SYSTEMATIC STUDIES IN THE GENUS <u>SOLANUM</u>

IN AFRICA

PETER-MARTIN LIND JAEGER B.Sc.

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Department of Plant Biology,
Faculty of Science,
University of Birmingham.

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SYNOPSIS

Africa is a major centre of diversity in the large cosmopolitan genus Solanum. The genus is an important component of the African flora, and, with a variety of uses, many of the species have a significant interaction with man. The objective of the present study was an elucidation of some of the many taxonomic problems found among the African species of the genus.

The systematic history of the African species of Solanum is reviewed to provide an insight into the origins of the nomenclatural problems that pervade the genus. Taxonomic characters are described and assessed, and the phytogeography of the genus is discussed.

The results of cross-pollinations and protein comparisons using polyacrylamide gel electrophoresis and serological techniques are discussed. No new insights into the taxonomy of the African species were revealed by these experimental studies and the potential for further work is reviewed. An adaptation of earlier methods of analysis of serological data is described.

In conclusion a taxonomic review is presented : species of Solanum occurring in Africa and the neighbouring islands are described accompanied by keys and comments on typification, distribution and synonymy. Around 80 species are believed

to be autochthonous; three new species are proposed. An

index to the species names in the review lists 382 epithets.

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present study.

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1. INTRODUCTION

Solanum is a large, cosmopolitan genus. It is estimated to comprise some 1,500 species, about 75% of the Solanaceae, but in the absence of a recent critical assessment these figures may well be too high. The genus is mainly tropical and there are comparatively few species of Solanum in cool temperate regions. The greatest diversity of species is to be found in South and Central America; Australia and Africa are less rich but have a significant number of endemics. Eurasia is poor in species numbers.

Many of the species in the genus have an important relationship with man as food plants, ornamentals, weeds or medicinal plants. Most notable of the food plants is the potato (S.tuberosum L.), a native of South America and introduced in parts of Africa, which in terms of acreage, tonnage and trade value, is one of the world's most important dicotyledonous crops. Other Solanum species of culinary importance in Africa are the native or introduced eggplants S.melongena L. (eggplant), S.aethiopicum L. (garden egg) and S.macrocarpon L., which are widely cultivated for their edible fruits or leaves. Garden ornamentals such as S.wendlandii Hook.f., S.pseudocapsicum L. and S.seaforthianum Andrews have been introduced to Africa and occasionally have escaped. Less benign introductions include the New

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World species S.erianthum D. Don, S.mauritianum Scop., S.torvum Sw., S.elaeagnifolium Cav., and S.rostratum Dunal which have all become serious pests as weeds in many parts of Africa and its neighbouring islands.

Several of the native African species have local uses including medicinal applications. Some non-African species, such as S.viarum Dunal, S.aviculare Forster f. and S.laciniatum Aiton, are cultivated outside Africa as a source of chemical intermediates useful in the industrial synthesis of contraceptive hormones and corticosteroid drugs.

It is important that the classification and nomenclature of a genus with such an extensive interaction with man should be understood and stabilised. The genus Solanum, however, has a certain taxonomic notoriety, derived in part from the large number of species names described, which complicates specimen identification, but also in part from the difficulty of identifying natural species groups. A number of factors are responsible for this and these include the poor definition of the generic limits, the occurrence of suites of attributes in varying combinations throughout the genus, the phenotypic plasticity and genetic variation in many of the species, and the continual reclassification of parts of the genus which has ended in nomenclatural confusion. Until recently, there was only a poor

understanding of the infra-generic divisions but relationships are being clarified gradually, and a synopsis by D'Arcy (1972) of the typification of the generic sub-divisions has simplified the nomenclature of the accepted species groups.

Most taxonomic research to date has concentrated on the cultivated species and their wild relatives (e.g. subgenus Potatoe (G. Don) D'Arcy: Correll, 1962; Hawkes, 1963; Hawkes and Hjerting, 1969; Hawkes, 1979), but some groups of wild species, such as the sections Brevantherum Seithe, Solanum, Androceras Bitter ex Marzell and Lasiocarpa (Dunal) D'Arcy, have also been the subject of recent study (Roe, 1967; Edmonds, 1972 and 1977; Whalen, 1979; Whalen et al., 1981 respectively). Today's knowledge of the African species of this genus is based on a series of publications early this century by Georg Bitter, which are collectively known as Solana africana (Bitter 1913, 1917, 1921 and 1923). Little work has been completed on these species since the 1920's, and none of the sections incorporating African species has been monographed.

Bitter's treatment of the genus in Africa is comprehensive but pedantic, and with the development of new methods and concepts in biosystematics the account is also out of date. Bitter had a tendency to split taxa on the basis of minor variation and although this

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is more marked in his assessment of the South American species, it is particularly noticeable at infraspecific levels in the African species, which he divided into numerous subspecies and varieties. The _Solana africana_ is a difficult work to use, notably because of the absence of an overall key. Each section has a key to its constituent species, but there is no key to the eighteen sections that Bitter recognised. Furthermore, there are no infraspecific keys to the many subspecies and varieties, and this causes difficulties in such species as _S.delagoense_ Dun. for example, which is divided into seven subspecies and nine varieties. At first sight the lengthy species descriptions which Bitter compiled, usually well over 300 words long, appear helpful for identification; but often when two or more descriptions are compared it is clear that they only differ on the most trivial characters. It is not uncommon to be confronted with a specimen that adequately matches more than one description.

The eclipse of Germany as a colonial power in Africa was contemporary with the completion of the _Solana africana_. Thereafter interest in African taxonomic botany was maintained by workers whose mother-tongue was generally not German. The _Solana africana_ was written in German and Latin and having to translate it compounded the difficulties in its use. In the sixty years since its publication the _Solana africana_ has been widely ignored

and it has had only a limited effect on the treatment of African species of _Solanum_ in herbaria and literature. Confusion has increased as the inadequate accounts in the _Flora of Tropical Africa_ and the _Flora of West Tropical Africa_ (Ed.1) continue to be used more widely than the _Solana africana_. However more than a translation of Bitter's works is now necessary. A modern treatment of the genus is overdue, particularly as several African regional Floras are in preparation, all of which will require an account of the Solanaceae. A start has been made at the Centro de Botanica (LISC) in Lisbon for the _Flora Zambesiaca_ but still outstanding are accounts for the _Flora of Tropical East Africa_, _Flore du Cameroun_, _Flore du Gabon_, _Flore d'Afrique Centrale_, _Flora of Ethiopia_, _Flora of Southern Africa_ and _Flore de Madagascar_

Such floristic accounts are essential for general use in naming specimens but piecemeal treatments of as large a genus as _Solanum_ have their disadvantages. In particular the artificial geographic boundaries which are set by Flora treatments impose arbitrary limits on the material to be consulted. The variation over the full geographic range of a taxon is often not appreciated, the taxon delimitations may be misunderstood and, most important, the author of an account for one Flora may fail to recognise the complete synonymy so that nomenclatural confusion remains

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unresolved.   Regional Floras impose constraints that
hinder the full comprehension of species and their
relationships.

With these considerations in mind I have undertaken a
study of the systematics of <u>Solanum</u> throughout Africa.
The intention has been to elucidate many of the problems
found at species level, to attempt to recognise natural
species groupings and to consider phylogenetic
relationships.   I hope, at least, to have highlighted
those areas of study where concentrated research would
most benefit the understanding of the genus.

I have studied the <u>"alpha"</u> taxonomy (Davis and Heywood,
1973) at the Royal Botanic Gardens, Kew, making use of
the herbarium collections and the library.   Other
herbaria visited include BM, BIRM, C, E, EAH and RNG
(abbreviations for herbaria throughout the present
thesis from Holmgren <u>et al.</u>, 1981) and I have received
loans fom FI and L.   I have followed experimental
approaches at the Department of Plant Biology in the
University of Birmingham using living material
cultivated at Birmingham and at Kew, grown from the
Birmingham Solanaceae Collection and from seed sent from
various sources in Africa.   Two visits to Africa, the
one to East Africa (1978) and the other to West Africa
(1982), have provided the invaluable experience of
observing the plants growing in their natural habitats

but, for the most part, my knowledge of the genus is derived from herbarium studies.

As a beginning to the present thesis I review the systematic history of the genus _Solanum_ (Chapter 2), focusing on treatments of the African species. Historical studies are an important part of taxonomy as they reveal the origins of present-day classifications and confusions. An understanding of these indicates a path to the solution of nomenclatural problems and helps to reduce the repetition of errors in a classification.

In Chapter 3, I discuss the taxonomic characters useful in _Solanum_ classification. Again, the emphasis is on the African species but it would be too limited to ignore other relevant observations on extra-African species of _Solanum_ or other genera of Solanaceae. A wider review serves two purposes. Firstly, it places the genus _Solanum_ in the context of other related genera, while secondly, it highlights areas of investigation which have been productive elsewhere in the genus or family, but have yet to be explored among the African species of _Solanum_.

I have followed this with observations on the geography and ecology of the African species (Chapter 4) such as can be gained from herbarium and library studies and, to a lesser extent, two visits to Africa. This represents

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an attempt to place bald specific epithets in their living context as well as to contribute to a knowledge of the African flora.

Experimental work is described next (Chapter 5) followed by a concluding discussion (Chapter 6) on the findings of the present study and the potential of other approaches.

Finally I present a review of the African species of the genus providing a synopsis of the classification with keys to the species and short descriptions with pertinent notes both on the native and on the introduced species (Chapter 7). In no way is this intended as a revision; it is a preliminary study giving an insight into the taxonomy of <u>Solanum</u> in Africa, clarifying the nomenclature and identifying species groups which can be the subject of detailed revision when the extra-African constituent species are included.

As I noted earlier, the notoriety of <u>Solanum</u> as a difficult genus is based in part on the problems of identification of specimens when there are a large number of described species. This plethora of epithets is to some extent a result of the combination of the variability of many of the species with the narrow species concept held by previous authors leading to minor variants being given specific status. For the

present thesis I have adopted a species concept which is taxonomic (Grant, 1981) and in a sense nominalistic (Mayr, 1969). I consider local populations to be real units of interbreeding individuals and species to be collections of populations definable by certain attributes. There is potential gene flow within a species, but this is extremely limited in reality, and can be ignored beyond the local population level. This stance opposes the classical biological species concept and will be defended elsewhere in the present thesis.

I have employed the concept of aggregate species, on occasion. This is a confession of ignorance of specific limitations, but having taken a taxonomic approach to species I believe it is quite acceptable. The aggregate species is analogous to the traditionally used species collectiva and has a major advantage in that it maintains the stability of a classification. Thus, for example, *S.incanum agg.* includes *S.incanum* L. in the precise sense as well as *S.lichtensteinii* Willd., *S.panduriforme* E. Meyer, *S.campylacanthum* Dunal and *S.cerasiferum* Dunal amongst over 50 synonyms. The status of these is uncertain and future research may offer an improved arrangement, but the concept of the aggregate species indicates a close relationship and does not force nomenclatural decisions that may be premature.

I have intended the synopsis of the African species of

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Solanum to be a clarification of the existing classifications and to provide a framework for further research. It is an introduction to _Solanum_ in Africa which I hope is more accessible and practical than Bitter's (l.c.) painstaking work from which it is derived.

2. SYSTEMATIC HISTORY

An important component of any systematic study is the comprehension of the origins and bases of the existing classifications. This facet is emphasised in those genera where nomenclatural confusion is evident : the solutions to such complexities so often lie in an understanding of their historical development. Further, an appreciation of the inadequacies of earlier classifications helps to prevent the repetition of errors, and provides a satisfying perspective to a current classification. The present chapter will discuss the development of systematic studies of the genus Solanum with particular attention to the African species.

The International Code of Botanical Nomenclature (ICBN, 1978) stresses the use of priority in resolving nomenclatural problems (Principle III) returning to the publication of Linnaeus' Species Plantarum in 1753 as the earliest valid publication of Spermatophyta species names. Linnaeus knew the genus Solanum well, and included 23 species in the first edition of Species Plantarum, but his treatment of the genus was neither perfect nor original. His understanding of the species was based on the works of others and mistakes can be traced back to his sources, such as the works of Tournefort, Cesalpino and Bauhin for example (see

Linnaeus, Classes Plantarum 1738). These in turn were based on earlier works and how far back into history a genus can be traced is defined by the earliest written record. As Bartlett (1940) discussed, the concept of a genus is rooted in pre-literate folk science, the grouping under a single name of objects considered to have some affinity to one another being an attribute of the human mental process.

For species of Solanum one of the earliest records still extant is the Enquiry into Plants by the Peripatetic philosopher, Theophrastus (370 - 285 BC). In various places in this work (see Chapters 7/7.2 and 15.4; Chapters 9/11.5-6 and 15.5 and 19.1) he discussed the virtues and characters of three kinds of Strychnos. This name is now applied to a genus in the Loganiaceae but tentative identification of the three kinds suggests that one is a Solanum (perhaps S.nigrum), one a Withania species and one Hyoscyamus (though Hort (1916) believed this last to be Datura). Further evidence that the Strychnos of Theophrastus comprised three species of Solanaceae is supplied by Pliny the Elder who in his Historia Naturalis (77 AD) mentioned that plants known as Strychnos in Greek were called Solanum in Latin.

The etymological roots of the generic epithet Solanum are obscure, but possibly they are connected to the Latin noun 'solamen' meaning a relief or comfort,

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assumed from the palliative effects of the nightshades. The medicinal use of species of Solanaceae was discussed in the _Materia Medica_ written by the Roman physician Dioscorides, a contemporary of Pliny. This work, written in Greek during the first century AD., contained descriptions and discussion of some 600 species of plants arranged according to their pharmacological characteristics. A copy prepared around the third or fourth century AD also incorporated illustrations, these most likely being derived from the _Rhizotomikon_ written by Crateuas early in the first century BC (Morton, 1981). A copy of this combined work was prepared in Byzantium about 500 AD : it is known today as the _Codex Vindobonensis_ and has discussions and illustrations of four kinds of _Strychnos_. Two of these are referable to _Solanum_ and two to _Physalis_.

The works of Pliny and Dioscorides survived through the cultural torpor of the Dark Ages as the major sources of botanical knowledge in Europe; their importance stimulated the preparation of copies and these in turn were copied, so leading to the gradual loss of the standards of illustration and description. Other texts were written but the first significant developments in European botany are not recognisable until after the appearance on the Continent of printing with movable type around the year 1440. This invention eased the process of book production and so increased the range

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and speed of the dissemination of knowledge. It was a catalyst to the concatenation of commercial, philosophical and theological developments which started the Renaissance in Europe. Interest in science at the time was practical in its approach and plants were studied for their medicinal virtues : botanical publications for the following 200 years took the form of herbals with the plants classified and described according to their pharmacological characters.

One of the first major works of this period was the _Herbarum vivae Eicones_ of Otto Brunfels published in Strasbourg in 1530. This was compiled from the writings of Theophrastus, Pliny, Dioscorides and others. Although it contains no classification or advances in nomenclature, the quality of the illustrations indicates that botanists were studying from life again rather than from copied and recopied texts. No _Solanum_ species were included by Brunfels but twelve years later his fellow countryman Fuchs published the _De historia stirpium_ (1542) in which at least three species of _Solanum_ appear including _S.melongena_ under the name _Mala insana_.

Botanical work at the time was directed, for the most part, towards providing floristic catalogues of plants available and classifying them on a pharmacological basis. With the development of herbarium techniques in the early sixteenth century it became possible to dry

and preserve botanical specimens for subsequent study. Travellers could now bring samples from abroad.

For a short period from the mid-fifteenth century onwards the Portuguese and Spanish were most active in exploring beyond Europe, sending expeditions into the African interior (in search of the legendary ruler 'Prester John' (Cortesao, 1961)), with Vasco da Gama circum-navigating Africa to India (1497-1498) and Columbus reaching the Americas a few years earlier. However, comparatively few findings from the expeditions were published, perhaps so that any commercial interests which might be derived would be protected.

After this early activity, Africa lay unexplored by Europeans until the eighteenth century, but at least one African species of Solanum had appeared in cultivation in Europe. The two Dutch botanists Lobel (1576,1591) and Dodoens (1583) included S.aethiopicum in their herbals, both relating that the plants had come to them from Spain. This species is widely cultivated in West Africa today and the plants described in Holland most likely originated from this area.

In the process of cataloguing plants the herbalists began to consider the theoretical question of which characters might be useful in distinguishing one kind of plant from another (differentiae) as opposed to the

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characters which would group one plant with another (affines). Thus Cesalpino (1583) could produce the beginnings of a natural classification by studying fructification but, by this stage, developments in systematics were already being held up by the problems of synonymy. Botanical authors were accustomed to name plants with short descriptive phrases and as the general perception of morphology improved so the phrase names grew longer. In consequence there was no agreement on the name of a particular species or on the application of published names until Gaspard Bauhin published his Pinax (1623). This work of remarkable industry included over 6,000 plants for which the nomenclature was simplified by the elucidation of the synonymy, the supply of references and the frequent use of binomials to indicate genus and species.

The Pinax includes 31 species of Solanum; there are no species descriptions as there are numerous references to earlier descriptions and illustrations. Bauhin placed the genera of Solanaceae Mandragora, Hyoscyamus and Nicotiana with three other unrelated ones in the same alliance as Solanum (Liber Quintus, Sectio Prima), and within Solanum he included species which today would be recognised as representatives of Physalis, Atropa, Withania, Paris, Trillium, Datura, Lycopersicon, Mirabilis, Circaea and Capsicum.

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Linnaeus made extensive use of Bauhin's _Pinax_ as a guide
to earlier literature and he cited it throughout his
Species Plantarum. The connection between Linnaeus and
the _Pinax_ was reinforced by the presence at Uppsala,
Sweden of the herbarium assembled by Joachim Burser
(1583-1639). This collection had been named and
arranged in accordance with the _Pinax_ and was thoroughly
studied by the young Linnaeus at Uppsala (Savage, 1936).
The herbarium contains the lectotype of _S.aethiopicum L._
for example.

Bauhin's higher levels of classification lacked
comprehensive order but his _Pinax_ provided a foundation
for the development of systematics by firmly
establishing genera and species as fundamental units of
taxonomy. In 1689 Pierre Magnol published his _Prodromus_
in which he proposed the family as a taxonomic unit : he
listed the families as tables and his 'Tabula XXXII' in
'Sectio Sexta' corresponds to the Solanaceae (see Table
2.1). Within 'Sectio Sexta' were other alliances
recognisable as the families Boraginaceae,
Scrophulariaceae, Convolvulaceae and Labiatae, which
with the Solanaceae are all included by Takhtjan (1980)
in the superorder Lamianae.

Contemporary with Magnol, the Englishman John Ray
published a classification (Ray, 1686-1704) which in
many respects survives today. The algae, fungi, mosses

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Table 2.1 : 'TABULA XXXII' in 'Sectio Sexta' in the Prodromus
historiae generalis plantarum by Magnol (1689).

Plantae floribus monopetalis, pomiferae, aut fructiferae,
semine compresso, Solanorum familia.

			(Tentative Determinations)
		(Solanum fruticosum (bacciferum. (	(S.pseudocapsicum)
	(Nudo & solitario.	(Belladonna. (	(Atropa)
	((	(Herba paris Alsine (baccifera. (	(Paris) (Alsine)
	((Nudo, in umbellam(	(Solanum hortense (	(S.nigrum)
	(disposito. (	((Solanum scandens	
Aliae sunt,(pomo minore(		(bacciferum.	(S.dulcamara)
	(Nudo striato & (spicato. (	(Solanum racemosum (indicum.	(?)
	((	(Alkekengi. (	(Physalis)
	(Vesiculis (incluso.	(Solanum vesicarum (indicum. (	(Physalis angulata)
		(Solanum somniferum (verticillatum.	(Physalis somnifera)
		(Mandragora (	(Mandragora)
		(Fructu non (striato.	
		((Melongena	(S.melongena)
	(Foliis integris.	(((Piper indicum	(Capsicum)
	((	(Fructu striato.(Mala aetiopica	(S.aethiopicum)
Aliae, pomo(majore (	((Foliis pinnatis.	(Fructu non (striato. (	(Solanum racemosum (Lycopersicon) (cerasorum forma (esculentum)
		(Fructu striato.(Solanum pomiferum (fructu striato (molli	(Lycopersicon) (esculentum)
Aliae, fructu majore echinato, aut aculeat.		(Stramonium. ((Datura.	(Datura) (Datura)

Determinations might be verified by study of
Magnol's herbarium now in LINN (or BM-SL & OXF.)

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and ferns (the _Imperfectae_) were separated from other flowering herbs (the _Perfectae_) which were divided into _Monocotyledones_ and _Dicotyledones_, the trees being kept separate. His achievements in systematics were at the higher levels of classification but showed no major advances at the generic levels : _Solanum_ was defined vaguely and included _Physalis_ and _Atropa_.

In the early seventeenth century several visits to the Cape of Good Hope had been recorded by travellers bound for India and beyond, and by 1652 a settlement had been established on the Cape (Gunn and Codd, 1981). Subsequently plants from the Cape began to appear in botanical accounts and Ray included two African species of _Solanum_ - the one probably _S.linnaeanum_ Hepper and Jaeger (_S.sodomeum_ auctt. non L.) from the Cape.

J. P. de Tournefort produced a clearer definition of genera in his _Institutiones Rei Herbariae_ (1700) than had Ray, by using characters of the corolla and fructification. His 'Sectio VII' in 'Classis II' contained the following eight genera :

<div align="center">

I   _Solanum_

II   _Lycopersicon_

III   _Alkekengi_ (i.e. _Physalis_)

IV   _Melongena_

V   _Capsicum_

</div>

VI   _Nymphoides_

VII   _Cyclamen_

VIII   _Moschatellina_

Meanwhile he had established _Mandragora_ and _Belladonna_ (i.e. _Atropa_) as genera in 'Classis I' and _Nicotiana,_ _Hyoscyamus_ and _Stramonium_ (i.e. _Datura_) in 'Classis II Sectio I'. In other words his concept of the genus _Solanum_ was a closer approximation to that held today than had been achieved previously. This was by virtue of the exclusion of such genera as _Physalis,_ _Atropa_ and _Datura_ from within _Solanum,_ but in his zeal for clearly defined genera Tournefort went on to erect a genus _Melongena_ (for _S.melongena_ and others) as distinct from _Solanum._

While Tournefort was to some extent a splitter both at the specific and the generic levels, Linnaeus, perhaps in reaction to this, tended to lump Tournefort's taxa together. The magnitude of Linnaeus' collected publications reveal his encyclopedic intellect (a facet which is sometimes overshadowed by his consistent use of binomial nomenclature from 1753) and from such an overview he was able to develop the 'Sexual System' of classification. This gave the best classification to that date.

In the _Species Plantarum_ (Ed. 1, 1753) Linnaeus' 'Classis V _Pentandria Monogyna_' included the genera of

Solanaceae _Datura_, _Hyoscyamus_, _Nicotiana_, _Mandragora_, _Atropa_, _Physalis_, _Solanum_, _Capsicum_, _Brunfelsia_, _Cestrum_ and _Lycium_ as well as genera from such closely related families as Boraginaceae, Convolvulaceae and Scrophulariaceae. His concept of _Solanum_ included the genera _Lycopersicon_ and _Melongena_ recognised by Tournefort; he accepted 23 species within the genus and he divided them into two groups according to whether they were prickly (11 species) or not (12 species). Of the unarmed species _S.guineense_ (now = _S.scabrum_ Miller) was known from Guinea, West Africa and _S.pseudocapsicum_ from Madeira. The armed species included _S.melongena_, _S.sodomeum_ and _S.incanum_, though only _S.melongena_ was known to grow in Africa.

Having developed the 'Sexual System' and a standard nomenclature, Linnaeus continued to publish by refining his classification and more importantly by adding in new species. For the second edition of the _Species Plantarum_ (1762) 30 species of _Solanum_ were recognised adding _S.aethiopicum_, _S.tomentosum_ and _S.trilobatum_ from Africa. By edition five of _Species Plantarum_ edited by Willdenow (1798) the genus comprised 83 species of which 19 were acknowledged as growing in Africa, the neighbouring islands or the Arabian Peninsula.

The botanical exploration of Africa started again in the second half of the eighteenth century, 250 years after

the first Portuguese expeditions. Before Linnaeus, knowledge of the African flora had been confined to the Mediterranean coast and the Cape of Good Hope. Now collectors, pupils of Linnaeus amon~ them, began to send or bring back material from other parts of Africa. In West Africa Adanson travelled by the Senegal River (1757), Baron Palisot de Beauvois visited Nigeria (1786), and collections were made in Sierra Leone by Smeathmann (1771-1772) and Afzelius (1792), and in Ghana by Isert (1786-1789) and Thonning (1799-1803) (Keay, 1961). In north-eastern Africa the most extensive collection of that time was made in Ethiopia by James Bruce in his attempt to discover the source of the Nile (1768-1773) (Cufodontis, 1961). The botanical understanding of South Africa developed from the collections of Auge (1751), Sparrman (1772 and 1775-1776), Thunberg (1772-1774) and Masson (1772) (Gunn and Codd, 1981).

In Europe, the next development of importance in the systematics of <u>Solanum</u> originated from the Botanic Gardens at Montpellier, one of the long established centres of botany in Europe. From study at Montpellier under A. P. De Candolle, Michel Felix Dunal published a thesis in 1813 entitled <u>Histoire naturelle, medicale et economique des Solanum, et des genres qui ont ete confondue avec eux</u> which sought to collate his findings with all available information on the genus and its

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close relatives. Dunal's taxonomic work was based on the herbaria of De Candolle, Bouchet, Gouan and the gardens and herbarium of Montpellier.

The introduction to the thesis reveals how thoroughly Dunal knew his subject and how far systematics had progressed in the century since Ray and Tournefort. The introduction begins with a review of the systematic history of Solanum, from the Bible onwards, and comments on the more recent generic concepts of Tournefort, Linnaeus and Adanson. For the thesis, Lycopersicon and Solanum were recognised as separate; but within Solanum Dunal included Melongena of Tournefort, Aquartia of Jacquin, Ventenat's Nycterium, Moench's Dulcamara, and Pseudocapsicum and Psolanum of Necker.

Dunal commented on the use of the presence or absence of prickles as a character to divide the species of Solanum into two sections as Linnaeus and subsequent botanists had done. He noted that the character was too variable in some species to be relied upon, but he believed that such a large genus needed to be split and prickliness provided two convenient initial groups. Each group was then subdivided into smaller alliances of species and he gave names to those groups which he considered to be natural. The hereditary constancy of characters was important to Dunal in recognising species and was cited as a reason for splitting the Linnaean varieties of

<u>S.nigrum</u> into species.

On nomenclature, Dunal held the modern views of priority except when he considered a name to be imprecise in which case it was changed. As an example he quoted <u>S.sodomeum</u> which he believed to originate from the Cape of Good Hope and not Judea where the ancient city of Sodom was sited : the epithet <u>sodomeum</u> was rejected and the species renamed <u>S.hermanni</u>. Such arbitrary nomenclatural alterations are considered illegitimate today (ICBN, 1978) but the epithet <u>sodomeum</u> has had to be rejected anyway to be replaced by <u>S.linnaeanum</u> (Hepper and Jaeger, In press).

After an extensive discussion of the morphology, uses, chemistry and medicinal applications of species of <u>Solanum</u>, Dunal provided a conspectus to the 199 species that he recognised. The species are listed in groups defined by certain characters and the groups occasionally are named. Each species name is followed by a brief description of 12 words or less distinguishing each from others in its group. The result is a key to all the species; each half of the genus being subdivided into progressively smaller alliances and ultimately into species. The initial division of the genus is based on the presence or absence of prickles and each half of the genus is then

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divided on aspects of leaf outline, in the degree and type of lobing, before more particular characters are employed.

The bulk of the thesis is taken up with the final section which comprises species descriptions, synonymy, provenance information and some illustrations. Dunal attempted to resolve all the synonymy that was already confusing Solanum taxonomy. At the end of his thesis he was obliged to list a few names without discussion either in a section Species non satis nota, for those names where the original descriptions were too poor to identify the species, or in a section Solana excludenda for those species once wrongly attributed to Solanum. Thus he hoped to include in his thesis all the species of Solanum ever described.

Dunal accepted around 30 species of Solanum from Africa. His placement of these species is mostly acceptable although S.macrocarpon, S.aethiopicum and S.zuccagnianum would be considered misplaced at present in the unarmed half of the genus, even though they lack prickles, as their affinities are certainly to the armed species. In the armed part of the genus, most of the species which today would be included in section Oliganthes (Dunal) Bitter are found together, today's section Torva Nees is recognisable and Dunal's section Melongena is unchanged.

Dunal's thesis represents a considerable advance in theoretical and practical taxonomy of Solanum in the 60 years since the first Species Plantarum account of the genus. Had Dunal not undertaken the thesis at the time he did and with such perception, the amount of new material from collectors over the following decades would have precluded the presentation of such a clear overview. However, with an established infrageneric classification new material could be added in or the classification modified accordingly; otherwise a unified system would have been a long time developing.

In 1816 Dunal published a conspectus of Solanum in which the major divisions were unchanged from 1813. Through the study of the herbaria of Desfontaines, Jussieu, Humboldt and Bonpland, Lamarck, and Richard, the overall number of species was increased to 287. The increase in number of species was almost entirely due to the new collections from South America and the number of species known to grow in Africa remained at about 30.

In 1846 Sendtner provided an account of the Solanaceae for Martius' Flora brasiliensis (Sendtner, 1846). He recognised a correlation within Solanum between certain characters of the anthers and the presence or absence of prickles. He noted that the unarmed species generally exhibited short, stout anthers with introrse apical pores while the prickly species possessed elongate,

tapered anthers with minute extrorse or upward facing
pores. He separated the species into a division
Pachystemona with short anthers and a division
Leptostemona with long anthers. Five species did not
fit this system being unarmed but with elongate anthers:
these were removed to a division Hypocritica.

Six years later Dunal supplied a complete treatment of
the Solanaceae for De Candolle's great Prodromus
systematis naturalis (Dunal, 1852). He followed
Sendtner in dividing the genus on anther shape and
dehiscence, erecting two sections, Pachystemonum and
Leptostemonum, with species of the former being unarmed
while those of the latter were generally armed. He
included Sendtner's division Hypocritica within
Leptostemonum and all infrageneric groups were now
named. Section Pachystemonum was divided into five
subsections on the basis of such characters as leaf
dissection, inflorescence type and position, corolla
dissection, pedicel articulation and fruit shape.
Section Leptostemonum was divided into three subsections
mainly on the basis of corolla dissection but also on
the presence of stellate hairs.
Some 94 species of Solanum had now been recorded from
Africa, the neighbouring islands or the Arabian
Peninsula. The bisection of the genus on the basis of
anther characters provided a more satisfactory
arrangement and the species S.aethiopicum,

S.zuccagnianum and S.macrocarpon were now placed amongst more closely related species in section Leptostemonum. The subsections and lesser divisions are broadly acceptable when only the African species are considered but Dunal attempted to define relationships between all the species known to him and it is here that the classification weakens. Nevertheless, it is a monumental work covering 851 species (with another 50 non satis notae) of Solanum alone. It represents the last attempt at a complete revision of the genus, and of the family, and it is a well observed work with keys to the species and with detailed description.

For Bentham and Hooker's Genera Plantarum (1862-1883) Bentham followed Dunal's broad division of Solanum into two sections but considered that the characters defining the subdivisions were often too uncertain. Twenty years later von Wettstein contributed an account of the Solanaceae to Engler and Prantl's Die Naturlichen Pflanzenfamilien (1895). This was a more detailed treatment than that of Bentham and the genus was now split into five sections viz: Pachystemonum, Lycianthes, Leptostemonum, Lycopersicum and Nycterium. Again anther characters were considered to be of greatest importance systematically but inflorescence arrangement, prickliness and floral symmetry were also used to delimit the sections. Von Wettstein estimated there to be 27 species known from Africa; these were not

enumerated but some of the cultivated species, for example S.aethiopicum and S.macrocarpon, were discussed.

In 1860 Speke and Grant set out from Zanzibar on a journey through Africa and assembled the first plant collections from the African interior (Gillett, 1961). As the century progressed explorers opened up the 'Dark Continent' and an increasing number of plant specimens were returned to Europe. C. H. Wright contributed accounts of the Solanaceae for Flora Capensis (1904) and the Flora of Tropical Africa (1906). In these works he accepted 113 species of Solanum, but as floristic catalogues there was no attempt at classification. There are, however, keys to all the species and again the presence or absence of prickles was seen as critical and was used for the first dichotomy in the key in both works. These two treatments represent the only attempt, after Dunal, to provide keys to all the African species. However, Wright was a splitter and he introduced much confusion by describing new species on the basis of minor variation with only the specimens available to him in London as a source.

Splitting was the dominant trend in European taxonomic botany at the turn of the century. There seems to have been a sentiment that taxonomy became scientific only if all deviants from a Type were described and named; there was no tolerance for species variability. At the

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Botanical Museum in Berlin, U. Dammer made a study of
the African Solanaceae. His first publication on the
genus (1905) described eight new species of _Solanum_.
Next he commenced a revision of the genus in Africa
adding another 23 new species (1906). Subsequent
publications (1912, 1915) added another 58 new species,
and this for Africa alone. Almost without exception,
his species were described from single specimens and
apart from the attempted revision in 1906 none are
presented within a systematic framework. The revision
that was issued (Dammer, 1906b) is fragmentary and
inadequate. For example, the account opens with the
heading 'Sectio I _Pachystemonum_' which evidently
comprised six subsections including a subsection
Euleptostemonum; there is no section complementary to
Pachystemonum.

Dammer's publications multiplied the confusion already
incipient in the taxonomy of African _Solanum_ species.
However, also working in Berlin, was Georg Bitter who,
in a series of publications (Bitter, 1913, 1917, 1921
and 1923) collectively titled _Solana africana_, produced
a sound revision of most of the known African species of
Solanum. The _Solana africana_ is a painstaking work with
detailed observations and descriptions, and despite the
prevailing war in Europe, which impeded the exchange of
material between herbaria, it is as comprehensive as the
times would allow. Bitter was particularly fortunate in

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having access to Dammer's Types in Berlin and the Dunal Types in the De Candolle herbarium in Geneva. The only part of the work which is incomplete is the treatment of the section Solanum (or section Morella (Dunal) Bitter) which Bitter partially covered in 1913 and 1917 but for which he intended a separate monograph.

Part I of the Solana africana (Bitter, 1913) covered seven new or less well known species of section Solanum. In Part II (Bitter, 1917) the revision proper was started with a lengthy introduction. Here, Bitter emphasised his concern that his understanding of the genus was incomplete but he observed that there had been no thorough study of the species published since Dunal's work in 1852, and therefore the present publication was justified. No overall key to the species could be provided without further study.

After discussing the geographical distributions of the sections, Bitter wrote about the cultivated species. He noted that prickly species might be unarmed in cultivation since there would be a tendency for man to select against prickles. He found that this had been a particular source of confusion in previous treatments of the genus, with unarmed varieties of prickly species being accepted as species in their own right. Of course it is often argued that cultivated varieties should indeed be given species rank, but when the

distinguishing character was presence or absence of prickliness, and this too was used to divide the genus, the result was that cultivated taxa were considered taxonomically remote from their wild progenitors. Bitter believed that there were more such irregularities than had been recognised already.

Bitter attempted to avoid dividing the genus on the basis of anther form and the presence or absence of prickles alone but to use the overall organisation of the plants to establish relationships. He hoped to discover other good characters with further study but at publication could only suggest that the presence or absence of stone cells in the fruits might be significant. As a framework Bitter divided the African species of <u>Solanum</u> into three subgenera and then 18 sections (<u>see</u> Table 2.2). Since he did not provide a key, the definitive characters for dividing the genus are not obvious but from the section descriptions it seems that he attached importance to the position of the inflorescence, filament lengths, the shape of the anthers, the presence or absence of prickles, the hair type (whether stellate or simple) as well as the presence or absence of stone cells. He also paid attention to leaf shape, anther fusion and certain corolla characters at lower taxonomic levels.

In his work on the South American Solanaceae Bitter has

Table 2.2:   Bitter's Classification of <u>Solanum</u> in Africa

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I   Subgenus Lyciosolanum Bitter

II   Subgenus Eusolanum Bitter

<u>Section</u>	<u>Series</u>
Quadrangulare Bitter	
Macronesiotes Bitter	
Lemurisolanum Bitter	
Afrosolanum Bitter	Nakurensia Bitter
	Bifurca Bitter
Benderianum Bitter	
Anthoresis (Dunal) s.str. Bitter	
Morella (Dunal) Bitter	
Pseudocapsicum (Dunal) s.str. Bitter	
Normania (Lowe) Bitter	

(Basarthrum Bitter)   )
) Introduced
(Tuberarium (Dunal) s.str. Bitter))
) Species
(Lycopersicon (Dunal) Wettst.)   )

Somalanum Bitter

Anisantherum Bitter

(continued overleaf)

Table 2.2 continued...

III Subgenus Leptostemonum (Dunal) s.str. Eitter

Section	Series
Torvaria (Dunal) s.str. Bitter	Eutorvum Bitter
	Giganteiforria Bitter
	Anomalum Bitter
Oliganthes (Dunal) Bitter	Afroindica Bitter
	Aethiopica Bitter
	Capensiformia Bitter
	Austroafricana Bitter
	Macracanthum Bitter
	Albicaule Bitter
	Eoafra Bitter
	Pyracanthum Bitter
Ischyracanthum Bitter	
Simplicipilum Bitter	
Androrronoecum Bitter	Sodomela Lowe
	Afrodecumbens Bitter
	Aculeastrum Bitter
	Acanthocalyx Bitter
	Rhodacanthum Bitter
	Macrocarpa Bitter
	Incaniforria Bitter
Monodolichopus Bitter	
Nycterium (Dunal) s.str. Bitter	

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been criticised for his approach as a splitter. However, for the African species he adopted a wider 'spezies-begriff' and he did much to reduce the number of species, particularly those described by Dammer, to varietal status. It is true that for infraspecific taxa he was a splitter (note, for example, the 12 subspecies and 27 varieties of S.indicum (L.) Nees sensu ampl. Bitter) but this is easier to ignore than at higher ranks. Bitter's sections seem to be relatively natural alliances, as do his subgenera, although sections Somalanum and Anisantherum should have been placed in subgenus Leptostemonum rather than subgenus Eusolanum. His division of the sections into series is usually understandable, if unnecessary in those instances when few species are involved.

Bitter died in 1927 without completing his work on Solanum worldwide. Since his Solana africana there have been no attempts at a revision of all the African species. The sufficiency of Bitter's observations can hardly be doubted when the detail of his descriptions, notes, comments on geographical distributions and specimen citations are considered. However, his opus is of limited use for identifications : the absence of an overall key is a hindrance and the comparison of the long (usually over 300 words) Latin species descriptions is tedious and often inconclusive. The sectional classification and the reduction of Dammer's species to

synonymy were major contributions.

Since Bitter's revision a number of floristic works on regions of Africa have been published that include accounts of the Solanum flora. A. A. Bullock (1931) contributed a treatment of the Solanaceae to the Flora of West Tropical Africa which unfortunately repeated many of Wright's (1906) earlier errors, but Heine's (1963) entry in the second edition resolved most of the problems. Other regional accounts of the family have been included by Chiovenda (1929 and 1932) for Somalia, Adamson and Salter (1950) for the Cape Peninsula, Andrews (1956) for the Sudan, Berhaut (1967) for Senegal, Jacot Guillarmod (1971) for Lesotho, Agnew (1974) for Upland Kenya and Compton (1976) for Swaziland. Six new species were published by Chiovenda. Other floristic treatments are planned as I have listed in the Introduction to the present thesis.

While the existing Floras, both popular and more detailed, have catalogued the Solanum species in their respective regions, no further consideration has been given to the classification except in an unpublished manuscript (at K), by Polhill (1961), on the East African species. On a wider scale, without restricting their studies to any region, Danert (1958, 1967) and Seithe (1962, 1979) have provided reviews of the branching patterns and hair types respectively in the

genus with a view to their use in systematics. The work of Danert has been reviewed and extended by Child (1979a, 1979b) who has noted, for example, a similarity in the branching patterns seen in sections of subgenus Petota (G.Don) D'Arcy and subgenus Solanum. Danert's approach supported certain taxonomic placements, but his comment (Child, 1979b) that derived branching patterns in Solanum have apparently evolved several times induces caution in the use of such characters.

Having observed the ontogenetic development and the temporal and topographical variation of the hairs, Seithe concluded that it was possible to divide the genus into two chori subgenerum - Solanum and Stellatipilum. The former comprised species bearing branchlet hairs, while species with stellate hairs constituted the latter. Analysis of other characters of the species with gland-tipped finger-hairs revealed that their nearest relatives were to be found in the chorus subgenerum Solanum. This division of the genus could be combined with Bitter's classification and a comparison with Dunal's system is shown in Table 2.3.

Recently, taxonomic work on the genus Solanum has been concentrated on revising species groups (Correll, 1962; Roe, 1967; Hawkes and Hjerting, 1969; Edmonds, 1972 and 1977; Whalen, 1979, 1981 and 1984; Child, 1983) although one regional monograph (Symon, 1981) has appeared as

Table 2.3: Seithe's (1962) arrangement of the taxa in the
genus Solanum L.

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Übersicht über die Taxa der Gattung Solanum L.

'orläufiges System nach BITTER und SEITHE-v.HOFF   System von DUNAL 1852

:horus subgenerum Solanum
  Subgen.Solanum   Sect.I Pachystemonum
    Sect.Solanum   Subsect.2 Morella
    Sect.Chamaesarachidium BITT.   'Morellae spuriae
    Sect.Campanulisolanum BITT.   "Morellae verae
    Sect.Cyphomandropsis BITT.   (Genus Cyphomandra pr.pte.)
    Sect.Gonatotrichum BITT.
    Sect.Episarcophyllum BITT.

    Sect.Anthoresis(DUN.)BITT.emend.SvH.   Subsect.4 Micranthes
    Sect.Lysiphellos(BITT.)SvH.   1⁰Anthoresis
    Sect.Oppositifolium(DUN.)SvH.   2⁰Anthopleuris
      Subsect.Oppositifolium   §1 Oppositifolia
      Subsect.Indubitaria(DUN.)SvH.   'Indubitaria
      Subsect.Silicosolanum BITT.   "Lepidota
    Sect.Pseudocapsicum(DUN.)BITT.   '"Leiodendra
                                                             §2 Pseudocapsicum
                                                             §3 Bassovioides
    Sect.Dulcamara(DUN.)BITT.
    Sect.Afrosolanum BITT.   Subsect.3 Dulcamara
    Sect.Benderianum BITT.   'Regmandra
    Sect.Quadrangulare BITT.   "Polybotryon
    Sect.Macronesiotes BITT.   '"Dulcamara
    Sect.Lemurisolanum BITT.   ""Subdulcamara
    Sect.Jasminosolanum BITT.ex SvH.
    Sect.Aculeigerum SvH.
    Sect.Herpysticum BITT.
                                                           Subsect.1 Tuberarium
    Sect.Tuberarium(DUN.)BITT.   'Potatoe
      Subsect.Tuberarium   "Pterophyllum
      Subsect.Basarthrum BITT.
    Sect.Rhynchantherum BITT.
    Sect.Herposolanum BITT.
    Sect.Anarrhichomenum BITT.
    Sect.Normania(LOWE)BITT.

  Subgen.Lycopersicum(HILL)SvH.   (Genus Lycopersicum)
  Subgen.Bassovia(AUBL.)BITT.   (Genus Bassovia pr.pte.)
  Subgen.Archaesolanum BITT.ex MARZ.
  Subgen.Lyciosolanum BITT.   Subsect.5 Lycianthes

:horus subgenerum Stellatipilum SvH.
  Subgen.Stellatipilum   Sect.II Leptostemonum
    Sect.Stellatipilum   Subs.3 Asterotrichotum
    Sect.Brevantherum SvH.*)   §1 Oliganthes
    Sect.Lepidotum(DUN.)SvH.   §2 Cryptocarpum
    Sect.Anisantherum BITT.   §3 Nycterium
    Sect.Somalanum BITT.   §4 Mogenoplum
    Sect.Monodolichopus BITT.   §5 Melongena
    Sect.Nycterium(DUN.)BITT.   Subsect.2 Torvaria
    Sect.Androceras(NUTT.)BITT.ex MARZ.   Subs.1 Euleptostemonum
    Sect.Protocryptocarpum BITT.ex MARZ.   §1 Graciliflora
    Sect.Oliganthes(DUN.)BITT.   'Persicaefolia
    Sect.Ischyracanthum BITT.   "Aquartia
    Sect.Simplicipilum BITT.   '"Polygama
    Sect.Torvaria(DUN.)BITT.   §2 Juripeba
    Sect.Irenosolanum BITT.ex SvH.   'Heteracantha
    Sect.Micracanthum(DUN.)BITT.emend.SvH.   "Micracantha
    Sect.Graciliflorum(DUN.)SvH.   §3 Acanthophora
                                                               'Psilocarpa
Genus Lycianthes(DUN.)HASSL.emend.BITT.   "Lasiocarpa

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well. None of the African species groups has been studied. D'Arcy (1972) has published a synopsis of the typification of the generic subdivisions which has provided a nomenclatural system by which the species groups can be identified, at least temporarily. Whalen (1984) has completed a conspectus of the species of subgenus Leptostemonum which reveals species alliances suitable for intensive study. Thus a gradual revision of the whole genus, group by group, should emerge and this approach has the advantage of ignoring the arbitrary geographic limits set by Floras.

From the recent revisions of species groups of Solanum it may be assumed that remaining nomenclatural confusion within the genus gradually will be resolved as studies proceed, but the inter-relationships of the infrageneric groups are as yet a mystery. Over two centuries of study have revealed few characters that might define affinity : Linnaeus (1753) used the presence or absence of prickles, Sendtner (1846) noted a correlation between prickles and anther characters, Dunal (1813, 1816, 1852) used leaf dissection, inflorescence position and corolla dissection as well as the presence of stellate hairs which was also used by Bitter (1913, 1917, 1921, 1923) and intensively by Seithe (1962, 1979). An assessment of the taxonomic characters available in the genus is required.

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3. TAXONOMIC CHARACTERS OF AFRICAN SOLANUM SPECIES

This chapter is intended as a review of the morphological, anatomical, cytological and biochemical characters of the African species of Solanum. Where relevant, non-African species of Solanum and species of other genera of Solanaceae are considered with the intention that the African species may appear in the context of the genus, and the genus in its place in the family. Areas of investigation which have been fruitful in the taxonomy of the non-African species of Solanum are highlighted.

3.1 Habit, roots, stems and branching patterns :

The species of the genus Solanum exhibit a wide diversity of habit with trees, shrubs, climbers, creepers, herbaceous perennials and annuals all represented in the genus. Among the African species the dominant growth form is the small to medium sized shrub. True annuals are rare in the native species, certainly some of the annual representatives of section Solanum are introduced, but of the many shrub species grown under glass at Birmingham all flowered in their

first year. There are several African species with a climbing or scrambling habit such as S.terminale, S.welwitschii, S.benderianum and S.runsoriense from subgenus Solanum but also S.pampaninii, S.taitense and S.cyaneo-purpureum, for example, in subgenus Leptostemonum. Several forest or forest-margin species grow into large shrubs up to 3m tall but fully grown plants of S.giganteum and S.aculeastrum will attain 6m in height having the appearance of small trees. The Madagascan species S.truncicolum is reputedly an epiphyte on recently fallen tree trunks (Bitter, 1917; D'Arcy, pers. comm.).

Few studies on the roots of species of Solanum have been reported, but according to Holm (1910), Artschwager (1918), Thiel (1931) and Whalen (1979a) they seem to be anatomically uniform with a typical exarch, diarch protostele. The root system may be quite extensive, spreading horizontally and sending up adventitious shoots to form dense stands of many stems. The phenomenon is seen in S.mauritianum and S.elaeagnifolium, two particularly successful weedy species introduced in Africa and now of economic importance as pests. Among African species the feature has been noted in S.sepicula, for example, growing at Birmingham and it is evidently widespread in the genus (Symon, 1981). This form of reproduction is undoubtedly an important component of a plant's

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tolerance to fire as well as contributing to the overall competitive strategy of a species.

As a family the Solanaceae are characterised by the bicollateral vascular bundles in the stems with internal as well as external phloem. This feature, which is rare among the dicotyledons, distinguishes the Solanaceae from such closely related families as the Scrophulariaceae, but it is also found, for example, in Cucurbita (Curcurbitaceae) (Esau, 1977).

The stems of the African species are usually woody, and when young may be green or, as in some S.aethiopicum cultivars, they may be violet from anthocyanin coloration. Among species of subgenus Leptostemonum the stems often bear prickles or, as in S.schumannianum and S.setaceum, bristles. In the herbaceous members of section Solanum the stems are sometimes slightly winged and species with toothed wings are found. Highly modified stems are seen in section Petota where the underground stems form the tubers for which the genus is commonly known. None of the African species are known to be tuberiferous.

The growth form in Solanum is for the most part sympodial. Each vegetative shoot is terminated with an inflorescence and a new shoot emerges from the axil of the last leaf. This again ends with an inflorescence

and a new shoot emerges from the youngest leaf. In other words, the terminal meristem becomes determinately differentiated as an inflorescence and is replaced by a lateral meristem. Each unit of vegetative growth terminated by an inflorescence is referred to as a sympodial unit or anthoclade (Goebel, 1931). This underlying pattern of growth can be considered a generic character within the family, and Danert (1958, 1967) and Child (1979a and b) have reviewed the infrageneric systematic significance of the various modifications. Danert noted that the branching systems found within many infrageneric taxa were either uniform or were closely related. Where diversity of branching patterns was seen within a taxon he believed this to be an indication of polyphyly.

According to Danert (1967) the primary level of sympodial organisation in the genus is a dichasial branching pattern with plurifoliate sympodial units. In such a scheme, two axillary shoots grow out at a shallow angle from the last two leaves below an inflorescence; the top axillary shoot is invariably the strongest. Modifications to this pattern involve the progressive reduction of the lower axillary shoot. Rather than growing laterally at a shallow angle, the upper axillary shoot takes on the direction of the primary axis so pushing the inflorescence into a lateral position. This leads to monochasial sympodia

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with plurifoliate sympodial units. Subsequent modification involves progressive reduction to one leaf per sympodial unit.

Danert (l.c.) observed that patterns which he considered to be derived seemed to have evolved several times in _Solanum_, and therefore infrageneric taxa should not be defined by their branching patterns. However, a reasonable correlation with existing subgenera seems to exist. Dichasial sympodia with plurifoliate units are characteristic of subgenus _Brevantherum_. Monochasial sympodia with plurifoliate sympodial units are particularly common in subgenus _Potatoe_ although in Africa they are also found in sections in subgenus _Solanum_. It is a pattern particularly found in climbing species and is also seen in _S.pampaninii_ in subgenus _Leptostemonum_. Other species of subgenus _Leptostemonum_ are usually monochasial with di- or tri-foliate sympodial units.

A significant exception to the sympodial pattern of growth is seen in the South African _S.guineense_ in the monotypic subgenus _Lyciosolanum_. This species has from one to three flowers clustered on the ends of short woody spurs. This form, otherwise unknown in _Solanum_, is characteristic of _Lycium_ and other genera in the Solanaceae, and it has been suggested by Child (1979a) that it is a xerophytic or halophytic adaptation;

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S.guireense is indeed found in xeric habitats and the leaves may be somewhat succulent.

3.2 Leaves :

The number of leaves in a sympodial unit varies within Solanum but is usually constant for a particular species. Few-leaved sympodial units were seen by Danert (1967) to represent the derived state as opposed to the primitive plurifoliate condition. Essentially, the leaves of the genus are alternate, but through the concaulescence of successive vegetative shoots, variations are seen and the leaves may appear to be paired or the inflorescences to be leaf opposed. In some species in the subgenus Leptostemonum (Danert (1.c.) quoted S.melongena and S.macrocarpon) the two leaves found between each inflorescence belong to two different shoot generations. Thus, the ontogeny of the units must be understood if sympodia are to be compared, but Danert believed that evolutionary convergence of branching patterns was common in Solanum.

Leaf size varies greatly throughout the genus, and often within a species, depending on the growing conditions endured by individual plants. African dry-country species tend to be small leaved (e.g. S.gracilipes) while bushland species have larger leaves (e.g. S.zanzibarense), and the largest leaves are seen

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in forest species (e.g. S. giganteum up to 38 x 15 cm).
The character is of limited diagnostic value except as
an indicator of the likely habitat of an individual.
The leaves (or leaflets) of Solanum species are
generally ovate or lanceolate in outline. The apex is
usually acute or acuminate, with a drip-tip in some
forest species (e.g. S.madagascariense). The leaf
bases are more variable and a range of forms from
decurrent (often seen in African species of subgenus
Solanum) to cordate (common in subgenus Potatoe and
occasionally seen in subgenus Leptostemonum) are found
throughout the genus.

There is some systematic value in the form of the leaf
margin as lobing seems to be confined to subgenus
Leptostemonum. The leaves of species of subgenus
Solanum are entire, toothed or lightly sinuate but
never lobed. Some sections of subgenus Leptostemonum,
such as section Irenosolanum or the Old World species
of section Torva, include species with entire leaves.

However, elsewhere in this subgenus, such as in section
Melongena and parts of section Oliganthes, a variety of
lobing is found. This is accentuated particularly in
such New World alliances as section Androceras, but
while the lobes of the leaves of the New World species
tend to be angular in outline, those of the Old World
species are more rounded. This can be seen, for

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example, in a comparison of the African section Melongena with the meso-American section Acanthophora.

The leaves of the South African species S.linnaeanum are described as pinnatisect, but the pinnate dissection of leaves, typical of subgenus Potatoe, is not seen outside America. On inspection, the lobing seen in subgenus Potatoe is entirely different from that found in species of subgenus Leptostemonum (see Fig. 3.2.1). In subgenus Potatoe the lobes take the form of sub-basal outgrowths of lamina, and each leaflet has a similar venation pattern to the terminal leaflet. It seems that during the development of the leaf, marginal meristems become separated along the foliar axis by intercalary growth of the rachis, and subsequently they develop into discrete leaflets rather than contributing to the lamina of an entire leaf.

Within subgenus Potatoe a progression of forms can be seen from the cordate leaf bases (Fig. 3.2.1a) of S.jasminoides, to the appearance of one, two, or more subtending leaflets (Fig. 3.2.1b), as in S.dulcamara or S.wendlandii to the development of the pinnately lobed leaf (Fig. 3.2.1c) typical of S.tuberosum. Although cordate leaf bases are found in some African Solanum species (e.g. S.setaceum Dammer), the only species known to have developed lateral leaflets is the
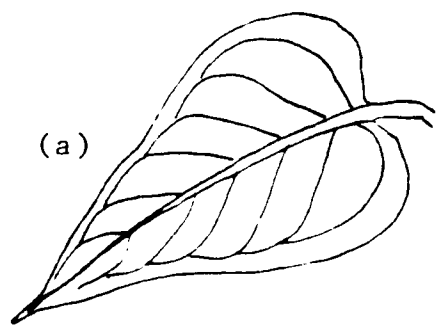
(a)
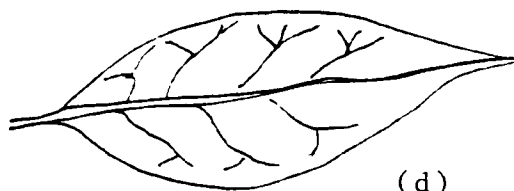
(d)
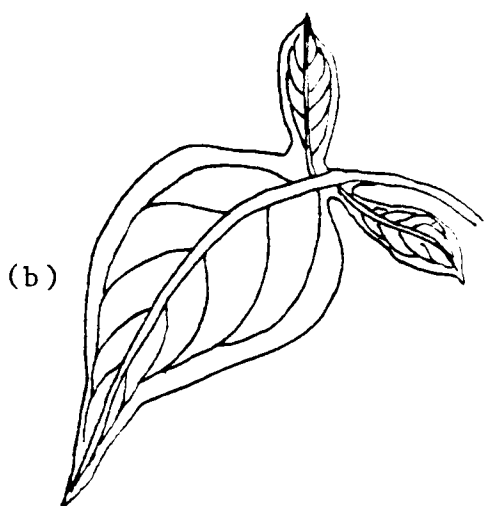
(b)
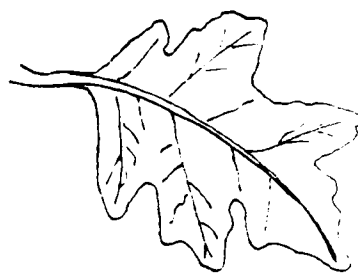
(e)

(c)

a,b,c = Camptodromus

d,e = Craspedromus

Fig. 3.2.1. Leaf venation and lobing in the genus <u>Solanum</u>

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Macaronesian _S.trisectum_, currently acknowledged as a

constituent of subgenus _Potatoe._

Recently, venation patterns have been studied in 12

species of Solanaceae by Inamdar and Murthy (1978).

Using the terminology defined by Hickey (1973) they

found the venation to be pinnately camptodromus (Fig.

3.2.1) in all species. The number of secondary veins

was not constant either between, or within, species and

it was found to vary irrespective of leaf size.

Branching of the secondaries was noted in two of the

species of _Solanum_ which they studied.

An initial survey of the African species of _Solanum_

revealed a similar pattern to that noted by Inamdar and

Murthy. Most of the species exhibit camptodromus

venation types, but the venation of the lobed leaves of

species of subgenus _Leptostemonum_ would be more

accurately described as mixed craspedromus. Although

the number of secondary veins per leaf is somewhat

variable within species, differences between species

can be recognised, as Whalen _et al_ (1981) have reported

for the neotropical section _Lasiocarpa._ Statistical

analysis would be needed to confirm this. The detailed

study of venation patterns in _Solanum_ has yet to be

undertaken but it seems that there is some systematic

information available from this approach.

3.3 Epidermal Characters :

The most extensive studies of any epidermal characters of _Solanum_ species are those reported by Seithe (1962, 1979, Seithe and Anderson, 1982) of observations on the hairs, glands, prickles and bristles to be found in the genus. Seithe noted that nearly all juvenile plants of _Solanum_ bore gland-tipped finger hairs as well as some multicellular glands on single celled stalks. The gland-tipped finger hairs were found to develop either into branchlet (dendritic) hairs or into stellate hairs, but never both in the same species, and Seithe considered these two distinct developments to represent parallel lines of evolution. The genus was therefore divided into two _chori subgenerum_ : species with stellate hairs were confined to the _chorus subgenerum Stelatipilum_, those without to _chorus subgenerum Solanum_. This division of the genus was found to correlate well with such characters as anther shape and dehiscence, and the presence or absence of prickles which have been used traditionally to define the infrageneric groups.

Within the genus _Solanum_ each of the hair types recognised by Seithe shows considerable variation. The systematic importance of the trichomes was limited by the imprecise use of terms to define them until Roe (1971) published a suggested terminology in an attempt

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to enhance their taxonomic value. More recently, detailed studies of the hairs of sections _Solanum_ (Edmonds, 1982) and _Basarthrum_ (Seithe and Anderson, 1982) have been reported; the latter work revealed that the morphology of hairs can be of some systematic use for taxa well below the subgeneric level at which such data was first applied. A detailed study of the African species has not been completed, but while a survey of the species with stellate hairs during the present work indicated variability in such features as hair size, stalk height and the length of the central ray, only limited correlations to accepted species groups were noted. Species from both sides of Seithe's division of the genus are represented in Africa.

Any systematic study of the hairs of _Solanum_ species must take into account the topographical and temporal variations in hairs on an individual. There are significant differences between the stellate hairs on the upper and on the lower leaf surfaces, and also as compared to those on the corolla lobes. Seithe remarked on variants connected with the time at which the hairs formed in relation to the developmental stage of the plant. Furthermore, environmental parameters may need to be considered, as it has been noted in _Encelia farinosa_ (Compositae), for example, that the pubescence will increase in response to such factors as a drop in leaf water potential, or a rise in the air

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temperature (Ehleringer, 1982).

Such increases in leaf pubescence reduce water loss and also lower the absorptance of solar radiation (Smith and Nobel, 1977), and this may indicate the adaptive significance of epidermal hairs to Solanum species. Certainly, some of the African dry country species, such as the North East African S.incanum, have an exceptionally dense pubescence, particularly on the abaxial leaf surface where the stomata are concentrated. Equally, other dry country species in Africa such as S.hastifolium and S.gracilipes do not, but rather have small leaves thereby increasing the convective heat dissipation. Hairs on other parts of the plant, such as the style and ovary, will play little significant part in reducing water loss, or in lowering the plant temperature; perhaps they contribute a defence against insect attack.

The prickles which are characteristic of many species of Solanum are probably another defence against herbivory (Symon, pers. comm.). As discussed in Chapter 2 of the present thesis, the presence or absence of prickles has featured prominently in the infrageneric classification of Solanum since Linnaeus' Species Plantarum (Ed. 1, 1753). Seithe (1962, 1979) included observations on prickles and bristles in her studies of Solanum trichomes, and she found that while

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bristles were developmentally long-stalked stiffened stellate hairs, the prickles were derived from gland-tipped or simple finger hairs. Thus possession of bristles is restricted to those species with stellate hairs, but because gland-tipped or simple finger hairs develop into the branchlet or into the stellate hairs which Seithe used to divide the genus, prickles could theoretically be related to either hair type. In practice, it is generally only the species with stellate hairs that are armed with prickles, although an exception is seen in the small hooked prickles of the species of section Aculeigerum which do not have stellate hairs.

The appearance of prickles in Section Aculeigerum (perhaps as an adaptation for a climbing or scrambling habit) and in the armed sections of subgenus Leptostemonum (possibly as a deterrent against herbivory) implies that the presence of prickles has developed at least twice in the evolution of the genus Solanum.

Within subgenus Leptostemonum, certain sections, such as section Somalense, section Anisantherum and some of the African species of section Torva, have no prickles and may never have had them. Other African species in this subgenus, such as the cultivated species S.macrocarpon and S.aethiopicum, may lack prickles, but

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from their relationship to other wild species it is
clear that prickles have been lost rather than not
developed.   In the domestication of these leaf and
fruit vegetables it is likely that there would be a
strong selection pressure by man against prickliness.
From their studies, Attavian et al (1983) have
concluded that prickliness is, in the species of
Solanum studied (their determinations are suspect),
under single gene control, and that the prickly
condition is dominant to the absence of prickles.
Selection against prickles would not be a complicated
procedure if they are indeed under single gene control.

Apart from section Aculeigerum, whose overall
affinities seem to be to subgenus Potatoe, all the
prickly species of Solanum are confined to subgenus
Leptostemonum. Typically, the prickles are found on
the stems, branches and twigs of the plants, but they
often extend to the petioles and leaves as well as the
pedicels and calyces.   The African species usually
have only a few prickles on the leaves and these are
often confined to the upper and lower surface of the
primary vein. By comparison, some of the Australian
species, for example S.prinophyllum (section
Oliganthes), have numerous prickles on the leaves
arising above and below the primary, secondary, and
some of the tertiary veins. Among Old World species it
is common to find species with the pedicels and calyces

densely armed with acicular or slender prickles.

The prickles in <u>Solanum</u> occur in a diversity of forms, with variation in shape, size, numerical density and colour, and this is often helpful in recognising species. There are broad-based stout prickles, small hooked prickles often found on scrambling shrubs, long and slender ones and sometimes needle-like, acicular prickles. In some species in Africa, notably <u>S.arundo</u> and <u>S.dennekense</u>, two prickle types are found on the same plant : there are recurved prickles on the stems and branches, and straight, narrow prickles on the leaves.

Prickle density is often relatively constant within a species, but, in some cases, particularly those with straight, narrow prickles, such as <u>S.coagulans</u>, there is much variation in the number of prickles per unit area of stem. Most prickles in the African species are shades of brown, from dark to the colour of straw. Among several Madagascan species of <u>Solanum</u> the prickles are red, but is is not clear whether this is always so on the living plant, as in <u>S.pyracanthum</u>, or an artifact of the drying process.

The lower half of a prickle is frequently pubescent, but, as the prickles are developmentally trichomes, an apical hair is often also present early on. Seithe

(1979) noted that the hairs on the prickle apex may be either gland-tipped, or simple finger hairs, indicating that the development of a prickle is determined early in the trichome ontogeny. Prickles with stellate apical hairs have been noted on a single accession of S.incanum grown at Birmingham (accession number S.859):. whether this phenomenon is more widespread is not known. Although Seithe found that bristles, rather than prickles, developed from stellate hairs, the development of finger hairs to either branchlet or stellate hairs is genetically determined, and in most cases only those destined to become stellate hairs are capable of further development into prickles. The apical hairs of accession S.859 have presumably simply continued their predetermined development.

In the South American section Leiodendron, small tufts of simple hairs are found in the axils between primary and secondary veins on the abaxial surface of the leaves. It might be suggested that these are domatia, but no studies have attempted to reveal their functional significance. No equivalent structures have been found in the African species of the genus.

Finally on epidermal characters, studies by Ahmad (1964a and b) and Bessis and Guyot (1979) attempted to use stomatal attributes in a systematic appraisal of the Solanaceae. The stomata of those Solanum species

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studied were generally of the mesogenous anisocytic
(cruciferous) type which Bessis and Guyot considered to
be an advanced form. These workers also found that all
the species studied in the family had the more
primitive perigenous anomocytic (ranunculaceous) type.
From other epidermal studies Ahmad (1964a) suggested
rearrangements to certain generic relationships
accepted by Bentham and Hooker (1876) and von Wettstein
(1895). For example, on the basis of epidermal
characters <u>Brunfelsia</u> did not stand with <u>Schizanthus</u>
and <u>Streptosolen</u> in the Salpiglossideae.

Bessis and Guyot were led to the conclusion that the
Solanaceae were clearly polyphyletic, and they
presented a hypothetical phylogeny of the genera based
on their data. While stomatal characters may have some
systematic value above the generic level in the
Solanaceae, there seems to be insufficient variation
within the genus <u>Solanum</u> to provide evidence for
infrageneric classification.

3.4 <u>Inflorescence</u> :

The position of the inflorescence varies throughout the
genus <u>Solanum</u> but may be diagnostic of a section. It
is often the case in <u>Solanum</u> that the inflorescence

appears to be lateral. This is a result of the sympodial growth form whereby a terminal inflorescence is superseded by an axillary vegetative shoot continuing to grow in the direction of the primary axis. The displaced inflorescence may be adnate to the new shoot and so appear in a variety of positions from internodal extra-axillary to leaf opposed. In those species with a dichasial, rather than monochasial, habit the terminal inflorescence is subtended by the two branches which continue the vegetative growth. Adnation of the inflorescence to the upper shoot may draw the inflorescence to an internodal position on that shoot (e.g. in S.giganteum).

The inflorescence of Solanum is in essence a cyme, but different degrees of elaboration have led to a bewildering variety of forms which defy the existing terminology as refined by Troll (1964/69), Briggs and Johnson (1979) and Weberling (1981). A readily apparent feature of the inflorescences of the genus is the complete absence of bracts from the inflorescence, and this too confuses the comparison of Solanum inflorescences with diagrammatically defined descriptive terms. It is important to note however that naming an inflorescence type is purely a descriptive exercise, and provides little information as to the possible relationships to other amplified or

reduced patterns. Furthermore, the inclusion of the inflorescences of two taxa under a single name is an assumption of homology which may be without foundation.

Danert (1967) noted a relationship between the size of the inflorescence and the number of leaves in a sympodial unit in Solanum. The plurifoliate species generally have more richly flowered inflorescences than those with few-leaved sympodia. This relationship seems to be true of the Solanum species in Africa, and it is particularly noticeable in the ostentatious inflorescences of sections Afrosolanum and Benderianum, which vary from compound cymes to thyrsoid and spike-like forms.

Reduction in inflorescence complexity and size is common in the genus, and species of subgenus Leptostemonum generally display few-flowered monochasial cymes. These too take a variety of forms, being often racemose in section Oliganthes, while in the andromonoecious species of section Melongena the hermaphrodite proximal flower is almost sessile on the stem, and the functionally male distal flowers are arranged thereafter in a pattern similar to a helicoid cyme.

The anomalous subgenus Lyciosolanum is characterised by inflorescences of one to three flowers on slender

pedicels arising from the leaf axils of short woody shoots. This form of flowering is not found elsewhere in the African Solanum species, although much reduced inflorescences are also found in section Somalanum.

The pedicels of African species are all articulated at or near the base, and it is from here that the unfertilised flowers are abscised. The articulations of some species of subgenus Solanum are markedly above the pedicel base, but articulation well below the mid-point is diagnostic of section Petota.

3.5 Perianth :

The morphological constancy of the flowers within the genus Solanum has been related by Symon (1979b) to the specialised nature of the pollination effected by a narrow range of insects. The perianth of Solanum is dicyclic, and generally actinomorphic. The calyx and corolla are both pentamerous, but this may be variable within a species, and sometimes within an individual; tetramerous and hexamerous flowers are not uncommon. Tetramerous flowers occur in some Old World species of section Torva as well as some of the species in section Oliganthes and the mostly Australasian section

Irenosolanum, but whether or not this is indicative of taxonomic relationship requires further evidence.

The gamosepalous calyx is green, often densely tomentose and sometimes armed with prickles. The calyx tube is usually campanulate, and the rim varies from toothed to deeply lobed. The lobing may first appear in bud as small teeth on the growing calyx, but generally is accentuated as the calyx splits when the bud emerges. Among African species the shape of the calyx lobes is often diagnostic, as are the acuminate lobes of S.somalense or the leafy lobes of section Monodolichopus for example.

The calyx is persistent in fruit and generally surrounds the young berry. Later the calyx may remain appressed to the fruit or be reflexed away as in S.hastifolium. The calyx occasionally continues to enclose the fruit by further increase in size. Thus the extremely prickly calyx of S.coagulans protects the fruit until maturity by elongation of the calyx tube, while the calyx of S.macrocarpon extends by continued growth of the lobes but fails to enclose the large fruit.

The corollas of the African species of Solanum vary from pentagonal to deeply lobed and stellate. The pentagonal form appears to be a stellate corolla, with

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interstitial tissue developing between the lobes. The
corolla is often hairy on the outside, or only on the
lobe edges, but some hairs may appear on the inside of
the flower. The most common form of flower is rotate,
but the larger pentagonal flowers, such as in
S.macrocarpon, may be campanulate. Conversely, the
stellate corolla of some species (e.g. S.hastifolium)
is sharply reflexed.

The corolla is either white or assorted shades of
purple or violet in the African species of Solanum.
There are no native yellow flowered species. The
colour of the corolla is usually consistent within a
species, although some white flowered species of
section Oliganthes may have purple streaks in the
corolla lobes of some races. It should be noted that
Nielsen (1965) and Symon (1981) have observed that
corolla colour may vary with age and ambient
temperature.

Most of the African species have actinomorphic
corollas, but zygomorphy is seen in section Nycterium.
The aestivation of the perianth whorls throughout the
genus is valvate or induplicate valvate.

3.6 Androecium :

Each of the five stamens of the androecium of _Solanum_ comprises a short filament attached to adnated yellow anther thecae. The basal portions of all five filaments are fused to form an annular structure in the tube of the corolla. Each filament adheres to the lower end of the anther between the extremes of the thecae. Hunziker (1979b) has contrasted this pattern with that seen in other tribes of the subfamily _Solanodeae_.

The following variants are found in the genus :

1. The size of the stamen is variable and in general is correlated to the perianth size. In section _Solanum_ the stamen size is often diagnostic of a species. Although there are usually five stamens per flower, some tetramerous species have only four (e.g. _S.anomalum_), while other species may have six or more.

2. The filament is generally very short in the genus, but in species of subgenus _Solanum_ it may be more pronounced than is seen in subgenus _Leptostemonum_. In subgenus _Lyciosolanum_ the filament can be as much as 2.5mm long, which is unusual. Section _Monodolichopus_ is characterised by the unequal

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filaments in each flower. This is particularly noticeable in S.melastomoides where the four filaments are 1mm long and the fifth 5mm long. The filaments in most African species are glabrous, but those of S.benderianum and S.runsoriense have scattered simple hairs.

3. Variation in the size and shape of the anthers, and their correlation to the presence or absence of prickles on the plant, was first used as a taxonomic character to divide the genus by Sendtner (1846). The prickly species usually have long, tapered anthers, while the anthers of the unarmed species are shorter and more robust in appearance. The anthers of species of the Macaronesian sections Normania and Nycterium are obviously unequal in each flower. This is a curious parallel adaptation as section Nycterium in subgenus Leptostemonum and section Normania in subgenus Potatoe are generally accepted as phylogenetically widely separated. The anthers of the Central American section Androceras also exhibit unequal anthers, and here the phenomenon has been shown to promote outcrossing by differences in the orientation of the long anther and the style in separate individuals (Bowers, 1975).

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4. The anthers of most of the African species are free
    from one another, but in S.welwitschii they seem to
    be fused into a tube. Bitter (1917) saw this as
    doubtful evidence of the species' affinity to the
    Eurasian S.dulcamara. Bitter (l.c.) also noted
    various degrees of anther coalescence in
    S.humblotii, S.truncicolum and S.madagascariense.
    It is difficult to assess the validity of these
    observations as the anthers become separate with
    age, or may be freed in the preparation of a
    herbarium specimen.

5. The androecium in Solanum is often said to be
    characterised by the apical dehiscence of the five
    stamens. However, this is too great a
    simplification as the anthers of many species split
    longitudinally at dehiscence. This splitting may
    proceed basipetally from a stomium at the apex, but
    the anthers of some species (e.g. S.benderianum)
    show little evidence of apical pores. An initial
    survey of the variation in shape and location of
    the stomium among African species indicated that
    there is some systematic value, at least at the
    species level, if not above, in such characters.
    The stomia of subgenera Lyciosolanum and Solanum
    are usually apical slits which may or may not
    extend down the length of the anther. The
    Madagascan sections Lemurisolanum and

Macronesiotes, however, have well defined apical pores. The stomia of most African species in subgenus _Leptostemonum_ are circular pores rather than slits, with the exception of section _Monodolichopus_, and the pores may have rims or lips. Occasionally the pores are introrsely offset from the apex of the anther.

3.7 Pollen :

Typically, the pollen grains of _Solanum_ species are either prolate or spherical in shape. They are tricolporate with comparatively long colpi and conspicuous ora, and have a granular exine. The morphology of the grains is not particularly variable through the genus, and very few of the 71 references to _Solanum_ pollen cited by Tanikaimoni (1972, 1973, 1976 and 1980) have considered the pollen in systematic terms. Symon (1979b) has related the uniformity of the grains and the lack of ostentatious surface ornamentation to the need for the pollen to flow freely out of the small apical pores of the anthers when vibrated by pollinating insects.

A survey of some of the species grown in the course of the present study assessed the variation in the shape

and size of the pollen grains as well as the surface patterning. Fresh pollen was usually prolate, with the exception of S.macrocarpon, while acetolysed grains were nearly spherical. Some interspecific variation in the numerical density and size of the granules on the exine was noted but intraspecific variability may be sufficient to invalidate the systematic use of granule patterns.

Size and shape of the grains of a selection of species was studied using fresh pollen mounted in glycerol under a light microscope. The smallest grains to be found were those of S.seaforthianum (mean: 15.5 x 12.3µm) while S.mauritianum gave only slightly larger grains (mean: 21.5 x 13.3µm). S.anguivi and S.aethiopicum were found to possess pollen grains with similar dimensions (23-26 x 14-17µm) to each other and the rounded sides and pointed poles gave an elliptic shape. Pollen of S.violaceum was seen to be larger (mean: 29.9 x 16.4µm) but with the same shape. Other species of section Oliganthes that were observed (S.pyracanthum and S.tomentosum) exhibited pollen grains of similar shape with dimensions in the range between S.anguivi and S.violaceum.

The pollen grains of section Melongena studied here (S.incanum, S.melongena, S.marginatum and S.linnaeanum) were generally slightly longer (25-30 x 15-17µm) than

those of section Oliganthes and, with rounded poles and straight sides, they had an oblong shape on which the two sections might be distinguished. One species, S.macrocarpon, produced pollen which was almost spherical (mean: 23.1 x 20.7μm) and quite distinct from the other species of section Melongera to which it belongs.

Intraspecific variation in size is quite marked in some species, such as S.anguivi, and may be related to variability in gross morphology. Henderson (1974) reported that for the polyploid species of section Solanum, pollen size, although not directly proportional to chromosome number, gave an accurate prediction of ploidy level when considered in conjunction with inflorescence characters. All the species in the present investigations are diploid (2n=24).

Of the scattered reports on the application of pollen studies to Solanum systematics, Sowunmi (Gbile and Sowunmi, 1979) found sufficient characters in grain size, and exine thickness and patterning, to construct a key to the Nigerian species of Solanum using these characters. He found the difference in pollen morphology sufficient to recommend that S.terminale subsp. inconstans, subsp. sanaganum and subsp. welwitschii be given specific status, although no

account of the variation within these taxa was given. While I agree that subsp. _welwitschii_ should be raised to species level on the basis of gross morphology, Sowunmi's recommendations for the other two subspecies seem unjustified.

Sharma (1974), in a palynological survey of 63 mostly Indian species of _Solanum_, found 18 distinct pollen types which could be grouped into four size classes. He commented that aperture (i.e. colpi and ora) characters varied considerably within species although in some species the os might show potential as a diagnostic character. He revealed further evidence for the separation of _Lycianthes_ (Dunal) Hassl. from _Solanum_ but drew no other taxonomic conclusions from his pollen types.

Anderson and Gensel (1976) completed an extensive review of _Solanum_ section _Barsarthrum_ pollen and concluded that size and granule density might be useful in a taxonomic study. Their results were based on observations of many specimens of each species and the statistical analysis of their data indicated that there were significant differenes between species. They also noted apparently viable, inapperturate pollen in certain species.

Anderson (1979b) has reported discovery of non-viable

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inapperturate pollen in two Meso-American species, S.appendiculatum and S.inscendens, which appear to be dioecious. The species are heterostylous and the inapperturate pollen is produced only by the long-styled "female" plants, possibly as a pollinator attractant. The short-styled plants have normal tricolporate pollen. No such variations have been reported to occur in the African species of Solanum.

3.8 Gynoecium :

The superior ovary of Solanum comprises two fused carpels and is usually bilocular. Internally, the numerous unitegmic, tenuinucellate ovules are derived by monosporic embryogenesis and are arranged on axile placentae. A single style generally emerges for some distance beyond the anthers and terminates in a more or less enlarged stigma. The ovary and style may be hairy.

Deviations from this pattern can be useful for determining species, but good correlations between types of organisation of the gynoecium, and higher taxonomic ranks within Solanum, have yet to be recognised. The following variations are found :

1. The ovary may be 4- or more locular by the occurrence of false septa derived from the fusion of extended placentae to the pericarp (Whalen et al, 1981). Thus ovules may appear to be arranged on the secondary septa. This feature has been reported in the Neotropical section Lasiocarpa (Whalen et al, l.c.) and may occur in the fleshy-fruited African species. In a certain cultivar of S.aethiopicum (cv Kumba) the number of carpels has multiplied, leading to possibly 15 or more locules but a single fused style. In the formation of the fruit, all the carpels fuse to result in a single much lobed multilocular berry. This grotesque result is no doubt a consequence of selection pressure applied by man for increased fruit size.

2. The length of the style varies between species not only in its overall proportions but also in the degree to which it emerges beyond the anthers. This second feature will vary with the age of the flower, but between certain species it may be clearly different at equivalent flower ages. As some styles are also reflexed towards the apex, it might be suggested that such variation could be correlated to specific pollinators.

3. Certain species demonstrate andromonoecy with only the proximal one, two, or three flowers of an

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inflorescence being hermaphrodite. In the distal flowers, the gynoecium fails to develop and the style remains vestigial. This is a diagnostic feature of section Melongena, but such stylar heteromorphism (often incorrectly called heterostyly) has also been reported in S.torvum by Hossain (1973), in S.khasianum (= S.myriacanthum) by Murty and Abraham (1975), in S.virginianum by Reddy and Bir Bahadur (1977) and in S.macranthum by Baksh and Iqbal (1978). Recently, dioecy has been noted in several species of Solanum in Australia by Symon (1979b) and in America by Anderson (1979b). This breeding system is not found among the African species of Solanum.

4. Between species of Solanum there may be recognisable differences in the size of the stigma as compared to the style, and also in the extent of the lobing of the stigmatic surface. In some species, particularly in section Oliganthes, the style barely swells at its apex to form the stigma.

5. There is considerable variation in the density and extent of the indumentum on the gynoecium. The ovaries and styles of African species of subgenus Solanum are usually glabrous, while those of species of subgenus Leptostemonum are often hairy. The hairs may cover the ovary completely,

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partially, or not at all, and they may extend up to two thirds of the way to the apex.

3.9 Fruits :

The fruit of Solanum is classified as a berry. Among the African species the berry is generally spherical, and there is variation in size from the 0.6-1.0cm diameter fruits of species of section Solanum to the 8-10cm diameter fruits of S.macrocarpon. The fruits vary in texture from the juicy fruits of subgenus Solanum, which are also found in section Torva and Oliganthes, to the fleshy fruits of section Melongena, the tough dry fruits of section Ischyracanthum and the dry papery fruits of section Monodolichopus. The mature fruits may be green, yellow, orange, red or black. White or purple fruits are found in some domesticated species.

Bitter (1911, 1915, 1917) recorded the presence of sclerotic granules in the fruits of some Solanum species and believed this feature to be taxonomically useful. Danert (1969) found that the sclerotic granules developed in the pericarp of the ovary just prior to anthesis. He considered their presence indicative of rudimentary drupaceous fruits. They are commonly found in the subgenera Potatoe and Solanum,

including some of their African representatives, with the exclusion of sections Afrosolanum and Benderianum. The number of sclerotic granules present may be diagnostic of a species. Sclerotic granules have not been found in subgenera Brevantherum of Leptostemonum.

3.10 Seeds :

Hunziker (1979a and b) recognised that the Solanaceae could be divided into two subfamilies on the basis of seed characters : the Solanoideae possess discoidal, flat, more or less compressed seeds with clearly curved embryos, while the Cestroideae develop prismatic, reniform, or subglobose seeds in which the embryos are straight or only slightly bent. The seeds of Solanum are flattened, slightly biconvex and discoidal, or reniform in outline. The subsurface sculpturing of the testa is under study at the University of Birmingham and initial results indicate that data from the comparison of patterns have some systematic value (Lester and Durrands, 1983).

The seeds of the African species of Solanum vary in size from the minute seeds of section Solanum, measuring 1-1.5mm in diameter, to the large, flat, seeds of S.pampaninii and S.vespertilio 6mm in

diameter. The seeds are often pale brown straw coloured, but in section Melongena they are a darker brown. The seeds of section Monodolichopus are black and shiny. Variation in seed size and colour is often useful in determining the section to which a species belongs.

3.11 Cytology :

The species of Solanum are predominantly diploid (2n = 24) and the base chromosome number is x = 12). The two sections Petota and Solanum have evolved as polyploid series, and reach to octoploid levels, but elsewhere in the genus polyploidy is rarely found naturally. The antipodean section Archaesolanum is an oddity with a base number x = 23 (Symon, 1981).

Federov (1969) lists the published chromosome numbers of a few African species. All are recorded as 2n = 24, with the exception of species of section Solanum and, strangely, S.macrocarpon which was reported to be 2n = 36. This count seems unlikely, and Omidiji (1979) has reported 2n = 24 for S.macrocarpon. Given the uniformity of chromosome numbers in the genus Solanum, no counts have been made in the course of the present work. However, where there is a published count of a

<u>Solanum</u> species which occurs in Africa, this is recorded in the species description to be found in Chapter 7.

3.12 <u>Comparative Chemistry :</u>

The potential value of comparative chemistry to systematics has been accepted since the last century. Its development however has been much more recent. Progress was delayed for a long time by the cumbersome nature and poor resolution of the techniques of analytical chemistry which precluded the widescale screening of plants for their metabolic products. The breakthrough came with the advent of chromatography and electrophoresis : these procedures allowed the rapid and repeatable separation of chemical constituents, and were capable of dividing small quantities of crude plant extracts into homogeneous components. Furthermore, because chromatographic or electrophoretic separation techniques resulted in patterns of spots, or bands representing individual metabolites, further analysis was unnecessary as taxa could be characterised by the presence or absence of individual unknown chemicals. As a consequence of the development of these techniques, chemotaxonomy has progressed rapidly

in the last 30 years or so.

Recent developments in the procedures of analytical chemistry (such as ultra-violet absorption spectroscopy, chemical manipulation procedures, nuclear magnetic resonance spectroscopy and mass spectrometry), have simplified the art of molecular indentification and structural elucidation. This has accelerated the application of chemical characters to taxonomy and a substantial amount of phytochemical information has been accumulated, as can be seen in the reviews by Hegnauer (1973) and Gibbs (1974). Comparative chemistry is widely accepted now as providing a reliable new set of data against which existing classifications may be tested, and which can be used at many levels of the taxonomic hierarchy for constructing new classifications. Chemotaxonomy has been applied usefully to the infrageneric classification of <u>Solanum</u>, although so far the African species have been largely neglected.

The compounds which form the basis of comparative chemistry are often divided into the 'macromolecules' and the 'micromolecules', reflecting differences in molecular weight. Macromolecules include the high molecular weight proteins and nucleic acids which are also collectively known as 'semantides'. These are further subdivided into primary, secondary and tertiary

semantides incorporating deoxyribonucleic acids (DNA), ribonucleic acids (RNA) and proteins respectively, reflecting the sequential transfer of genetic information. The use of macromolecules in the chemotaxonomy of Solanum will be discussed in Chapter 5, together with other experimental work which has been part of the present investigation.

Traditionally, micromolecules have been divided into primary and secondary metabolites. This distinction was based upon the understanding that the primary metabolites were involved in the chemical processes essential to life, while the secondary metabolites were by-products which were not essential to the plant. This is now considered to be untrue : many secondary metabolites are believed to have important roles in, for example, defence or pollinator attraction, and the assumption that a compound is of no importance to a plant because its use has not been recognised has been abandoned. The distinction between primary and secondary metabolites however is maintained, to divide those compounds which are directly involved in the primary metabolic processes from those products of biosynthetic pathways which are not. It is a vague but useful distinction.

Primary metabolites, by definition, are involved in the essential metabolic processes, and the distribution of

individual compounds in the plant kingdom is usually widespread if they are not ubiquitous. Consequently they are of limited use as taxonomic markers, except where there is quantitative variation, or there are differences in metabolic pathways as, for example, is seen in the various carbon dioxide assimilation and fixation routes found in C_3, C_4 and CAM plants. The fundamental roles played by the primary metabolites restricts their variability and to the taxonomist they are only of use at the higher levels of classification. By contrast, there are a multitude of secondary metabolites, and these have been shown to be useful at all levels of classification (Gershenzon and Mabry, 1983). Their use in the classification of Solanum will be the focus of the following discussion.

Advances in analytical chemistry have led to the possibility of identifying the routes followed by biosynthetic pathways, using, for example, isotopic tracers, sequential analysis of intermediate compounds or microbial auxotrophic mutants unable to synthesise precursors in a sequence of reactions. From such studies it is clear that two metabolites of the same type, such as two alkaloids, may be synthesised by completely different pathways. It may also happen that the same compound is synthesised in two taxa by two slightly different routes. If the routes are different it may be assumed that there are differences in the

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genome and so in any comparative study, homology in the formation pathways is most important.

Fig. 3.12.1 provides a synopsis of the major biosynthetic pathways in plants. Taking the alkaloids as an example : this class of compounds was originally defined on the basis of wide-ranging physicochemical and pharmacological properties which has led to a heterogeneous grouping under a single name. It is now appreciated that the 'true' alkaloids are biosynthesised from amino acid precursors, while some of the pseudoalkaloids, the steroidal alkaloids, are derivatives of the acetate-mevalonate pathway, and the protoalkaloids (or aromatic amines) are derived from the shikimate products. Further, the indole alkaloids may be divided into the simple compounds biosynthesised from the shikimate precursor tryptophan and the complex compounds derived from trytophan and mevalonic acid. It is plain that for comparability, the biosynthetic pathway must be known. Each of the four biosynthetic pathways indicated in Fig. 3.12.1, and their taxonomically useful products relevant to the study of Solanum, will be considered briefly in turn.

Firstly, the tricarboxylic acid cycle, and the production by transamination of glutamate or glutamine, compounds which are involved directly or indirectly in the biosynthesis of all amino acids. While amino acids

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CARBOHYDRATES

PENTOSE
PHOSPHATE
PATHWAY

GLYCOLYSIS

AROMATIC
COMPOUNDS

CARBON DIOXIDE
+ WATER

SHIKIMIC
ACID
PATHWAY

TRANSAMINATION

PYRUVIC ACID

AMMONIA

ACETYL CoA

TRICARBOXYLIC
ACID CYCLE

AMINO ACIDS

ACETATE-MALONATE
PATHWAY

ALKALOIDS

FATTY ACIDS

ACETATE-
MEVALONATE
PATHWAY

PROTEINS

NUCLEIC ACIDS

POLYKETIDES

TERPENOIDS

AROMATIC
COMPOUNDS

STEROIDS

**Fig. 3.12.1   Outline of the Biosynthetic Pathways
in Plants. (From Vickery & Vickery, 1981)**

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are considered to be the building blocks of proteins (whose use in taxonomy will be discussed in Chapter 5), over 240 non-protein amino acids are known in plants. Bell (1981) has demonstrated the use of the non-protein amino acids as taxonomic markers in the Leguminosae, but they are so far unstudied in the Solanaceae.

Several amino acids, particularly ornithine, lysine and nicotinic acid, are precursors in the synthesis of the true alkaloids as are the aromatic amino acids phenylalanine, tyrosine and tryptophan which, being derivatives of the shikimate pathway, will be discussed later. Some alkaloids have a medicinal value and so there has been extensive screening of plants in the search for new compounds and new sources.

Ornithine is involved in the biosynthesis of three classes of alkaloid : the tropane, pyrollidine and pyrollizidine alkaloids. The tropanes (e.g. hyoscyamine) are of particular interest as they chiefly occur in the Solanaceae, but while they are not found in Solanum they have been recorded in Cyphomandra (Schreiber, 1968). The taxonomic limits of these two genera are not clear, but such evidence tends to support their separation. Evans (1979) has discussed the distribution of tropane alkaloids in the Solanaceae. It seems that tropanes are probably biosynthesised from pyrollidine derivatives and these

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are also abundant in the Solanaceae but not seen in Solanum. Evans however noted sporadic occurrence in Solanum of cuscohygrine which is a side product of the principal tropane biosynthetic pathway. It may be that tropane biosynthesis, being found in several genera in the Solanaceae, represents the least derived state for the family, and in the course of evolutionary history the biosynthetic pathway has been reduced.

Lysine gives rise to the quinolizidine (or lupin) alkaloids, amongst others, which are found in the Chenopodiaceae, Berberidaceae and Leguminosae. Gibbs (1974) recorded dl-lupanine in Solanum lycocarpum but this is the only record in the Solanaceae. Nicotinic acid is the precursor of the tobacco alkaloids such as nicotine. This is characteristically accumulated by Nicotiana, but is also found in the other solanaceous genera Duboisia, Salpiglossis and Withania (Gibbs, 1974). Trace amounts have been noted in many other families.

The porphyrins, purines and pyrimidines should also be mentioned as derived from amino acids. By themselves these compounds are of little chemosystematic importance, but the ordering of nucleotides (derived from the purines and pyrimidines) in the nucleic acids, when studied by sequencing and DNA hybridisation procedures, can give taxonomically useful information.

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Such techniques have not been reported in the study of Solanum taxonomy.

The second pathway to be discussed is the shikimate pathway which leads to the biosynthesis of aromatic compounds, notably phenylalanine, tyrosine and tryptophan. An outline of the pathway by Gottlieb (1980) is presented in Fig. 3.12.2.

Gottlieb's (l.c.) 'First Principle of Micromolecular Systematics' states that for a biosynthetic sequence of metabolites

$$A \begin{cases} B \longrightarrow C \longrightarrow D \\ E \end{cases}$$
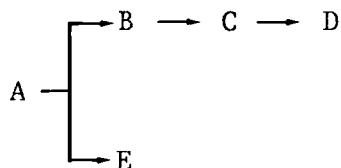
"when B, C and D represent primary metabolites of the shikimate pathway, if

a taxon accumulates derivatives of C it comes from a taxon characterised by derivatives of D".

In other words, Gottlieb considers that there has been a reduction of the shikimate pathway in the course of evolution. Thus, the benzylisoquinoline alkaloids, for example, occur in the Magnolianae (sensu Dahlgren, 1975), but only sporadically elsewhere. A recent family such as the Solanaceae should have few

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derivatives of this pathway.

Precursors   Products

Carbohydrates ──────────────────────────────► Cellulose
          │
          │   Pyruvic Acid──►Mevalonic Acid════►Iridoid
          ▼   ▼   Alkaloids
Shikimic Acid   Tryptophan ────────►Indole
          │   ▲   Alkaloids
          ▼   │
Chorismic Acid────────►Anthranilic Acid──►Quinoline
          │   Alkaloids
          ▼
Phenylalanine────────►BTIQ──────────────►Benzylisoquinoline
          │   Alkaloids
          ├──(PAL)   (Oxidases)
          ▼
Cinnamic Acids ──────────────────────────►Lignoids
          │
          ▼
Cinnamyl Alcohols ◄──────────────────────►Lignins

Fig. 3.12.2   Outline of the Shikimate Pathway
               (from Gottlieb, 1980)

Gottlieb's 'First Principle' seems to be a useful
generalisation, but it must be acknowledged that
inevitably exceptions will be found. A particular
anomaly seems to be that all higher plants, from the
liverworts and mosses upwards, possess flavonoids, and
parts of these compounds are biosynthesised from the
cinnamic acids which in turn are end products of the
shikimate pathway (Fig. 3.12.2). Apart from the
flavonoids, which will be discussed more fully below,
other derivatives of the shikimate pathway seen in the
Solanaceae include the simple indole alkaloid
tryptamine biosynthesised from trypotphan. Gibbs

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(1974) recorded the presence of tryptamine in 'Lycopersicon and Solanum (eggplant)'.

The shikimate pathway also leads to the production of the 'hydrolysable' tannins, especially the esters of gallic and ellagic acids. These tannins are biogenetically different from the condensed tannins (or proanthocyanidins) which share a biosynthetic pathway with the flavonoids. Tannins are associated with lignification, a supposedly primitive feature, but Gibbs (1974) reported the presence of unspecified tannins in the Solanaceae. Coune and Denoel (1975) found the roots of Solanum dasyphyllum Thonn. to be rich in tannins which also were unidentified. The fruits of certain African species of Solanum, in particular S.marginatum L.f., are used by some Africans for tanning leather, though no tannins have been reported. Gornall et al (1979) observed that the flavonol myricetin often co-occurs with ellagic acid, and Whalen (1978b) has reported myricetin in the leaves of species in the meso-American section Androceras in Solanum : this is a highly specialised group but Whalen did not record the presence of tannins. With several reports of tannins in the Solanaceae further investigation of this group of compounds may be merited.

The third biosynthetic pathway for consideration is the

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acetate-malonate pathway of which the main products are the fatty acids. This pathway also contributes to the aliphatic and aromatic compounds via the side production of polyketides, and an early intermediate, malonyl CoA, is involved in flavonoid production. The pathway is of little use in the taxonomy of higher plants : polyketides are abundant in the fungi but less so in higher plants where they are usually aromatic derived and their possession seems to be a primitive characteristic. The ubiquitous major and minor fatty acids are of limited use as taxonomic markers, although some unusual ones may be found in seed oils.

Fourthly, the acetate-mevalonate pathway, which leads to the biosynthesis of terpenoids and steroid compounds which are derived from isoprene five-carbon units. The pathway is ubiquitous and all organisms can biosynthesise some terpenoids although the pathway is only found fully elaborated in the angiosperms. The derivation of compounds is shown in Fig. 3.12.3. Of particular interest in the Solanaceae are the steroids, these being produced through the intermediates squalene and cycloartenol. The steriods vary according to the number of carbon atoms they contain (Fig. 3.12.4), but it is the C_{27} (cholestane) derivatives which are of greatest interest in the taxonomy of the Solanaceae.

The steroidal sapongenins (or spirostanols) are usually

ACETYL CoA

|
↓

MEVALONIC ACID

|
↓

DIMETHYLALLYL PYROPHOSPHATE————————————————→HEMITERPENOIDS C_5

|
↓

GERANYL PYROPHOSPHATE ————————————————————→MONOTERPENOIDS C_{10}

|
↓

FARNESYL PYROPHOSPHATE—————————————————————→SESQUITERPENOIDS C_{15}

SQUALENE

CYCLOARTENOL

STEROIDS   TRITERPENOIDS C_{30}

GERANYLGERANYL PYROPHOSPHATE——————————————→DITERPENOIDS C_{20}

————————————→CAROTENOIDS C_{40}

POLYISOPRENES
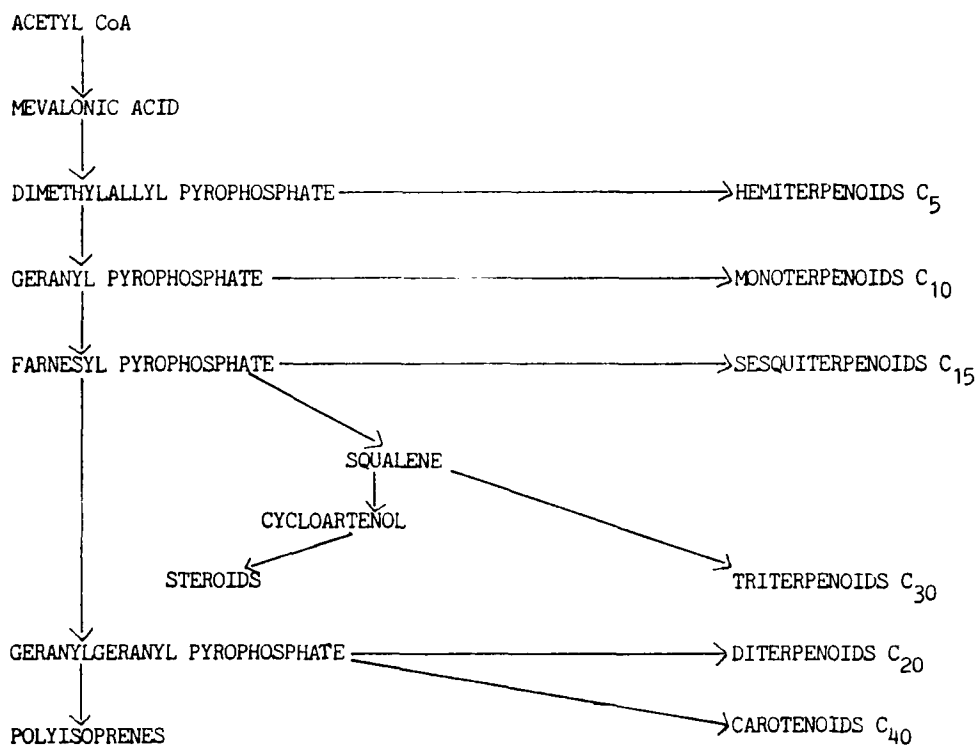
Fig. 3.12.3   Outline of the Acetate-Mevalonate Pathway.

(Adapted from Vickery & Vickery, 1981.)

CYCLOARTENOL

C_{29} STEROIDS C_{28} STEROIDS   CHOLESTEROL

|
├——→C_{27} SAPOGENINS
↓
C_{27} ALKALOIDS

C_{21} STEROIDS

C_{21} ALKALOIDS C_{19} & C_{18} STEROIDS

C_{24} BUFADIENOLIDES

C_{23} CARDENOLIDES
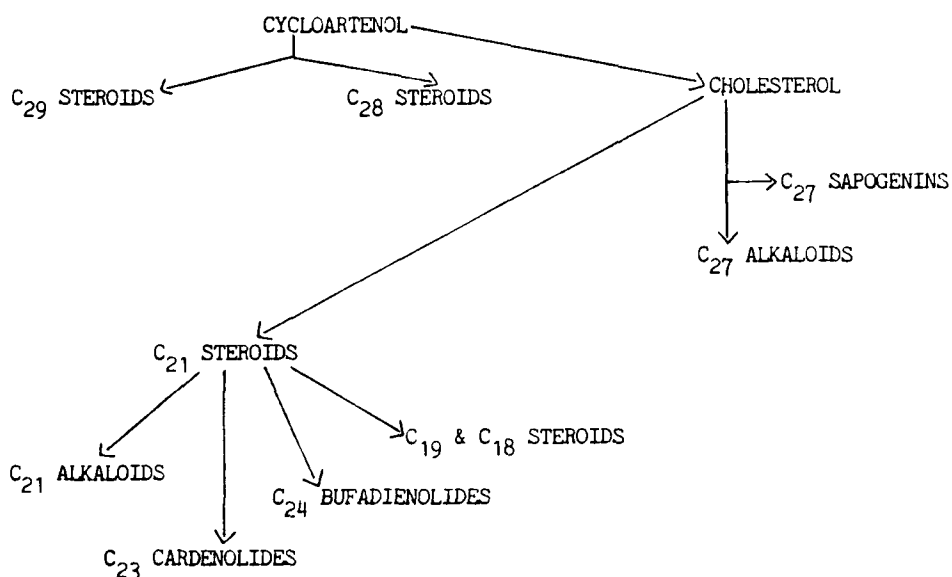
Fig. 3.12.4   Phytosteroid Derivation.

(From Vickery & Vickery, 1981)

found as glycosides (called saponins), and are common in the Liliaceae, Agavaceae, Dioscoreaceae and Solanaceae, as well as having been found in the genus Digitalis of the Scrophulariaceae. They should not be confused with the more widespread pentacyclic triterpenoid sapogenins, also derived from squalene, but subsequently following a different biosynthetic route. Some of the saponins occurring in the Solanaceae and Liliaceae contain nitrogen and are classed as alkaloids : to distinguish these from biosynthetically distinct alkaloids they may be referred to as pseudoalkaloids, steroid alkaloids or isoprenoid alkaloids. They are probably biosynthesised from cholesterol via the sapogenin diosgenin and are particularly characteristic of the genus Solanum. Some examples of steroidal sapogenin and alkaloid structures are given in Figs. 3.12.5 and 3.12.6 respectively.

A considerable amount of data on the occurrence of the cholestane derivatives has accumulated now as a result of their use in the industrial synthesis of such steriod drugs as contraceptives and corticosteroids. The sapogenins diosgenin and hecogenin derived from Dioscorea and Agave have been the traditional sources of the precursors for industrial synthesis, but rising prices and the political instability of supplier countries (notably Mexico) have encouraged the search for alternative sources. Attention was drawn to the

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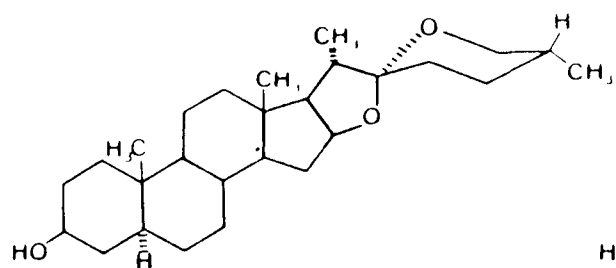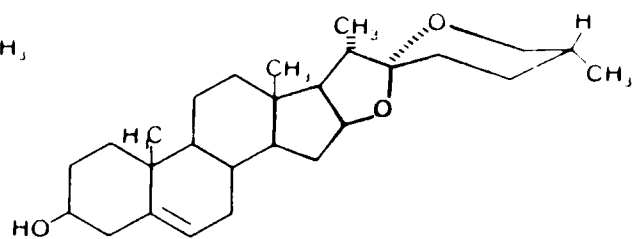
I Tigogenin

II Diosgenin
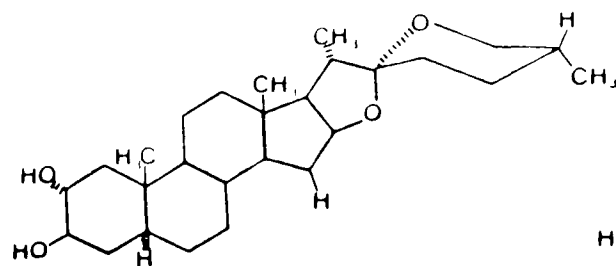
III Gitogenin
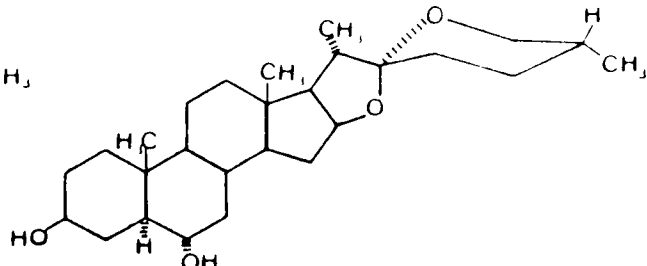
IV Chlorogenin
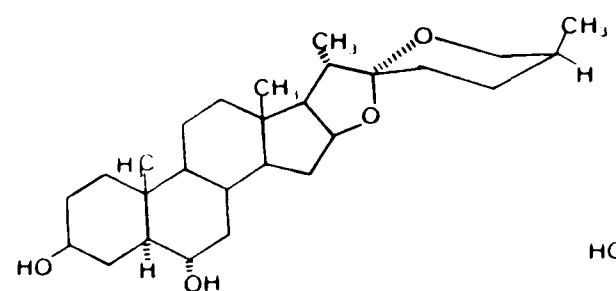
V Neochlorogenin
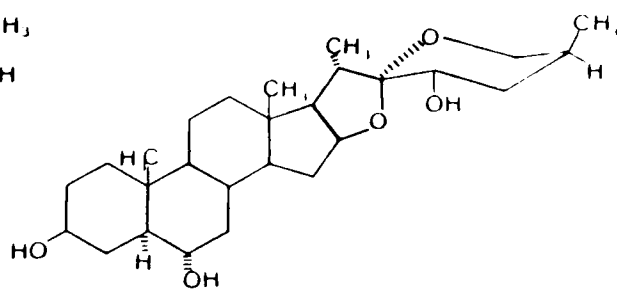
VI Paniculogenin
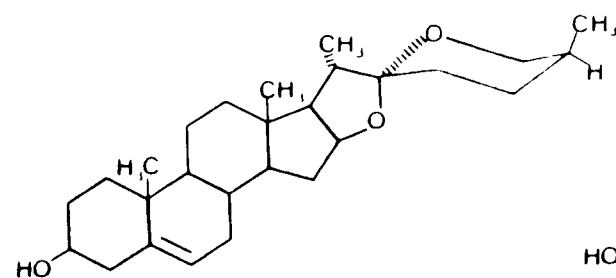
VII Yamogenin
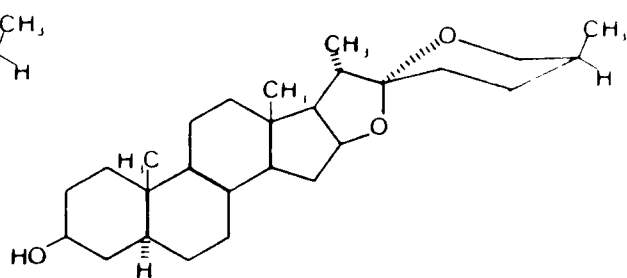
VIII Neotigogenin

Fig. 3.12.5 Examples of Steroidal Sapogenins (Spirostanols) found in the genus Solanum.
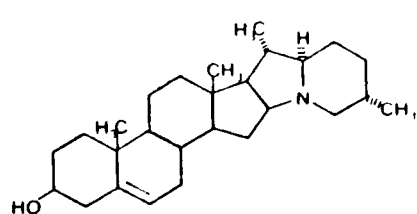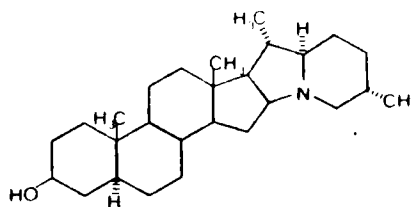
I Solanidine II Demissidine
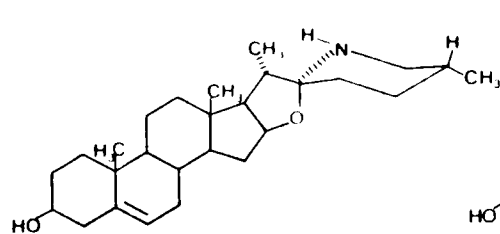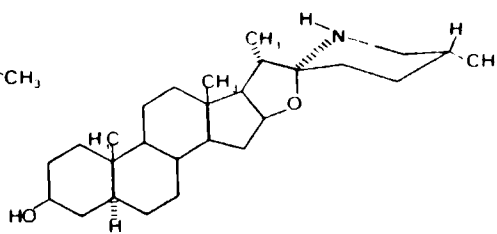
III Solasodine IV Soladulcidine
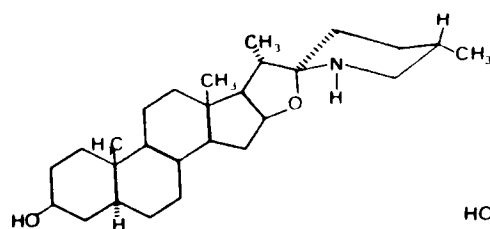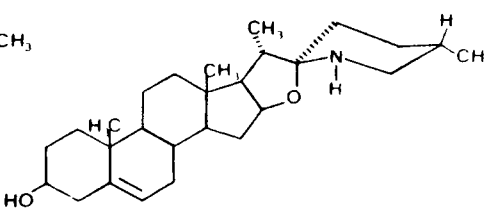
V Tomatidine VI Tomatid-5-en-3-ol
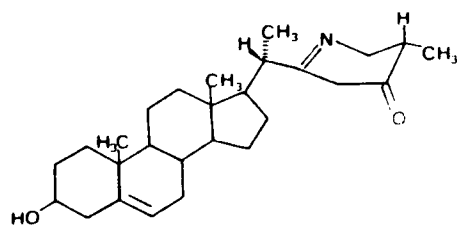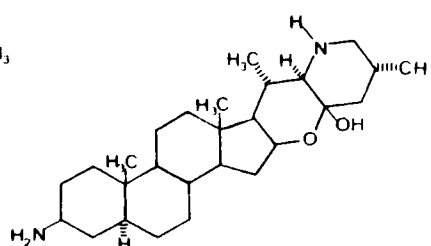
VII Tomatillidine VIII Solanocapsine
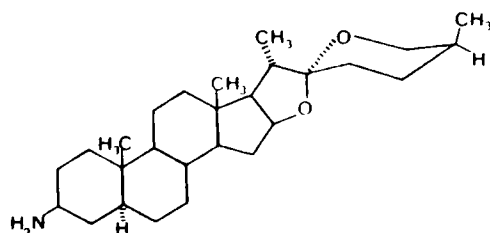
IX Jurubidine

I-II = Solanidanes
III-VI = Spirosolanes
VII = 22,26-epiminocholestane
VIII = Solanocapsine
IX = 3-aminospirostane

Fig. 3.12.6 Examples of Steroidal Alkaloids found in the genus Solanum.

Solanaceae after reports announcing the chemical transformation of the solanaceous steroidal alkaloids solasodine and tomatidine into the industrially important intermediates 3β-acetoxy-pregna-5,16-dien-20-one and its 5,6-dihydro derivative respectively. As a result, much work has been carried out surveying species of Solanum for the presence of sapogenins or steroidal alkaloids and this has been followed up by research into the physiology of biosynthesis and the agronomics of commercial cultivation of high-yielding species. At present, perhaps five species of Solanum are grown on a commercial scale for steroid production (Coppen, 1979):

> S.aviculare and/or S.laciniatum are grown in New Zealand and by some eastern bloc countries.

> S.viarum is cultivated in India.

> S.marginatum is under trial in Ecuador and a chemovariety of S.dulcamara was tested by some eastern bloc countries.

Although much information on cholestane derivatives in Solanum has now been published, the literature is scattered and review articles such as that of Schreiber (1968) are needed to collate the data. The identities of the species studied, however, cause a major problem:

too often obsolete specific names are used and the existence of voucher specimens is rarely mentioned. For the taxonomist, it is a pity that the search has not followed systematic lines as the value of a chemical compound, as a taxonomic marker, may not be appreciated unless its distribution is known. Carle (1981) has attempted a systematic screening of species of _Solanum_ section _Solanum_ for sapogenins and steroidal alkaloids, but the value of this work is undermined by certain species determinations - four of the species studied as named by Carle should not have been included in a survey of section _Solanum_. On the other hand, Bradley _et al._ (1978) reviewed the solasodine content of Australian species of _Solanum_ with voucher specimens cited and determinations by a co-author, D. E. Symon, the acknowledged authority on the taxonomy of _Solanum_ in Australia.

Maiti _et al._ (1979) have reported initial findings from alkaloid studies of Indian species of _Solanum_, and the South American species have been widely screened (Schreiber, 1968). As yet the steroidal alkaloids of only a few African species of _Solanum_ have been studied, and Coune and Denoel (1975) and El Kheir and Salih (1979) have recently published additional data. Table 3.12.1 lists the published steroidal alkaloids and sapogenins, both of introduced and of native African species of _Solanum_. Few species endemic to

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Table 3.12.1. The steroidal alkaloids and sapogenins
reported in species of <u>Solanum</u> native or
introduced to Africa. (Key to Refs overleaf)

Species	Alkaloid Aglycone	Sapogenin	Ref.
S. AETHIOPICUM	SOLASODINE		(5)
S. ALBICAULE	SOLASODINE		(1)
S. AMERICANUM	SOLASODINE		(5)
S. ANGUIVI	SOLASODINE		(5)
S. COAGULANS	SOLASODINE		(4)
S. DASYPHYLLUM	TOMATIDENOL		(3)
S. ELAEAGNIFOLIUM	SOLASODINE		(5)
S. ERIANTHUM	SOLASODINE		(5)
	TOMATIDENOL		(2)
S. GIGANTEUM	SOLASODINE		(5)
	SOLANOGANTINE		(2)
S. LINNAEANUM	SOLASODINE	DIOSGENIN/GITOGENIN	(5)
S. MACROCARPON	SOLASODINE		(5)
	TOMATIDENOL		(5)
S. MARGINATUM	SOLASODINE		(5)
S. MAURITIANUM	SOLASODINE	DIOSGENIN	(5)
S. MELONGENA	SOLASODINE		(5)
S. NIGRUM	SOLASODINE	TIGOGENIN	(5)
S. PSEUDOCAPSICUM	SOLANOCAPSINE		(5)
S. PYRACANTHUM	SOLASODINE		(5)

Table 3.12.1 (continued)

S. SARRACHOIDES	SOLASODINE		(5)
S. SCHIMPERIANUM	SOLASODINE		(5)
S. TOMENTOSUM	SOLASODINE		(5)
S. TORVUM	SOLASODINE	CHLOROGENIN	(5)
	JURUBIDINE	NEOCHLOROGENIN/ PANICULOGENIN	(5)
S. UMBELLATUM	SOLASODINE		(5)
S. VILLOSUM	SOLASODINE	TIGOGENIN	(5)

Key to the references :

(1)   Ahmad et al. (1980)

(2)   Bradley et al. (1978)

(3)   Coune and Denoel (1975)

(4)   El Kheir and Salih (1979)

(5)   Schreiber (1968)

Africa have been studied.

In reviewing the steroidal alkaloids of Solanum, Schreiber (1968, 1979) has identified five structural groups of alkaloid as set out below.

Group		Example	Fig.	
A	Solanidanes	Solanidine	3.12.6	I
B	Spirosolanes	Solasodine	3.12.6	III
C	22,26-epimino-cholestanes	Tomatillidine	3.12.6	VII
D	Solanocapsine	Solanocapsine	3.12.6	VIII
E	3-aminospirostanes	Jurubidine	3.12.6	IX

All usually occur as glycosides with a variety of sugars attached through the C-3 hydroxyl group. The same sugar moieties are found in conjunction with all the different steroidal alkaloid groups and the sapogenins, and as the identity of the sugars is not taxonomically important only the aglycones will be discussed.

Of the five groups of steroidal alkaloid, groups A and B, the solanidanes and spirosolanes, are the most widespread, though tomatillidine of group C is also common. The solanidanes have been reported in the genera Physochlaina, Scopolia, Capsicum, Lycopersicon and Solanum (Gibbs, 1974). In Solanum they are

restricted to the subgenus Potatoe (G.Don) D'Arcy. The
dibasic solanocapsine of group D is characteristic of
species of section Pseudocapsicum Bitter, and would
seem to be a good taxonomic marker except for a report,
quoted by Schreiber (1979), that it is also found in
S.seaforthianum Andr. (section Jasminosolanum). So
far, jurubidine (group E) has been recorded only in the
species S.paniculatum L. and S.torvum Sw.; structurally
it is closely related to diosgenin.

The spirosolanes (group B) are found throughout the
genus Solanum. They occur as either of two steric
types, with reference to the orientation of the
nitrogen containing ring. Similarly, the steroidal
sapogenins (= spirostanols) also occur in two forms
depending on the orientation of the methyl group on
ring E. The two types are referred to as 25D and 25L.
Sander (1963) pointed out that in any one species of
Solanum the spirosolanes and the spirostanols are of
the same steric series. Thus the 25D solasodine and
soladulcidine co-occur with diosgenin, tigogenin,
gitogenin or chlorogenin while the 25L tomatidenol and
tomatidine co-occur with, for example, yamogenin and
neotigogenin. (Figs. 3.12.5 and 3.12.6).

Solasodine is found in the subgenera Solanum,
Leptostemonum (Dun.) Bitter, Archaesolanum (Bitter ex
Marz) Danert and Brevantherum (Seithe) D'Arcy but it is

not known to occur in subgenus Potatoe (G.Don) D'Arcy.
Schrieber (1979) quoted reports of its occurrence in
Cestrum and Cyphomandra but these results require
confirmation.

Vickery and Vickery (1981) have speculated that
solasodine is a precursor in the biosynthesis of the
solanidanes, such as solanidine, which are more complex
molecules. They proposed that the widespread
tomatillidine might be an intermediate in this pathway.
However since only 25L spirosolanes occur in subgenus
Potatoe (with the exception of S.dulcamara detailed
below) in which the solanidanes are to be found, it
seems that these are more likely to be involved in the
biosynthesis. The solanidanes are found in four other
genera in the Solanaceae, apart from Solanum, so
perhaps their presence represents the less derived
state of steroidal alkaloid possession. The wide
distribution of the 25D spirosolanes in Solanum points
to an early separation of the subgenus Potatoe from the
other subgenera.

Weiler et al. (1980) have developed a radioimmunoassay
for detecting the presence of steroidal alkaloids, in
particular solasodine. The technique is both rapid and
sensitive, but given the apparent taxonomic importance
of the 25D and 25L forms it is regrettable that the
procedure is unable to distinguish tomatidine (25L) and

solasodine (25D). Further surveys for these steric types are needed, as there are exceptions to the separation of the genus into subgenera which produce 25D spirosolanes and those which do not. For example, one chemovariety of S.dulcamara produces the 25D soladulcidine and solasodine with tigogenin and diosgenin (Sander, 1963) which conflicts with the usual placement of the species in subgenus Potatoe, but another chemovariety produces the 25L tomatidenol/yamogenin which in fact agrees with such a placement. In subgenus Leptostemonum, S.macrocarpon and S.dasyphyllum both produce the 25L tomatidenol (Schreiber, 1968 and Coune and Denoel, 1975 respectively) otherwise only found in subgenus Potatoe. Analysis of the steroidal alkaloids of the Macaronesian section Normania (Lowe) Bitter could provide further evidence for the inclusion in subgenus Potatoe.

It is evident that the steroidal alkaloids are of some use in the infrageneric classification of Solanum, however considerably more data on distribution and a clearer understanding of biosynthesis are required before more positive conclusions can be drawn. Ending discussion of the steroids, it should be mentioned that, despite extensive studies of the steroidal alkaloids, their biological function remains obscure. Several suggestions have been proposed including their use as nitrogen excretory products analogous to urea,

their use as a nitrogen reserve, a role as growth regulators, especially as germination inhibitors, and also their use in maintaining the cell ionic balance by virtue of their chelating powers. There is evidence for and against each suggested role, and although protection against predation may not be a primary function, the steroidal alkaloids must afford some defence being toxic or inhibitory to a wide range of living organisms (Roddick, 1979).

Finally, the flavonoids : a group of compounds which are bio-synthesised by a combination of the shikimate and the acetate-malonate pathways. The flavonoids are one of the most widely distributed classes of secondary compounds in higher plants, and some 2000 flavonoid structures have been identified (Harborne et al., 1975). They are most obvious as floral pigments serving as pollinator attractants, but their occurrence is not restricted to the flowers and they are found in all plant parts. Their function outside the flowers is poorly understood, and various suggestions and accompanying evidence have been reviewed by McClure (1975), including their use in the leaves as filters against potentially harmful ultra-violet radiation and a role as phytoalexins. Their widespread distribution in the higher plants, their variability, their stability, and their ease of detection make the flavonoids one of the most taxonomically useful groups

of secondary compounds.

Flavonoid structure is based on a C_{15} skeleton of two aromatic rings linked by a ring C (Fig. 3.12.7) which may also occur in isomeric open form. Ring A is formed from three acetate units from malonyl CoA (i.e. via the acetate-malonate pathway) while the cinnamic acids (at the end of the shikimate pathway) contribute ring B and C_2, C_3 and C_4 of ring C. The central intermediates in the combined pathways are the chalcones and isomeric flavanones, and from these a diversity of flavonoids is produced (Fig. 3.12.8). The types of flavonoid are classified according to the oxidation state of ring C and the position of ring B. Most occur as glycosides and the sugars may be further substituted by acyl residues.

Flavonoids are particularly obvious in the flowers where they contribute to the flower colour and patterning : pigmentation is largely due to the presence of anthocyanidins, flavonols, chalcones and aurones. Anthocyanidins are widespread, usually occurring in glycosidic form known as anthocyanins, and give rise to the blue, mauve and red colours in flowers, fruits and leaves. Six main substitution patterns on ring B of an anthocyanin molecule modify the colour of the pigment : increasing hydroxylation provides a bluer hue, while increasing methylation
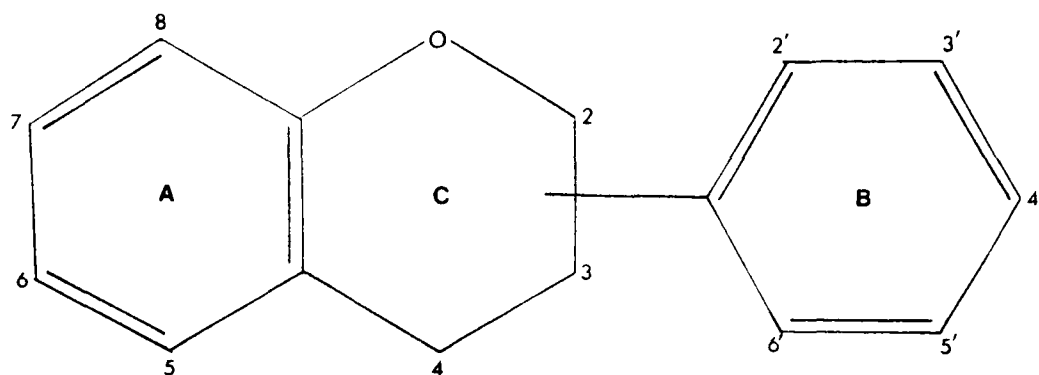
Fig. 3.12.7 Basic Flavonoid Structure.

Ring B may occur in positions 2, 3 or 4.
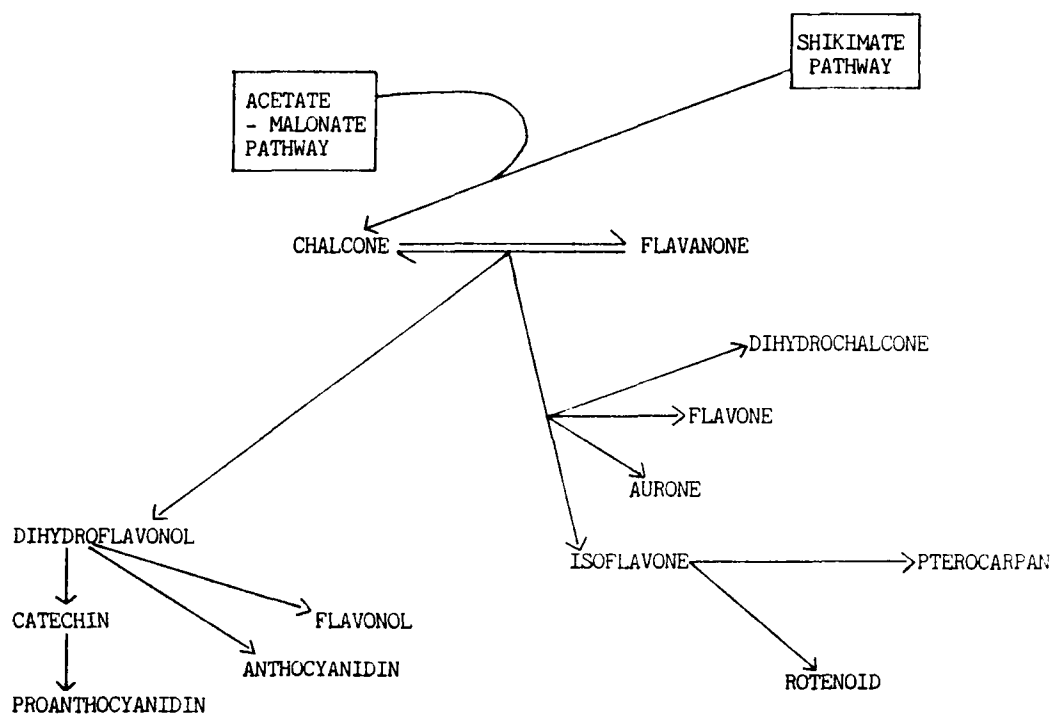
Fig. 3.12.8 Proposed Interrelationships between

Flavonoid Types. (From Markham, 1982)

gives a redder colour. Flavonols give "body" to white flowers, which in their absence would be nearly transparent, and it is important to note that their absorption of the near ultra-violet range of the spectrum is visible to insects. Most yellow pigmentation is provided by carotenoids but in certain families, for example Compositae, Scrophulariaceae, Acanthaceae and Liliaceae, bright yellow flowers are the results of chalcones and aurones. Flower colour is not solely dependent on flavonoid or anthocyanin type and several other factors are involved : these include the pH of the cell sap, the presence of certain metal ions and co-pigmentation with other flavonoids. Thus similar colours need not imply possession of identical flavonoids.

In the Solanaceae, Harborne and Swain (1979) have written that they consider the most characteristic anthocyanidin to be the blue-purple petunidin which usually occurs as the acylated glycoside petanin. Acylated pigments are also considered characteristic of the Convolvulaceae, Polemoniaceae and the Labiatae. Harborne (1975) noted that bees generally preferred to visit blue or yellow flowers, and these, particularly shades of blue, are dominant colours in the flowers of the genus Solanum. Pigments based on the anthocyanidins petunidin, delphinidin and malvidin are largely responsible for the blue to mauve colours in

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the flowers of the genus, but no reports have been traced positively identifying the pigments in the yellow flowers found in some of the New World species. Gibbs (1974), using an ammonia test, found no aurones in S.peruvianum flowers, but several other species remain to be tested. White flowered species occur in the genus, notably in section Solanum and some species of section Oliganthes, but again the identity of the pigments, presumably based on flavonols, does not seem to have been reported.

It is clear that little work has been completed on the identity and systematic value of Solanum floral pigments, and since flower colour is difficult to use taxonomically, being affected by several variables, a survey of the pigments responsible seems to be overdue. This might be correlated with a screening of fruit pigmentation, another understudied field, as there is considerable variation in skin colouration. Within section Solanum, black, purple, red, orange, yellow and green (at maturity) fruits are known. In section Melongena there are white, yellow and purple fruited species, while in section Oliganthes the scarlet fruits of the white flowered species are a different shade of red from the orange-red fruits of the violet flowered species. The only report traced of the identity of Solanum fruit pigments is a mention by Harborne and Swain (1979) of the occurrence of delphinidin in the

purple fruit skins of S.melongena L.

Whalen (1978b) has demonstrated the systematic value of leaf flavonoids in Solanum with a study of the Mesoamerican section Androceras. In this specialised group he found extensive elaboration of new flavonoid biosynthesis and he noted that the diversity of flavonoids was greater in the series which he considered to be more advanced. The flavonoid profiles of most species were easily distinguished but he was able to recognise three species groups in accord with his concept, based on morphological studies, of three series within the section. It is important to note that he found frequent but not extensive infraspecific and seasonal variation in flavonoid content.

Whalen (l.c.) reported evidence that the more primitive species alliance within the section, series Androceras, was phyletically closer to section Nycterium than to section Cryptocarpum on the basis that the section Cryptocarpum lacks the isorhamnetin glycosides found in both section Androceras and section Nycterium. However, only specimens of S.tridynamum Dun. of section Nycterium and of S.sisymbriifolium Lam. of section Cryptocarpum were analysed, so considerably more evidence is required. Whalen also attempted a reconstruction of the events of flavonoid evolution in section Androceras and concluded that trends in

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biochemical evolution should be sought independently in each group studied rather than conceived as general statements. This arose from his opinion that the flavonoid evolutionary trend within section Androceras was towards increased complexity, as opposed to a general trend in other angiosperm groups towards simplification, as noted by Mabry (1974) and others.

The proanthocyanidins (or condensed tannins) are derived from the same mixed biosynthetic pathway as other flavonoids, being chalcone derivatives (Fig.3.12.8). They are biogenetically distinct from the previously mentioned hydrolysable tannins that are derived directly from the shikimate pathway, but both can be included in the definition of tannins as :

"water-soluble phenolic compounds having a molecular weight between 500 and 3,000 and besides giving usual phenolic reactions have special properties such as the ability to precipitate alkaloids, gelatin and other proteins".

Bate-Smith and Swain (cited by Haslam, 1981)

A purely defensive function has been ascribed to the tannins but this is continuously debated as discussed by Zucker (1983).

As I noted earlier, tannins have been reported in the genus Solanum, but without indication as to the type of tannin. Harborne and Swain (1979) stated that proanthocyanidins are completely absent from the Solanaceae even though very few examples have been studied. The presence of proanthocyanidins in leaves seems to be related to lignification, and to be a primitive character (first appearing with vascular tissue), so further investigation of the leaves of the genus Solanum may be unrewarding; nevertheless, the various reports of tannins in the genus require investigation.

In conclusion, it is evident that many published studies of comparative chemistry are open to serious criticisms. Particularly outstanding are those reports in which there has been insufficient care given to species determinations, and voucher specimens are not cited or even preserved. Such reports are of negligible value to taxonomy and the citation of voucher specimens ought to be made a condition of publication. When specimens are cited it is often clear that the taxa under study are represented by a single accession on which taxonomic judgment is then based. Such an approach has long been disdained in morphological studies as totally ignoring the possible phenotypic variation due to environmental, seasonal, developmental or genetic differences between

populations. It may not be possible to analyse more than one accession per taxon in a survey, because of restrictions in time and available material, but conclusions must be tempered by the possibility of unassessed variability.

Although techniques are available now for the identification and structural analysis of chemical compounds, such detail may be unnecessary and time consuming in a purely taxonomic study. Developed chromatograms reveal the presence or absence of components in a crude extract, and the spots, representing separated compounds, compared by their position and colour on the chromatogram can be used as taxonomic characters. This approach has been used successfully (e.g. on Trifolium, Aquilegia, and Potentilla : Harborne, 1975) but ignores two factors : firstly, it is conceivable that two different compounds may arrive at the same co-ordinates on a chromatogram and so be considered identical, and, secondly, a single compound may occur naturally in a variety of forms, for example as different glycosides, and therefore appear more than once on the chromatogram, so increasing the apparent intertaxon distance.

There are still problems for the evolutionary taxonomist even if the identity and biosynthetic pathways of the compounds studied are known. As

Gottlieb (1980) has pointed out : for a hypothetical pathway

$$A \begin{cases} \rightarrow B \\ \rightarrow E \end{cases} \quad B \rightarrow C \rightarrow D$$
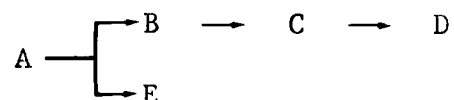
If a taxon contains C the question arises as to whether it evolved from :

(1)   a taxon accumulating B, by expansion of the reaction sequence.

(2)   a taxon accumulating D, by reduction of the reaction sequence,

(3)   a taxon accumulating E, by concomittant blocking of the pathway to E and enhancement of the route B to D.

Humphries and Richardson (1980) have criticised the "narrative approach" which they consider many phytochemists have pursued in merely publishing reports of chemical compounds new to science. A preferable approach would consider the compounds in biological, evolutionary or taxonomic terms, rather than merely adding to the list of known metabolites rather in the manner of collectors of curios. The taxonomic

usefulness of a particular compound is limited by its range within a group. Clearly, the range can only be assessed if there are records of both the presence and the absence of that compound in the constituent taxa. But the narrative approach leads to publication only of reports of compounds new to science, or newly recorded in a taxon. Absence of a searched for chemical in a taxon may go unpublished. Thus although reviews (such as that of Schreiber (1968) on the steroidal alkaloids in Solanum) collate the published data, the taxonomic range of a chemical compound can, at best, be guessed at. A systematic study would overcome this problem and furthermore would encourage care in the determination of the identity of the research specimens.

Collation of the scattered literature has shown that flavonoids and steroidal alkaloids, and their sapogenin analogues, have potential as taxonomic markers in Solanum as has been discussed. Research into the distribution of other secondary compounds in the genus may reveal other metabolites of systematic value : phytoalexins and non-protein amino acids have been employed successfully elsewhere (e.g. in the Leguminosae by Ingham (1981) and Bell (1981) respectively. Food storage products may show variation, though perhaps only at a higher level, and mineral accumulation might be considered : Chenery (1948) and Webb (1954) found no aluminium accumulation

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in the Solanaceae though Gibbs (1974) recorded that

S.americanum (as S.nodiflorum) was an aluminium

accumulator. Despite criticisms, the value of

comparative chemistry to taxonomy is generally accepted

if only as providing new data with which to test

existing classifications. There is plenty of room for

extensive chemotaxonomic study in the genus Solanum.

4. PHYTOGEOGRAPHY

There are two approaches to the study of plant distributions, and together or separately these are described as phytogeography. One approach is ecological in reasoning, and is concerned with the study of the environmental factors pertinent to an explanation of the dispersion of individuals and populations. The other is taxonomic, and endeavours to explain the distribution of plant taxa on the basis of historical factors such as speciation, long-range dispersal and continental drift. According to Wiley (1981), this methodological distinction was first recognised by De Candolle : it has persisted, and the term phytogeography is now used to cover two, rather different studies.

Classifications are hierarchic : individuals form the populations that constitute the species that are parts of genera, and so on. If it is assumed that each rank is monophyletic (an ideal), such a scale is continuous, and for an understanding of the phytogeography of a taxon, a synthetic approach is needed, combining both ecological and taxonomic approaches. Environment and history have interacted in shaping the plant distribution seen today.

Distribution of the family and the genus:

According to Hunziker (1979b), the Solanaceae comprises 88 genera. Of these, 64 are endemic to the Americas, 16 are endemic to the Old World and four (Solanum, Lycium, Physalis and Nicotiana) are widespread. The remaining four (Heteranthia, Atrichodendron, Atropanthe and Pauia) are of uncertain systematic position.

In the genus Solanum D'Arcy's (1972) classification recognised seven subgenera. Ignoring the recent introduction of representative species to other areas, five of these subgenera are regional endemics : Bassovia, Brevantherum and Potatoe are confined to South America; Lyciosolanum is only known from South Africa; Archaesolanum is restricted to New Guinea, New Zealand, Australia and Tasmania. Of the remaining two, subgenus Solanum has a fairly wide range with centres of diversity in South America and Africa but is also encountered in Eurasia, while subgenus Leptostemonum is widespread, occurring in many parts of the Old and New World.

These figures raise two general questions about the distributions of the taxa : why are only some of the genera/subgenera widespread, and secondly how did these genera/subgenera come to be widespread?

Possible solutions to the first question might suggest that

the endemics are confined by their narrow ecological range and their inability to compete in, or indeed tolerate, different habitats; or that the endemics have had insufficient opportunity for long-distance dispersal to equivalent habitats elsewhere. A third explanation might be that all the taxa were once widespread; but many have now become extinct in most areas, and are thus limited in their present day distributions. This last solution then raises the second question of how the taxa came to be widespread.

When the distribution of a taxon is more or less continuous throughout its overall range there seems to be no conceptual problem to the phytogeographer. The observer can invoke hypotheses of gradual migration by dispersal of propagules, and it can be envisaged that, given sufficient time and a suitable environment, once narrow ranges could expand to their present size. However, in the Solanaceae four genera have intercontinental distributions with oceanic interruptions in their range. The explanation of such disjunctions forms one of the central problems in plant geography.

Over the past century three theories have been postulated to account, in general terms, for intercontinental, disjunct distributions. One theory proposes the past existence of large islands or land-bridges between the continents that would allow direct migration, with only occasional small dissections. A second theory relies on the long-distance

dispersal of plant parts by, for example, birds or marine currents. Thirdly, it has been proposed that the continents are mobile : that an earlier splitting-up of supercontinents, on which the plants were distributed, led to a rearrangement of the land fragments as they drifted apart, into the present configuration of the continents and distribution patterns of the flora.

None of the theories, taken alone, satisfactorily accounts for the trans-oceanic disjunctions seen today. The hypothesis of land-bridges is now out of fashion through a lack of any geological evidence in its support. If long-distance dispersal were the only means by which intercontinental distributions had come about, a more uniform pattern of vegetation around the world might be expected. The concept of continental drift has gained much support from palaeomagnetic and other data gathered in the past decade, but for this to account for the present-day distribution of the flora the taxa themselves must have been present in some form as the continents split apart. This last possibility needs to be discussed in more detail.

Figure 4.1 shows a possible sequence of the break-up of the great continent Pangaea and the subsequent fragmentation of the southern land mass, Gondwanaland. The main points of note are that Gondwanaland began to fragment around 130 million years ago; Australia and South America were
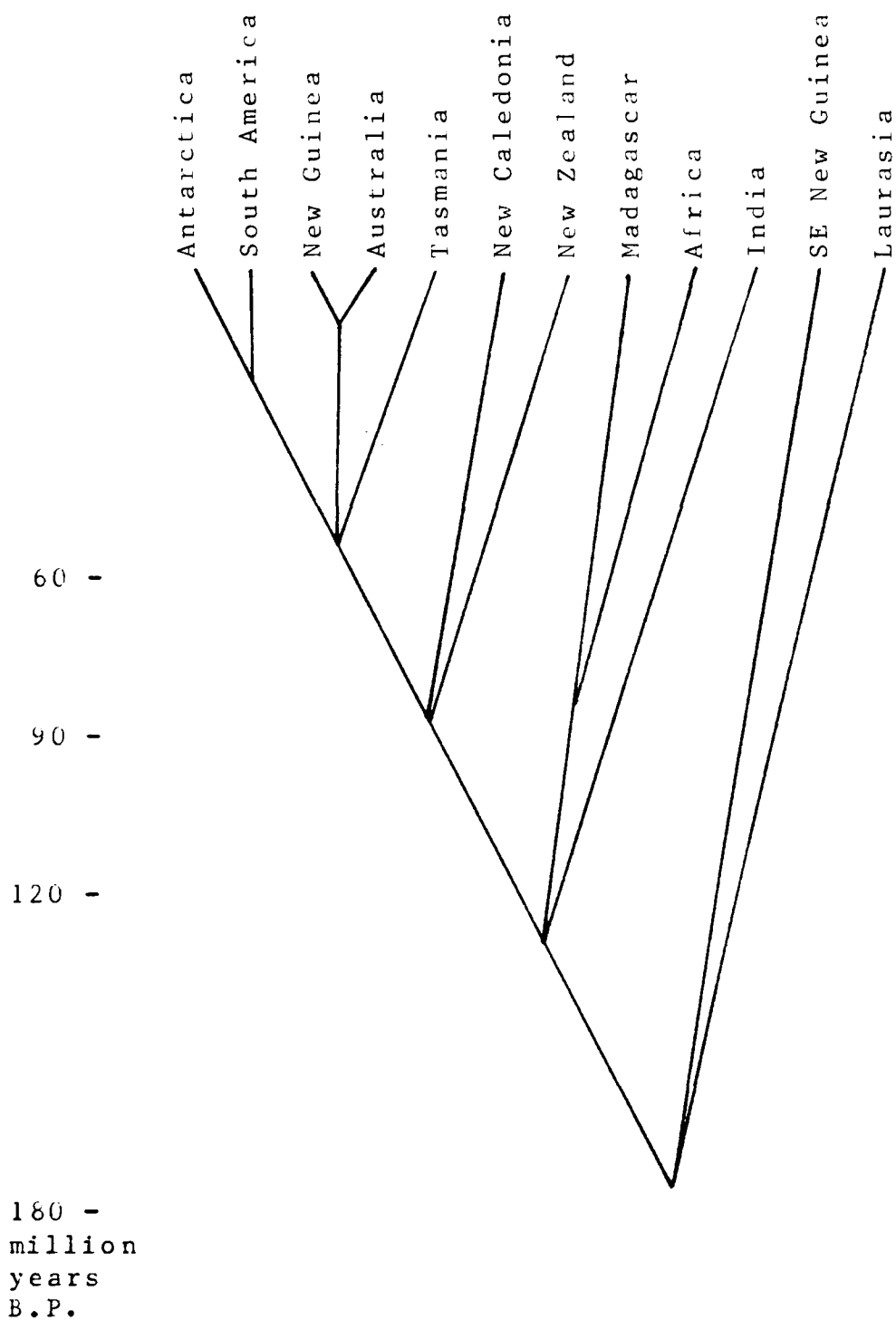
Fig. 4.1   The sequence of fragmentation of Pangaea and

Gondwanaland (after Humphries, 1981)

connected via continental Antarctica until perhaps 50 million years ago, and the Antarctic continental ice-cap was built up 4-5 million years ago.

In an early paper on the possibility of plant dispersal by continental drift, Hawkes and Smith (1965) concluded that the widely distributed genera Gossypium, Bromus and Solanum must have existed in something like their present form by the early Cretaceous, approximately 120 million years ago. However, the earliest angiosperm records are some 127 million years old, and it is believed that by the end of the Cretaceous (65 m.y. BP) the angiosperms had differentiated as far as originating many modern orders, a number of families but only some genera (Raven and Axelrod, 1975). One of the earliest fossil records of Solanaceae was noted by Muller (cited by Raven and Axelrod, l.c.) in Eocene deposits laid down only 54 million years ago.

In this context, recent work on the genus Nicotiana is of interest. The full distribution of this genus, between South America, southwestern Africa and Australia, can only be explained by continental drift if the genus had been present towards the end of the Cretaceous.

However, the genus is represented in Africa by a single, apparently native, species. Analysis of the amino acid sequences of Rubisco in Nicotiana by Martin (pers. comm) suggests a more recent common ancestry between the African

and the South American species than the proposed time of the split up of Gondwanaland. In the light of this evidence, it is more likely that the presence of _Nicotiana_ in Africa is the result of a chance long-distance dispersal, albeit a long time ago. In considering the disjunction in the genus between South America and Australia, it should be remembered that the two continents were connected via Antarctica until 50 million years ago.

If it is unlikely that angiosperm genera were present at the time that Gondwanaland fragmented, then continental drift cannot, alone, account for the pattern of distribution seen in _Solanum_. However, the continents drifted apart slowly : dispersal of the ancient flora between Africa and South America would have been straight-forward for a long time, and even by the end of the Cretaceous, some 65 million years ago, the two continents were only some 800km apart with many islands in between.

A combined theory of continental drift coupled with long-range dispersal offers a possible explanation of the disjunct distributions. That only some lines of the evolving taxa should be widely distributed while others were not, is an indication, in the first place, that the ancestral taxa were growing in such an area that dispersal across the widening ocean was possible; secondly that the conditions for such dispersal are strict.

The high endemism seen in isolated islands demonstrates the inefficiency of long-range dispersal : there must be an appropriate means of distribution, propagules must be available for dispersal, they must survive transport and arrive in a tolerable habitat with suitable conditions for growth. The immigrants must be able to compete with the existing flora in the new environment. Taking just one aspect of the genus _Solanum_ it is noteworthy that the species of the most widely distributed subgenus (_Leptostemonum_) are self-compatible, a necessity for colonisation, whereas self-incompatibility is common in other parts of the genus.

Distribution of the genus in Africa:

The study of chorology allows the map of Africa to be divided into areas of relatively homogenous flora. The most recently defined system was proposed by White (1976) and the 20 major phytochoria which he recognised (White, 1983) are outlined in Fig. 4.2. The Centres of Endemism have been provisionally defined as regions in which more than 50% of the species are endemic and there are more than 1,000 endemic species (White, 1979). These Centres are separated by Transition Zones with relatively few endemics. Three small parts of Africa do not fit this scheme and are entitled Regional Mosaics alluding to the patterned

occurrence of two or more distinct floristic elements.

Taking each phytochorion in turn, selected examples can be given of the species of <u>Solanum</u> which grow within them as an indication of their distribution patterns. Since the boundaries of the phytochoria based on endemism tend to delimit vegetation types based on physiognomy, notes have been added on the vegetation with which the species are associated. Not all native species of <u>Solanum</u> are endemic to a region and some are true chorological transgressors having extended their range into other phytochoria without completing speciation. Well-known in many parts of Africa are the two widespread and polymorphic species <u>S.anguivi</u> Lam. s.l. (sect. <u>Oliganthes</u>) and <u>S.incanum</u> L. s.l. (sect. <u>Melongena</u>) whose specific limits have yet to be defined. The <u>Solanum</u> species characteristic of Africa's neighbouring islands are also discussed.
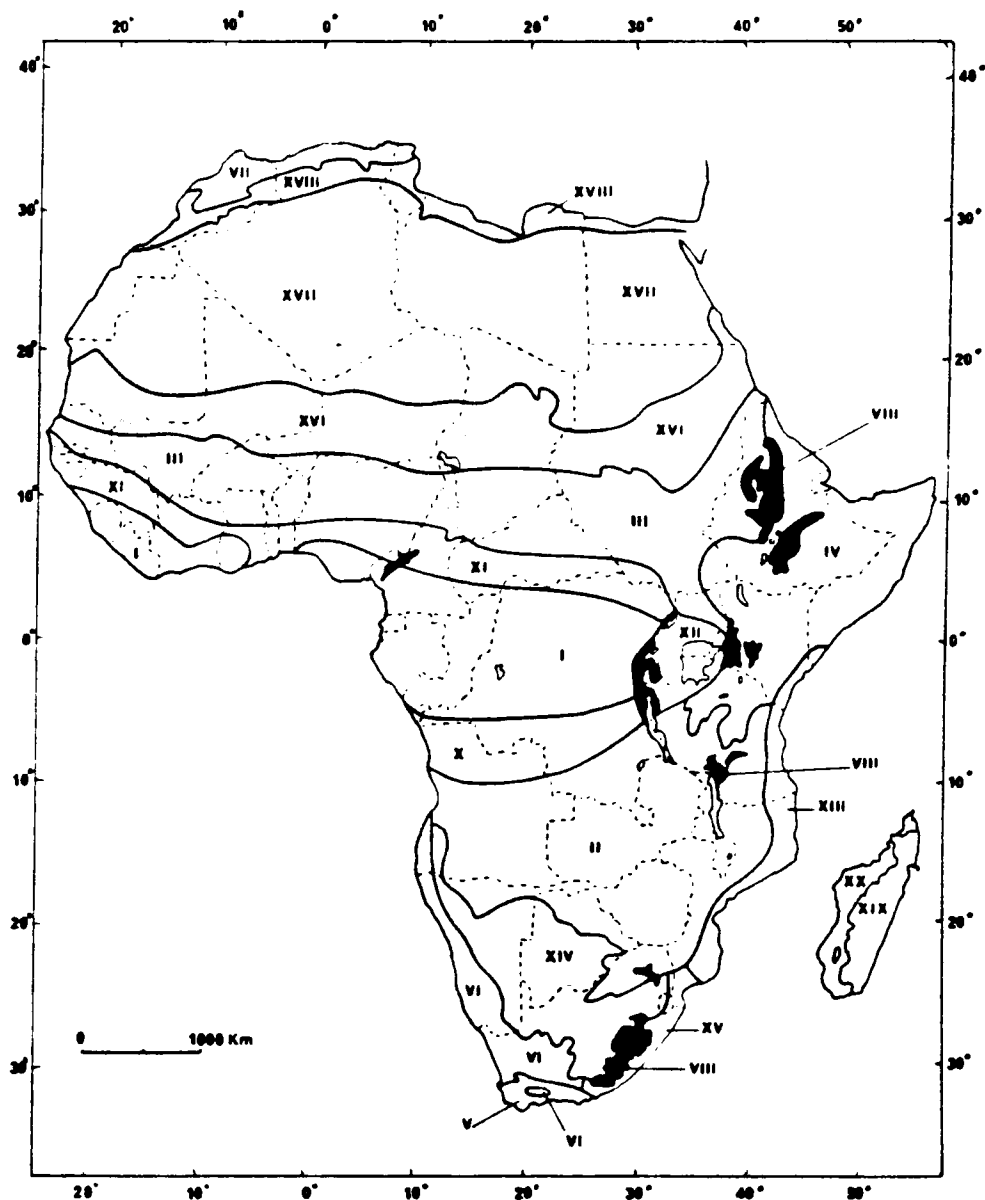
Main phytochoria of Africa and Madagascar

I. Guineo–Congolian regional centre of endemism II. Zambezian regional centre of endemism III. Sudanian regional centre of
endemism IV. Somalia–Masai regional centre of endemism V. Cape regional centre of endemism VI. Karoo–Namib regional centre
of endemism VII. Mediterranean regional centre of endemism VIII. Afromontane archipelago-like regional centre of endemism,
including IX. Afroalpine archipelago-like region of extreme floristic impoverishment (not shown separately) X. Guinea–
Congolia/Zambezia regional transition zone XI. Guinea–Congolia/Sudania regional transition zone XII. Lake Victoria regional
mosaic XIII. Zanzibar–Inhambane regional mosaic XIV. Kalahari–Highveld regional transition zone XV. Tongaland–Pondoland
regional mosaic XVI. Sahel regional transition zone XVII. Sahara regional transition zone XVIII. Mediterranean/Sahara regional
transition zone XIX. East Malagasy regional centre of endemism XX. West Malagasy regional centre of endemism

Fig 4.2 The main phytochoria of Africa and Madagascar
(from White, 1983)

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I. <u>Guineo-Congolian Centre</u>: The lowland equatorial evergreen and semi-evergreen forest of tropical Africa. It is humid with rain almost throughout the year. <u>S.anomalum</u> (sect. <u>Torva</u>) is endemic to the area, but has outlying populations in II. Afromontane species such as <u>S.giganteum</u> (sect. <u>Torva</u>) and <u>S.aculeastrum</u> (sect. <u>Melongena</u>) are found here in the upland forests, as is <u>S.welwitschii</u> (sect. <u>Afrosolanum</u>) a close relative of <u>S.terminale</u> from the East African highlands.

II. <u>Zambezian Centre</u>: One of the largest phytochoria in Africa, with a rich and diversified flora in a wide range of vegetation types. In general, there is one summer wet season followed by two dry seasons (one cool, one hot) per year. The few <u>Solanum</u> species that grow here are mostly either outlying populations from other areas, or they are chorological transgressors such as <u>S.renschii</u> (sect. <u>Torva</u>) which is widespread in IV. Only <u>S.richardi</u> (sect. <u>Melongena</u>) is centred here.

III. <u>Sudanian Centre</u>: A narrow band from Senegal to Ethiopia with a single summer rainy season. Woodland is characteristic of the area, and while there are many tree species in common with II, the Sudanian region is not so floristically rich. <u>S.forskalii</u> (sect. <u>Oliganthes</u>) grows here, with a range which extends from Senegal across Africa and Arabia to north-western India. The 'cerasiferum' group of <u>S.incanum</u> agg. (sect. <u>Melongena</u>) also occurs within this

regional centre.

IV. Somalia-Masai Centre: A dry country of deciduous bushland and thicket. This is an important region in terms of the diversity of Solanum species, with at least a dozen species endemic or nearly so. Sections Monodolichopus and Ischyracanthum are confined to this area, as are two of the three species of section Somalanum. Several species of section Oliganthes are endemic here including S.hastifolium, S.sepicula, S.setaceum, S.cordatum and S.cymbalarifolium. Species of section Torva, such as S.renschii, occur at the higher altitudes below the Afromontane region (VIII).

V. Cape Centre: A winter rainfall area with poor sandy soils. The characteristic vegetation is shrubland (fynbos), which is extremely rich in species. S.guineense (subgen. Lyciosolanum), S.africanum (sect. Africanum), S.tomentosum (sect. Oliganthes) and S.linnaeanum (sect. Melongena) are all indigenous to the region. Of these, only S.tomentosum grows in the fynbos, the others are all species of the coastal habitats. S.linnaeanum also occurs in VII.

VI. Karoo Namib Centre: A geologically varied area of desert and semi-desert, dominated by shrubland. The small shrubs S.burchellii, S.giftbergense agg. and S.namaquense (all sect. Oliganthes) are found here.

VII. Mediterranean Centre: A winter rainfall area with hot

dry summers. During the moister period the region supports numerous herbaceous plants in the 'matorral' of bush and shrubland. <u>S.linnaeanum</u> (sect. <u>Melongena</u>) grows here but is most likely native to V. Other records of <u>Solanum</u> are limited to the dry country herbaceous species of section <u>Solanum</u>.

VIII. <u>Afromontane Centre</u>: High mountain vegetation scattered across the continent in the manner of an archipelago. The lower altitudes are dominated by forest which gives way higher up to shrublands in which the Ericaceae are characteristic. Several species from sections <u>Afrosolanum</u>, <u>Torva</u>, <u>Oliganthes</u> and <u>Melongena</u> grow in the lower levels of this region. Some have quite restricted geographical ranges while others are more widespread. Local endemics include <u>S.schliebenii</u> (sect. <u>Torva</u>) and <u>S.inaequiradians</u> (sect. <u>Oliganthes</u>) found in the Uluguru Mts. of Tanzania, <u>S.kitivuense</u> (sect. <u>Oliganthes</u>) on the Usambara Mts. also in Tanzania, <u>S.sessillistellatum</u> (sect. <u>Melongena</u>) growing in Central Kenya and <u>S.sodomaeodes</u> (sect. <u>Oliganthes</u>) from the eastern side of the Drakensberg Mts. in South Africa. Among the widespread species are <u>S.giganteum</u> (sect. <u>Torva</u>), <u>S.aculeastrum</u> (sect. <u>Melongena</u>) and <u>S.terminale</u> (sect. <u>Afrosolanum</u>) which occur in Afromontane regions in West, East and South Africa.

IX. <u>Afroalpine Region</u>: Scattered areas of vegetation which are peculiar to the high peaks of Africa. The region is

subject to climatic extremes, and its total flora is small.
No species of <u>Solanum</u> are known from this region.

X/XI. <u>Guinea-Congolia/Zambezia and Guinea-Congolia/Sudania</u>
<u>Zones</u>: Transition zones between the regional centres of
endemism, containing elements of both neighbouring floras.
There are very few endemic species, and a gradual
replacement of one flora by another is seen across their
width. No <u>Solanum</u> species are endemic here.

XII. <u>Lake Victoria Mosaic</u>: A high rainfall area with
extensive swamp vegetation and forest remnants. The region
is low in endemic species, being a mosaic of the floras of
I, II, IV and VIII. Several <u>Solanum</u> species from
neighbouring regions grow here including the very widespread
species aggregates <u>S.anguivi</u> (sect. <u>Oliganthes</u>) and
<u>S.incanum</u> (sect. <u>Melongena</u>). <u>S.cyaneo-purpureum</u> (sect.
<u>Oliganthes</u>), often found on termitaria, is apparently
endemic; it has close taxonomic affinity to <u>S.zanzibarense</u>
(in XIII) and <u>S.kitivuense</u> (in VIII).

XIII. <u>Zanzibar-Inhambane Mosaic</u>: A coastal belt from
Somalia to the Limpopo River. Except for the East Usambara
Mts. (1500m) in Tanzania, most of the land lies below 200m.
The climax vegetation is mostly forest. <u>S.goetzei</u> (sect.
<u>Torva</u>) grows in this region as do <u>S.taitense</u>, <u>S.monotanthum</u>,
<u>S.vagans</u> and <u>S.zanzibarense</u> (all sect. <u>Oliganthes</u>).

XIV. Kalahari-Highveld Zone: A region occupying the great Interior Plateau of southern Africa. The climate is intermediate between that of the neighbouring phytochoria, but winter frosts are quite widespread. The varied vegetation is largely a complex of the neighbouring regions with scrub forest, shrublands and grasslands. S.supinum and S.rautanenii (both sect. Oliganthes) are endemic to the wooded grasslands here. S.rubetorum (sect. Oliganthes) has a scattered distribution within the region.

XV. Tongaland-Pondoland Mosaic: The coastal belt continuing from XIII south to Port Elizabeth. Locally, it rises up to 1600m and carries a mixed vegetation of forest, bushland and grassland. S.africanum extends its range into this region from V, while S.capense (sect. Oliganthes) is endemic here.

XVI. Sahel Zone: A region of unreliable summer rainfall. It forms a transition zone between III and the Sahara Desert. The wooded grasslands of the southern part give way to bushlands and grassland further north. The 'cerasiferum' group of S.incanum agg. (sect. Melongena) extends into this region from III.

XVII/XVIII. Sahara and Mediterranean/Sahara Zones: A region across the north of Africa which incorporates the Sahara Desert. Scrub forests and shrublands, when not degraded by man, predominate in XVIII, but in XVII only the

wadis and oases support trees and bushes. Otherwise sparse areas of grassland or dwarf shrubland are to be found, or, of course, absolute desert. Elements of the neighbouring phytochoria extend into these zones.

XIX. _East Malagasy Centre_: The eastern half of Madagascar, including the central highlands, with an annual rainfall generally in the range 2000-3000mm per annum. The rain forests, very rich in endemic species, which originally covered most of the area, have been widely replaced by grassland. The species of sections _Macronesiotes_ and _Lemurisolanum_ as well as _S.flagelliferum_, _S.pyracanthos_ and _S.erythracanthum_ (all sect. _Oliganthes_) grow in the forests here.

XX. _West Malagasy Centre_: The western half of Madagascar lying in the rain shadow of the south-easterly monsoon. Again, rich in endemic species. The three species of section _Croatianum_ and _S.sp. nov._ = _Lorence 1940_ (at K) (sect. _Oliganthes_) grow in the deciduous thickets near Tulear in the extreme south-west of the island.

XXI. _Other Offshore Islands_: In the Atlantic Ocean only the islands of Macaronesia off the north-west coast of Africa merit mention in the geography of _Solanum_. The groups of islands vary in physical geography, but are generally mountainous, and overall support a range of vegetation from xerophytic to cloud forest. Section

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Nycterium, which otherwise includes a group of Meso-American species, is represented in the Canary Islands by two endemics. The small section Normania, possibly related to the subgenus Potatoe, is endemic to the region, with S.nava in the Canary Islands and S.trisectum on Madeira.

On many of the islands in the Indian Ocean (excluding Madagascar) the indigenous vegetation has either disappeared or is poorly known. The genus Solanum is not well represented here. Notable among the species in the area are S.aldabrense (sect. Oliganthes) which is endemic to Aldabra and S.richardi (sect. Melongena) which has been collected on the Comoro Islands but otherwise grows in II.

Habitats and Adaptations:

It can be seen from the foregoing discussion that, in Africa, species of Solanum are to be found growing in a wide variety of habitats. They occur throughout a range of elevations, between sea level and about 2500m; they grow in forest, woodland, bushland, shrubland and grassland; some species will tolerate quite xeric conditions, although most show a preference for more mesic environments. The only major floristic regions of Africa from which species of Solanum are completely absent are the Afro-Alpine region and the desert areas of the Saharo-Sindian centre; the acid

soils of the Zambezian Centre seem to exclude Solanum
species as well.

At the sectional level, many of the species groups have a
restricted range, while others are ecologically more
heterogeneous. Section Normania, for example, is confined
to Macaronesia, and sections Somalanum, Ischyracanthum and
Monodolichopus are restricted to the dry country of North
East Africa. Meanwhile, section Torva is more widespread,
and comprises species from forests and more open spaces,
growing from sea level up to 2500m. Most widespread of all,
however, is section Oliganthes, whose species are to be
found in such diverse habitats as the xeric conditions of
South West and North East Africa, as well as the scrub
forests of Central Africa, and the mountain forests of East
Africa.

The morphological variation found among the African species
of Solanum has been discussed in Chapter 3 of the present
thesis. Limited comment on the possible adaptive
significance of some of the characters was made there. It
might be tempting to extend such discussion here, linking
notes on the diversity of habitats with comments on the
adaptations seemingly appropriate to each environment.
However, 'adaptation' implies the derived state of a
character. Adaptive value can, therefore, only be discussed
in synapomorphies identified in taxa growing in similar
environments. Further discussion of the adaptive

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significance of the characters of <u>Solanum</u> species must await

phylogenetic analysis of the group.

<u>Reproductive Biology</u>:

In a survey of self-incompatibility (SI) in the genus

<u>Solanum</u> Whalen and Anderson (1981) found that SI was

restricted largely to the subgenus <u>Potatoe</u>. The SI

mechanism involved is predominantly of the gametophytic

type, controlled by 'S' loci operating in the style. Of the

other four subgenera which the authors examined, the

majority of species were self-compatible (SC).

In the pollination experiments detailed in Chapter 5 of the

present work all the species studied were members of

subgenus <u>Leptostemonum</u> and were found to be SC. None of the

African members of subgenus <u>Solanum</u> were included in this

study. Whalen and Anderson found no SI species in section

<u>Solanum</u>, but they did not incorporate other African sections

of subgenus <u>Solanum</u> in their survey. The monotypic subgenus

<u>Lyciosolanum</u> has not yet been studied.

Pollination in the genus is effected by the visits of bees.

By holding the stamens, and vibrating the indirect flight

muscles, the bee shakes pollen from the terminal pores of

the thecae onto its venter, before leaving for another flower (Whalen, 1984). The morphological constancy of Solanum flowers was noted in Chapter 3 of the present thesis, and the value of unequal anthers as an outcrossing mechanism in the Central American section Androceras was discussed in 3.6. Unequal stamens are also seen in the African sections Monodolichopus, Normania and Nycterium, but the effect of this asymmetry on pollination in these taxa has not been studied.

Andromonoecy is found in section Melongena, but otherwise has not been found with certainty in other African sections. The phenomenon is, however, quite common in the extra-African species of subgenus Leptostemonum (Whalen, 1984). In the African andromonoecious species the fruits are rather larger than in other species; they are generally yellow when ripe (except in cultivars of S.melongena) and have a tough, thickened pericarp. Little is known of the ecological significance of andromonoecy, although it may be expected to promote out-crossing by the sequential opening times of the hermaphrodite and staminate flowers.

The African species of Solanum generally have few-flowered inflorescences. This is particularly true in sections Oliganthes and Melongena. Danert (1967) noted a general relationship in Solanum between the size of the inflorescence and the number of leaves in a sympodial unit : many-flowered inflorescences, for example, are usually seen

on plurifoliate species. Among the African species the larger inflorescences are found on those species growing in forests or enclosed environments : here perhaps a showy inflorescence is a better pollinator attractant in dull light, while the plurifoliate condition suggests longer periods of competitive vegetative growth. For the species of Solanum with many, few-flowered inflorescences, the increase in number of inflorescences spreads the reproductive load all over the plant. The raceme-like form of the smaller inflorescence ensures that only one or two flowers are available for pollination at any one time; the implications of this as an out-crossing mechanism might be investigated.

Dispersal, Seed Biology and Weediness:

There are few published records of the dispersal biology of Solanum species. Symon (1979a) reported observations on the Australian species, and there are scattered reports in the literature of the dispersal of fruits by such agents as bats, birds, reptiles, mammals and marsupials. Whalen (1979a) has noted a censer-mechanism in species of section Androceras, a section which also includes the tumbleweed S.rostratum.

In an extensive search of the literature, I have found only

two records of observed dispersal among the species of Solanum in Africa. The one concerns S.aldabrense : Fosberg and Renvoize (1980) noted that the fruits of this species were eaten and seed locally dispersed by tortoise, pigeon, dove and bulbul. The other (Alexandre, 1982) recorded the role played by forest duickers in the distribution of S.erianthum. It is likely that the succulent berries of most of the African species are taken by birds and other small frugivores, but the fruits with tough pericarps such as are found in species of sections Melongena and Ischyracanthum, or the dry fruits of section Monodolichopus, are often seen to be persistent on the plants.

Man has played a part in the dispersal of some of the species. The spread from the Americas of the weeds S.erianthum, S.mauritianum and S.umbellatum has been related by Roe (1979) to 16th century trade routes. All three species are now pernicious weeds in Africa. No doubt man has been the agent responsible for the distribution of the cultivated species S.melongena, S.aethiopicum and S.macrocarpon. Man may also have assisted in the distribution of such species as S.aculeastrum which is used, quite widely, as a hedge plant.

Many Solanum species have a deserved reputation for weediness. However, only a few of the African species demonstrate the facilities for long-distance dispersal and rapid, opportunistic colonisation seen, for example, in the

American S.mauritianum. By far the most common species of disturbed land I have encountered in West Africa are S.torvum and S.erianthum, both introductions from the New World. As a rule, the seeds of the native African species are larger than those of these two American species, and there seems to have been a sacrifice of seed number per fruit (and dispersibility) for seed weight (and seedling establishment). S.anguivi and S.incanum are the African species of the genus which show the greatest weediness and are, perhaps, the most frequently encountered African Solanum species in disturbed ground. Both species fruit prolifically, both species are easy to germinate, they grow rapidly and vigorously, and they are both self-compatible. Both also show considerable phenotypic plasticity.

Speciation:

The biological species concept holds that species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from all other such groups (Mayr, 1942). Central to this concept is the belief that gene-flow is the mechanism maintaining the homogeneity within a biological species. It is widely accepted that speciation can only take place if gene-flow is interrupted: the divergence of disjunct populations leading to speciation has been a frequently cited model in

evolutionary biology.

Although the concept of gene-flow has been widely taken for granted, doubts about the 'cohesion' of gene-flow (a term used by Wiley and Brooks, 1982) in maintaining the integrity of a species have also been published (eg Ehrlich & Raven, 1969; Sokal, 1973; Levin, 1979). As evidence for their case, the supporters of cohesive gene-flow cite the homogeneity of continuous populations in contrast to the heterogeneity of disjunct ones. It is assumed that gene-flow permeates the former, but is interrupted in the latter. The detractors from this point of view have argued that selective forces and founder effects can equally well explain the homogeneity or heterogeneity in continuous or disjunct populations.

The two main components of gene-flow are pollen dispersal and seed dispersal. A considerable body of evidence (reviewed by Levin & Kerster, 1974) has now accumulated, indicating that for pollen and seed movement away from a donor plant, the curves of density against distance are strongly leptokurtic. For insect pollinated plants, the vast majority of pollen grains may be deposited within 10m of the donor, though this range may increase somewhat in less dense populations. The movement of seeds away from a parent may, depending on the dispersal agent, cover a much greater distance, but the distribution is leptokurtic nevertheless.

While pollen dispersal within a stand of plants is likely to

be random, it will only rarely reach another population. In the event of pollen from one population reaching another, the effect of the incoming pollen on the local gene-pool will be virtually swamped by the locally produced, much more abundant pollen. Similarly, for seed dispersal the probability of spread to, and establishment in, a distant conspecific community is small, and unless the incoming seed arrives in sufficient quantity, it is unlikely to have a unifying effect on the gene-pool.

It seems, then, that gene-flow is too restricted to be a relevant consideration in speciation, or indeed species definition. Only a population which is limited in extent can be considered to be a real interbreeding unit of individuals. Since testing the potentiality of interbreeding is not practicable, except on a very limited scale, the biological species concept cannot be considered a workable definition. For the present thesis, I have considered species to be groups of populations which exhibit a degree of homogeneity, whether in morphology, anatomy, biochemistry or any other data set. As such, the species definition is taxonomic (Grant, 1981).

Such gene-flow as there is between populations, rather than reinforcing the homogeneity of the species, will maintain the variability of the populations. In the absence of gene-flow, species homogeneity is maintained by unifying selection; that is, different populations being subject to

similar selection pressures. Speciation, while constrained by the genotype, is a consequence of disruptive selection. The divergent populations may well be remote from each other, satisfying the traditional allopatric criteria of speciation. But if gene-flow is limited then disruptive selection can act on populations distributed along ecological gradients. Areas of steep ecological gradients can provide suitable conditions for speciation (Linder, 1985).

Whalen (1984) noted that sections Brevantherum, Torva, Lasiocarpa and Acanthophora displayed "strikingly parallel patterns of species diversity, with local areas of species richness" in various parts of South America. After phylogenetic study, he noted some evidence of vicariant speciation, but more often the sister species were sympatric. All the areas of species richness in the study were montane, suggesting the steep ecological gradients which might generate high diversity.

The ecology of Solanum in Africa is very poorly known. Looking for areas of species richness, East Africa predominates, while South West Africa is a subsidiary area of diversity. In East Africa the Somalia-Masai Centre, the Afromontane Centre and the Zanzibar-Inhambane Mosaic are regions of diversity for the sections Torva, Oliganthes, Monodolichopus and Ischyracanthum. All three chorological regions have a varied topography with areas of ecological

heterogeneity. The geologically varied terrain of the Karoo-Namib Centre is a secondary centre of diversity in section Oliganthes. The question of why Solanum has not diversified in other floristically rich regions of Africa merits further investigation.

Among the species of Solanum which are widespread in Africa, the aggregate species S.anguivi and S.incanum are probably the most widely dispersed. Herbarium collections of these aggregates show a tremendous range of variation, but, despite intensive study, I have been unable to divide either of them satisfactorily beyond loose groupings of morphotypes. The same characters constantly arise in different combinations in specimens from widely separated collection sites. It is tempting to suggest that this plasticity has an adaptive value in allowing the two species to become generalist in their ecological requirements. They may thus have succeeded in extending their range, so generating diversity and distributing the species beyond local fluctuations in the environment (fire, drought, over-grazing etc) which might cause the species' extinction.

5. EXPERIMENTAL STUDIES

In the course of the present work a number of African species of _Solanum_ were grown, mainly for the study of living plants, as a complement to herbarium investigations, but also to produce seed for the protein comparisons discussed later in this chapter (5.2). With living plants available, some artificial pollinations were attempted in order to obtain information on the reproductive biology and the cross-compatibility of the species involved.

5.1 Pollination Studies :

5.1.1 Introduction

Artificial pollination avoids those extrinsic barriers, such as geographical isolation and specific vectors, which prevent cross-pollination occurring in nature. It thereby allows investigation of the intrinsic barriers which may prevent hybridisation between taxa. Successful reproduction requires appropriate co-ordination between the genomes of both parents. Assuming that the species are fully fertile and that there are no self-incompatibility mechanisms involved, successful cross-fertilisation must imply a close relationship between the two parents.

Most hybridisation studies in Solanum have been directed at the subgenus Potatoe for the obvious reason of its economic value. A search through the literature has failed to reveal any reports of such investigations on the African members of subgenus Solanum, but some studies have been made of African species of subgenus Leptostemonum. Pearce (1975), Omidiji (1975, 1979), Rao (1979) and Niakan (1980, Lester and Niakan, In press) have crossed cultivars of S.aethiopicum L., S.anguivi Lam., S.macrocarpon L. and S.melongena L. with each other and a range of other species. Niakan, in particular, carried out an extensive crossing programme using cultivars of S.aethiopicum and S.anguivi, which she found to be highly interfertile. Both Pearce and Niakan included other wild species from Africa and Asia in their studies, and the present work has extended this approach.

Failure of inter-specific crosses in Solanum has been reported to be due to failure of the zygote to develop properly (Pearce, l.c.). However, Omidiji (1979) noted that the crosses involving S.macrocarpon or S.melongena with S.aethiopicum failed to produce ovary stimulation. He found that pollen germination was restricted and that pollen tube growth was abnormal.

Self-incompatibility is widespread in the angiosperms (Nettancourt, 1977), and in the Solanaceae it is predominantly gametophytic being under the control of 'S'

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loci functioning in the style. However, a survey of the taxonomic distribution of self-incompatibility in the genus <u>Solanum</u> has shown this phenomenon to be restricted to the subgenus <u>Potatoe</u> (and <u>Lycopersicon</u>) (Whalen and Anderson, 1981). It is very rarely found in other subgenera. The present work tested self-compatibility amongst the species grown, to confirm that no self-incompatibility mechanisms were operating which might complicate cross-compatibility studies. It also tested for stylar incompatibility between a few accessions of one species, <u>S.anguivi</u>.

5.1.2   <u>Materials and Methods</u>:

Plants were grown from seed from the Solanaceae collection of the University of Birmingham. Additional seed was obtained from various sources in Africa. Seeds were germinated on wet filter paper in petri dishes, pricked out and grown up at Birmingham and the Royal Botanic Gardens, Kew. The plants at Birmingham were grown under glass whilst those at Kew were grown under glass the first year and outdoors the second year.

The identities of all the plants grown were checked by reference to the herbarium collection at Kew (K). Provenance details of the accessions used are to be found in the 'Appendix to Chapter 5' of the present thesis, while

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further information regarding the species concerned is given in Chapter 7. Voucher specimens of most accessions have been deposited in the herbarium of the University of Birmingham (BIRM).

It is important to pollinate the flowers at the right time. Rao and Ponnaiya (1970) reported that in certain Indian Solanum species the stigma became receptive 12 hours before the flowers opened and remained so for $3\frac{1}{2}$ days. They also quoted the findings of other workers that the duration of pollen viability varied between one and ten days. Quagliotti (1979) reported that the anthers of S.melongena dehisced at 05.00-08.00 hours, and Niakan (pers. comm.) confirmed this timing in other African and Indian species. It can be expected, therefore, that a reasonable chance of fertilization might be achieved if a flower is emasculated the day before opening and pollinated within 24 hours.

Several techniques for pollinating Solanum species have been described (see Pearce, 1975 for a review), but Niakan (pers. comm.) found that the following method, adopted for the present study, was both reliable and easy. Emasculated flowers were pollinated immediately or bagged until treatment the following day. Pollen was transferred from the donor plant by tapping the dehiscent anthers of an open flower on to a clean microscope slide. When sufficient pollen had been accumulated on the slide it was drawn gently across the stigma of the recipient flower so depositing

pollen on the stigmatic surface. The flowers were then labelled before being enclosed in cellophane bags which permitted both gaseous exchange and easy observation of the results. The number of flowers pollinated for each attempted cross varied according to the availability of simultaneously open flowers.

To study stylar incompatibility the ultra-violet fluorescence technique described by Johnson (1971) was used. The stigma and style were collected into Carnoy Solution (Ethanol, Chloroform, Glacial Acetic Acid 6:3:1 by volume) about 24 hours after pollination. They were stored in a refrigerator. For examination, the Carnoy Solution was replaced by 1N NaOH and the tissue softened by heating at $60^{\circ}C$ for 50 minutes. The styles were stained with decolourised Aniline Blue (0.2% Aniline Blue and 2% K_3PO_4 by weight) and squashed in Glycerol between a slide and coverslip. Examination at X100 magnification using ultra-violet light revealed the pollen tubes fluorescing bright yellow against a dark background.

5.1.3   <u>Results of Cross-Pollinations</u>:

The present study incorporated three growing seasons. For the first year the plants were divided between Birmingham and the Royal Botanic Gardens, Kew, a division which was made necessary by the shortage of growing space available at each institution. Generally, flowering began in June and continued throughout the summer and well into the autumn. However, the summer of 1978 suffered from dull weather and flowering was correspondingly poor. That year, the plants in Birmingham were grown in the ground in an unheated greenhouse while those at Kew were grown in pots in a controlled temperature greenhouse. Flowering was noticeably better at Kew than in Birmingham.

The division of time between Kew and Birmingham resulted in considerable wastage of potentially useful flowers which opened while pollinations were being attempted 100 miles away. This situation was impractical and the following year the bulk of the plants were grown at Kew. Owing to further restrictions on growing space the plants at Kew had to be grown outdoors in frames and this apparently caused very late flowering. For the third growing season a reduced number of experimental plants were grown in a controlled temperature greenhouse in Birmingham.

A wide range of species was grown in all three years, and with limitations on the space available only a few

accessions of each species could he grown. The poor
flowering coupled with the need for seed from self-
pollinations severely restricted the number of cross-
pollinations that could he attempted. Occasionally four
pollinations for one cross were achieved, hut more usually
not even this many were possible.

Selfings were usually successful after a number of
attempts, and failures were prohably attributable either to
pollination technique or to the notable decline in fruit-set
late in the season. The range of cross-pollinations which
were attempted involved crosses hetween accessions of the
same species (particularly S.anguivi), as well as crosses
hetween accessions of species within section Oliganthes and
within section Melongena, and also hetween species of these
two sections. The results are summarised in the Figs. 5.1.1
to 5.1.6. All accession numbers refer to accessions in the
University of Birmingham Solanaceae Collection. Provenance
details are to he found in the 'Appendix to Chapter 5' of
the present thesis.

5.1.3.1. Stylar incompatibility:

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Stylar incompatibility was tested amongst several accessions of <u>S.anguivi</u>. The following pollinations were carried out :

<u>Male</u>		<u>Female</u>
S.871	x	S.1336
S.871	x	S.48
S.871	x	S.1380
S.871	x	S.857
S.871	x	S.871
S.857	x	S.871
S.1336	x	S.1336
S.48	x	S.48
S.1380	x	S.1380
S.857	x	S.857

In all cases pollen tubes were seen to reach the ovary.

5.1.3.2. Crosses within and between species:
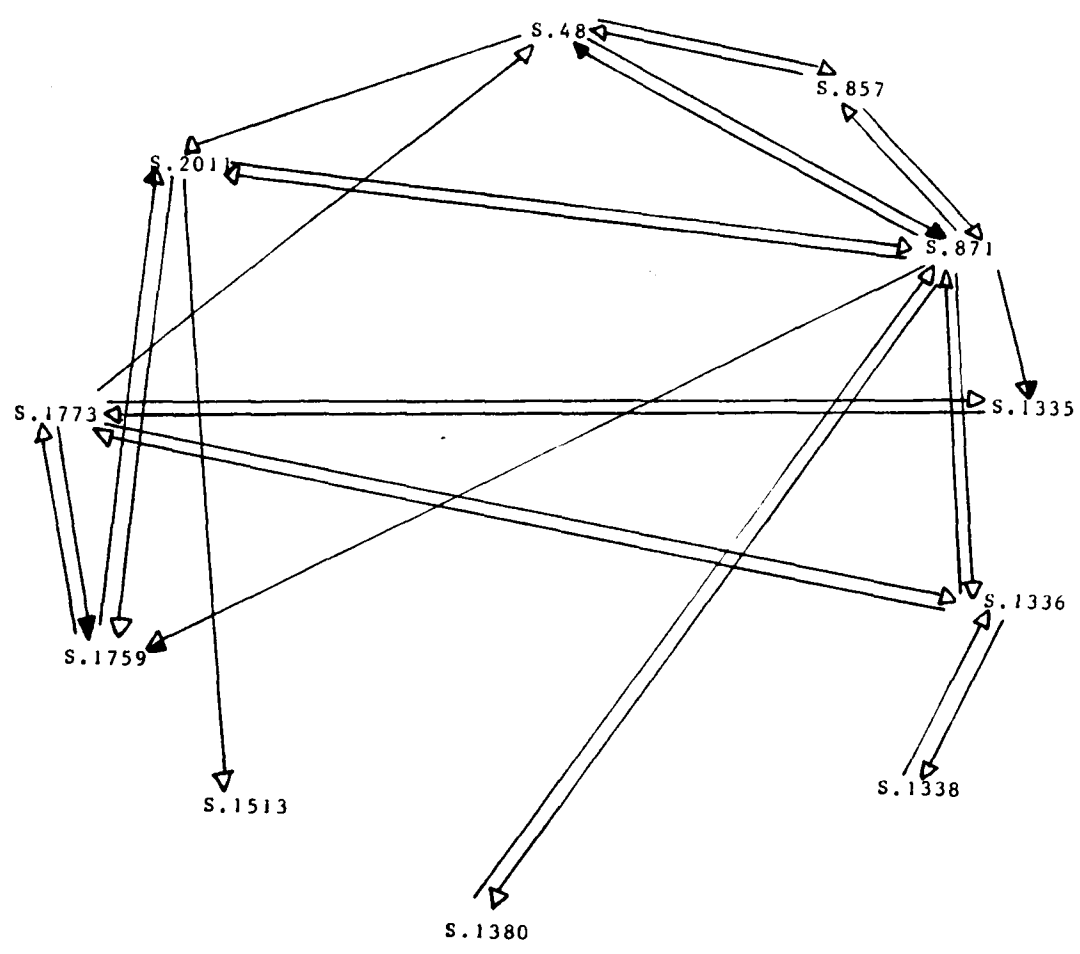
Fig. 5.1.1. Diagram representing cross-pollinations attempted between accessions of <u>S.anguivi</u>.

Key : Arrows indicate attempted cross-pollinations

⟶▶ F1 plant grown.

⟶▷ Fruit set, non-germinable seed produced.

⟶▷ No fruit set.

Fig. 5.1.2.   Diagram representing cross-pollinations attempted between accessions of S.aethiopicum.

Key : Arrows indicate attempted cross-pollinations

⟶▶ Fl plant grown.

⟶▷ No fruit set.
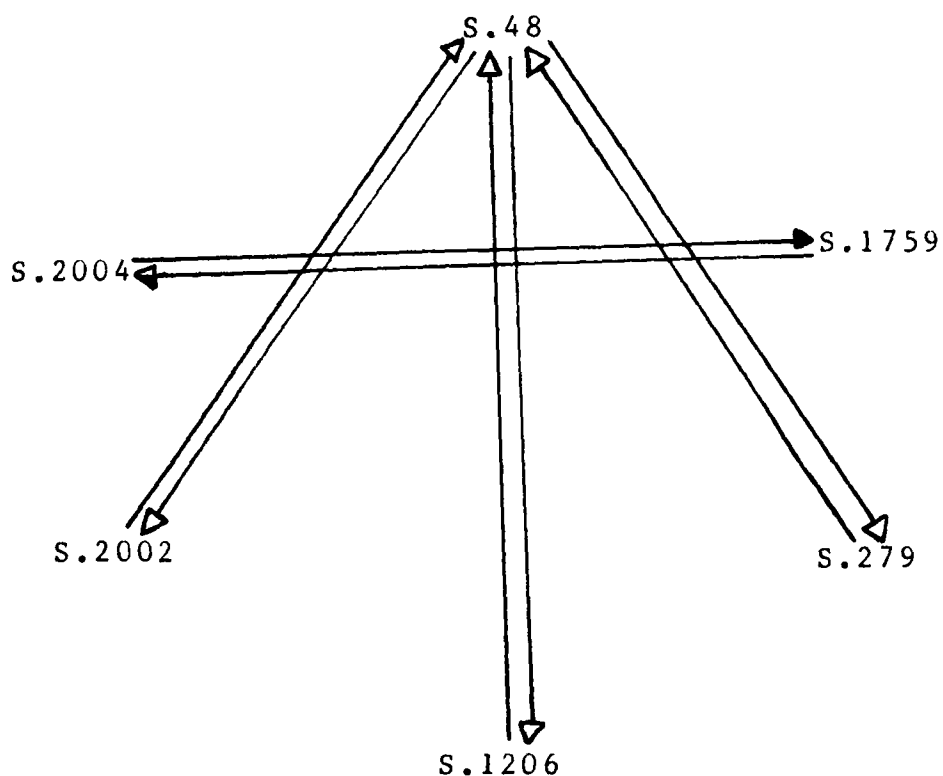
Fig. 5.1.3.   Diagram representing cross-pollinations attempted between accessions of S.anguivi and S.aethiopicum. S.48 and S.1759 are S.anguivi, the other four accessions are S.aethiopicum.

Key : Arrows indicate attempted cross-pollinations

————▶ F1 Plant grown.

————▷ Parthenocarpic fruit produced.

————▷ No fruit set.
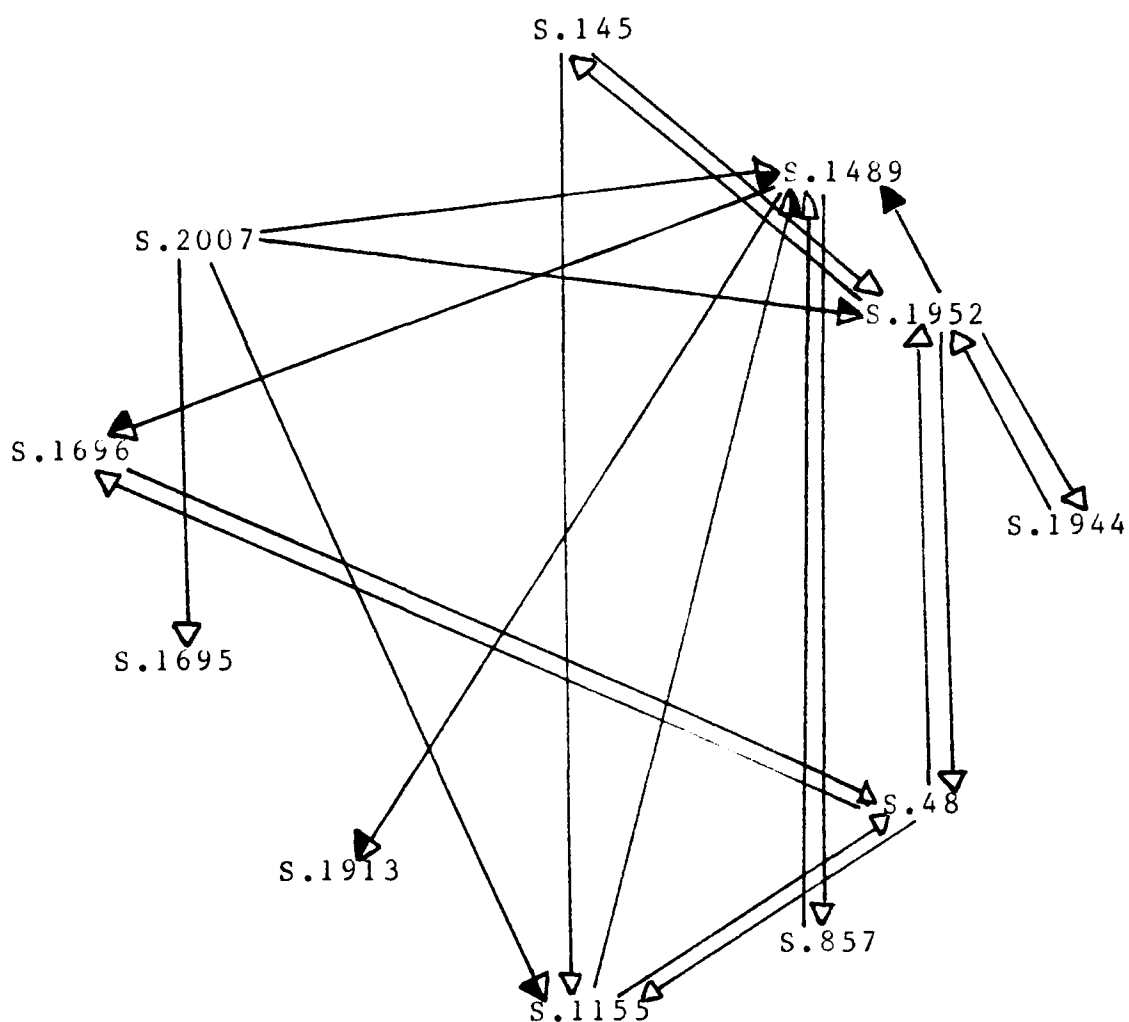
Fig. 5.1.4. Diagram representing cross-pollinations attempted between species belonging to section Oliganthes.

Key :

S.145	= S.pyracanthum	S.1155	= S.tomentosum
S.1489, S.1952	= S.violaceum	S.1913	= S.coccineum
S.1944	= S.kurzii	S.1695, S.1696	= S.rubetorum
S.48, S.857	= S.anguivi	S.2007	= S.hastifolium

Arrows indicate attempted cross-pollinations

F1 Plant grown.
Fruit set, non-germinable seed produced.
No fruit set.

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Fig. 5.1.5. Diagram representing cross-pollinations attempted between species belonging to section Melongena.

Key :

S.incanum	S.marginatum	S.linnaeanum	S.macrocarpon
S.859	S.256	S.101	S.133
S.1398		S.210	S.1264
S.1778			S.1337
S.1793			
S.2021			
S.2026			

Arrows indicate attempted cross-pollinations

Fruit set, non-germinable seed produced.

No fruit set.
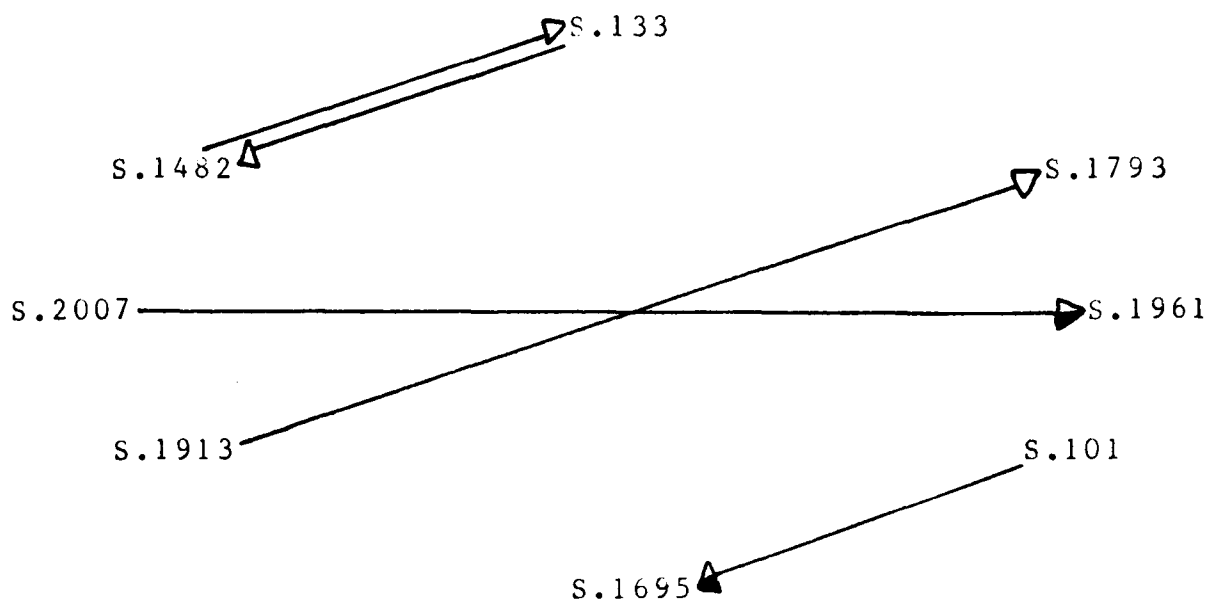
Fig. 5.1.6. Diagram representing cross-pollinations attempted between species belonging to section Oliganthes and section Melongena.

Key :

Section Melongena

S.133   = S.macrocarpon

S.1793, S.1961 = S.incanum

S.101   = S.linnaeanum

Section Oliganthes

S.1695 = S.rubetorum

S.1913 = S.coccineum

S.2007 = S.hastifolium

S.1482 = S.aethiopicum

Arrows indicate attempted cross-pollinations

➤ Fruit set, non-germinable seed produced.

▷ No fruit set.

5.1.4 Discussion :

The preceding diagrams (Figs. 5.1.1 - 5.1.6), summarising the results of cross-pollinations, indicate a disappointing rate of fruit-set. Generally, after repeated attempts, self-pollinations were successful, but a surprising number of intraspecific crosses failed to set fruit, and it seemed that these were no more likely to set fruit than were the interspecific crosses.

When fruit-set was achieved with interspecific crosses, the usual consequence was abortion of the hybrid seed. Even though many of the crosses duplicated those reported to be fertile by other workers such as Pearce (1975) and Niakan (1980), only one interspecific cross resulted in an F1 generation, that between S.aethiopicum and S.anguivi (S.2004 x S.1759).

The particularly low rate of fruit-set noted in conspecific crosses of S.anguivi provoked a study of stylar incompatibility to assess the possible involvement of this phenomenon. Pollen tubes were seen to have grown through the length of the style in all the crosses tested and it seems that there were no barriers to fertilisation operating there. Although Omidiji (1979) reported that pollen germination was reduced and tube growth abnormal in some crosses between S.macrocarpon and S.aethiopicum, and between S.melongena and S.gilo (= S.aethiopicum), stylar

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incompatibility appears to be restricted to subgenus <u>Potatoe</u> and without significant influence in subgenus <u>Leptostemonum</u>. However, as Whalen <u>et al</u>. (1981) observed, the presence of stylar incompatibilities are almost never absolute, and as yet they are not understood. Recent discussion of their involvement in interspecific incompatibility in the Solanaceae can be found in papers by Pandey (1979) and Hogenboom (1979).

If stylar incompatibilities cannot be invoked as a reason for failure to obtain fruit-set, then the causes most likely lie in the artificial conditions for plant growth and pollination. Several factors can be identified that may have had an adverse influence on the chance of successful pollination and fertilisation. For example, the environmental conditions were less than optimal, and what effect growth conditions in England may have had on the fruit-set pattern, as compared to the natural environment, is unknown. In the first season of study flowering was affected by the wet and relatively cool summer, and possibly the weather may have had other physiological effects on the plants and their ability to set fruit. In the second year, the weather was warmer and drier, but growing the plants outdoors apparently delayed the flowering, and many of the plants did not start flowering until they were moved under glass in September. Pearce (1975) and Quaggliotti (1979) both commented on the decline in fruit-set by <u>Solanum</u> species late in the flowering season.

In the present study the best rate of fruit-set was achieved in the third year of experiment when the plants were grown in a controlled temperature greenhouse. This improvement might also be related to experience with the technique of artificial pollination : it is a delicate procedure often complicated by the difficulties of handling a spiny plant.

While imperfections in technique and growing conditions can sometimes be identified and reduced, little is known of the effect of internal physiological factors on fruit-set. The phenomenon of developing fruits depressing flowering is widespread, but scientific investigation of its influence in _Solanum_ species has so far been neglected. Casual observations indicate that the rate of fruit-set is affected by the number of fruits already developing on the plant; it is therefore recommended that in any study of artificial pollinations the unwanted flowers and fruits should be removed. Here, however, the maximum output of fruit was required for seed production towards a study of seed proteins, and removal of the fruits and flowers was impractical.

No doubt there are many other factors which impinge on the rate of fruit-set. Cross-pollination should be repeated as many times as possible to increase the probability of over-riding the external barriers to fertilization. With limitations on the flowers available no cross-pollination was attempted more than four times during the present study,

and no conclusions can be drawn from those pollinations which failed to set fruit.

Of the instances when pollination led to fruit-set all but one of the interspecific crosses gave non-viable seed. Whalen et al. (1981) have noted, citing other workers, that abortion of hybrid seed is the most commonly reported crossing barrier that is encountered in Solanum. The results of the present study indicate that this post-zygotic barrier operates in the African species tested as well.

The seed failure observed in crosses between accessions of S.anguivi may be of some significance : I consider this to be an aggregate species with several phenetically discontinuous taxa incorporated under a single specific epithet. The accessions involved, S.371, S.1335, S.1759 and S.2011, were grown from seed sent from Uganda, Zimbabwe, Cameroun and Tanzania respectively, and divergence is, perhaps, reflected in the crossability pattern. Cytological investigations should be the next stage of the study, to explore the possibility of chromosome races being responsible for the variation in intraspecific compatibility.

The cross between S.aethiopicum and S.anguivi which gave germinable seed resulting in an F1 generation is of less interest. Niakan (1979; Lester and Niakan, In press) has already demonstrated convincingly the interfertility of

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these two species. She concluded that S.aethiopicum is a domesticated form of S.anguivi. The cross reported in the present study adds limited support to Niakan's findings.

Apart from Niakan's investigations of the cross-compatibility between S.anguivi and S.aethiopicum few experimental studies have included African species of Solanum. Pearce (1975) incorporated S.aethiopicum, S.anguivi and S.tomentosum in her researches on the crossability of S.incanum and S.melongena : they all gave healthy F1 hybrids with S.incanum and S.melongena, but pollen stainability was low. Omidiji (1979) tested the cross-compatibility of S.aethiopicum, S.macrocarpon and S.melongena and found them partially interfertile.

While this neglect of the African species of Solanum leaves a vacuum in our biosystematic understanding of the genus in Africa, crossability studies may not contribute greatly to the taxonomy. Certainly, hybridisation has an important conceptual place in taxonomic studies that are based on Mayr's (1942) definition of the 'biological' species ('species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'), but as Sokal and Crovello (1970) discussed, this definition is unusable on several counts. Their objections to the definiton include the laboriousness of a crossing programme to test interbreeding, the fallacy of extrapolating experimental crossability in

cultivation to micro-evolution of populations in the wild, the unworkable word 'potentially' in the definition and the subjective nature of assessment of reproductive isolation - whether to use 50% pollen stainability in the F1 as indicative of isolation or 70% or 80%, or should the F2 be studied?

Furthermore, it might be asked whether cross-pollination studies should carry more weight in species delimitation than other methods of taxonomic assessment. Clausen (1951) reported infertility between conspecific crosses of Layia glandulosa, while Vickery (1964) found some species of Mimulus to be interfertile and others not.

Finally, looking at crossability in cladistic terms, hybridisation must be the plesiomorphic condition. Disharmony between the gene complexes involved in reproduction implies divergence, and therefore cross-incompatibility should be interpreted as the derived state in a compatible/incompatible comparison of taxa. Since symplesiomorphies are ignored in cladistic taxonomy, only the crosses which are incompatible will theoretically be of interest, and at the species level the information content of such a widely distributed character is likely to be minimal.

Artificial pollination and experimental hybridisation can contribute to many fields of botanical study such as the

genetics of character inheritance, the nature of reproductive barriers, the genecology, or the interest per se in producing a hybrid plant otherwise unknown. As such, further investigations on the African species of Solanum will add to an understanding of the biology of the group, but taxonomic expectations should be restrained.

5.2   Protein Studies

5.2.1   Introduction :

In Chapter 3.12 of the present thesis the taxonomic utility of 'micromolecules' in relation to Solanum was considered. The high molecular weight organic compounds such as proteins and nucleic acids, collectively known as the 'semantides', have also been used extensively by taxonomists, and their value to the systematics of Solanum will be considered here.

The term 'semantides' was applied to the nucleic acids and proteins by Zuckerkandl and Pauling (1965). The term alludes to the genetic information content, with DNA and RNA being primary and secondary semantides respectively, and proteins being tertiary semantides. For most of this century the taxonomic characters available from the macromolecules were provided by serology, using proteins to raise antibodies which could be used to recognise similar proteins. With the discovery of the genetic code and the establishment of the direct link between protein amino acid sequence and the nucleotide bases, the importance of proteins to systematics seemed to be reinforced. In consequence, more experiments have been done with proteins in a systematic context than with any other type of biochemical character (Harborne & Turner, 1984).

Now, with developments in laboratory techniques, it has become possible to determine the sequence of nucleotides in DNA and RNA, and an absolute measure of differences in the genome between organisms is theoretically possible. In practice, however, the techniques are laborious, expensive and skilled and thus unsuited to wide taxonomic application. A short cut via DNA hybridisation techniques provides a measure of the similarity of the DNA of two species. Here, DNA is denatured by heat into single strands and a mixture of the DNA of two species is allowed to recombine into hybrid DNA. The degree to which they recombine, measured by recording the temperature at which they separate on reheating, is directly proportional to the similarity of the DNA strands. As yet few such hybridisation studies have been attempted on plants, but results on grasses supported the separation of oats into a different tribe from wheat, rye and barley (Bendick & McCarthy, 1970). No such work seems to have been reported on the Solanaceae.

The methods of study of proteins for systematic purposes can be divided into two groups : there are the comparative techniques of electrophoresis and serology, in which the underlying structure of proteins is largely ignored, and there are amino acid sequencing procedures in which the ordering of the peptides is determined and compared between taxa. Both types of survey have their advantages and disadvantages, and much depends on the taxonomic rank under

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comparison and the choice of experimental material. Clearly, there must be sufficient variation amongst the proteins studied within the taxon investigated; however too much variation will require intrataxon analysis before intertaxon comparisons can be made. At one time, it was considered that the difficulties involved in comparing the differences among the several hundred peptides of a protein molecule were best kept to a minimum by choosing proteins of low variability : thus meaningful results would only be gained at the higher taxonomic levels.

A significant attraction of sequence data was the possibility of a phylogenetic interpretation with diversity being considered a phyletic measure. Sets of sequence data have now been accumulated by Boulter (1980) for cytochrome c, plastocyanin and ferredoxin. The initial enthusiasm for the techniques, however, seems to have worn somewhat, and Boulter (l.c.) noted that no firm phylogenetic inferences could be made, not least because of the numerous parallel substitutions of amino acids. There is some evidence that the plastocyanin data give taxonomically more acceptable results than sequence comparisons of cytochrome c, which, for example, show more differences between maize and wheat than between maize and some dicotyledons (Cronquist, 1976). As regards the plastocyanin-generated tree, it should be noted that Capsicum is separated from Lycopersicon and Solanum by the Caprifoliaceae (Boulter et al., 1979).

The problems of parallel substitutions in amino acid sequences suggested to Boulter (1980) that widespread comparisons were of limited value, and that studies should be restricted within the familial or tribal levels. Preliminary results from Martin have reinforced this view with recent work involving the genus Solanum (Symon, pers. comm.). The findings of this work are in complete accord with the traditional division of the genus into two groups of species, one with prickles, stellate hairs and elongate anthers, the other being prickleless with simple hairs and stout anthers. Furthermore, the Australian species grouped together with each other as did the African species. At present, only a few species have been studied, but further work using this technique appears to have the potential to supply some taxonomically useful data.

Of the comparative techniques of protein study not involving a detailed knowledge of structure, investigations involving Rubisco have been rewarding. Rubisco is the most abundant protein in the leaves of most green plants and has been identified as ribulose 1,5 bisphosphate carboxylase, the enzyme responsible for catalysing the CO_2 fixation step in the Calvin cycle. Structurally it comprises two different subunit types, having eight large subunits (m.w. 55,000) and eight small subunits (m.w. 12,000 - 15,000). The large subunits have catalytic sites while the function of the small subunits is unknown. Murphy (1978) raised antisera to Rubisco from Nicotiana and Spinacia. He then compared the

Rubisco of a wide range of angiosperms and gymnosperms using quantitative microcomplement fixation techniques, demonstrating close antigenic similarities between the Rubisco of tobacco and that from species in the Solanaceae, Nolanaceae, Cuscutaceae and Convolvulaceae. This is in accord with the traditional taxonomy based on morphological comparisons.

Gray (1977) used serology to compare Rubisco in species of Nicotiana and found correlations with morphological and cytogenetic classifications. Further work has revealed that the large subunits of Rubisco are inherited from the maternal parent while the small subunits are inherited from both parents. Using isoelectrofocussing it is possible to detect the origin or parentage of genomes by comparing band patterns of a putative amphiploid with those of likely parents (Gray, 1980).

While Murphy (l.c.) used a single purified protein to raise antisera, crude protein extracts have also been used in serological studies. Gell, Hawkes and Wright (1960) used serology to compare the tuber proteins of Solanum and found a good correlation with morphological classifications. Lester (1965) and Hawkes and Lester (1966, 1968) continued and expanded this approach. Hawkes and Tucker (1968) and Tucker (1969) deduced some relationships of various genera of Solanaceae and other families. Lester (1979b) analysed the serological data from a comparison of the proteins of

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eight species of <u>Solanum</u>, and found some agreement with Seithe's (1962) division of the genus into the chori subgenerum <u>Solanum</u> and <u>Stellatipilum</u>. Lester and Roberts have continued to explore serological relationships within the genus and also the family (Lester <u>et al.</u>, 1983; Lester and Roberts, in press). Cladistic analysis of the data has been attempted by them with partial success.

Perhaps the most popular method for comparing protein profiles has involved electrophoresis, a technique which is cheap, relatively simple and uses small samples. In particular, electrophoresis has been applied to the seed storage proteins of plants, which are suitable for a variety of reasons : their storage function does not appear to demand a rigorously defined sequence of amino acids, and while they are more variable than enzymes, whose catalytic sites are largely fixed, they are, for the most part, unaffected by climate or season. Furthermore, a seed is rich in protein and therefore offers a high yield of experimental material from a small amount of the plant.

Electrophoresis has been used in several comparative studies of <u>Solanum</u> proteins. Desborough and Peloquin (1968) found species specific electrophoretic bands in a comparison of the tuber proteins of 16 species of <u>Solanum</u>. Stegemann (1975) used electrophoresis to characterise certain species and varieties of <u>Solanum</u> on the tuber proteins and isoenzymes. Edmonds and Glidewell (1977) found that the

electrophoretic patterns of 20 species belonging to the section Solanum reflected the morphological differences and the genetic isolation of accessions within species. Pearce (1975; Pearce and Lester, 1979), Roberts (1978) and Lester and Niakan (In press) all used electrophoresis of the seed proteins in their studies on Solanum species and noted intraspecific variability.

For the present study the techniques of serology and electrophoresis were applied to crude protein extracts from the seeds of a range of African species of Solanum, with a view to testing the existing classification based on morphological criteria.

5.2.2 Materials

All the seed used in the present study had been harvested from the living collection of Solanaceae at the University of Birmingham. After harvesting, the seeds were extracted from the fruits, washed and then allowed to dry. Seeds were stored in sealed bags at $4^{o}C$, dried over silica gel.

Provenance details of the accessions used are given in the 'Appendix to Chapter 5' of the present thesis while further information regarding the species can be found in Chapter 7.

5.2.3 Polyacrylamide Gel Electrophoresis (PAGE) :

5.2.3.1. Principles

Proteins are polyelectrolytes bearing a net charge that is dependent on the pH of the surrounding medium. Electrophoresis exploits this property by causing a sample of proteins to migrate in an electric field. The mobility of a protein is dependent on a number of factors including its net charge, its molecular size and shape, the size of the electric field potential and the properties, such as adsorption and viscosity, of the surrounding medium. A sample of mixed proteins will separate in an electric field because of the differences in mobility. If the surrounding medium is semi-solid, the position of the proteins can be fixed when the electric field is removed, and the application of a suitable stain will reveal them as bands. The patterns of bands produced by electrophoresis of crude extracts from different species provide a simple, phenetic comparison of the protein content of each extract.

A polyacrylamide gel is widely used as a support medium for electrophoresis since the pore size is simple to control and the gel is relatively inert. In a standard arrangement a two gel system is used : a short length (ca. 1cm) of a large pore gel (2-3% acrylamide) is cast on top of a longer (7cm+), small pore gel (7% acrylamide). Each end of the double gel is placed in a separate reservoir of buffer and

the protein sample is applied on top of the large pore gel along with a marker dye. The reservoirs are connected to a direct current power supply.

The large pore gel has a stacking effect on the proteins so that by the time they arrive at the interface with the small pore gel they have separated into discs of individual proteins : this improves the resolution of the technique. These discs separate in the small pore gel, some travelling faster than others, and when the marker dye reaches the bottom of the gel, the current is switched off and the gel fixed and stained.

Such a routine uses one buffer to make the gels and another in the reservoir : it is a discontinuous system. Other techniques omit the large pore gel and use a continuous buffer system. Sometimes, urea or a detergent is employed to dissociate the proteins. The detergent has the added effect of swamping the net charge of a protein, and, as a result, the polypeptide molecular weight can be found as there is an inverse relationship between the log of the molecular weight and the mobility (Payne, 1976). Varying the pore size of the gel or the pH may help to resolve proteins which otherwise do not appear as separate bands.

5.2.3.2 Methods

Protein Extraction : Seed, which had been washed and dried, was shaken in a Dangoumau Analytical Pulveriser for ten minutes. The resulting fine flour was defatted with petroleum ether, dried and stored at -15°C.

Protein was extracted by soaking the flour overnight at 4°C in TRIS-glycine buffer, pH 8.3, in a ratio of 1:5 w/v. The suspension was centrifuged at 15,000g for six minutes. The supernatant was decanted and urea added to make a 3M solution which was stored at -15°C.

Electrophoresis : The disc electrophoresis procedure that was used followed Davis (1964) with some modifications. Glass tubes, 8cm long, were sealed at the base with rubber stoppers. 7% acrylamide gels (in TRIS- HCl-TEMED buffer pH8.9 + 3M urea) were cast in the tubes to 2cm from the top. The gels were allowed to polymerise with a layer of water on top to occlude the air and to prevent a meniscus forming. The water was removed when the gels had set, and a large-pore 2% acrylamide gel was cast to 1cm from the top of the tubes. Again, water was layered on top.

After polymerisation of the second gel the stoppers and the water were removed and the tubes were mounted vertically in

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the Shandon Column Electrophoresis Apparatus. The upper and lower reservoirs were filled with TRIS-glycine buffer and $0.05cm^3$ of protein extract was placed on top of each large pore gel. Bromophenol Blue was added to the upper reservoir as a marker. An initial current of 2 mA per tube was increased to 5 mA per tube after ten minutes and electrophoresis was run until the marker dye reached the bottom of the tubes.

The gels were reamed from the tubes and fixed and stained in 0.1% w/v Naphthalene Black in 7% v/v acetic acid for two hours. The gels were washed in continual changes of 7% acetic acid for 2-3 days to remove excess stain and then stored in the dark in 7% acetic acid.

Test Experiments : Some variations were added to the technique described above in an attempt to improve the resolution of the protein bands. It was established that the addition of 3M urea to the extracts and the gels produced a pattern with more bands than when no urea was added. This phenomenon was presumed to be the result of the urea depolymerising the larger molecules by breaking the H-bonds. Further depolymerisation was attempted by heating the sample in the presence of the reducing agent 2-mercaptoethanol and the detergent sodium dodecyl sulphate (SDS). However, the results were not reproducible and the

large number of bands produced made the assessment and comparison of patterns difficult.

Electrophoresis was also carried out in a vertical slab of acrylamide gel. A single 5%, 7.5% or 10% acrylamide gel was used here because a two-gel system was not possible in the apparatus available. Poor separation, in both a discontinuous buffer system as described above and a continuous sodium phosphate buffer system (pH7.2), together with the long run-time, showed disc electrophoresis to be a preferable technique.

5.2.3.3. <u>Results</u>

Protein extracts from the seeds of 25 species of <u>Solanum</u> were subjected to electrophoresis. In order to assess the infraspecific variability, most of the species were represented by more than one accession from the Birmingham Collection and a total of 90 accessions was used. Electrophoresis was carried out at least twice on each protein extract and when sufficient seed was available more than one extract was made. For those accessions with seed that had been harvested separately in two or more years, extracts were made from each year's seed.

Comparison of the stained protein bands proved to be

difficult. The Bromophenol Blue marker dye did not move the same distance from the origin in gels run simultaneously and protein bands could not be identified by Rp values alone. Rather, it was necessary to compare the patterns of the bands, and so, by deduction, identify the novel or absent bands.

Some limited variation was found between replicates, both of seed of the same accession harvested in different years as well as the same extract run on separate occasions. The results of interaccession and interspecific comparisons should therefore be treated with caution.

All gels were compared without knowing the identity of the extacts that had been applied. The gels were grouped according to similarity of pattern as judged by eye, and then identified by their extracts. The groupings that resulted are presented in Table 5.2.1 (a) with diagrams of the protein bands diagnostic of each group shown in Table 5.2.1 (b). No particular significance is intended in the sequence of groups in Table 5.2.1.

Table 5.2.1(a) Groups of accessions of **Solanum** species recognised by comparison of protein band patterns after zone electrophoresis of the seed proteins.

Group 1   –   S.renschii   S.1774

Group 2   –   S.schimperianum   S.1794

Group 3   –   S.pyracanthum   S.145
S.926

Group 4   –   S.violaceum   S.1489
S.1951
S.1952
S.2030

                 S.kurzii   S.1944

Group 5a –   S.anguivi   S.871   S.tomentosum   S.1040
                         S.1338
                         S.1380
                         S.1759
                         S.1772
                         S.2017

S.aethiopicum Gilo group	Aculeatum group	Shum group
S.156	S.240	S.1206
S.270	S.344	S.1415
S.395	S.1268	
S.1234	S.1331	
S.1236		
S.1381		

Group 5b – S.aethiopicum Gilo group   Shum group

	Gilo group	Shum group
	S.225	S.1267
	S.279	S.2000
	S.1395	S.2001
		S.2002
		S.2003
		S.2004

Table 5.2.1(a) continued:

Group 5c - S.anguivi S.964

                          S.1336

                          S.1773

                          S.1954

                          S.2011

                          S.2012

Group 5d - S.anguivi S.1335

Group 5e - S.anguivi S.48

Grouf 5f - S.aethiopicum Kumba group   Gilo group

                              S.1485   S.1748

                                             S.1749

Group 6 - S.tomentosum S.927

                          S.1155

Group 7 - S.rubetorum S.1690

Group 8 - S.capense S.1689

Group 9 - S.macrocarpon S.133

                          S.1269

                          S.1337

                          S.2005

                          S.2006

Table 5.2.1(a) continued:

Group 10a - S.incanum S.1780
                         S.1961
                         S.2021

Group 10b - S.incanum S.50
                         S.859
                         S.1942

Group 10c - S.melongena S.46
                           S.241
                           S.448

              S.ovigerum S.657

Group 11   - S.linnaeanum S.101
                            S.210
                            S.1174

Group 12   - S.marginatum S.128
                            S.256
                            S.396

Group 13   - S.viarum S.1065

Group 14   - S.pectinatum S.1181

Table 5.2.1(a) continued:

Group 15   -   S.atropurpureum   S.641

                                   S.668

                 S.capsicoides   S.96

                                  S.214

                                  S.1307

Group 16   -   S.torvum   S.839

Group 17   -   S.virginianum   S.1237

                                  S.1382

                                  S.1389

                                  S.1417

Group 18   -   S.cinereum   S.142

                               S.202

                 S.campanulatum   S.387

                                   S.773

Group 19   -   S.mauritianum   S.1762

Table 5.2.1(b) The diagnostic protein band patterns

of the accession groups.

Group 1

2

3

4

5a

5b

5c

5d

5e

5f

6

7

8

9

10a

10b

10c

11

12

13

14

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16

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5.2.3.4. Discussion

Only those protein bands that were found to be constant and diagnostic of a group of accessions have been shown in Table 5.2.1(b). The number of bands on an individual gel was often far greater than the number drawn here, with up to 18 bands being distinguishable on some gels. Clearly, the number of diagnostic bands is influenced by the variability of the constituent accessions : the groups with the greatest number of diagnostic bands shown in Table 5.2.1 (b) are those comprising a single accession where all the replicates showed the same banding pattern.

In making comparisons between gels it was found that the most successful way to identify a particular band was to note its position within the pattern of bands on the gel, as Rp values were almost useless. The slower moving bands, possibly globulins, were relatively simple to identify on separate gels since the bands were thick and the variation in the distance moved by the marker dye was less significant. In the middle range, it seemed that the bands occasionally merged to form a thicker, slower-moving band that may have retarded some of the more mobile proteins. This phenomenon tended to confuse pattern comparisons, and was a source of variability in intra-accession replicate experiments as well as being noted among inter-accession comparisons. Possibly, the merging resulted from a greater quantity or concentration of protein extract being applied

to the top of the gel, although the quantities of extract used for electrophoresis were reasonably constant. However, the amount of protein per gram of seed is variable and may have been the source of error. The narrow, faster-moving bands were quite variable in position and thus extremely difficult to recognise between gels.

Gels were compared on the basis of similarity of protein band patterns with the assumption that two bands in equivalent positions, both being approximately equal in width and colour density, were the result of the same protein. This assumption is not reliable however, since the electrophoretic mobility of a polypeptide is influenced by more than one factor, and it is possible that a large, highly charged molecule will travel the same distance as a smaller molecule with a lower charge. This particular problem can be counteracted by treatment of the protein extract with sodium dodecyl sulphate (SDS) which, in effect, swamps all the molecular charges so that mobility is directly related to molecular size. The use of this detergent was tested in the present study, and also by Roberts (1978), but in both cases it was abandoned as it resulted in too many bands which made comparisons between extracts difficult.

If the presence of a protein band is treated as a taxonomic character, then it might appear that the techniques of numerical taxonomy could be applied to group the gels on the

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basis of their character states. However, for the present study numerical analysis would be specious. Bands were only readily identified in comparisons below the species level, or in gels with similar patterns, yet the comparisons of interest here are between species and between sections. Where there was little or no similarity in pattern in the interspecific or intersectional comparisons, it was impossible to reliably identify bands in common between two gels, and most bands would be scored as different. Numerical analysis, being only as good as the data put in, would merely group the accessions with very similar patterns, while the rest would appear distinct; this is no different from comparison by eye. If bands can only be identified in comparable patterns, then numerical analysis is only applicable below the species level where relative similarities may become apparent.

Overall, insufficient intraspecific variability was sampled in the present study, but there was some evidence of the increased variation in seed proteins being correlated to the morphological diversity within species. For example, the three accessions of S.marginatum, a morphologically uniform species, all gave broadly similar patterns of protein bands; while in S.anguivi, a highly variable species, the protein band patterns could be grouped but were less uniform. Edmonds and Glidewell (1977) presented this effect more clearly, demonstrating the parallel electrophoretic and infraspecific morphological variability in species of

Solanum Section Solanum.

A subjective comparison of band patterns in the present study showed some correlation to the current sectional arrangement of the species. The two accessions of the South American species S.atropurpureum (S.641 and S.668) gave a similar pattern which was more similar to S.capsicoides than to other species, so forming Group 15 of the present study. In turn, Group 15 was quite similar to S.viarum in Group 13 and these three species are all members of section Acanthophora Dunal.

In section Melongena, the accessions of each species tested gave sufficiently uniform results that each species could be recognised. The accessions of S.incanum, S.melongena and S.ovigerum all produced similar patterns and they were placed in the same group (10) which was then divided into three before the gels were identified. The division of Group 10 shows two sub-groups of S.incanum and a third sub-group consisting of S.melongena and S.ovigerum. These three species share several morphological attributes and it would seem that the similarity extends to the seed proteins. S.incanum is generally assumed to be the wild progenitor of S.melongena, of which S.ovigerum is widely treated as a variety.

Among the other species of section Melongena tested, namely S.macrocarpon, S.linnaeanum and S.marginatum, there were few

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similarities, the strongest perhaps being between S.incanum and S.linnaeanum. However, Group 9, the group of S.macrocarpon accessions, was characterised by a distinctive, large, slow-moving band which was diagnostic of some of the species of section Oliganthes, in particular S.anguivi, S.aethiopicum, S.rubetorum and S.violaceum. Omidiji (1979) has reported that S.macrocarpon and S.aethiopicum are partially inter-fertile.

Among the species of section Oliganthes there was a diversity of band patterns, but for the most part the species could be recognised. S.anguivi and S.aethiopicum were not clearly separable, even as sub-groups in Group 5, but as Lester and Niakan (In press) have convincingly shown, S.aethiopicum is a domesticated form of S.anguivi and is only arguably a separate species. The various cultivar groups of S.aethiopicum recognised by Lester and Niakan (l.c.) were not distinguished into separate sub-groups of Group 5. One accession of S.tomentosum also fell in Group 5 but the identity of this accession is in doubt.

Zone electrophoresis of the seed proteins of the Solanum species in the present study successfully separated most of the species. Some sectional groupings were noted, but the clearest delimitation at the sectional level was of the South American section Acanthophora which is anyway taxonomically distinct from the African species. Apart from some similarity between S.macrocarpon and S.anguivi/

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S.aethiopicum, the present study did not provide any new insights into the interrelationships of the African species of Solanum. Roberts (1978) suggested that the systematic value of zone electrophoresis of seed proteins reaches its upper limit at the rank of section in a genus of such taxonomic diversity as Solanum. The present findings concur with this view.

5.2.4. <u>Serotaxonomy</u> :

5.2.4.1 <u>Principles</u> :

Immunology has its basis in the discovery by Pasteur (1876) that defence reactions against infectious agents could be acquired. From this discovery a system in which antibodies arose in a serum in response to the introduction of antigens was proposed, and Kraus (1897) demonstrated the precipitation reaction between antibodies and antigens <u>in vitro</u>. The specificity of this reaction was soon realised and taxonomists saw this property as a method of molecular recognition which did not require protracted analytical techniques. In a seminal paper, Nuttall (1901) published his results from comparisons of blood from different primates and demonstrated a clear relationship between human blood and that of the higher primates. Subsequently, the techniques have been employed more widely (see Smith, 1976) as the range of materials which can cause antibody production has become established.

For most of this century work on serology has been empirical, but with recent advances in biochemical and molecular understanding the science has gained a sound theoretical basis. An antigen may be defined as any agent (protein, carbohydrate, nucleic acid or lipid) which, when transferred to a living cell system containing immunologically competent cells, will elicit antibody

formation specific to that agent. An antibody is a protein formed when an animal is immunised with an antigen. It is known that antibodies constitute the γ- globulin fraction of serum and five classes of antibodies are recognised based on their physicochemical and biological properties.

Antibody molecular structure in general is understood, and the specificity of the antibody/antigen reaction is thought to arise from the complementarity of certain sites on the antibody molecule to sites on the antigen. One antigen molecule will have several such 'antigenic determinant sites' and each one will stimulate the production of an antibody molecule specific to it. The antibody molecules are usually bivalent while most antigens are multivalent. Therefore, if an antigen and the corresponding antibodies are mixed in the appropriate proportions, each antibody molecule will bind on to two antigen molecules, both of which will be bound via other antibody molecules to further antigen molecules. Thus a molecular lattice is produced which is seen as a precipitate. At proportions other than this equivalence point, less or even no precipitate is seen as the lattice will be incomplete and soluble, and the antigen or antibody molecules which are in excess will have spare binding sites.

In the application of serology this maximum precipitation at the equivalence point was achieved previously by numerous test experiments with the antigens and antibodies in

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different proportions to one another. At the equivalence point, the amount of precipitate produced by different antigen systems with an antiserum was compared with the amount produced by the homologous or reference reaction (i.e. the antiserum with the antigen system against which it was raised) and described as a percentage. This technique has been superseded by a routine known as double diffusion which was developed by Ouchterlony (1948). It overcomes the necessity for finding the equivalence point by allowing the antibodies and antigens to diffuse towards each other in a semi-solid medium such as agar. A line of precipitate will appear where each antigen meets its complimentary antibodies in the optimal proportions.

The result of a multiple antigen test is a spectrum of lines of precipitate between the origins of antibody and antigen diffusion. Each line represents the reaction of a set of antibodies with one kind of antigenic molecule. The spectra of different antigen systems may be compared according to the number, density and position of the lines of precipitate. However, the spectra tend to be densely packed and immunoelectrophoresis (IEP) has been developed to improve the resolution. First, the antigen system is subjected to electrophoresis so that the antigens are separated along the length of a gel. Then, antiserum is allowed to diffuse through the gel, perpendicular to the direction of electrophoresis. The result is a spectrum of arcs of precipitate, each of which can be characterised by

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the electrophoretic mobility of the antigen.

The technique of double diffusion with absorption (DDA) has been developed to simplify the spectra of straightforward double diffusion. Here, antibodies are removed from an antiserum by precipitation with an antigen system, and the remaining antibodies are tested against a second antigen system. Therefore, if the antiserum is absorbed by the reference antigen system to which it was raised, all the antibodies will be removed, whereas if a less similar cross-reacting antigen system is used for absorption, some antibodies will still be free to react. Any lines of precipitate in the gel will be the result of antigens common to the cross-reacting test antigen system and the reference antigen system, but not possessed by the absorbing antigen system. Using antisera raised against a variety of antigen systems, such as protein extracts from different species, a three-dimensional matrix of results can be built up : each antiserum is absorbed in turn with each antigen system for testing against the other antigen systems. These data provide measures of similarity of the antigen systems, but the analysis is complex (Lester, 1979b; Lester et al., 1983).

Other routines for serological comparison, for example two-dimensional immunoelectrophoresis and immunoelectro-focussing, have been developed but were not employed in the present study.

5.2.4.2 Methods :

Antigen and Antibody Preparation : Seed was run through a coffee grinder, which on the appropriate setting sliced the seed coats off without causing too much damage to the embryos. The embryos were separated from the seed coats by adding the grist from the grinder to a mixture of carbon tetrachloride and petroleum ether. In the correct proportions (approximately 20:1 v/v petroleum ether : carbon tetrachloride) the density of the liquid was such that the embryos rose to the surface and the seed coats sank. The embryos were removed and dried and then shaken in a Dangoumau Analytical Pulveriser for ten minutes. The resulting fine flour was defatted in petroleum ether and stored at $-15^{o}C$.

Protein was extracted by soaking the flour overnight at $4^{o}C$ in distilled water in a ratio of 1:5 w/v. The suspension was centrifuged at 15,000g for six minutes and the supernatant decanted and stored at $-15^{o}C$. This extract was used both to raise antisera and for serological tests.

Antisera to six species of _Solanum_ were raised in six mature female 'New Zealand White' rabbits. A ten week course of intramuscular and subcutaneous injections of the extracts mixed with Freund's Complete Adjuvant was followed to effect immunisation.

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Before the course of injections, $10cm^3$ of blood was taken from each rabbit. This was used to test the serum for any response to the antigens which might confuse later serological tests. No reactions were found.

After the course of injections, about $60cm^3$ of blood was taken from the ear of each rabbit and the serum decanted and stored at -15^oC with 0.5% sodium azide as a bacteriostatic agent.

The following antisera were raised:-

R.122 against S.linnaeanum S.210

R.123 against S.marginatum S.256

R.124 against S.tomentosum S.1155

R.125 against S.giganteum S.1208

R.126 against S.violaceum S.1489

R.127 against S.macrocarpon S.1653

Two antisera which had been raised in 1974 were added to the study:-

R.97 against S.incanum S.50

R.98 against S.aethiopicum S.395

Agar Preparation : Clean microscope slides (7.6 x 2.6cm) were lightly sprayed with 0.1% agar which was allowed to dry before a second and then a third spraying (see Sangar et al., 1972). This coated one surface of the slide with

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spots of agar to which the agarose gel could adhere.

1% w/v agarose in borate phosphate buffer pH7.6 was heated until clear and $2cm^3$ applied to each microscope slide. The gels were left overnight in a humid atmosphere before being used.

Immunoelectrophoresis (IEP) : The techniques used followed Sangar et al. (1972). A central trough and two wells were cut in the agar on the slides in the pattern shown in Fig. 5.2.1a. The wells were filled twice with the antigen system (i.e. protein extract) to be tested and the slides placed between two reservoirs of borate phosphate buffer. A wick from each reservoir was laid across the ends of the slides and electrophoresis was run at 5 v/cm for 60 minutes. Antiserum was then applied to the central trough and the slides were incubated for 25-30 hours at room temperature in a humid atmosphere.

To remove unwanted proteins the slides were washed for 36 hours in a borate buffered saline solution which was changed every 12 hours. A final 12 hour wash in distilled water removed the salts and the slides were dried, stained in Ponceau S (0.2% in 3% Trichloracetic acid), destained in 2% acetic acid and stored dry.

<u>**Double Diffusion with Absorption (DDA)**</u> : The technique used

for pre-absorbing antisera followed that of Dray and Young

(1959). A pattern of two wells each surrounded by four

peripheral wells was cut in the agar on the microscope

a/.   b/.
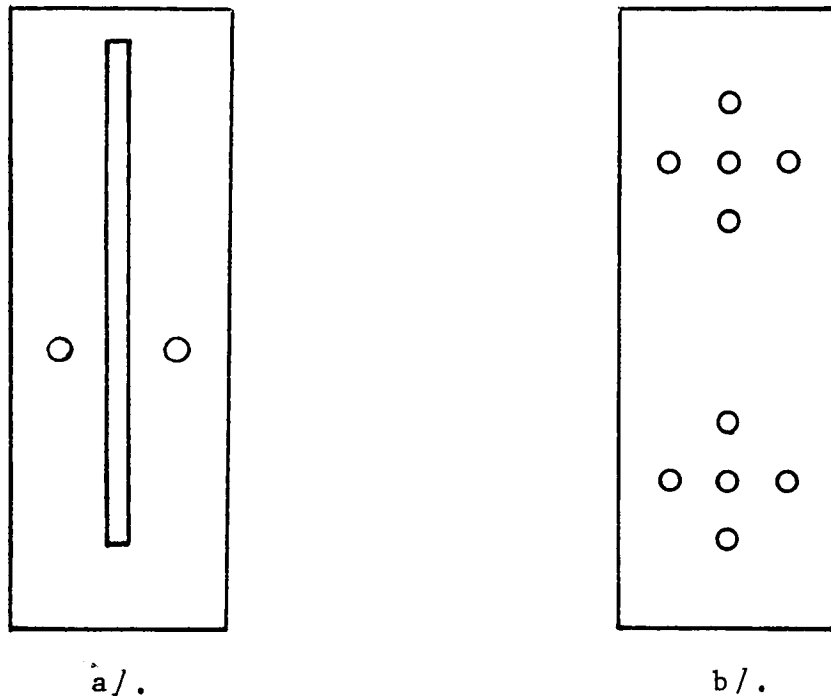
Fig. 5.2.1 The patterns of wells cut in agar for a/. IEP and b/. DDA.

slides (Fig. 5.2.1b). This allowed one pre-absorbed

antiserum in the two central wells to be tested against

eight antigen systems per slide. The wells were filled as

follows :

1. Absorbing antigen system added to central wells.

2. Absorbing antigen system added to central wells.

3. Antiserum added to central wells and test antigen
    systems added to peripheral wells.

4. Absorbing antigen system added to central wells.

5. Antiserum added to central wells and test antigen

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systems added to peripheral wells.

The wells were filled when all of the previous application of antiserum or antigen system had diffused into the agar.

The eight antisera were each absorbed by all eight antigen systems which had been used to raise them and tested against all eight antigen systems.

5.2.4.3 Results :

The developed slides were examined against a light box to reveal the arcs of precipitate formed between antiserum and antigen systems. Immunoelectrophoresis resulted in a spectrum of arcs of precipitate distributed according to the electrophoretic mobility of the antigens (Figs 5.2.2a-h) : arcs of similar size, shape and position were considered as likely to be the result of the same or similar antigens. Each of the eight antisera was tested against each of the eight antigen extracts which had been used for immunisation. Each cross-reaction (of an antiserum and one of the seven non-homologous antigen systems) was compared to the reference - reaction (between the same antiserum and the antigen system against which it was raised) and the results are summarised in Table 5.2.2.

The results of the double diffusion with absorption experiments were scored in four states : absence, possible presence, definite presence and strong presence (-, $\overset{+}{-}$, +, ++ respectively) of precipitate. The 8 x 8 x 8 matrix of data presented in Table 5.2.3 collates the results of absorbing each antiserum with each antigen system before testing against each antigen system.
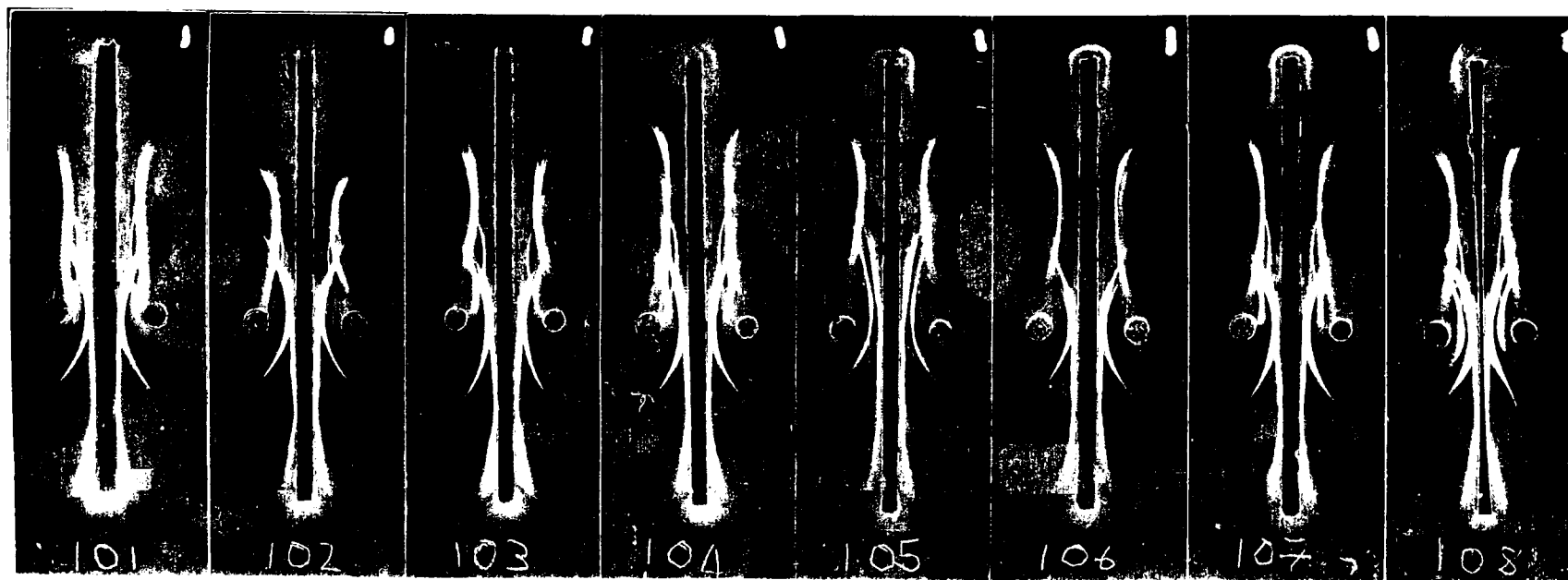
Fig. 5.2.2a :

IEP reactions with antiserum R.122 against S.linnaeanum (S.210).

Antigen extracts tested :   101   S.linnaeanum (S.210)   102   S.marginatum   (S.256)

                           103   S.tomentosum (S.1155)   104   S.giganteum   (S.1208)

                           105   S.violaceum   (S.1489)   106   S.macrocarpon (S.1653)

                           107   S.incanum   (S.50)   108   S.aethiopicum (S.395)
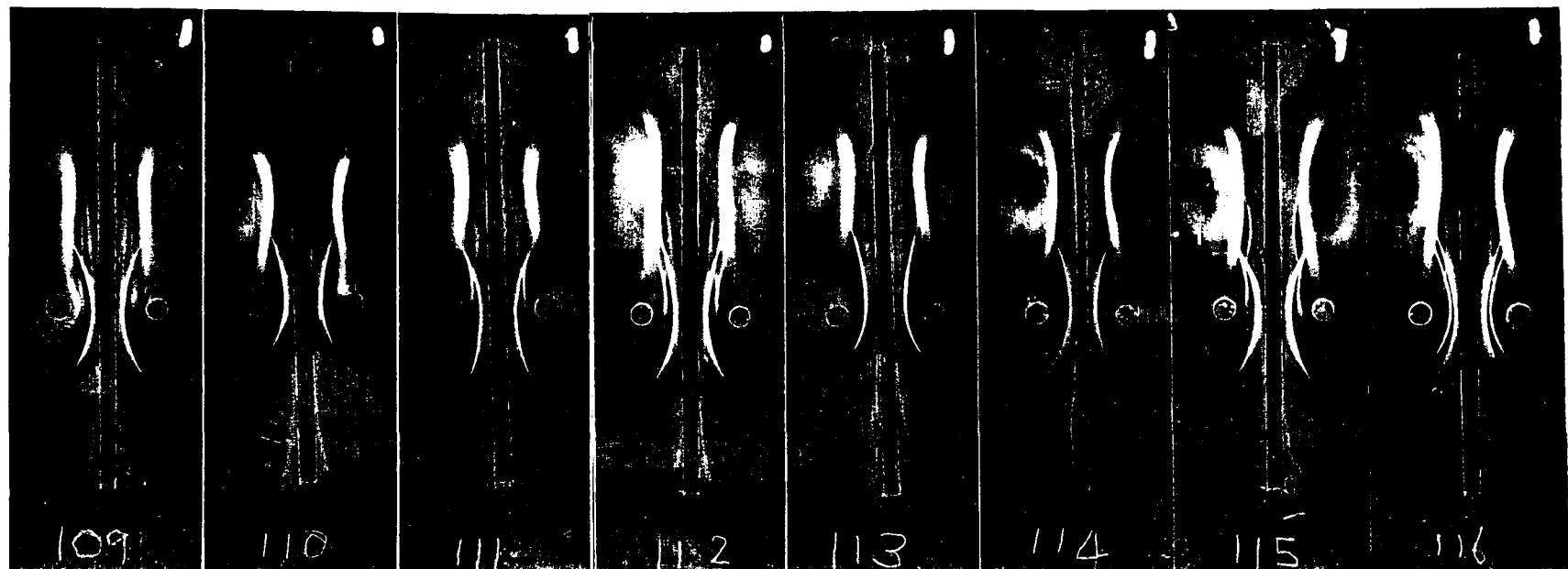
<u>Fig. 5.2.2h</u> :

IEP reactions with antiserum R.123 against <u>S.marginatum</u> (S.256)

Antigen extracts tested : 109 <u>S.linnaeanum</u> (S.210)   110 <u>S.marginatum</u>   (S.256)

111 <u>S.tomentosum</u> (S.1155)   112 <u>S.giganteum</u>   (S.1208)

113 <u>S.violaceum</u> (S.1489)   114 <u>S.macrocarpon</u> (S.1653)

115 <u>S.incanum</u>   (S.50)   116 <u>S.aethiopicum</u> (S.395)
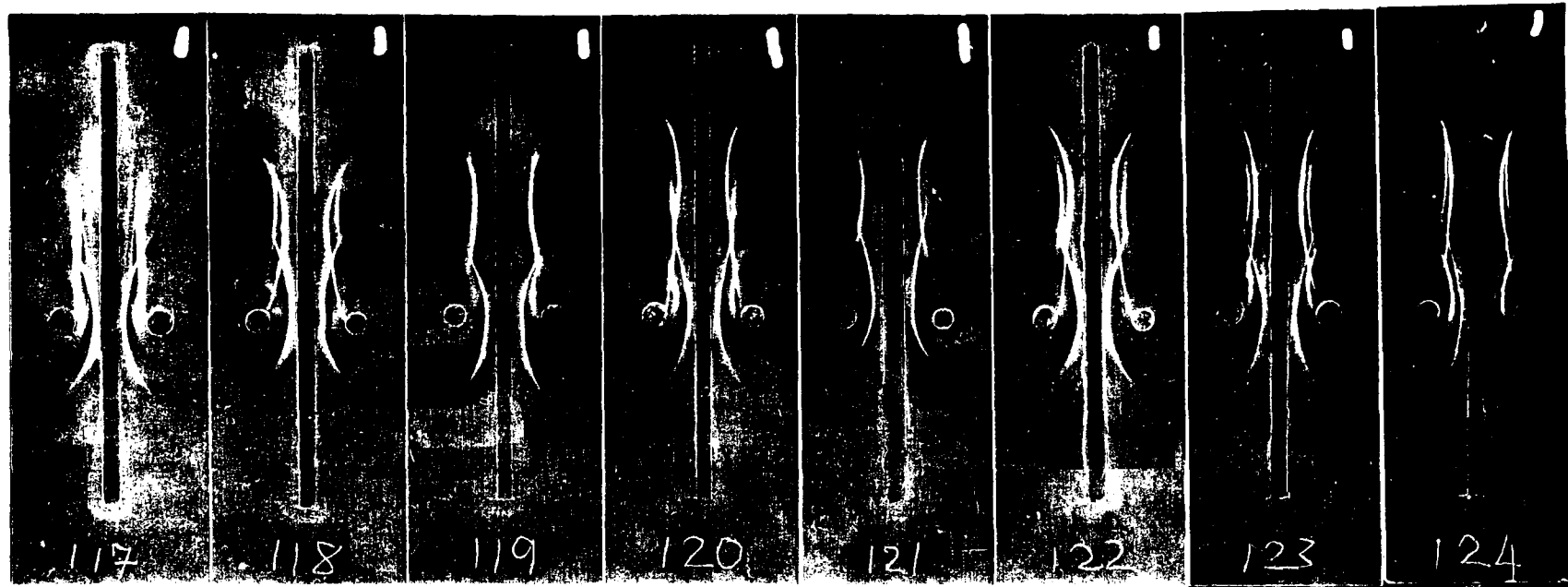
Fig. 5.2.2c :

IEP reactions with antiserum R.124 against S.tomentosum (S.1155)

Antigen extracts tested :   117   S.linnaeanum (S.210)   118   S.marginatum (S.256)

119   S.tomentosum (S.1155)   120   S.giganteum   (S.1208)

121   S.violaceum (S.1489)   122   S.macrocarpon (S.1653)

123   S.incanum   (S.50)   124   S.aethiopicum (S.395)

Fig. 5.2.2d :

IEP reactions with antiserum R.125 against S.giganteum (S.1208).

Antigen extracts tested : 125 S.linnaeanum (S.210)   126 S.marginatum   (S.256)

127 S.tomentosum (S.1155)   128 S.giganteum   (S.1208)

129 S.violaceum   (S.1489)   130 S.macrocarpon (S.1653)

131 S.incanum   (S.50)   132 S.aethiopicum (S.395)
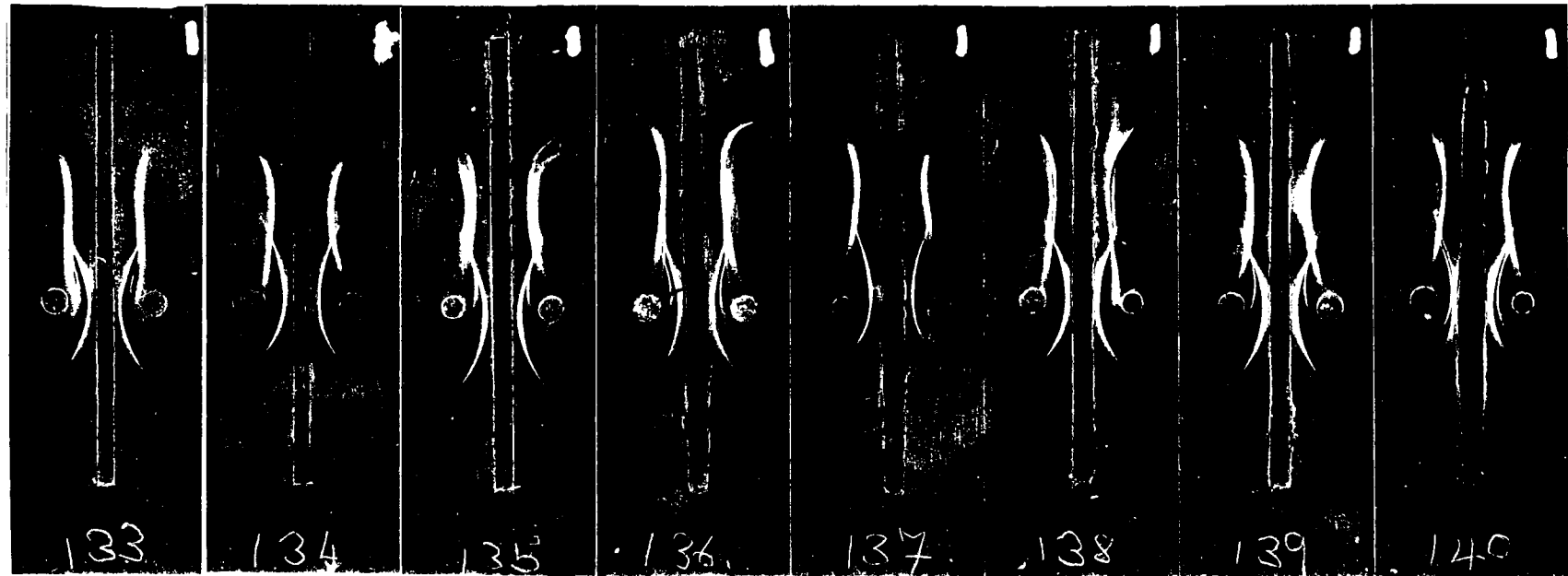
Fig. 5.2.2e :

IEP reactions with antiserum R.126 against S.violaceum (S.1489).

Antigen extracts tested : 133 S.linnaeanum (S.210)   134 S.marginatum   (S.256)

133 S.tomentosum (S.1155)   136 S.giganteum   (S.1208)

137 S.violaceum   (S.1489)   138 S.macrocarpon (S.1653)

139 S.incanum   (S.50)   140 S.aethiopicum (S.395)
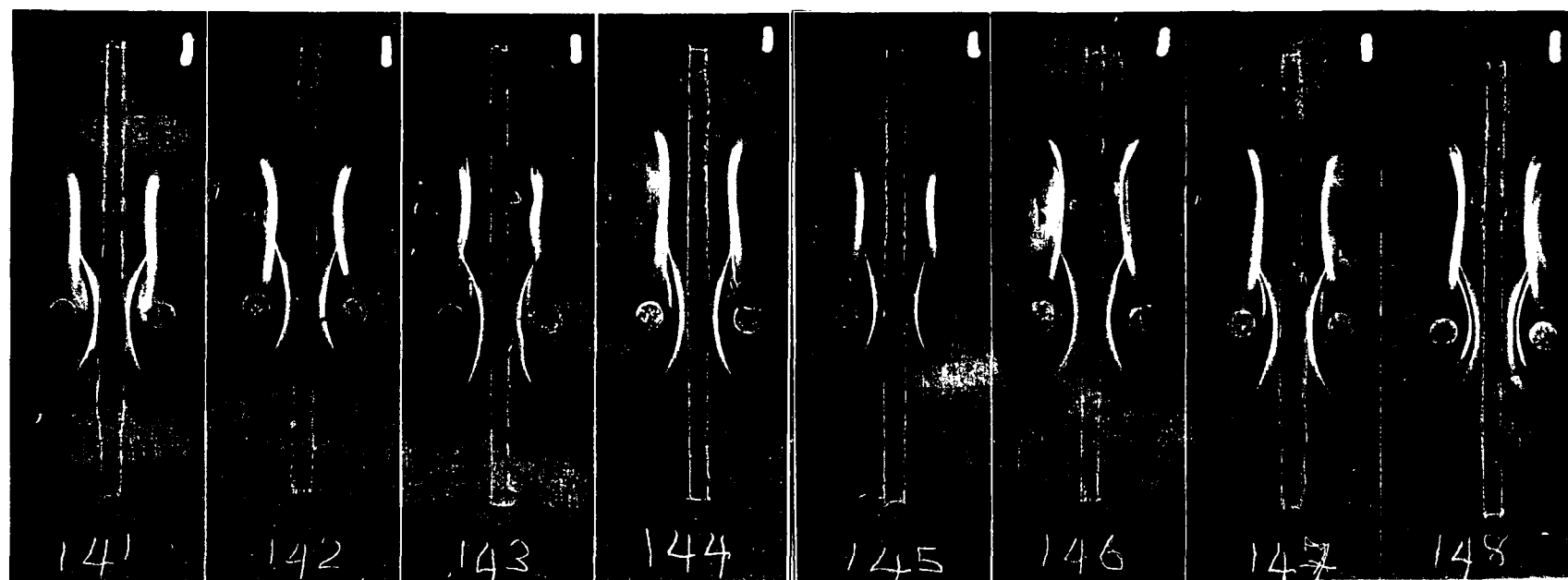
Fig. 5.2.2f :

IEP reactions with antiserum R.127 against S.macrocarpon (S.1653).

Antigen extracts tested : 141 S.linnaeanum (S.210)   142 S.marginatum (S.256)

                           143 S.tomentosum(S.1155)   144 S.giganteum   (S.1208)

                           145 S.violaceum (S.1489)   146 S.macrocarpon (S.1653)

                           147 S.incanum   (S.50)   148 S.aethiopicum (S.395)
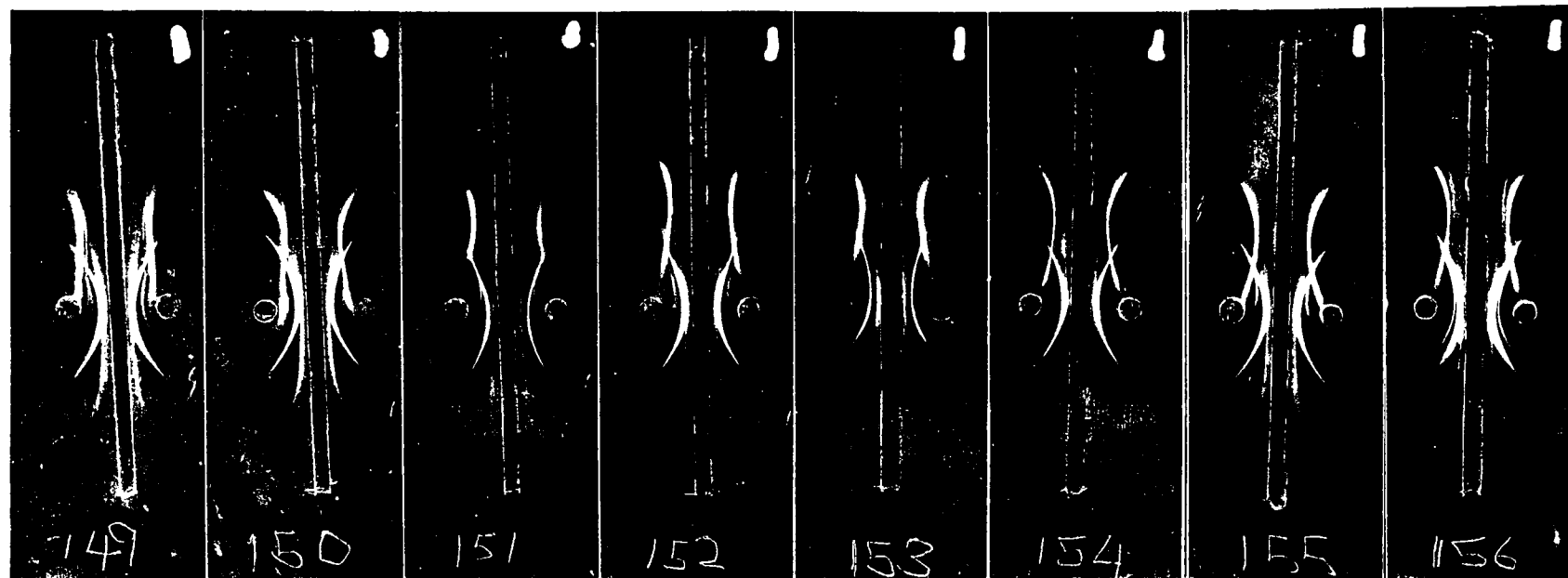
Fig. 5.2.2g :

IEP reactions with antiserum R.97 against S.incanum (S.50).

Antigen extracts tested : 149 S.linnaeanum (S.210)   150 S.marginatum (S.256)

151 S.tomentosum (S.1155)   152 S.giganteum (S.1208)

153 S.violaceum (S.1489)   154 S.macrocarpon (S.1653)

156 S.incanum   (S.50)   156 S.aethiopicum (S.395)
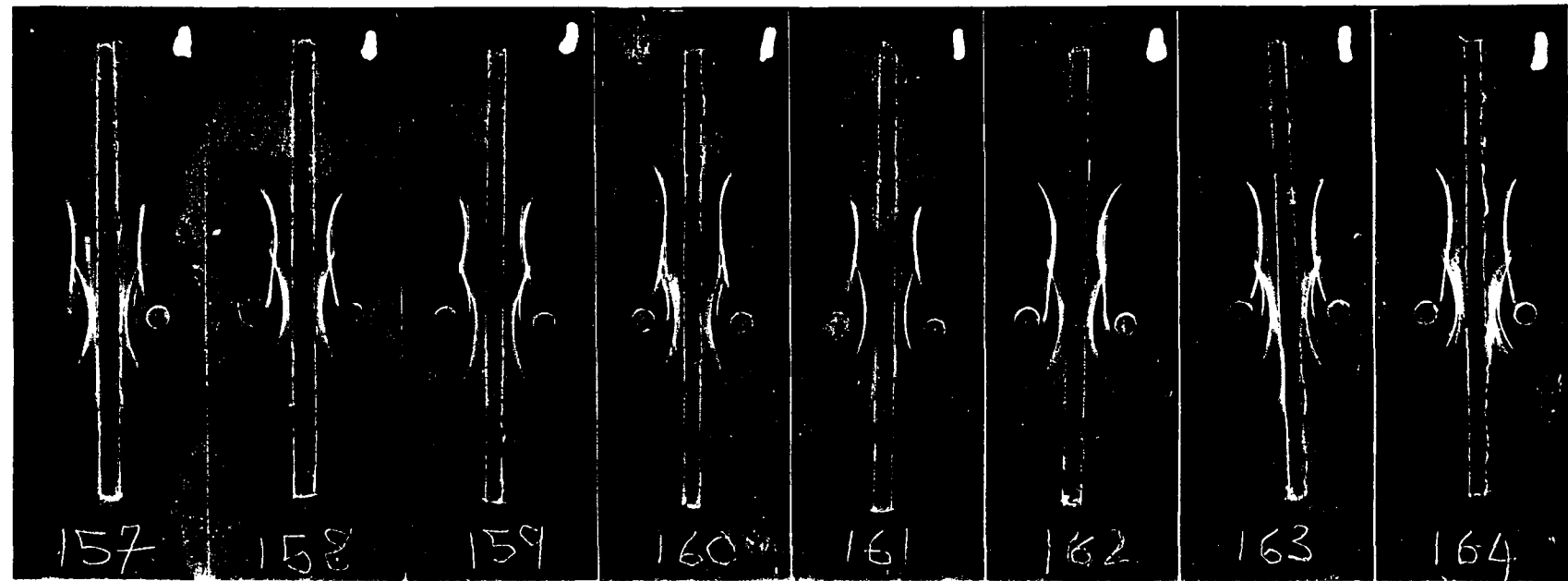
Fig. 5.2.2h :

IEP reactions with antiserum R.98 against <u>S.aethiopicum</u> (S.395).

Antigen extracts tested :   157   <u>S.linnaeanum</u> (S.210)   158   <u>S.marginatum</u> (S.256)

159   <u>S.tomentosum</u> (S.1155)   160   <u>S.giganteum</u>   (S.1208)

161   <u>S.violaceum</u> (S.1489)   162   <u>S.macrocarpon</u> (S.1653)

163   <u>S.incanum</u>   (S.50)   164   <u>S.aethiopicum</u> (S.395)

Antigen System	R.97 a	b	R.98 a	b	R.122 a	b	R.123 a	b	R.124 a	b	R.125 a	b	R.126 a	b	R.127 a	b
S.50	6	–	5	–	4	–	5	–	6	1	4	–	3	2	3	2
S.395	5	–	6	–	5	1	5	–	6	–	4	–	3	2	4	1
S.210	5	1	4	–	9	–	6	–	5	2	3	1	4	1	4	1
S.256	5	–	5	1	3	2	6	–	3	1	4	–	4	1	4	–
S.1155	4	1	5	–	3	2	5	–	7	–	4	2	4	1	5	–
S.1208	4	1	4	1	3	2	5	–	6	–	6	–	5	1	5	–
S.1489	4	–	3	1	3	–	3	1	3	–	3	2	6	–	2	1
S.1653	3	1	4	1	3	1	3	–	5	–	4	1	3	2	5	–

Table 5.2.2 : Summary of the numbers of arcs of precipitate

after immunoelectrophoresis

Key : R.97   antiserum against S.incanum   S.50
       R.98   antiserum against S.aethiopicum S.395
       R.122 antiserum against S.linnaeanum   S.210
       R.123 antiserum against S.marginatum   S.256
       R.124 antiserum against S.tomentosum   S.1155
       R.125 antiserum against S.giganteum   S.1208
       R.126 antiserum against S.violaceum   S.1489
       R.127 antiserum against S.macrocarpon S.1653

Column a = Number of arcs in common with the reference

reaction.

Column b = Number of arcs different from those in the

reference reaction.

The reference reactions are underlined.

Each 8 x 8 matrix represents the reactions to one antibody system (Abs). Each column within a matrix corresponds to the antigen system (Ags) which was used to pre-absorb the antibody system. Each row consists of the results obtained when each antigen system is tested against the variously absorbed antibody system.

Antigen systems are referred to by their accession numbers which are as follows :

S.incanum	S.50
S.aethiopicum	S.395
S.linnaeanum	S.210
S.marginatum	S.256
S.tomentosum	S.1155
S.giganteum	S.1208
S.violaceum	S.1489
S.macrocarpon	S.1653

Results were scored according to the quantity of precipitate :

-	=	Absent
+ -	=	Possibly present
+	=	Present
++	=	Strongly present

Abs. R.97 to S.50 (<u>S.incanum</u>)

<div align="center">Absorbing Ags</div>

	S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
S.50	−	+ −	−	−	−	+ −	−	−
S.395	−	−	−	−	+ −	+ −	−	−
Test S.210	−	−	−	−	+ −	−	−	−
Ags S.256	−	−	−	−	−	−	−	−
S.1155	−	−	−	−	−	−	−	−
S.1208	−	−	−	−	−	−	−	−
S.1489	−	+ −	−	−	−	−	− .	−
S.1653	−	−	−	−	−	−	−	−

Abs. R.98 to S.395 (<u>S.aethiopicum</u>)

<div align="center">Absorbing Ags</div>

	S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
S.50	−	−	−	−	−	−	+	−
S.395	−	−	−	−	−	−	+	−
Test S.210	−	−	−	−	−	−	+	−
Ags S.256	−	−	−	−	−	−	+ −	−
S.1155	−	−	−	−	−	−	+	−
S.1208	−	−	−	−	−	−	+	−
S.1489	−	−	−	−	−	−	−	−
S.1653	−	−	−	−	−	−	+	−

<u>Table 5.2.3</u> − Results of Double Diffusion with Absorption.

Abs. R.122 to S.210 (<u>S.linnaeanum</u>)

<div align="center">Absorbing Ags</div>

		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	+	−	+ −	+	+ −	+	−
	S.395	−	−	−	+ −	−	+ −	+	−
Test	S.210	−	+	−	+ −	+	+ −	+	−
Ags	S.256	−	−	−	−	−	−	+	−
	S.1155	−	+ −	−	+	−	+ −	+	−
	S.1208	−	+ −	−	+	−	−	−	−
	S.1489	−	+	−	−	+	−	−	−
	S.1653	−	−	−	+ −	+	−	+ −	−

Abs. R.123 to S.256 (<u>S.marginatum</u>)

<div align="center">Absorbing Ags</div>

		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	+	−	−	+	+	+	−
	S.395	−	−	−	−	+	+	+	−
Test	S.210	−	+	−	−	+	+	+	−
Ags	S.256	+	+	+	−	+	+	+	−
	S.1155	−	+	−	−	−	+	−	−
	S.1208	−	+	−	−	+	−	+	−
	S.1489	−	+	−	−	+	+	−	−
	S.1653	−	+	−	−	+	+	−	−

<u>Table 5.2.3</u> continued.....

Abs. R.124 to S.1155 (S.tomentosum)

Absorbing Ags

Test Ags		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	−	−	+	−	−	++	+
	S.395	+/−	−	−	+	−	−	++	+
Test	S.210	+/−	−	−	+	−	−	+	+
Ags	S.256	−	−	−	−	−	−	+	+/−
	S.1155	+	−	−	+	−	−	++	+
	S.1209	−	−	−	+	−	−	−	+
	S.1489	+	−	−	−	−	−	−	−
	S.1653	+/−	−	−	+/−	−	−	+/−	−

Abs. R.125 to S.1208 (S.giganteum)

Absorbing Ags

Test Ags		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	−	−	−	−	−	+	−
	S.395	−	−	−	−	−	−	+	−
Test	S.210	−	−	−	−	−	−	+	−
Ags	S.256	−	−	−	−	−	−	+	−
	S.1155	−	−	−	−	−	−	+	+
	S.1208	−	−	−	−	+/−	−	+	+
	S.1489	−	−	−	−	−	−	−	−
	S.1653	−	−	−	+	−	−	+	−

Table 5.2.3 continued....

Abs. R.126 to S.1489 (<u>S.violaceum</u>)

<div align="center">Absorbing Ags</div>

		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	−	−	−	−	−	−	−
	S.395	−	−	−	−	−	−	−	−
Test	S.210	−	−	−	−	−	−	−	−
Ags	S.256	−	−	−	−	−	−	−	−
	S.1155	−	+/−	−	−	−	−	−	−
	S.1208	−	+/−	−	−	−	−	−	−
	S.1489	−	+	−	−	−	−	−	+/−
	S.1653	−	−	−	−	−	−	−	−

Abs. R.127 to S.1653 (<u>S.macrocarpon</u>)

<div align="center">Absorbing Ags</div>

		S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
	S.50	−	−	+	+/−	+	−	+	−
	S.395	−	−	+	−	+	−	+	−
Test	S.210	−	−	+	+/−	+	−	+	−
Ags	S.256	−	−	+	−	+	−	+	−
	S.1155	−	−	+	+/−	+	−	+	−
	S.1208	−	−	+	+/−	+	−	+	−
	S.1489	−	−	+	−	+	−	+	−
	S.1653	−	−	++	+	+	−	+	−

<u>Table 5.2.3</u> continued....

5.2.4.4. Discussion

Immunoelectrophoresis (IEP) :

The spectra resulting from immunoelectrophoresis were carefully compared but identification of the arcs proved difficult. The spectra were not well spread out, as can be seen in Figs. 5.2.2a-h, and there were many problems in deciding which arcs were identical and which arcs were different. Some misidentifications may have occurred : future work might use a higher voltage or longer time in order to spread the arcs more effectively.

A general similarity of reaction was noted, indicating, perhaps, the close taxonomic relationship among the tested species. Taking the reactions of antiserum R.123 to S.marginatum as an example, it can be seen from Table 5.2.2 that the reference-reaction produced six arcs which were also found in the cross-reaction with S.210 (S.linnaeanum) : five of these arcs, the same ones in each case, were also found in S.50 (S.incanum), S.395 (S.aethiopicum) and S.1208 (S.giganteum). Cross-reaction with S.1155 (S.tomentosum) gave four of the five arcs shown by S.50, S.395 and S.1208 and one found only in S.210 and the reference-reaction.

The total number of arcs was fewer than expected when results are compared with other work on similar species. Roberts (1978) found up to fourteen arcs, and not less than

eight arcs, in the reference reactions of antisera raised against the seed proteins of six species of <u>Solanum</u>. In the present work a maximum of nine and minimum of five arcs were found in the reference-reactions, and this may be indicative of an incomplete immune response by the rabbits to all the antigenic determinant sites on all the different proteins in the seed extracts. This is reinforced by the asymmetry of Table 5.2.2 : an antiserum raised against antigen system A tested against antigen system B might be expected to give the same result as antiserum against B tested against antigen system A, but they rarely did so. For example, the reaction of the antigen system (=Ags) S.50 (<u>S.incanum</u>) with antibody system (=Abs) R.124 (anti-S.1155 <u>S.tomentosum</u>) produced seven arcs, whereas the reciprocal reaction of Ags S.1155 with Abs R.97 (anti-S.50) produced only five arcs. However, although there were considerable qualitative differences between antisera, due to the differing immune responses of individual rabbits, for any one antiserum, the reference reaction was not exceeded by any of the cross reactions.

There is no obvious solution to the problem of incomplete immune responses, particularly as there is variation in the response of individual rabbits exposed to the same antigen systems. Replicate antisera, using several rabbits to raise antiserum against the same antigen system, would provide a means of checking results, and a longer course of injections might induce a more complete response. With the

present results, the higher reaction in each pair of reciprocal comparisons (Ags B tested with Abs A, and Ags A tested with Abs B) was assumed to be the more complete response.

For any one antibody system several of the arcs shown by the reference reaction were shown similarly by the various cross-reacting antigen systems; but other arcs had different electrophoretic mobilities (columns b in Table 5.2.2), and yet others were missing altogether. The arcs of different electrophoretic mobility were assumed to be the result of homologous proteins, but with some amino-acid substitutions. The absence of some arcs need not necessarily imply the complete absence of these proteins, but may be the result of too many amino-acid substitutions rendering a homologous protein unrecognisable to any of the antibody molecules, and thus preventing any reaction.

Extensive numerical analysis of the data was not appropriate here as only eight species were tested. The total number of arcs in a cross-reaction as compared to the number in the reference-reaction was interpreted as a measure of the similarity of the proteins in the two antigen systems. The antigen systems could be ranked in order of their similarity to each antiserum. The most similar and least similar antigen systems are listed below without those of intermediate affinity as their positions in the order were often interchangeable.

Antiserum	Most Similar	Least Similar
S.incanum	S.linnaeanum	S.macrocarpon
S.aethiopicum	S.marginatum	S.violaceum
S.linnaeanum	S.aethiopicum	S.violaceum
S.marginatum	S.linnaeanum	S.macrocarpon
S.tomentosum	S.incanum	S.violaceum
S.giganteum	S.tomentosum	S.linnaeanum
S.violaceum	S.giganteum	S.incanum
		or S.aethiopicum
		or S.macrocarpon
S.macrocarpon	S.tomentosum	S.violaceum
	or S.giganteum	

The list shows occasional correlation with contemporary classification but anomalies are just as freqent. When tested against antiserum R.97 (to S.incanum), S.marginatum and S.linnaeanum gave spectra that were the most similar to the reference-reaction. These three species belong to section Melongena and might be expected to have similar seed proteins. However, S.macrocarpon also belongs to section Melongena but gave the least similar reaction to antisera against S.incanum and S.marginatum. S.aethiopicum, from section Oliganthes gave the highest reaction to S.linnaeanum antiserum, despite the normal placement in two separate sections, while S.linnaeanum gave one of the lowest reactions to S.aethiopicum antiserum.

Studies using IEP on species of <u>Solanum</u> have been carried
out with some success by Pearce (1975) and Roberts (1978),
both of whom tested a wide range of species against a few
antisera. Roberts found a good correspondence to species
arrangements based both on orthodox morphological characters
as well as results from zone electrophoresis. The present
survey might be extended with less closely related species
so that differences are more readily identified, but the
number of anomalies noted in the data presented here
indicate some of the limitations of this approach to
taxonomy.

Double Diffusion With Absorption (DDA) :

Inspection of the matrices presented in Table 5.2.3 reveals
that the majority of test reactions failed to produce a
precipitate. In DDA tests, failure to react implies a
similarity of seed proteins either between the species used
to raise the antiserum and the species used as absorber or
between the absorber and the test antigen species. In the
former, all the antibodies are removed by the absorber,
while in the latter all the antibodies relevant to the test
antigen species are removed prior to testing. The general
lack of precipitate in the present set of experiments
indicates that the seed storage proteins of the species
studied are similar in terms of immunological reactivity.

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The more detailed analysis of the results of DDA experiments in general has been a subject for debate for over 20 years and, as yet, there is no widespread agreement on how the data should be interpreted. Moritz and Jensen (1961), Kirsch (1967) and Moore and Goodman (1968) have discussed the inherent problems. Jensen (1968) has interpreted the data as phyletic evidence while Lester (1979b) treated his results as phenetic data, but also attempted cladistic analysis (Lester, Roberts and Lester, 1983; Lester and Roberts, In press).

Kirsch (l.c.) was the first to apply the mathematical theories of sets to the problem of the analysis of taxonomic immunological data. While he was unable to use it to analyse the data, set theory is a useful medium for discussion.

In terms of set theory, the collection of antigenic determinant sites of the seed proteins of each species may be thought of as mathematical sets. Since there are similarities between the seed proteins of all the species under discussion, all the sets will overlap to a greater or lesser extent. On injection into the rabbit, each set of antigenic determinant sites should stimulate an equivalent, complementary set of antibody receptor sites. In theory, one might expect the set of antigenic determinant sites to incorporate exactly the same number of sites as its complementary set of antibody receptor sites. In practice,

however, there is some variation as there may be an incomplete immune response, but for the argument it will be assumed that the two complementary sets are equivalent.

When the antibody system raised from species A (designated A_{Abs} here) is combined with the antigen system of the seed proteins of species B ($=B_{Ags}$) the intersect of the sets A_{Abs} and B_{Ags} will be visible as precipitate. This may be represented diagrammatically as
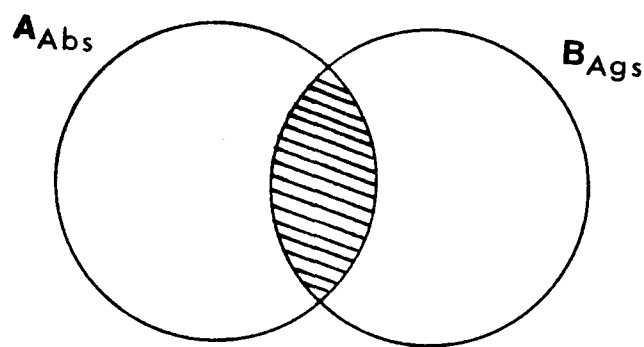
where the shaded portion represents the antigenic determinant sites in common between species A and species B. In mathematical notation the shaded area is $A_{Abs} \cap B_{Ags}$.

Since theoretically $A_{Abs} = A_{Ags}$ and $B_{Ags} = B_{Abs}$

then $\qquad A_{Abs} \cap B_{Ags} = B_{Abs} \cap A_{Ags}$

In practice, as mentioned above, the formula is not always commutative, and for this reason it is important that a number of reciprocal test reactions are carried out to check the completeness of a rabbit's immune response.

Applying set theory to DDA, the reactions may he represented

as
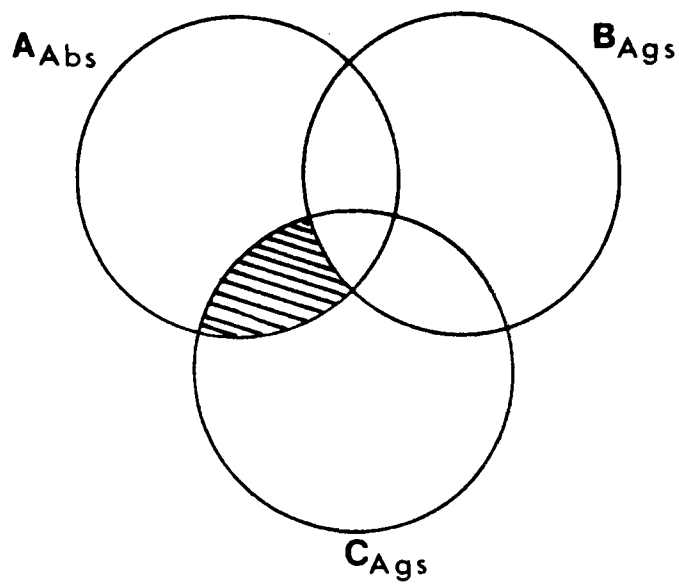
A_{Abs} B_{Ags} C_{Ags}

where the shaded area represents the reaction of $C_{A\varepsilon s}$

with A_{Ahs} after A_{Ahs} has heen ahsorhed hy $B_{A\varepsilon s}$.

Mathematically this is $(A_{Ahs} - A_{Ahs} \cap B_{Ags}) \cap C_{Ags}$.

The reciprocal reaction is :
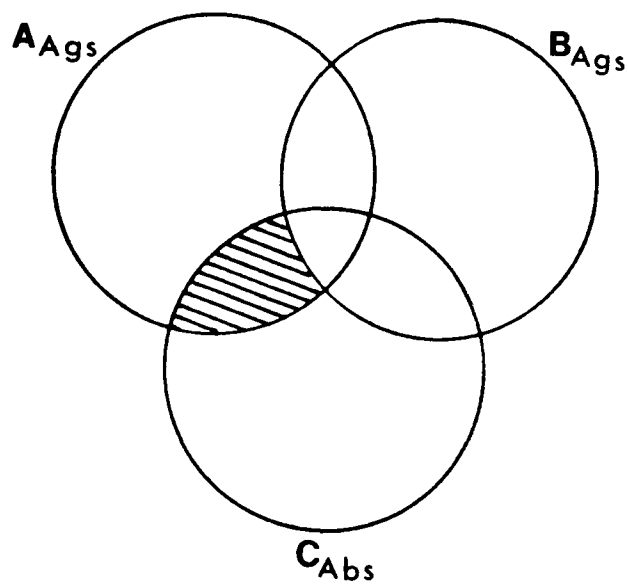
A_{Ags} B_{Ags} C_{Abs}

or $(C_{Abs} - C_{Abs} \cap B_{Ags}) \cap A_{Ags}$

and theoretically

$$(A_{Abs} - A_{Abs} \cap B_{Ags}) \cap C_{Ags} = (C_{Abs} - C_{Abs} \cap B_{Ags}) \cap A_{Ags}.$$

In practice, the formula is not always commutative, and it must be assumed that if the equation of reciprocal reactions is not equal, then there must be an incomplete immune response on one side. Thus, if reciprocal DDA tests are compared and are unequal, the reaction giving the greatest amount of precipitate is assumed to be the better response, and that result is used as data for analysis.

For the data from the present DDA study a table (Table 5.2.4) has been drawn up with the columns representing the reaction after the various species have been used as absorber, and the rows being the reactions between antibody system and test antigen. All the tests carried out here were done reciprocally, that is

$(A_{Abs} - A_{Abs} \cap B_{Ags}) \cap C_{Ags}$ and $(C_{Abs} - C_{Abs} \cap B_{Ags}) \cap A_{Ags}$

In each case the reaction giving the greater amount of precipitate has been used as data for the table.

The absorbing antigen systems can now be compared. Clearly if $(A_{Abs} - A_{Abs} \cap B_{Ags}) \cap C_{Ags}$

and the reciprocal

$(C_{Abs} - C_{Abs} \cap B_{Ags}) \cap A_{Ags}$

give no precipitate, and if

$$(A_{Abs} - {}^{A}_{Abs} \cap D_{Ags}) \cap C_{Ags}$$

and its reciprocal do not either, then the absorbers B and D

have some antigenic determinant sites in common since they

both remove all the antibody receptor sites common to A and

C. Thus, looking at Table 5.2.4, absence of precipitate is

read as the possession of a character for the absorbing

antigen system.

The similarity of the absorbing antigen systems can be

computed using the techniques of numerical taxonomy. In the

present study the simple matching coefficient was used to

assess similarity, followed by the 'unweighted pair-group

method using arithmetic averages' (UPGMA) clustering method

to produce a dendrogram, Fig. 5.2.3 (see Sneath and Sokal,

1973, for discussion of these taximetric techniques).

Table 5.2.4 : Summary of Double Diffusion with

Absorption Results

Overleaf, the columns indicate the absorbing antigen system while the rows are the antibody and test antigen reactions. Reciprocal reactions have been combined and the greater amount of precipitate entered in the table.

Key : +   =   Presence of precipitate.

$\frac{+}{-}$ =   Some (doubtful) precipitate.

−   =   No precipitate.

Accession No.	Species	Antiserum
S.50	S.incanum	R.97
S.395	S.aethiopicum	R.98
S.210	S.linnaeanum	R.122
S.256	S.marginatum	R.123
S.1155	S.tomentosum	R.124
S.1208	S.giganteum	R.125
S.1469	S.violaceum	R.126
S.1653	S.macrocarpon	R.127

Table 5.2.4

Absorbing Antigen System

	S.50	S.395	S.210	S.256	S.1155	S.1208	S.1489	S.1653
S.50/S.395	−	−	−	−	±	±	+	−
S.50/S.210	−	+	−	±	+	±	+	−
S.50/S.256	−	+	−	−	+	+	+	−
S.50/S.1155	−	−	−	+	−	−	++	+
S.50/S.1208	−	−	−	−	−	−	+	−
S.50/S.1489	−	±	−	−	−	−	−	−
S.50/S.1653	−	−	+	±	+	−	+	−
S.395/S.210	−	−	−	±	−	±	+	−
S.395/S.256	−	−	−	−	+	+	+	−
S.395/S.1155	±	−	−	+	−	−	++	+
S.395/S.1208	−	−	−	−	−	−	+	−
S.395/S.1489	−	−	−	−	−	−	−	−
S.395/S.1653	−	−	+	−	+	−	+	−
S.210/S.256	−	+	−	−	+	+	+	−
S.210/S.1155	±	±	−	+	−	±	+	+
S.210/S.1208	−	±	−	+	−	−	+	−

Table 5.2.4 continued

<div align="center">Absorbing Antigen System</div>

	S.50	S.395	S.210	S256	S.1155	S.1208	S.1489	S.1653
S.210/S.1489	−	+	−	−	+	−	−	−
S.210/S.1653	−	−	+	±	+	−	+	−
S.256/S.1155	−	+	−	−	−	+	+	±
S.256/S.1208	−	+	−	−	+	−	+	−
S.256/S.1489	−	+	−	−	+	+	−	−
S.256/S.1653	−	+	+	−	+	+	+	−
S.2155/S.1208	−	±	−	+	−	−	+	+
S.1155/S.1489	+	±	−	−	−	−	−	−
S.1155/S.1653	±	−	+	±	+	−	+	−
S.1208/S.1489	−	±	−	−	−	−	−	−
S.1208/S.1653	−	−	+	±	+	−	+	−
S.1489/S.1653	−	−	+	−	+	−	+	−

Key : Section Melongena   Section Oliganthes
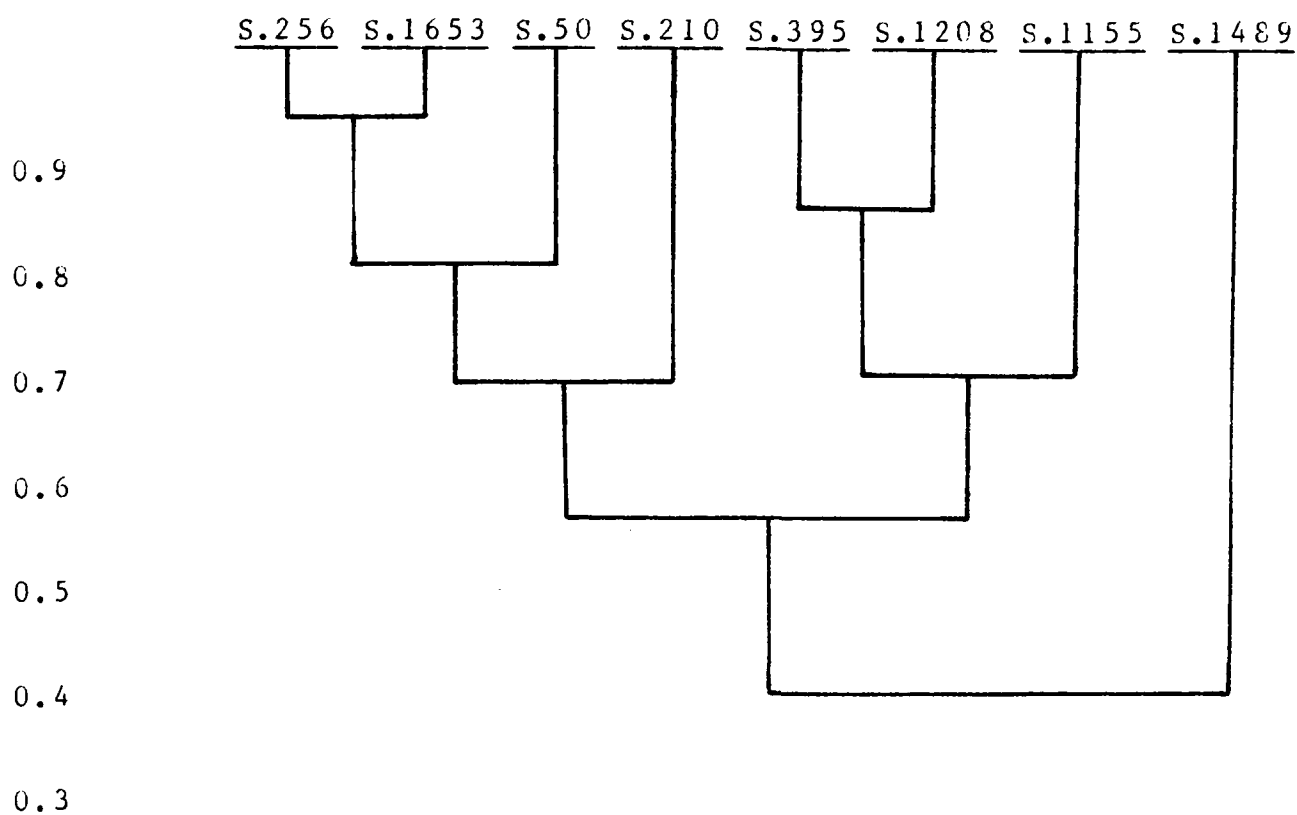
      S.50   = S.incanum   S.395   = S.aethiopicum

      S.210   = S.linnaeanum   S.1155 = S.tomentosum

      S.256   = S.marginatum   S.1489 = S.violaceum

      S.1653 = S.macrocarpon

                                Section Torva

                                S.1208 = S.giganteum

Fig. 5.2.3 Dendrogram showing the species groupings derived from the analysis of data from double diffusion with absorption experiments.

The dendrogram, Fig. 5.2.3, shows the species of section Melongena clustering in one group and two of the species of section Oliganthes clustering in another with S.giganteum of section Torva. S.violaceum appears to be remote from either cluster, and sections Melongena, Oliganthes and Torva cluster together before S.violaceum links in at a low level of similarity. This analysis supports the traditional separation of the species of sections Melongena and Oliganthes, but S.violaceum would, on the basis of morphology, normally be included in section Oliganthes whereas S.giganteum would not. Here, there is greater similarity between section Oliganthes, section Torva and section Melongena than there is between S.violaceum and section Oliganthes.

Roberts (1978) used DDA techniques in an immunotaxonomic study of Solanum species, mostly from South America. He used a similar analysis to that of Lester (1979b) but found the results taxonomically unacceptable. Reinterpretation of the data using cladistic analysis showed some agreement with classification based on morphology (Lester et al., 1983). Roberts suggested that the value of DDA tests might increase above the sectional level, and Lester (l.c.) also working on Solanum, found satisfactory agreement between the results of DDA study and the sub-generic divisions. The present analysis however seems to indicate that some acceptable results can be obtained from intersectional comparisons.

The novelty of the analysis developed here lies in the recognition that within a complete matrix of DDA data there are reactions which are reciprocal and which should give identical results. When the data which are believed to be erroneous are removed, a lot of background 'noise' is taken out which might otherwise corrupt calculation of similarity or distance measures.

5.2.5 **Conclusion**

Looking at the combined results from zone electrophoresis and serology, there are no clear taxonomic conclusions which emerge. Limited support for the existing classification of parts of the genus Solanum are given by zone electrophoresis and double diffusion with absorption, while the anomalies in immunoelectrophoresis data preclude interpretation.

Zone electrophoresis indicated that, in some cases, species could be delimited by the patterns of protein bands. Species of section Acanthophora showed some similarity to one another but the patterns both of section Oliganthes and of section Melongena were insufficiently uniform or similar to suggest any distinction or cohesiveness between the sections. One similarity of note, however, was found between accessions of S.macrocarpon and some species of section Oliganthes, but this evidence was contradicted by

the data from double diffusion with absorption in which S.macrocarpon clustered tightly with S.marginatum and other species of section Melongena.

The analysis, developed here, of double diffusion with absorption data gave a good separation of the species of section Melongena and section Oliganthes. However, S.giganteum, from section Torva, clustered in the centre of the section Oliganthes species, and S.violaceum joined the rest of the species in the dendrogram after the representatives of sections Melongena, Oliganthes and Torva had clustered at a higher level of similarity.

It is clear from the present work that the techniques of serology and zone electrophoresis should be applied at different taxonomic levels. Differences in molecular immunological reactivity seem to be insufficient to clarify relationships below the sectional level, and published serological work (see Grund and Jensen (1981), Fairbrothers and Petersen (1983), Jensen and Greven (1984), Lee and Fairbrothers (1978) and Hillebrand and Fairbrothers (1970) for example) has concentrated around the familial or order level. Cristofolini (1980) has suggested that immunological reactivity only directly involves 1-2% of the whole molecule, and then only its external surface. It follows that variation is more likely to be discernible at the higher levels of classification.

Meanwhile, zone electrophoresis shows variation below the species level. This may be taxonomically useful in a population study, but if species are to be compared, it is necessary to test the population variability and to exclude from the comparison any protein band which is not constant within the species. Furthermore, it is only in the comparison of a closely knit group that it is reasonable to assume that protein bands occupying the same position in a gel are homologous. Thus zone electrophoresis might be used in interspecific comparisons, perhaps to delimit sections, but it will be more valuable in a study of the taxonomy of populations or sympatric species.

If there are no taxonomic inferences to be drawn from the present study of seed proteins, it is at least possible to assess the value of further work with zone electrophoresis and serology. Zone electrophoresis seems to offer the ability to clarify species limits, and to suggest relationships between infraspecific taxa. This may be particularly useful in a study of the large, morphologically variable species aggregates such as S.incanum and S.anguivi whose infraspecific taxonomy remains confused. Studies at the sectional level are problematic as has been discussed, and the present work has shown the need for adequate sampling of the variation between and within species.

The bulk of the African species of Solanum fall into sections Oliganthes and Melongena and it seems that these

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may be insufficiently distinct to justify further serological study. In any case, the following problems need to be overcome before serology can be considered a worthwhile approach.

Firstly, it is usual that only one specimen per species (per higher taxon) is used, yet this takes no account of variation within the species (or higher taxon). Serology is not in some way better than other approaches to taxonomy that this should be permissible, but the technique would be laborious and expensive if an adequate sample were to be taken.

Secondly, more than one rabbit should be used to raise antiserum to each protein extract so that the variation in immunological response can be assessed. Jensen (1973) used two to four rabbits for the injections of the same antigenic material, but whether even this is adequate is not known.

Thirdly, with multiple-protein extracts the analysis of the data is complicated by ignorance of what is being measured : is the precipitate that is seen in one cross-reaction due to the same antibody-antigen complex as in another cross-reaction; and how often is the same character being counted in a numerical analysis? Single protein studies might reduce the uncertainty here.

Fourthly, Friday (1980) has noted that the correlation

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between immunological cross-reaction and the amino acid sequence is very approximate, and that problems with phylogenetic analysis of the data are such that only phenetic interpretation is possible.

Finally, the suitability of serology to taxonomy can be judged from published results. Cronquist (1980) has written that :

> "..... serology works when it works, and doesn't work when it doesn't. Serological reactions correlate with other features often enough so that they must be taken seriously by taxonomists, but they so often fail to correlate that they can never be taken as definitive."

If this is accepted, then it is difficult to see what gain in information is to be derived from serology.

APPENDIX TO CHAPTER 5

Listed below are the accessions of <u>Solanum</u> species which have been used for the experimental studies recorded in Chapter 5 of this thesis. The accession numbers are those used to catalogue the Solanaceae Collection at the University of Birmingham. The identities of those accessions which were grown in the course of the present studies were verified by reference to the herbarium of the Royal Botanic Gardens, Kew (K). For the accessions which were not grown, I have accepted the determinations currently used in the cataloguing system at Birmingham, most of which have been verified either by Dr. R. N. Lester or other experts who have visited the collections, for example during the 1976 Solanaceae Conference. Most of the accessions are represented at BIRM by voucher specimens.

Accession No.	Identity	Provenance
S.46	S.melongena	Thompson & Morgan, U.K.
S.48	S.anguivi	Madagascar, Tananarive.
S.50	S.incanum	Tanzania, Dar-es-Salaam,
S.51	S.seaforthianum	Zimbabwe, Sanyati Tribal Area.
S.96	S.capsicoides	Bot. Gdns. Glasgow, U.K.
S.101	S.linnaeanum	Bot. Gdns. Glasgow, U.K.
S.128	S.marginatum	Bot. Gdns., West Berlin, Germany.
S.133	S.macrocarpon	Bot. Gdns., Brussels, Belgium.
S.142	S.cinereum	R.B.G., Kew, U.K.

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Accession No.	Identity	Provenance
S.145	S.pyracanthum	R.B.G., Kew, U.K.
S.156	S.aethiopicum Gilo group	Univ. Bot. Gdns, Nijmegen, Holland.
S.202	S.cinereum	Australia, Pt. Augusta.
S.210	S.linnaeanum	Bot. Gdns., Adelaide, Australia.
S.214	S.capsicoides	Smith College Bot. Gdns., Mass., U.S.A.
S.225	S.aethiopicum Gilo group	Bot. Gdns., Nancy, France.
S.240	S.aethiopicum Aculeatum group	Univ. Montpelier Bot. Gdns., France.
S.241	S.melongena	Univ. Montpelier Bot. Gdns. France.
S.256	S.marginatum	Mexico, Michoacan State.
S.270	S.aethiopicum Gilo group	Nat. Hist. Museum, Paris, France.
S.279	S.aethiopicum Gilo group	Univ. Bot. Gdns., Strasbourg, France.
S.344	S.aethiopicum Aculeatum group	Bot. Gdns., Barcelona, Spain.
S.387	S.campanulatum	Australia, Kulnura, New South Wales.
S.395	S.aethiopicum Gilo group	Univ. Adelaide, Australia.
S.396	S.marginatum	Univ. Adelaide, Australia.
S.448	S.melongena	S. Dobie & Sons, Ltd. Chester, U.K.
S.641	S.atropurpureum	Bot. Gdns., Nijmegen, Holland.
S.657	S.ovigerum	Bot. Gdns., Dijon, France.

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Accession No.	Identity	Provenance
S.668	S.atropurpureum	Bot. Gdns., Coimbra, Portugal.
S.763	S.mauritianum	Univ. Bot. Gdns., Amsterdam, Holland.
S.773	S.campanulatum	Univ. of Adelaide. Australia.
S.839	S.torvum	Australia, Queensland.
S.857	S.anguivi	Uganda, East Mengo Dist.
S.859	S.incanum	Uganda, Kampala
S.871	S.anguivi	Bot. Gdns. Makerere, Uganda.
S.926	S.pyracanthum	Bot. Gdns., St. Jean Cap Ferrat, France.
S.927	S.tomentosum	Bot. Gdns., St. Jean Cap Ferrat, France.
S.964	S.anguivi	Bot. Dept., Univ. of Ghana, Ghana.
S.1040	S.tomentosum	Botswana, Kgalagadi Dist.
S.1065	S.viarum	Glaxo Ltd. (No. 187), India.
S.1155	S.tomentosum	Bot. Gdns., St. Jean Cap Ferrat, France.
S.1174	S.linnaeanum	Bot. Gdns., Pisa, Italy.
S.1181	S.pectinatum	Belize.
S.1206	S.aethiopicum Shum group	Bot. Gdns., Uppsala, Sweden.
S.1208	S.giganteum	Bot. Gdns., Adelaide, Australia.
S.1230	S.melongena	Bot. Gdns., Ibadan, Nigeria.

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Accession No.	Identity	Provenance
S.1234	S.aethiopicum Gilo group	Bot. Gdns., St. Jean Cap Ferrat, France.
S.1236	S.aethiopicum Gilo group	Bot Gdns., St. Jean Cap Ferrat, France.
S.1237	S.virginianum	Bot. Gdns., Lucknow, India.
S.1264	S.macrocarpon	
S.1267	S.aethiopicum Shum group	Bot. Gdns., Copenhagen, Denmark.
S.1268	S.aethiopicum Aculeatum group	Bot. Gdns., Copenhagen, Denmark.
S.1269	S.macrocarpon	Bot. Gdns., Copenhagen, Denmark.
S.1307	S.capsicoides	Bot. Gdns., St. Jean Cap Ferrat, France.
S.1331	S.aethiopicum Aculeatum group	N. I. Vavilov Inst. U.S.S.R.
S.1335	S.anguivi	Zimbabwe, Belingwe Dist.
S.1336	S.anguivi	Zimbabwe, Melsetter Dist.
S.1337	S.macrocarpon	Uganda, Buganda.
S.1338	S.anguivi	Uganda, Buganda.
S.1380	S.anguivi	Uganda, Kigezi Distr.
S.1381	S.aethiopicum Gilo group	Uganda, Buganda.
S.1382	S.virginianum	India.
S.1389	S.virginianum	Glaxo Ltd., India.
S.1395	S.aethiopicum Gilo group.	Ghana
S.1398	S.incanum	Zimbabwe, Harare.
S.1415	S.aethiopicum Shum group	W.A.R.I., Univ. Adelaide, Australia.

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Accession No.	Identity	Provenance
S.1417	S.virginianum	Forest Res. Inst., India.
S.1482	S.aethiopicum Gilo group	Ghana, Accra Market.
S.1485	S.aethiopicum Kumba group	Mali (Market).
S.1489	S.violaceum	I.A.R.I., New Delhi, India.
S.1513	S.anguivi	India, Maharashitra.
S.1554	S.incanum	India, Nilgiris.
S.1653	S.macrocarpon	Bot. Gdns., Eala, Zaire.
S.1681	S.mauritianum	South Africa, Natal.
S.1689	S.capense	South Africa, Transkei.
S.1690	S.rubetorum (= S.rigescens Auctt.)	South Africa, Transkei.
S.1695	S.rubetorum (= S.rigescens Auctt.)	South Africa, Transkei.
S.1696	S.rubetorum (= S.rigescens Auctt.)	South Africa, Cape Province.
S.1748	S.aethiopicum Gilo group	Nigeria, Benin Market
S.1749	S.aethiopicum Gilo group	Nigeria, Benin Market
S.1759	S.anguivi	Cameroun.
S.1762	S.mauritianum	East Africa Herbarium, Nairobi, Kenya.
S.1772	S.anguivi	
S.1773	S.anguivi	Zimbabwe, Umtali.
S.1774	S.renschii	Kenya.
S.1778	S.incanum	Tanzania, Dar-es-Salaam.
S.1780	S.incanum	Tanzania.
S.1793	S.incanum	N. E. Ethiopia.

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Accession No.	Identity	Provenance
S.1794	S.schimperianum	Ethiopia.
S.1820	S.capsicoides	Brazil, Rio de Janeiro.
S.1913	S.coccineum	Nat. Bot. Gdns., Kirstenbosch, South Africa.
S.1942	S.incanum	Java.
S.1944	S.kurzii	Java.
S.1951	S.violaceum	India.
S.1952	S.violaceum	Burma.
S.1954	S.anguivi	Ghana.
S.1961	S.incanum	Sri Lanka.
S.2000	S.aethiopicum Shum group	Nigeria.
S.2001	S.aethiopicum Shum group	Nigeria
S.2002	S.aethiopicum Shum group	Nigeria
S.2003	S.aethiopicum Shum group	Nigeria
S.2004	S.aethiopicum Shum group	Nigeria
S.2005	S.macrocarpon	Nigeria
S.2006	S.macrocarpon	Nigeria
S.2007	S.hastifolium	N. Yemen.
S.2011	S.anguivi	Tanzania.
S.2012	S.anguivi	Tanzania
S.2017	S.anguivi	Tanzania
S.2021	S.incanum	Kenya.
S.2026	S.incanum	Kenya.
S.2030	S.violaceum	Mauritius.

6. CONCLUDING DISCUSSION

The objective of the present study was an elucidation of
some of the many taxonomic problems found among the African
species of _Solanum_. To this end, the study has made use of
herbaria and libraries, as well as following some
experimental approaches. It was hoped at the outset that a
review of the African species, such as is presented in
Chapter 7, would provide a framework for further research.

In a taxonomic context, the genus _Solanum_ is notable for its
nomenclatural disarray. The historical background to this
was discussed in Chapter 2 of this thesis, and, as regards
the African species, much of the blame can be laid on the
'splitting' by the researchers in the early years of this
century. Given that workers at that time were studying only
a fraction of the specimens available in herbaria today, it
is alarming to contemplate the number of species names that
might have been published had more collections been
available. Even so, in recognising 161 species of _Solanum_
in Africa, Bitter (l.c.) listed over 400 names in the index.

It seems that a 20th century Bauhin is needed now to collate
the synonymy of species names within _Solanum_. However, the
size of the problem (5,000 or more names?), and the
intricacies of applying the International Code for Botanical
Nomenclature, are such that it would be unrealistic to
consider a single purge of the accumulated synonymy. Of

course, the sooner the nomenclature is stabilised the better, yet even a start by typification of all published species names would be a major undertaking. It is unavoidable, therefore, that nomenclatural changes will be made by instalment.

The nomenclatural problems in the genus are not confined to the species but pervade the higher infrageneric ranks too. The situation here was improved somewhat by D'Arcy's (1972) publication of the typification of the subdivisions of Solanum. This, at least, provided reference points for the names, even if the subgeneric and sectional limits are far from clear.

Chapter 3 of this thesis assessed the taxonomic characters available for the systematic interpretation of Solanum. Above the species level, very few characters have been found to be taxonomically useful : there seem to have been many instances of parallel evolution. The infrageneric groups tend, therefore, to be defined not on the basis of diagnostic characters, but on combinations of attributes unique to each taxon. The same applies at the species level too, where it causes particular problems to the taxonomist constructing a dichotomous key.

Without a satisfactory classification the value of phytogeographic studies is limited. The two approaches to phytogeography, based either on ecology or taxonomy, were

discussed in Chapter 4. It was argued there that for a real understanding of the phytogeography a synthesis of the two approaches is required. With an unreliable classification the taxonomic aspect of such a study is meaningless. Nevertheless, the ecological approach is important to the study of speciation. Furthermore, at the higher infrageneric ranks an appreciation of the ecology of species may identify homoplastic similarities, possibly evolved in response to analogous selection pressures.

Neither the pollination studies nor the protein comparisons described in Chapter 5 suggested any alterations to the existing classification. The artificial pollinations were notably unsuccessful, and would have yielded scant information in any field of study. As regards the application of crossability studies to taxonomy only limited conclusions can be drawn anyway, but some support for the pollination studies of other researchers (e.g. Pearce, 1975; Niakan, 1980) was implied by the present studies.

The protein comparisons by gel electrophoresis gave results which corresponded reasonably well with species delimitations. However, there was little indication of interspecific relationships. It seems, therefore, that the techniques of gel electrophoresis of seed proteins are best applied to assessing relationships below the species level.

Conversely, from the present studies and a review of the

literature, serology gives its best results in the
resolution of taxonomic problems at or above the generic
level. Regrettably, neither technique of protein comparison
seems suitable for systematic studies at the supra-specific,
sectional levels.

As a genus, Solanum is an unsatisfactory, heterogeneous
grouping. While a member of the genus is usually easy to
recognise as a Solanum, it is a particularly difficult genus
to define. An overall perception of a plant specimen may
tell the observer that it is a Solanum, yet there are no
good diagnostic characters which reliably identify all the
species with the genus. This situation is attributable in
part to the diversity within the genus, and in part to the
unclear distinction between Solanum and other genera, in
particular Lycopersicon, Cyphomandra and Lycianthes.

Of course, in taxonomic theory the rank of genus cannot be
defined, and therefore it is possible to argue that the
limits of any genus should be expanded or contracted.
However, in practice, while the systematic history of a
genus may be agglomerative, with new species having been
added as they were discovered, at some point an analytical,
divisive approach is applied, and the limits of the genus
are circumscribed. In the case of Solanum, I know of no
post-Linnaean attempts at an analytical approach.

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There are very few characters that describe _Solanum_ in general. In fact only one character, that of the anthers opening by apical pores, is used often as diagnostic. Yet even this is not a good character. In subgenus _Lyciosolanum_ and some species of subgenus _Solanum_ the anthers may open initially at the apex, but the pore widens basipetally to form a longitudinal slit. The diversity within the genus is such that it is not possible, at present, to write a description which simultaneously includes all _Solanum_ species while excluding _Cyphomandra_, _Lycopersicon_ and _Lycianthes_.

If _Solanum_ is so difficult to define then it may be that it should be split into groups of relative homogeneity. Certainly, evidence is accumulating that might justify such an action. Firstly, it has been shown that gametophytic self-incompatibility in _Solanum_ is largely restricted to species of subgenus _Potatoe_, but is also found in the genus _Lycopersicon_ (Whalen and Anderson, 1981). Secondly, as discussed in Chapter 3 of the present thesis, pinnate leaves are a feature of subgenus _Potatoe_ (including section _Nemorense_ Child) not found elsewhere in the genus. They are, however, characteristic of _Lycopersicon_. Thirdly, only the 25L steric series of the spirosolane steroidal alkaloids occur in subgenus _Potatoe_, while the 25D series are characteristic of the other subgenera (see Chapter 3). Thus, a case emerges for separating subgenus _Potatoe_ from the rest of _Solanum_, and perhaps even combining it with

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<u>Lycopersicon.</u>

Looking further at the genus, the stellate hairs, the attenuate, truly poricidal anthers, the prickles and the absence of stone cells in the fruits all suggest that subgenus <u>Leptostemonum</u> could be separated from the other subgenera. The protein sequencing work of Martin, discussed here in Chapter 5, reinforces this separation. Whether subgenus <u>Brevantherum</u> should be kept with <u>Leptostemonum</u> or with the rest of the genus would need further research.

It was noted above that the limits of any genus are arguable. To some extent cladistics would reduce this problem by the recognition and rejection of paraphyletic groups. However, a cladistic interpretation of <u>Solanum</u> is not imminent. Furthermore, although evidence may suggest that the genus <u>Solanum</u> should be divided, such a move would be most unwelcome for the nomenclatural chaos that it would bring. The subgenera <u>Leptostemonum</u> and <u>Potatoe</u> may be likely candidates for separation, yet both contain species of economic importance (e.g. <u>S.melongena</u> and <u>S.tuberosum</u>, respectively). It could therefore be argued that the name <u>Solanum</u> should be conserved for either taxon, but the type species of the genus <u>S.nigrum</u> is in subgenus <u>Solanum</u>.

A further barrier to splitting the genus is the ambiguity of the infrageneric classification; for example, the sections

Aculeigerum Seithe and Nemorense Child are placed in subgenus Leptostemonum by some authors (e.g. Whalen, 1984), while others have argued that they are better placed in subgenus Potatoe (e.g. Child, 1983). The presence of prickles in the species suggests the former placement, while the plurifoliate sympodia, pinnate leaves and simple hairs are evidence for the latter.

For the African species the sectional arrangement used for Chapter 7 of the present thesis is much the same as that developed by Bitter (1913, 1917, 1921 and 1923). Some alterations have been made here, others are suggested in the text of the survey; it would be premature to make further changes on the basis of the evidence so far.

Under the present arrangement of the species in Africa the autochthonous species fall into four subgenera, namely Lyciosolanum, Solanum, Potatoe, and Leptostemonum. Lyciosolanum is monotypic and there is no obvious species group elsewhere in the genus to which it might be associated. In subgenus Solanum I have accepted 23 species in six sections. Apart from section Solanum, all the sections are small or monotypic. Their interrelationships are unclear. There are no obvious associations between the sections that might lead to combination of two or more sections under one name.

I have followed D'Arcy (1972) in placing section Normania

from Macaronesia in subgenus _Potatoe_. There are no other native species of the subgenus in Africa or its neighbouring islands. Section _Normania_ has a distinctive floral morphology, and the section fits uncomfortably in subgenus _Potatoe_. It may be that it is best treated as a separate subgenus.

In subgenus _Leptostemonum_ I have accepted nine sections. This differs somewhat from Bitter's arrangement in that I have included sections _Anisantherum_ and _Somalanum_ here (which Bitter placed in subgenus _Eusolanum_), as well as the recently described section _Croatianum_ D'Arcy & Keating. While some of the African sections in this subgenus appear to be natural groupings, most are controversial.

Section _Torva_, as recognised by Bitter, comprises species from the Americas as well as Africa. The African elements of this section, with entire leaves and red fruits, should be separated from the New World species characterised by lobed leaves and yellow or brown fruits. The group of African species might be divided further on the basis of the sympodia which are either plurifoliate or difoliate. However, as has been noted elsewhere in this thesis, there has evidently been parallel evolution in the branching patterns of _Solanum_ species. Dividing the section on sympodia alone might, therefore, be rash, but the defoliate species tend also to have smaller inflorescences and, sometimes, tetramerous flowers. These species bear some

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resemblance to the S.zanziharense group in section Oliganthes, in which tetramerous flowers are also found. Furthermore the ovaries and styles in section Torva and the S.zanziharense group of species hear glandular hairs, whereas the gynoecia in nearly all other species in section Oliganthes hear stellate hairs. This possible relationship needs to he studied further.

Curiously, there is also a striking similarity between the difoliate African species of section Torva and the Oceanian S.dunalianum group of species. In particular, tetramerous flowers are found in both groups of species. As yet, this relationship has not been studied in detail.

Section Anisantherum is represented in Africa by S.somalense. Its stellate hairs clearly place it in subgenus Leptostemonum. There is some similarity to the African species of section Torva, hut the unequal anthers in S.somalense are distinctive. Dimorphic anthers are also found in the Indian species S.puhescens, which may he included in section Anisantherum, as well as the Macaronesian species of section Nycterium and the meso-American section Androceras. The possibility of a relationship between these species needs further study.

Section Somalanum was also placed in subgenus Eusolanum by Bitter, but again its stellate hairs are characteristic of subgenus Leptostemonum. It is not a clearly defined section

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and might well be combined with section <u>Oliganthes</u>. Section <u>Croatianum</u> too is poorly defined and rather heterogeneous. Its immediate affinity, however, is to section <u>Torva</u>.

For section <u>Oliganthes</u> I have recognised 35 species in Africa and the neighbouring islands. There are a few more species from Asia which belong here in the current understanding of the section, but the Australian and American species included by some authors should be excluded. While the African species of section <u>Oliganthes</u> have an overall similarity it is a difficult section to define. Although both Eitter (1923) and Whalen (1984) have attempted to recognise species groups within the section these are far from clear, and it is not obvious how the section might be split into discontinuous groups. The possible relationship between the <u>S.zanzibarense</u> group of species and parts of section <u>Torva</u> was noted above.

Section <u>Ischyracanthum</u> seems to be andromonoecious and the purple flowers and yellow fruits are reminiscent of section <u>Melongena</u>. However, the tough pericarp of the fruits is not seen in section <u>Melongena</u>.

Andromonoecy and large fleshy yellow fruits are characteristic of the section <u>Melongena</u>, which includes species with a surprisingly varied morphology. The diversity is such that it is tempting to suggest that the diagnostic characters might be the result of convergent

evolution in several phyletic lines.

Finally, the sections Monodolichopus and Nycterium are two distinctive sections. The former is confined to the dry country of North East Africa and includes the morphologically plastic S.coagulans. The section has no obvious close relatives. Section Nycterium meanwhile has a disjunct distribution from meso-America to Macaronesia, and, as noted above, shows similarities to the American section Androceras and the African/Asian section Anisantherum.

This brief review of the present state of the classification highlignts a few areas which merit further study. The current classification may appear to impose a degree of order on the many species, but it is far from satisfactory. If the principal goals of systematics are predictivity and a reflection of phylogeny then, clearly, the present classification of Solanum in Africa is particularly rudimentary. To progress towards these goals a critical appraisal of the known characters is required, and the search for further, taxonomically useful characters must be continued.

The present classification is almost entirely based on morphology. Many of the attributes which might be used taxonomically are to be found in several supposedly distinct parts of the genus. Clearly, it is important to avoid placing too much emphasis on one or two striking characters.

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However, a suite of characters is not necessarily stronger evidence of a shared phylogeny : ecological selection pressures may alter many different attributes of the phenotype. Thus, the joint possession in _Solanum_ of plurifoliate sympodia, large showy inflorescences and large pilose leaves is often characteristic of forest _Solanum_ species. Climbing or scrambling species may lack the pilose indumentum of the leaves but bear recurved prickles. Among the African species, those growing in a shaded environment tend to have white flowers and red berries, while those of open, sunny habitats have smaller leaves, mauve flowers and orange or yellow berries. If the species grows in arid conditions the indumentum may be very dense. The biological significance of these characters is a side issue, and should not enter into the taxonomic reasoning.

One approach to the study of the characters might be to attempt a classification of the species of _Solanum_ based on ecology. Characters of the phenotype which are congruent with the ecological classification might then be used with caution in supra-specific systematic studies as being possibly homoplastic. The characters discussed above would be expected examples.

A possible next stage in the reappraisal of the characters might be phylogenetic analysis (cladistics - Wiley (1981), for example, has reviewed the methodology). The attraction

of this approach lies in the logically sound manner in which
character homology is assessed, and in the derivation of
phylogenetic classifications with an inherent predictivity.
In theory, therefore, the principal goals of taxonomy should
be achieved.

If a cladistic approach is to be applied to the genus
Solanum then it is important to identify in advance species
groups which are natural. Without these, the whole genus
must be studied as one clade and that assumption is probably
suspect. Whalen's (1984) conspectus of subgenus
Leptostemonum has sought to identify such natural groups,
and within the subgenus each group can now be revised in
turn while the inter-relationships of the groups themselves
can also be studied.

Phylogenetic analysis results in a classification which is,
in effect, an hypothesis. The classification is a statement
based on the data available at the time of analysis. It can
be tested by adding data in the form of characters from
other sources. In the case of the African Solanum species
an initial cladistic classification would be based on
morphological data. Subsequently, this might be tested, and
perhaps amended, by anatomical, palynological, biochemical
or any other set of taxonomic data.

Whether a cladistic approach, or a phenetic approach, or an
intuitive approach is adopted for a revision of the African

<u>Solanum</u> species, there are large bodies of taxonomic data which have so far been ignored. It is axiomatic that a systematic study should draw on all available sources of data. A review of characters was presented in Chapter 3 of this thesis; certain fields for further study can be suggested.

Firstly, morphology can be studied in more detail. Secondly, variations in the anatomy of the African <u>Solanum</u> species are so far largely unknown : Lester and Durrands (1963) have made a start by studying the seed surface structures in some species with encouraging results; leaf venation appears to have some taxonomic value in <u>Solanum</u>. Thirdly, palynology of the species should be reviewed. A brief study was undertaken for the present thesis, and the general similarity of pollen was confirmed, but detailed research may yet reveal characters of systematic value. Fourthly, chemistry offers a potentially enormous array of data for systematic interpretation. The flavonoids, steroids, tannins and non-protein amino acids were highlighted in Chapter 3 of this thesis as meriting further study. Certainly, many other secondary products may well prove useful as well. The value of protein comparisons has already been discussed.

A taxonomic survey of <u>Solanum</u> in Africa is presented in the next and final chapter. It incorporates the findings of research described in this thesis. It is therefore a

conclusion, but it is also intended as a starting point. It provides a more modern and more accessible treatment of Bitter's _Solana africana_ as a framework for further research.

7. TAXONOMIC SURVEY OF SOLANUM IN AFRICA

The survey presented here is a review of all the species of Solanum known in Africa. A full taxonomic revision would necessitate consultation of many herbaria, rediscovery of all type specimens and also many decisions on synonymy. Complete and thorough studies of these and other basic taxonomic procedures would take many years. Rather than make premature taxonomic decisions I have aimed at providing an account of the Solanum species to be found in Africa, as a starting point for further research. My views on the taxonomy, as well as those of others, are expressed in the text. The species groupings are largely those used by Bitter (1913, 1917, 1921, 1923), but further research may well alter the infrageneric taxonomy.

References: Only the original place of publication of a name is cited here. Listing further references would take up much space, and the literature pertinent to the study of Solanum has been reviewed in Chapter 2 of the present thesis. Where I disagree with an author's interpretation of a species, this is usually mentioned in the notes on the species.

Typification: Unless otherwise specified, 'type' here refers to type material, without judgment as as to whether the specimen is a holo-, iso-, lecto- or other sort of type. Microfiches have been cited according to the system proposed

by Hepper (1968).

Synonymy: I have treated the synonymy informally : my views
of possible synonymy are given in the notes without setting
out a list of synonyms in the formal manner. This avoids
premature judgment in a genus already replete with published
errors of species delimitation and synonymy.

Herbaria: Abbreviations for herbaria follow Holmgren <u>et al.</u>
(1981). The publications of Lanjouw and Stafleu (1954),
Chaudhri <u>et al.</u> (1972) and Vegter (1976) have been useful
for tracing the most likely locations of type material.
Where the location of a specimen is uncertain a '?' is
used. '!' indicates that I have studied the specimen cited.
'+' is used to denote that the specimen has been lost or
destroyed. Most of the Berlin (B) herbarium was destroyed
in the Second World War and many of holotypes of Dammer and
Bitter were lost with it. Leeuwenberg (1965) has listed the
herbaria with istotype material of holotypes lost in Berlin.

Specimen citation: To save space no specimens have been
cited except where relevant to discussion or required to
identify an un-named species.

Classification: The classification of Bitter (1913, 1917,
1921, 1923) has been followed except where persuasive
evidence has led to revision of the species groupings. The
nomenclature of subgenera and sections has been corrected

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according to D'Arcy (1972). Comments on the validity of the sections are expressed in the notes.

Solanum Linnaeus, Sp. pl. ed. 1 184(1753); Gen. Pl. 85 (1754). Lectotype species: _S.nigrum_ L. (_fide_ Hitchcock and Green, 1929).

Characters of the African species of **Solanum** have been discussed in detail in Chapter 3 of the present thesis. The distribution of the genus, both worldwide and in Africa, has been described in Chapter 4.

Key to the sections represented in Africa :

1   Indumentum of simple, acute or gland tipped hairs and/or branched hairs; unarmed (except for section _Aculeigerum_ with small recurved prickles); anthers mostly stout, rarely tapering, opening by subapical introrse pores becoming longitudinal slits

.... 2.

1'   Indumentum of simple to stellate, multangular or echinoid hairs; usually armed with prickles and sometimes bristles; anthers usually lanceolate, tapering towards the apices (except for section _Brevantherum_ which has stout anthers) opening with

small terminal pores which only rarely become introrse slits
.... 14.

2   Inflorescence simple, few-flowered, compressed in the leaf axils of condensed lateral shoots or in branch forks of the longer shoots; corolla broadly companulate with a long (for Solanum) tube; filaments at least as long as the anthers; S. Africa

.... Subgenus Lyciosolanum (p.261)

2'   Inflorescence diverse, usually leaf remote or opposite; flowers stellate or campanulate; filaments less than half the length of the anthers

.... 3.

3   Erect herbs, rarely woody

.... 4.

3'   Woody climbers, creepers or shrubs

.... 5

4   Leaves simple, sinuate or shallowly lobed

.... Section 6. Solanum (p.287)

4'   Leaves imparipinate; pedicels articulate above the base

.... Section 7. Petota (p.313)

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5   Plants armed with small, brown, recurved prickles;
        cultivated
                        .... Section 13. <u>Aculeigerum</u> (p.335)

5'   Plants unarmed
                        .... 6.

6   Creepers, climbers, rarely erect; inflorescence
        terminal or towards the ends of branches; cymes often
        compound with several to many flowers
                        .... 7.

6'   Erect shrubs, inflorescence axillary, leaf opposed or
        remote from the leaves, few-flowered
                        .... 12.

7   Plants with haptotropic petioles if leaves entire (or
        with basal lobes), or leaves pinnately lobed and
        petioles not haptotropic
                        .... Section 9. <u>Jasminosolanum</u> (p.318)

7'   Petioles not haptotropic, leaves entire
                        .... 8.

8   Often somewhat succulent; stems angular; leaves
        decurrent onto flattened petiole; S. Africa
                        .... Section 1. <u>Africanum</u> (p.264)

8'   Not as above

         .... 9.

9   Inflorescence a large, lax, terminal cymose panicle

         .... Section 5. <u>Benderianum</u> (p.283)

9'   Inflorescence not paniculate, or if so with flowers

      congested at the apices of the rachides

         .... 10.

10   Inflorescence shortly pedunculate or sessile; calyx

      deeply lobed; corolla 1.8-3.0cm diam.

         .... Section 2. <u>Macronesiotes</u> (p.267)

10'   Inflorescence pedunculate; calyx cupulate; corolla less

      than 1.8cm diam.

         .... 11.

11   Leaves coriaceous, very glossy; Madagascar

         .... Section 3. <u>Lemurisolanum</u> (p.271)

11'   Leaves membranaceous; Africa

         .... Section 4. <u>Afrosolanum</u> (p.273)

12   Anthers markedly unequal, one much shorter than the

      other four; Macaronesia

         .... Section 10. <u>Normania</u> (p.321)

12' Anthers equal; cultivated or naturalised species

.... 13.

13 Hairs two-celled, basal cell thicker and longer than tapering apical cell; inflorescence of 10-12 flowers; peduncle 3-4cm long; pedicels pubescent; cultivated for the ellipsoid, or ovoid, fruit up to 15cm long

.... Section 8. Basarthrum (p.316)

13' Hairs not as above; inflorescence of up to 5 flowers; peduncle up to 0.5cm long or absent; pedicels glabrous; fruits red, ornamental, 1-2cm diam.

.... Section 12. Pseudocapsicum (p.331)

14 Unarmed, large shrubs with branching pattern of furcate, plurifoliate sympodia; leaves entire; indumentum of stellate or dendritic hairs; inflorescence terminal at anthesis, dichotomously branched, each of several branches terminating in a many-flowered cyme

.... Section 11. Brevantherum (p.325)

14' Plant not as above

.... 15.

15 Flowers hermaphrodite, corolla stellate; fruits red or orange, juicy with a thin pericarp (except in

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S.aethiopicum cvs) seeds pale brown

.... 16.

15' Inflorescence andromonoecious or not, corolla stellate or pentagonal; fruits yellow, vermillion or brown(or dark purple) with a thick or tough pericarp, fleshy or dry; seeds pale brown, dark brown or black

.... 22.

16 Anthers obviously unequal,

.... 17.

16' Anthers equal or sub-equal

.... 18.

17 Erect or procumbent shrubs, often armed; Macaronesia

.... Section 22. Nycterium (p.464)

17' Unarmed shrubs; N. E. Africa, Arabia

.... Section 15. Anisantherum (p.360)

18 Indumentum of porrect-stellate hairs with lateral rays somewhat fused, or peltate hairs; S. W. Madagascar

.... Section 17. Croatianum (p.368)

18' Lateral rays of stellate indumentum not fused; generally continental Africa, some species represented

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in mesic parts of Madagascar

.... 19.

19   Shrubs viscid-villous with simple glandular hairs; leaves pinnatifid; corolla 4cm diam; fruit enclosed by enlarged spiny calyx lobes

.... Section 25. Cryptocarpum (p.472)

19'   Plants not as above

.... 20.

20   Leaves entire or repand, 7 - 30cm long; inflorescence sub-fasciculate or corymbose, many-flowered

.... Section 14. Torva (p.337)

20'   Leaves entire or quite deeply lobed, usually less than 10cm long; flowers solitary, paired or few and generally with a single rachis

.... 21.

21   Unarmed shrubs, may be drought-deciduous; flowers solitary or paired or terminal

.... Section 16. Somalanum (p.363)

21'   Shrubs usually armed, not drought-deciduous; few-flowered

.... Section 18. Oliganthes (p.372)

22   Spreading shrubs or herbs; stamens unequal

.... 23.

22' Shrubs, usually erect; stamens equal

.... 24.

23   Flowers blue-violet; stamen filaments unequal, anthers

sub-equal; N. E. Africa, Arabia

.... Section 21. Monodolichopus (p.458)

23' Flowers yellow; stamen filaments equal, anthers

markedly unequal; naturalised in S. Africa

.... Section 24. Androceras (p.470)

24   Berries stellate-pubescent; cultivated or naturalised

in N. E. Tanzania

.... Section 27. Lasiocarpa (p.484)

24' Berries without trichomes (sometimes only when fully

mature)

.... 25.

25   Pericarp of berries usually thickened and fleshy or

bony, fruits 1-6cm diameter (or more in cultivated

varieties)

.... 26.

25' Pericarp tough but not thickened, fruits usually less

than 1.5cm diameter

.... 28.

26   Trichomes simple, often gland-tipped; armed with usually acicular prickles although some compressed recurved prickles may also be present; flowers stellate

.... Section 26. Acanthophora (p.474)

26' Trichomes stellate; prickles usually broad-based or absent; flowers stellate or pentagonal

.... 27.

27   Medium to large shrubs or bushes; with recurved prickles on the stem and straight prickles on the leaves; berry hard and dry at maturity

.... Section 19. Ischyracanthum (p.417)

27' Erect shrubs, usually with either straight or recurved prickles, rarely both types on the same plant; pericarp fleshy and mucilaginous at maturity

.... Section 20. Melongena (p.420)

28   Large shrubs to 3m or more; leaves large (17cm or longer) angular or deeply lobed; inflorescence a much branched corymb, of 30-50 or more flowers, corolla white

.... Section 14. Torva (p.337)

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28' Shrubs to 60cm tall, often armed with red acicular
     prickles; leaves 1-10cm long, entire or sinuate,
     pubescent with porrect stellate hairs; inflorescence 3-
     6-flowered, corolla blue (rarely white)

                .... Section 23. <u>Leprophora</u> (p.468)

`

Subgenus 1 **Lyciosolanum** Bitter in Bot. Jb. 54 : 425 (1917).
Type species: S.guineense Linn.

Unarmed shrub with ovate to elliptic leaves; inflorescence sessile in leaf axils of short shoots; flowers pedicellate violet; filaments up to 5mm long, longer than in all other African Solanum species.

Notes: A single species confined to the Cape area of South Africa with no close relatives among African Solanum species.

1. **Solanum guineense** Linnaeus, Sp. Pl.: 184 (1753); Heine in Kew Bull. 14 : 245-247 (1960). Lectotype (fide Wijnands, 1983) : 246.4 LINN! (IDC microf. 136 : III.1).

Small shrub, almost glabrous, up to 1m high. Leaves ovate to elliptic, 3.0-7.0 x 1.5-4.0cm, entire, decurrent on to petiole, sometimes succulent. Flowers on slender pedicels usually crowded on short branches; corolla violet, stellate, up to 2cm diam; filaments up to 5mm long, anthers opening by a terminal pore which becomes a longitudinal slit. Fruit yellow, 0.8-1.5cm diam, globose, without sclerotic granules.

Distribution: Southern part of the Cape Province of South Africa.

Notes: A characteristic species which has no obvious relatives amongst African Solanum species. Heine (1960) cleared the confusion which previously surrounded the application of the name S.guineense.

Bitter (1917, p. 421) thought that S.guineense deviated sufficiently from other Solanum species to merit its own subgenus whereas D'Arcy (1972) remarked that its distinctiveness at the subgeneric level was not apparent to him, and perhaps it should be considered a section of subgenus Solanum. I have found no group in the genus with which it might be associated, and therefore I have accepted Bitter's placement.

Bitter presumably named the subgenus from the similarity of this species to the genus Lycium, a cosmopolitan genus with several representatives in Africa. The similarities are striking in habit, leaf shape (but not size) and in arrangement of the flowers; but the flowers themselves, though having a longer tube than most Solanums, are campanulate with deeply divided corolla lobes, whereas Lycium flowers are tubular.

Subgenus 2 **Solanum** sens. D'Arcy in Ann. Mo. bot. Gdn. 59(2): 262-278 (1972). Type species: S.nigrum L.

Annual or perennial herbs or shrubs, unarmed, glabrous to pubescent with simple or branched (never stellate) hairs; leaves simple, entire to dentate, membranaceous or coriaceous; inflorescence lateral or terminal, peduncles branched or unbranched, flowers generally small, white to violet, stellate, anthers stout; fruits red, orange, yellow or black, juicy, not more than 1.5cm diam.

Notes: A subgenus composed of sections which share the attributes of simple pubescence, absence of prickles, simple leaves and similar flowers. These similarities are superficial and further study will no doubt result in the reorganization of this subgenus. In particular the African sections could probably be combined and they seem to show greater affinity to section Dulcamara (in subgenus Potatoe (G. Don.) D'Arcy) than they do to section Solanum.

The subgenus is represented in Africa by the sections Africanum, Macronesiotes, Lemurisolanum, Afrosolanum, Benderianum, and Solanum.

Section 1 **Africanum**.

(= section <u>Quadrangulare</u> Bitter in Bot. Jh. 54: 428 (1917)). Type species: <u>S.africanum</u> Miller.

Climbing shrub with young stems quadrangular; leaves often succulent, decurrent on to petiole; inflorescence terminal, paniculate; flowers violet, stellate; filaments up to 2mm long.

<u>Notes</u>: A single species restricted to the coast of South Africa. Bitter (l.c.) named the section in agreement with the constituent species, <u>S.quadrangulare</u>. That species should be known as <u>S.africanum</u> Miller and the name of the section therefore, is altered to conform with this name of the species.

2. **Solanum africanum** <u>Miller</u>, Gard. dict. ed. 8, art. Solanum No. 26 (1768), non Dunal, Hist. nat. Solanum 238 (1813). Type: Cape, cult. Hort. Eltham., 1726, <u>Dillenius</u> (OXF, Solanum dulcamarum Africanum, foliis crassis hirsutis. Dillenius Hort. Eltham. t. 273 f.352 (1732)).

A climbing unarmed semi-succulent shrub, up to 3m high. Stems quadrangular when young, sometimes pilose. Leaves lanceolate to ovate (sometimes obovate), tapering into the petiole, pilose or glabrous, 1.5-6.0 x 1.0-5.0cm; the lower leaves often lobed or hastate. Inflorescence terminal, paniculate often with 30+ flowers; flowers violet, 1.2-1.8cm

diam; filaments up to 2mm long, anthers dehiscing by longitudinal slits. Fruits black, spherical 1.2-1.5cm diam with sclerotic granules.

Distribution: South Africa; on the coasts of Cape Province, Transkei and Natal.

Notes: When Miller described S.africanum in the eighth edition of his Gardener's Dictionary (1768), he cited a polynomial and plate from the Hortus Elthamensis of Dillenius (p. 365 t. 273 (1732). I have been unable to find a specimen of S.africanum in Miller's herbarium with the phrase-name, but the plate in Hort. Eltham is a clear depiction of the species hitherto known as S.quadrangulare Thunb. ex Linn.f. A change of name is therefore necessary since Miller's valid publication of S.africanum antedates the description of S.quadrangulare in the Supplementum Plantarum of the younger Linnaeus.

Several other taxa are typified by the Dillenian description and are therefore automatically synonyms of S.africanum. Bitter (1917) included four Dunal species as synonyms of this species. I have seen the types of three of them on microfiche and agree with the inclusion of S.exasperatum and S.geniculatum under S.africanum, but not of S.longipes which appears to be material from section Afrosolanum. Some confusion is evident in S.longipes since Dunal cited Drege as the collector of the type, yet there is no mention of

this specimen in Drege's account (Drege, 1843) of the plants that he collected in South Africa. I have not seen any material of the fourth species of Dunal to be included by Bitter, namely S.a_erum, but from the description it seems likely to be a synonym of S.africanum. The type specimen in Boissier's herbarium in Paris must be seen in order to confirm this.

Section 2 **Macronesiotes** Bitter in Bot. Jb. 54: 432 (1917).

Type species: <u>S.imamense</u> Dunal (<u>fide</u> Seithe, 1962).

Unarmed shrubs, glabrous or tomentose: leaves sometimes crowded on short branches, ovate, lanceolate or elliptic, entire, membranaceous or coriaceous; inflorescence (always?) terminal, corymbose and up to 20-flowered, or sub-solitary; calyx deeply lobed; corolla violet, stellate; anthers with round apical pores with a definite lip; fruits not seen.

<u>Notes</u>: In this section Bitter (l.c.) placed three poorly known species which are endemic to the Madagascan forests. Bitter saw less affinity between this section and section <u>Afrosolanum</u> than between section <u>Lemurisolanum</u> and section <u>Afrosolanum</u>, and contemplated the possibility of its relationship to <u>S.guineense</u> in subgenus <u>Lyciosolanum</u>. There is insufficient material to allow further comments on the relationships of section <u>Macronesiotes</u> except that it seems to me that <u>S.guineense</u> is quite distinct.

Key to species:

    Leaves congested at the ends of branches, ovate, hairy, membranaceous, apices acute, bases rounded; inflorescence corymbose with up to 20 flowers

          .... 3 <u>S.imamense</u>

    Leaves arranged alternately along branches with

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internodes at least 1cm long, elliptic, glabrous
(at least above), subcoriaceous, apices acuminate,
bases attenuate; inflorescence 2-3-flowered

.... 4 S.humblotii

Leaves congested at the ends of branches,
lanceolate, glabrous, shiny, coriaceous, apices
obtuse, bases attenuate; flowers solitary

.... 5 S.truncicolum

3. **Solanum imamense** Dunal in DC., Prodr. 13(1): 85 (1852).
Type: Madagascar, Bojer s.n. (G-DC S.rupicolum Bojer mss.
1839 IDC microf.! 2068:I.1).

Unarmed shrub, with dense tomentum of branched hairs on the
young shoots. Leaves rather crowded on short branches,
ovate, apices acute, bases rounded, 4-8 x 2.5-4cm, tomentose
with branched hairs. Inflorescence terminating short leafy
branches, corymbose, up to 20-flowered, tomentose; calyx
deeply lobed, campanulate-stellate; corolla stellate,
violet, up to 2.75cm diam; filaments up to 2mm long, anthers
5mm long; style 11mm long. Fruit not seen.

Distribution: Central Madagascar.

var. **grandiflorum** Dunal in DC., Prodr. 13(1): 85 (1852).
Type: Madagascar, Bojer s.n. (G-DC, S.pentapetaloides
Bojer mss. 1833 IDC microf.! 2068:I.2).

Leaves smaller, 4.25 x 2.75cm. Flowers 3.75cm diam, filaments 2.5-3mm long, anthers 6mm long, style 15mm long.

Notes: The arrangement of the leaves in this species is reminiscent of that in S.guineense; however the differences, particularly in inflorescence and floral characters, are sufficient to distinguish them easily.

Two specimens at Kew are possible isotypes of this species and its variety. The one sheet is almost certainly a Bojer collection (the var. grandiflorum) whilst the other is more doubtful. Both correspond well with the holotypes in G-DC which I have seen on microfiche, but they cannot be confirmed as isotypes as there are no collection numbers.

4. **Solanum humblotii** Dammer in Bot. Jb. 38: 184 (1906). Type: Madagascar, Humblot 509 (K!).

Climbing shrub, almost completely glabrous. Leaves elliptic, acuminate, sub-coriaceous, shiny, 3.5-8.0 x 1.5-3.5cm. Inflorescence terminal, 2-3 flowered; calyx deeply lobed; corolla stellate, up to 2.0cm diam; filaments 1.5mm long, anthers 4-4.5mm long; style 8.5mm long. Fruit not seen.

Distribution: Madagascar.

Notes: A species only known from the type collection.

Vegetatively it appears to have a greater affinity to section Lemurisolanum than to S.imamense; however, it lacks the terminal panicle with numerous flowers common to that section.

5. **Solanum truncicolum** **Bitter** in Bot. Jb. 54: 435 (1917). Type: Madagascar, South Betsileo, Hildebrandt 3954 (K!).

Low shrub, most parts glabrous, lower branches and stem rather gnarled. Leaves congested on short branches, lanceolate, small, 1.5-3.0 x 0.7-1.0cm, coriaceous, shiny, apex obtuse. Flowers terminal, solitary, on a long pedicel; calyx deeply lobed; corolla stellate up to 1.8cm diam, violet; filaments 0.75mm long, anthers 5.0-5.5mm long; style up to 10mm long. Fruit not seen.

Distribution: Madagascar.

Notes: A species only known from the type specimen which, according to the collection data, was found growing on a mossy trunk. It has a rather wizened appearance, and it is possibly a stunted form of S.imamense Dunal.

Section 3 **Lemurisolanum** Bitter in Bot. Jb. 54: 436 (1917).

Type species: S.madagascariense Dunal.

Unarmed shrubs; leaves glabrous, coriaceous, shiny, inflorescence paniculate with numerous flowers; calyx cupulate; corolla stellate; fruit not seen.

Notes: Bitter placed three Madagascan species in this section. For the present thesis I have included those three species under one name, S.madagascariense Dunal, and I doubt whether it is necessary to maintain a section for the single species.

6. **Solanum madagascariense** Dunal in DC., Prodr. 13(1): 99 (1852). Type: Madagascar, collector unknown, herb. Lambert and G-DC (G-DC IDC microf.! 2069:I.3).

Climbing(?) shrub. Leaves oblong, elliptic or obovate, entire, often acuminate, 4.0-8.0 x 2.0-4.0cm, glabrous, coriaceous, very glossy, with secondary veins looping 2-3mm within the margin. Inflorescence a lax terminal panicle with 30-100 or more flowers; calyx cupulate; corolla violet, stellate, up to 2cm diam, lobes reflexed; filaments 1.5mm long, anthers 2.5mm long; stigma exerted by up to 5mm. Fruit not seen.

Distribution: Madagascar.

var. **apocynifolium** stat. nov. (= S.apocynifoliur Laker).

Liffers by having dense pale-brown branched hairs on the stem and inflorescence, and occasionally by the presence of two small leaves in the leaf axils.

Notes: Bitter accepted three species for this section, namely S.apocynifolium Baker, S.madagascariense Lunal and S.nitens Baker. They seem to me to be synonymous and I have placed them under the earliest name, separating S.apocynifolium as a variety to cover the tomentose material.

S.clerodendroides Hutch. and Dalziel was described from a specimen which according to its label (Talbot 3211 at K) was collected in Eket, Nigeria. This material is certainly S.madagascariense which is endemic to Madagascar, and the confusion must be the result of a misplaced label.

The species is typical of rain forest shrubs having deep green sclerophyllous leaves with acuminate apices, entire margins and glabrous, shiny surfaces.

Section 4 **Afrosolanum** <u>Bitter</u> in Bot. Jh. 54: 440-487 (1917).
Type species: <u>S.terminale</u> Forsskal.

Erect or climbing shrubs, unarmed, glabrescent or with
simple or branched hairs; leaves entire, membranaceous or
subcoriaceous; inflorescence terminal at least at first,
often many flowered, corolla violet to white, stellate,
anthers connate or free; fruits red, globose or ellipsoid;
sclerotic granules absent (Bitter (l.c.)).

<u>Notes</u>: A difficult section whose taxonomy is complicated by
both the variability of the constituent species and the
plethora of specific and infraspecific names which have been
applied in the section. About 35 specific names have been
used, but it is doubtful whether there are really more than,
at the most, one sixth of that number of species involved.

For the present treatment I have followed Heine (1960) who
adopted a broad view of the species in order to minimise the
confusion in naming material. He considered all material in
this section from the Flora of West Tropical Africa (Hepper,
1963) area to be <u>S.terminale</u> which he then split into the
subspecies <u>inconstans</u>, <u>sanaganum</u> and <u>welwitschii</u>. Gbile and
Sowunmi (1979) challenged this view, and, on the basis of
their limited palynological and morphological observations,
recommended that all the subspecies be reinstated to
specific status. They did not indicate whether they also
considered Heine's subspecies to be too broad and thus

whether some supposed synonyms should be reinstated. Having looked at material at K, BM and C from the distributional range of the section in Africa I find Heine's treatment to be the most useful, though I recommend that S.terminale subsp. welwitschii be returned to specific status.

Thus I have accepted three species for this section namely: S.nakurense, S.terminale and S.welwitschii. This is not a satisfactory arrangement since the subspecies of S.terminale are somewhat indistinct, but such problems will only be resolved by a full biosystematic study. A numerical analysis of morphological data might provide useful character correlation and distribution information which would go some way to outlining more satisfactory taxa.

Key to the species:

1. Inflorescence usually lateral, with less than 20 flowers

.... 2

1'. Inflorescence usually terminal, with more than 20 flowers

.... 3

2. Erect subshrub of woodland and open places; leaves up to 3.0 x 1.5cm, with scattered simple hairs; inflorescence umbellate; fruit globose

.... 7. S.nakurense

2'. Forest climber; leaves up to 12 x 5cm, glabrescent;
inflorescence racemose; fruit ellipsoid

.... 8c S.terminale

ssp inconstans

3. Inflorescence spiciform; leaves subcoriaceous

.... 9. S.welwitschii

3'. Inflorescence paniculate or umbellate; leaves
membranaceous

.... 4

4. Inflorescence with flowers arranged in a few umbels
subsessile on the main axis

.... 8a S.terminale

ssp terminale

4'. Inflorescence with flowers arranged in umbels on
conspicuous lateral branches

.... 8b S.terminale

ssp sanaganum

7. **Solanum nakurense** C. H. Wright in Bull. misc. Inf. R.
hot. Gdn., Kew : 275 (1897). Type: Kenya, akuru, Scott
Elliott 6800 (K!)

Erect subshrub up to 1m high, stems verrucose. Leaves
variable, generally 2.0-3.0 x 1.0-1.5cm ovate, with scattered
simple hairs on both surfaces. Inflorescence umbellate,
peduncle rarely branched, with 5-10(-20) flowers, white to
violet; corolla stellate, up to 1.5cm diam, strongly
reflexed at anthesis. Fruit red, globose, 0.8cm diam.

Distribution: East tropical Africa in upland woodland and
more open places up to 2800m alt.

Notes: A species which is not clearly defined. It is
difficult to distinguish in the herbarium from S.terminale
as its characteristic features are its erect habit and its
preference for more open habitats. Generally this species
has smaller leaves, often with more hairs, and a simpler
inflorescence than S.terminale. The material at Kew is
rather variable, but Bitter's variety lykipiense (C. H.
Wright) Bitter is not worth maintaining.

I would include the following as synonyms of this species:
S.lykipiense C. H. Wright, S.mangaschae Pax, S.aculeolatum
Dammer, S.massaiense Bitter, S.penduliflorum Dammer and
S.stolzii Dammer which should possibly be separated as a
variety for the material from southern Tanzania.

8. **Solanum terminale** Forsskal, Fl. aegypt.-arab. : 45 (1775); Bitter in Reprium Spec. nov. Regni veg. 18: 301 (1922); Heine in Kew Bull. 14: 247 (1960). Type: Yemen, Mokhaja, **Forsskal s.n.** (C! IDC microf.! 2200   102: II. 3-6).

Climbing shrub. Leaves lanceolate to narrowly elliptic, 12.0 x 4.5cm, membranaceous, glabrescent or with scattered simple or branched hairs. Inflorescence terminal, usually many-flowered, often branched, pedicels fascicled in groups; corolla deep violet to white, stellate, up to 1.5cm diam. Fruits red, globose or ellipsoid, 0.8cm. diam.

Notes: A poorly understood species in which, as mentioned under the section notes, I have included three subspecies but removed ssp. **welwitschii** (C. H. Wright) Heine to specific status. Most of the material which I have seen fits into this system but it can be difficult to separate the subspecies; the subspecies **terminale** and **sanaganum** in particular merge into one another. Material of ssp. **inconstans** is generally poor, which may be its real defining character.

Synonymy: With some 35 specific names and many subspecific ones having been applied to this section, synonymy presents a considerable problem. The following is an attempt to assign the many specific names to taxa which I have included in the present treatment, but most of the decisions are

based on the descriptions rather than on the type specimens. Other names have been included under S.nakurense and S.welwitschii.

8a   ssp. terminale

S.bifurcum Hochst.

S.bifurcatum A. Rich.

S.phytolaccoides C. H. Wright

S.comorense Dammer

S.bilabiatum Dammer

S.hemisymphyes Bitter

8b   ssp. sanaganum

S.buchwaldi Dammer

S.plousianthemum Dammer

S.leucanthum Dammer

S.bansoense Dammer

S.lateritium Dammer

S.rhodesianum Dammer

S.meyeri-johannis Dammer

S.holtzii Dammer

S.ruandae Bitter

S.sycInoteranthum Bitter

8c   ssp. inconstans

S.inconstans C. H. Wright

S.togoense Dammer

S.suberosum Dammer

8a   **S.terminale** subsp. **terminale**

Peduncles with a terminal umbel and sometimes a few lateral ones as well. Lateral umbels subsessile, or occasionally the lowest on short branches.

Distribution: Widely distributed in eastern Africa from Etiliopia to South Africa.

Notes: Specimens with the simplest unbranched inflorescences with only a terminal umbel are indistinguishable from S.nakurense except by habit and habitat. Material with inflorescences which have subsessile lateral umbels on the rhachis as well as the terminal one may resemble S.welwitschii, but this subspecies terminale is distinguished by leaf characters, the more condensed appearance of the inflorescence and the geographical distribution. Specimens of this subspecies may be separated from subsp. sanaganum by the number and vigour of the branches.

8b   **S.terminale** subsp. **sanaganum** (Bitter) Heine in Kew Bull. 14: 247 (1960). Type: Cameroon, nr. Deng Deng, Mildbraed 8619 (K!)

Strongly branched peduncles give the inflorescence a paniculate appearance, but there is considerable variation in the vigour of the branching.

Distribution: Widely distributed in the upland forests of tropical Africa but less common in the east.

Notes: In making this combination Heine (l.c.) incorporated two Dammer species, S.plousianthemum and S.bansoense, and he named the subspecies sanaganum from S.bansoense subsp. sanaganum which had been published by Bitter in Reprium. Spec. nov. Regni veg. 18: 304 (1922). However, earlier subspecific names are available in S.plousianthemum from Bitter's division of the species in Bot. Jb. 54: 456-469 (1917), and according to the ruling at the 13th International Botanical Congress in Sydney (1981) the earliest names of equivalent rank must be used with the autonym taking precedence. Therefore this taxon should be named S.terminale subsp. plousianthemum.

8c   **S.terminale** subsp. **inconstans** (C. H. Wright) Heine in Kew Bull. 14: 247 (1960). Type: Fernando Po, **Mann 62** (K!); Cameroons, **Kalbreyer 172** (K!).

Characterised by flexuose stems with long internodes and the few-flowered racemose inflorescence bearing ellipsoid fruits.

Distribution: A climber in West African lowland forests up to 900m alt.

9. **Solanum welwitschii** C. H. Wright in Bull. misc. Inf. R. bot. Gdn., Kew 1894: 126 (1894). Type: Angola, Welwitsch 6081 and 6098 (K).

Climbing shrub, up to 8m high. Leaves elliptic, base obtuse, apex acuminate or cuspidate, 6 x 3 - 16 x 7cm or larger, usually glabrous, subcoriaceous, secondary veins joining together in a series of prominent arches (brochidodromus). Inflorescence terminal, spike-like, up to 20cm long, rhachis with short pedicels arising in fascicles along its length; corolla violet, stellate when fully opened, 1cm diam., anthers connate. Fruits red, globose, 0.8cm diam.

Distribution: In the forests of western tropical Africa between 600-1,000m alt.

Notes: Heine (1960) reduced S.welwitschii to a subspecies of S.terminale in an attempt to ease the confusion caused by the large number of specific names which had been used in this section. However, it seems that material in this subspecies is quite distinct from the other subspecies of the S.terminale and I recommend that this taxon is returned to specific status. It is recognised by its long spike-like inflorescence and its rather thick leaves with characteristic brochidodromus venation. The varieties into which it was divided by Wright (l.c.) are of doubtful value.

Synonymy: Probable synonyms of S.welwitschii are: S.pendulum Welwitsch non R. & Pav.; S.symphyostemon De Wild. & Durand; S.laurentii Dammer non De Wild.; S.lujaei De Wild. & Durand; S.preussii Dammer; S.subcoriaceum Th. & H. Durand.

Section 5 **Benderianum** Bitter in Bot. Jb. 54: 487-489 (1917).

Type species: S.benderianum Schimper ex Dammer.

Climbing shrubs, unarmed, glabrescent or densely pubescent; leaves lanceolate, entire, bases shortly attenuate; inflorescence terminal, compoundly cymose, lax.

Notes: Bitter (l.c.) erected this section for the single North East African species S.benderianum. He was undecided as to where S.runsoriense should be placed, not having had the opportunity to study any material of it, and inserted it between this section and section Afrosolanum. There can be little doubt that S.runsoriense should take its place in section Benderianum and it seems likely that it should be combined with S.benderianum under one name. The two species are probably best considered as subspecies, and, being the first published, the name S.runsoriense should take precedence. This is unfortunate since it covers a rather local form and S.benderianum not only gives it name to the section but is the more widely known name and species. To avoid confusion, I have maintained them as separate species for the present thesis, but I recommend their combination.

The species are distinguished from section Afrosolanum by their complex, much-branched inflorescences. The flowers of this section are of interest since not only do they often have one filament longer than the other four but they also seem to exhibit a form of stylar heteromorphism. Bitter

(l.c.) noted that in some flowers of S.benderianum the stigma was exserted on a long style beyond the anthers whilst in others the stigma remained well below the anthers. It is not clear from his descriptions whether this heterostyly (as he called it) was found in flowers on the same inflorescence or whether the specimens differed in this respect.

In the material which I have seen (K), the majority of the specimens (a ratio of about 5:2) of both species appeared to be short-styled, and long-styled and short-styled flowers did not occur in the same inflorescence. Without further investigations on living material, it is not possible to know whether there is a difference in fertility in such heteromorphs, and thus whether the species are exhibiting true heterostyly in which both types of flower are fertile or if they are androdioecious or even dioecious. The phenomenon is significant since heterostyly is unknown in the genus; androdioecism (and andromonoecism) is known only in subgenus Leptostemonum (Symon, 1979b) and dioecism has been reported only one species, S.appendiculatum Kunth ex Dun. from South America in subgenus Potatoe (Anderson, 1979b).

Key to the species:

Plants densely pubescent with much-branched hairs

.... 10 S.runsoriense

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Plants glabrescent

.... 11 S.henderianum

10. **Solanum runsoriense** C. H. Wright in Johnston, Uganda
Prot. 1: 326 (1902). Type: Uganda, Ruwenzori Mts.,
Doggett s.n. (K!)

Climbing shrub, with dense mealy pubescence of much-branched
hairs. Leaves lanceolate, axillary leaflets sometimes
present. Inflorescence terminal, a lax cymose panicle with
up to 50 or more flowers; corolla violet, 2cm diam.;
filaments sometimes 3mm long, anthers slightly longer.
Fruits not seen.

Distribution: Montane forest in Uganda and Kenya, generally
growing at 2,500-3,000m alt.

Notes: From their descriptions S.longipedicellatum De
Wild., S.dewildemanianum Robyns and S.keniense Standley are
probably later synonyms of this species.

11. **Solanum henderianum** Schimper ex Dammer in Bot. Jb. 38:
184 (1906). Type: Ethiopia, near Gaffat, Schimper 1227
(1863) (E!); Uganda, Ruwenzori Mts., Scott Elliott 7733
(K!).

Differs from S.runsoriense by the absence of a dense
pubescence.

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<u>Distribution</u>: Frequent in Ethiopia, rare in Uganda and Kenya. Grows between 2,500-3,600m alt.

<u>Notes</u>: <u>S. macrothyrsum</u> Dammer from the Comoro Islands is probably synonymous.

Section 6 **Solanum** sens. Seithe in Bot. Jb. 81: 261-336 (1962), (**Maurella** Nees; **Morella** (Dun.) Bitter). Type species: S.nigrum L.

Erect or scrambling herbs, often suffrutescent, unarmed, sparsely to densely pubescent with simple, sometimes glandular, hairs; leaves simple, ovate to lanceolate (or rhomboidal) with entire to sinuate-dentate margins; inflorescence cymose, condensed to become umbellate or lax and appearing racemose, 2- to many-flowered, flowers white to violet, stellate; fruits succulent, black, dark purple, red, orange or green, with or without sclerotic granules.

Notes: This section is one of the most widespread and taxonomically difficult groups in the genus. Almost every continent has indigenous species which belong to this section, and the weedy properties of some of the species have enabled them to become widely naturalised. The section has been the subject of many taxonomic investigations around the world, for example in North America (Stebbins and Paddock, 1949), South America (Edmonds, 1972), Europe (Edmonds, 1979a), India (Tandon and Rao, 1964, 1966a and b), New Zealand (Baylis, 1958) and Australia (Henderson, 1974 and Symon, 1981) but the African species have received little attention. Bitter intended to complete a thorough monograph of the section (Bitter, 1917 p. 494), separate from his Solana africana, but he died before he had achieved this end.

The section was known previously as _Morella_ (or _Maurella_)
since Dunal (1813) gave the name to the group of species
close to _S.nigrum_. This name was dropped when Seithe (1962)
observed that since _S.nigrum_ is the type species of the
genus the section should carry the generic name in
accordance with Article 22 of the International Code of
Botanical Nomenclature.

The taxonomic complexity of the section arises from several
sources which have been reviewed by Edmonds (1979b).
Factors that she considered to be responsible included the
continual reclassification of the group which has led to
over 300 post-Linnaean specific and infraspeciic names, the
phenotypic plasticity of the species, the genetic variation
between populations of the species, the occurrence of
polyploidy, and perhaps also natural hybridisation between
species. All of these sources of complexity have
contributed to the taxonomic confusion in other parts of the
genus but the problems which they present are possibly more
severe in this section.

The species of this section constitute a polyploid series
starting from a base chromosome number of x=12, with
diploid, tetraploid, hexaploid and octoploid taxa in the
section. Since this was understood, cytological studies
have assisted in the definition of species limits, and,
although chromosome counts require living material, a good
estimate of ploidy level may be obtained from measurements

of pollen diameter and stomatal length. These tend to
increase with ploidy level (Edmonds, 1979b) and can be
studied on herbarium material.

Artificial hybridisation studies have demonstrated that many
of the species of the section can be induced to cross with
at least one related species, even if differing ploidy
levels are involved. This has suggested the possibility
that hybridisation occurs naturally between some species and
Edmonds (1979b) has proposed that hybridisation is probably
more widespread than has been appreciated previously. If
this is so, and introgression has followed the initial
hybridisation, then the phenotypic variability of some
species may be explained.

The origin of the polyploid taxa has received considerable
attention which has given rise to various theories as
discussed by Henderson (1974) and Edmonds (1979b). Edmonds
concluded from her own studies of hybridisation and cytology
in the section that:

> "The polyploid members of the section Solanum are
>
> probably mostly allopolyploids, with all species
>
> so far investigated cytologically, showing regular
>
> bivalent formation at meiosis. From the work now
>
> completed it is becoming clear that these
>
> polyploids have probably arisen from comparatively
>
> few diploid species contributing genomes in
>
> different combinations. This is a further factor

complicating the taxonomy of this section. The possession of common genetic material would, however, explain the similar ranges of morphological variation encountered in the species belonging to the section Solanum."

As I indicated earlier, the African species have received little taxonomic attention. Bitter died before he completed his monograph of the section, and he left only the results of his preliminary examinations published (Bitter, 1912, 1913, 1917). As far as the African material was concerned, he accepted four previously described species and described another twelve new ones himself. This treatment has not been followed since, partly because of the loss of many of Bitter's holotypes in Berlin and the consequent problems of identification, but more because subsequent authors (e.g. Adamson and Salter, 1950; Andrews, 1956; Heine, 1963; Berhaut, 1967; Herxmuller, 1969; Jacot Guillarmod, 1971; Compton, 1976) have tended to lump material under one or two names, such as S.nigrum L. and S.villosum Miller, for the sake of convenience. It would have been interesting to see how Bitter would have revised the section, for such infraspecific variability must have posed daunting problems to his detailed approach.

The problems inherent in this section are such that they will only be resolved by extensive studies involving living material both in the wild and the glasshouse. The

identifications and notes on the species which follow are based on a superficial study of herbarium specimens and some discussion with Dr. J. M. Edmonds (of the Department of Agriculture and Forestry at the University of Oxford). The section is too important a component of the African Solanum flora to be omitted from this thesis, but to attempt to resolve the problems would have precluded work on the other sections.

It appears that in Africa there are at least two hexaploid species, at least three tetraploid species and possibly more than six diploid species. Reports of the uses of the members of this section vary between countries, and the identifications are often unreliable, but most commonly the two hexaploid species, S.nigrum and S.scabrum, are collected for their fruits or as leaf vegetables.

Key to the most widely distributed species:

Construction of keys to the species of this section is severely complicated by the continual overlap in the range of variation of morphological characters and the lack of correlations between characters. Any form of key to this section, whether monothetic or polythetic, must rely on very few good characters to distinguish the species. Although I have recognised thirteen species in this section in Africa, I have constructed a key to only the six most widely distributed species. I am not sufficiently familiar

with the others, and I consider a satisfactory key to a few of the species to be more useful than a poor key to all of them.

1. Flowers to 1cm diam.

.... 2

1' Flowers more than 1cm diam.

.... 3

2. Plants glabrous or sparsely pubescent with eglandular hairs; stems angular; fruiting calyx not enlarged

.... 12 S.americanum

2' Plants villose with dense glandular hairs; stems rounded; fruiting calyx enlarged

.... 13 S.sarrachoides

3. Fruits red, orange or yellow

.... 14 S.villosum

3' Fruits black

.... 4

4. Leaves rhomboidal, dentate; cymes umbellate, 3-5-flowered, flowers white with narrow purple stripe

.... 15 S.retroflexum

4' Leaves ovate, entire or dentate; cymes umbellate or racemose, 5-12-flowered, flowers white

.... 5

5. Leaves broadly ovate or rotund, entire, up to 13 x 8cm; inflorescence umbellate, anthers purplish-brown; fruits about 15mm diam.
.... 16 S.scabrum

5' Leaves ovate-lanceolate, usually dentate, 3-7 x 1.5-3.5cm; inflorescence racemose, anthers yellow; fruits 6-10mm diam.

.... 17 S.nigrum

Species not included in the key:

18. S.chenopodioides Lam.

19. S.grossedentatum A. Rich.

20. S.hirtulum Steud.

21. S.pseudospinosum C. H. Wright.

22. S. sp. A.

23. S. sp. B.

24. S.triflorum Nutt.

12. **Solanum americanum** Miller, Gard. dict. ed. 8, art. Solanum No. 5 (1768). Type: Cultivated Chelsea Physic Garden, introduced from Virginia, North America, Miller s.n. (BM!).

Suffrutescent herb, spreading or scrambling, up to 1.5m

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high, glabrous or sparsely pubescent, hairs eglandular. Stems usually angular. Leaves ovate, entire, 5-15 x 2.5-8cm. Cymes simple, umbellate, 2-8-flowered, pedicels erect in fruit; flowers white, up to 1cm diam. Fruits black, 5-10mm diam., sclerotic granules sometimes present.

Chromosomes: 2n=2x=24 (Edmonds, 1977)

Distribution: Throughout Africa and widely distributed around the World.

Notes: A very widely distributed and morphologically variable species which is used here in a broad sense without subdivisions. The species is generally accepted as being the donor of at least two genomes to the hexaploid S.nigrum L. (Edmonds, 1979b), which may account for the morphological variability of the latter, but its involvement as a progenitor of the tetraploid S.villosum Miller is less certain.

In literature on the African flora S.nodiflorum Jacquin and S.nigrum have been widely and incorrectly used for this species. Edmonds (1972, p.103) has provided further details of the synonymy, though S.chenopodioides Lamarck should be excluded from her list (Edmonds, 1979a).

The species grows in a wide range of habitats and is often a weed of cultivation. There are occasional reports of the

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use of the fruits and the leaves for medicine or food, but there is no general agreement.

13. **Solanum sarrachoides** Sendtner in Martius, Fl. bras. 10: 18 (1846). Types: Brazil, Sellow s.n. (B+; P); Chile, Poeppig s.n. (A, W) (fide Edmonds, 1972, p.102).

Erect herb up to 75cm high, villose with dense glandular hairs. Stems rounded. Leaves ovate, sinuate-dentate, 3-7 x 1.5-4cm. Cymes simple, shortly racemose, 3-8-flowered, fruiting pedicels reflexed. Flowers white, up to 1cm diam; calyces enlarged in fruit. Fruits greenish when mature, 6-10mm diam, sclerotic granules usually present.

Chromosomes: $2n=2x=24$ (Edmonds, 1972)

Distribution: Originally from South America but now established across tropical Africa.

Notes: Edmonds (1979b) has suggested that this species might be a diploid progenitor of the tetraploid S.villosum Miller and therefore may have contributed to the origin of S.nigrum L.

The synonymy of this species has been discussed by Edmonds (1972, p.102).

14. **Solanum villosum** Miller, Gard. dict. ed. 8, art. Solanum No. 2 (1768). Type: Cultivated Chelsea Physic Garden, introduced from Barbados, Miller s.n. (BM) (Lectotype fide Edmonds (1979a), neotype fide Henderson (1977))

Erect herb, sometimes quite woody, much branched, up to 50cm high, glabrescent to villose, hairs glandular or eglandular. Leaves ovate, entire to dentate, 3-7 x 1.5-3.5cm. Inflorescence simple, lax, appearing racemose, 3-5-flowered, fruiting pedicels usually deflexed; flowers white, 1.0-1.7cm diam. Fruit red, orange or yellow, 6-10mm diam., sclerotic granules absent.

Chromosomes: $2n=4x=48$ (Edmonds, 1977)

Distribution: Established in North and East Africa in drier habitats as well as on the Atlantic Islands.

Key to the subspecies:

1. Stem smooth; plant pubescent with patent, multi-cellular, glandular hairs

.... ssp. *villosum*

Stem with dentate ridges; plant glabrescent with appressed, multicellular, eglandular hairs

.... ssp. *miniatum* (Bernh. ex Willd.) Edmonds.

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Notes: Edmonds (1979a) has reviewed the nomenclatural problems in this species and discussed the extensive synonymy associated with the two subspecies.

Both subspecies are found in Africa though there is considerably more material at K of subsp. miniatum. As is found elsewhere, the fruit colour of this species varies from red to orange to yellow. It is possible that S.grossedentatum A. Richard should be included in this species but I have found no information regarding its fruit colour.

S.villosum is considered to be a likely progenitor of S.nigrum by hybridization with the diploid S.americanum and subsequent chromosome doubling. The origin of S.villosum itself is less certain: Stebbins (1950) thought that S.americanum might be involved again and Edmonds (1979b) discussed the possibility that S.sarrachoides Sendtner was the other parent.

15. **Solanum retroflexum** Dunal in DC., Prodr. 13(1): 50 (1852). Type: Cape of Good Hope, Drege 7864a & b (syntypes G-DC IDC microf.! 800-61 2062: II. 1-2; isosyntypes K!).

Spreading annual herb, up to 50cm high and 1m across, pubescent with eglandular hairs. Leaves rhomboidal, incised with triangular lobes, up to 6 x 4cm. Cymes simple, umbellate, 3-5-flowered, pedicels deflexed in flower and

fruit; flowers white with characteristic narrow purple stripe, 1.2-1.5cm diam. Fruit dull black, 9mm diam, possibly with sclerotic granules.

Chromosomes: 2n=4x=48 (Edmonds, 1977)

Distribution: Originally described from South Africa, the species has also been found in North East Africa, Sierra Leone and northern Nigeria as well as outside Africa.

Notes: This tetraploid is distinguished from S.villosum by its purple striped flowers and black fruits. It is thought to be the Wonderberry which was introduced to the United States and sold as a new fruit early this century by Luther Burbank. The controversy which surrounded the marketing and indentity of Burbank's fruit is recounted in detail by Heiser in his book Nightshades, The Paradoxical Plants (Heiser, 1969 pp 63-105).

16. **Solanum scabrum** Miller, Gard. dict. ed. 8, art. Solanum No. 6 (1768). Type: Cultivated Chelsea Physic Garden, origin North America, Miller s.n. (BM) (fide Henderson, 1974).

Woody herb, up to 1m high, glabrous except when young then sparsely pubescent with eglandular hairs. Leaves broadly ovate or rotund, entire, up to 13 x 8cm. Inflorescence simple, umbellate, 7-12-flowered, fruiting pedicels erect or

recurved; flowers white, 1.8cm diam., anthers purplish-
brown. Fruit purple-black, glossy, about 15mm diam.,
sclerotic granules absent.

Chromosomes: 2n=6x=72 (Edmonds, 1977)

Distribution: Occasionally cultivated in West, East and
South Africa.

Notes: Sometimes known as the Garden Huckleberry, the
origin of this hexaploid species is unknown. The species is
described as a native of Guinea but Heine (1960) considered
it unlikely to be native to any part of Africa. Henderson
(1974) and Edmonds (1979a) have discussed the synonymy.

It is generally cultivated for its fruits but often the
shoots and leaves are eaten as well. It is not cultivated
on a large scale.

17. **Solanum nigrum** Linnaeus, Sp. Pl. : 186 (1753). Type:
LINN 248.18 (IDC microf.! 1775 138: III.4).

Erect herb, much branched, up to 70cm high, glabrescent to
villose, hairs eglandular and glandular. Leaves ovate-
lanceolate, entire to dentate, 3-7 x 1.5-3.5cm. Cymes
simple, lax appearing racemose, 5-10-flowered, pedicels
recurved in fruit; flowers white, 10-14mm diam. Fruit
black, 6-10mm diam. occasionally with one or two small

sclerotic granules.

Chromosomes: 2n=6x=72 (Edmonds, 1977)

Distribution: A weed of open, fairly dry areas throughout Africa as well as on the Atlantic Islands.

Notes: The species is widely distributed in the Old World and is considered to be an allopolyploid arising from the hybridization of the diploid S.americanum and the tetraploid S.villosum (Edmonds, 1979b). The variability in this species may be due to the combination of different biotypes of the progenitors.

The name S.nigrum is used here in a restricted sense having been used in the past to cover a wide range of species, if not all the species, in the section. Thus the literature on the species is unreliable.

18. **Solanum chenopodioides** Lamarck, Tabl. encycl. 2: 18 (1794). Type: herb. Lamarck s.n. (P IDC microf.! 6207 468: I.5).

Bushy perennial, up to 1m high and 1m across, pubescent with eglandular hairs. Leaves lanceolate, entire to repand, deep green above and whitish below, up to 7 x 2cm. Inflorescence simple, sub-umbellate, 4-8-flowered, peduncles usually reflexed in fruit; flowers white, 1.2-2cm diam. Fruits

black, 7-10mm diam., sclerotic granules usually absent.

Chromosomes: 2n=2x=24 (Edmonds, 1979a)

Distribution: Naturalised in open disturbed ground in southern Africa from South America.

Notes: The application of the name S.chenopodioides, discussed by Morton (1976) and Edmonds (1979a), has been in doubt since its original publication. The problem stems from Lamarck's comment in his description that the type specimen had originated from Mauritius, while an unidentified hand had written 'Reunion' on the specimen, and yet neither Morton nor Edmonds has found material of this species collected on either island. The earliest South African specimen at K is dated 1953 which would suggest a recent introduction to the area. Both Morton and Edmonds concluded that the type specimen was most likely collected by Commerson in Argentina and that the confusion over the locality came about later in Paris.

19. **Solanum grossedentatum** A. Richard, Tent. fl. abyss. 2: 101 (1850). Type: Ethiopia, 'Crescit in provincia Tchelikote', A. Petit s.n. (P).

Erect herb, up to 70cm high, villose with rust-coloured hairs. Leaves ovate, dentate to incised, 3-7 x 2-4cm.

Cymes simple, sub-umbellate, 3-4-flowered, pedicels reflexed in flower and in fruit; flowers white, ca. 1.5cm diam. Fruit not known (possibly green when ripe).

Chromosomes: Probably 2n=4x=48 but not counted.

Distribution: North East Africa and, depending on the accuracy of indentification, occasionally elsewhere on the continent.

Notes: A poorly known species which is not easily recognised. It may be that it is best included in S.villosum but its ploidy level and fruit colour are unknown.

20. **Solanum hirtulum** Steudel ex A. Richard, Tent. fl. abyss. 2: 101 (1850). Type: Ethiopia, Enschedcap, Schimper 977 (K!).

Suffrutescent herb with decumbent branches from the base, up to 20cm high, sparsely pubescent with eglandular hairs. Leaves lanceolate, 2.5-3 x 1-1.5cm. Inflorescence simple, umbellate, 2-3-flowered, fruiting pedicels spreading or reflexed; flowers mauve (?), 12-15mm diam. Fruits not known.

Distribution: Ethiopia.

Notes: A poorly known species whose low habit may be the result of grazing pressure.

21.   **Solanum pseudospinosum** C. H. Wright in F.T.A. 4(2): 220 (19u6).   Type: Cameroon, Mt. Cameroon, Mann 1938 (K!).

Prostrate or ascending herb, sometimes woody below, up to 1.5m high.   Stem with simple hairs, some on longitudinal ridges and becoming hard.   Leaves ovate, entire or bluntly toothed with a few lobes, 4 x 2.5cm.   Cymes, sub-umbellate to racemose, up to 6-flowered, fruiting pedicels reflexed; flowers white, 1.5-2cm diam.   Fruit violet-black, 5mm diam.

Distribution: Endemic to the Mt. Cameroon area.

Notes: Heine (1963) considered this taxon an easily recognised segregate of all the West African material of section **Solanum** which he lumped under **S.nigrum**.   However, the species limits are not so clear when all the African species are considered, and it may be that this is an introduced form of a species not normally growing in West Africa.

S.molliusculum Bitter is a synonym of this species.

22. **Solanum sp. A** (cf S.florulentum Bitter in Reprium Spec. nov. Regni veg. 10: 544 (1912).   Type: Tanzania, Albers 189 (B+, EA?).

Scrambling herb, up to 1.5m high, sparsely pubescent with eglandular hairs. Leaves ovate to lanceolate, entire, 8-14 x 5-7cm. Inflorescence branched once, racemose, 8-20-flowered, fruiting pedicels reflexed; flowers white, 6-8mm diam. Fruit purple, 4mm diam.

Distribution: 1000-2000m alt. in the grasslands of East Africa.

Notes: Very similar to S. sp. B but this taxon has a branched inflorescence. It is most probably diploid.

The species A and B are recognisable entities but might best be considered as two subspecies. I have been unable to trace a suitable name for either taxon but I have indicated a name for each which, from the description, fits best.

23. **Solanum sp. B** (cf S.tarderemotum Bitter in Reprium Spec. nov Regni veg. 10: 547 (1912). Type: Tanzania, Winkler 3856 (WRSL?).

Erect or scrambling herb, up to 1.5m high, glabrous or sparsely pubescent with eglandular hairs. Leaves ovate to lanceolate, entire or sinuate-dentate, 7-18 x 3.5-7cm. Inflorescence simple, racemose, 7-12-flowered, fruiting pedicels reflexed; flowers white, 7-9mm diam. Fruit purple, 4-6mm diam.

1000-2000m alt. in East Africa.

Notes: This, probably diploid, species shows affinities to S. sp. A and to S.americanum, but it is distinguished by its simple racemose inflorescence. It is often used as a leaf vegetable.

24. **Solanum triflorum** Nuttall, Gen. N. Amer. pl. 1: 128 (1818). Type: U.S.A., North Dakota, Nuttall s.n. (BM?).

Spreading suffrutescent herb up to 1m long, with scattered simple hairs, unarmed. Leaves up to 3 x 2cm, generally ovate, pinnatisect. Inflorescence 2-3-flowered, sub-umbellate; calyces 0.5cm diam, enlarged to 1.5cm in fruit, corolla white, stellate, 6mm diam. Fruit whitish-green, globose, 1.5cm diam, with numerous seeds and sclerotic granules.

Chromosomes: n=12 (Randell and Symon, 1976).

Distribution: Introduced to South Africa, originally from North America.

Notes: The first record at Kew of this species in Africa is a specimen collected in 1935 at Prieska, South Africa. The species does not seem to be widespread in Africa tending to favour more temperate climates. Further study of the genus in North America may indicate the true position of this

species in the genus since it is somewhat atypical of section __Solanum.__ It is included here for convenience.

The following is a list of specific names which have been used for African material in this section but are either insufficiently known or are synonyms of the species described above. The list is not exhaustive.

__S.aegyptiacum__ Forsskal, Fl. aegypt.-arab.: 46 (1775).

> __var. a__ Type: Egypt, nr. Cairo, two specimens __Forsskal s.n.__ (1762) (C!).
>
> > Probably synonymous to __S. villosum__ Miller.

> __var. b__ Type: Egypt, cultivated, three specimens __Forsskal s.n.__ (1762) (C!).
>
> > Synonymous with __S.hirsutum__ Dunal/__S.memphiticum__ J. Gmelin.

__S.dasytrichum__ Bitter in Bot. Jb. 49: 568 (1913).

> Type: Tanzania, Usambara, __Eick 227.__
>
> > From the description, aff. __S.americanum__ Miller.

__S.depilatum__ Bitter in Reprium Spec. nov. Regni veg. 12: 88 (1913). Type: Madagascar, __Paroisse 10__ (P?).

> Affinity not known.

S.fistulosum C. Richard ex Dunal in D.C., Prodr. 13(1): 49

(1852). Type: 'ex Mauritii in America tropicali

cultum', Richard s.n. (cited by Dunal as in herb.

Boissier at G and by D'Arcy (1974) as in P).

Synonym of S.americanum Miller (fide

D'Arcy (l.c.)).

S.florulentum Bitter in Reprium Spec. nov. Regni veg. 10:

544 (1912). Type: Tanzania, Kwai, Albers 189 (B+, EA?)

See Solanum sp. A above.

S.foliosum Link in Buch, Phys. Beschr. Canar. Ins.: 144

(1828). Type: Canary Islands, collector unkown

(described at B).

In Index Kewensis as

'=Lycopersicum humboldtii'.

S.guineense (L.) Lamark, Tabl. encycl. 2: 18 no. 2339 (1794)

Based on S.nigrum var. guineense L., Sp. Pl.: 186

(1753).

A synonym of S.scabrum Miller.

S.hildebrandtii Braun & Bouche, Ind. Sem. Hort. Berol. 8: 18

(1874). Type: cult. Berlin Bot. Gard. ex Somalia,

Hildebrandt 865 (B+, L).

Edmonds (1979a) suggested that this

is a synonym of S.villosum ssp.

miniatum (Bernh. ex Willd.) Edmonds.

S.hirsutum Dunal, Hist. nat. Solanum: 158 (1813).

Type: As S.aegyptiacum var. b. Forsskal.

In his description, Dunal cited
S.memphiticum J. Gmelin as a synonym
but this should take precedence
having been published 21 years
previously.

S.humile Bernhardi ex Willdenow, Enum. Pl. Hort. Berol. 1:
236 (1809). Type: herb Willdenow 4367 (B).

According to Edmonds (1979a) a
synonym of S.villosum ssp. miniatum
(Bernh. ex Willd.) Edmonds.

S.hypopsilum Bitter in Reprium Spec. nov. Regni veg. 10: 543
(1912) Type: Cameroon, Buea, Lehmbach 175.

Affinity not known.

S.imerinense Bitter in Bot. Jb. 49: 566 (1913)

Type: Madagascar, Hildebrandt 3796.

Affinity not known.

S.incertum Dunal, Hist. nat. Solanum: 155 (1813).

Type: Based on Rheede, Hort. malab. 10: t.73 (1690).

From the description, probabably a
synonym of S.villosum ssp. miniatum
(Bernh. ex Willd.) Edmonds.

S.kifinikense Bitter in Reprium Spec. nov. Regni veg.10: 545
(1912). Type: Tanzania Kilimanjaro, Volkens 1909.

               Affinity not known.

S.luteum Miller, Gard. dict. ed. 8, art. Solanum No. 3

    (1768). Lectotype: cult. Chelsea Physic Garden, origin

America, Miller s.n. (BM).

               According to Edmonds (1979a) a

               synonym of S.villosum ssp.

               villosum Miller.

S.memphiticum J. Gmelin, Syst. nat. 2(1): 385 (1791).

    Type: As S.aegyptiacum var. b Forsskal.

               An earlier name for S.hirsutum

               Dunal, possibly with an

               affinity to S.grossedentatum A.

               Richard.

S.miniatum Bernhardi ex Willdenow, Enum. Pl. Hort. Berol. 1:

    236 (1809). Lectotype: herb. Willdenow 4366, sheet 3

    (B) (Edmonds, 1979a).

               A subspecies of S.villosum.

S.molliusculum Bitter in Reprium Spec. nov. Regni veg.10:

    546 (1912). Type: Cameroon, Buea, Preuss 740a.

               A synonym of S.pseudospinosum

               C. H. Wright.

S.nodiflorum Jacquin, Collectanea 2: 288 (1789), Icon. Pl.

Rar. 2: t. 326 (1789). Type: cult. Vienna, introduced

from Mauritius, herb. Jacquin (BM).

A synonym of S.americanum Miller

(Edmonds, 1972).

S.pachyarthrotrichum Bitter in Reprium Spec. nov. Regni

veg.10: 542 (1912). Type: Cameroon, Deistel 631.

From the description, aff.

S.sarrachoides Sendtner.

S.patens Lowe, Man. fl. Madeira 2: 74 (1872).

Type: Madeira, Lowe 547 (BM).

Synonym of S.villosum ssp. miniatum

(Bernh. ex Willd.) Edmonds.

S.pentagonocalyx Bitter in Reprium Spec. nov. Regni veg. 10:

544 (1912). Type: Tanzania, Usambara, Holst 9021.

Affinity not known.

S.plebejum A. Richard, Tent. fl. abyss. 2: 100 (1850).

Type: Ethiopia, Chire, Quartin Dillon s.n. (P?)

From the description, probably a synonym

of S.villosum ssp. miniatum

(Bernh. ex Willd.) Edmonds.

S.sancti-thomae Bitter in Bot. Jb. 49: 560 (1913).

Type: San Tome, Quintas & Moller 47 (B, COI).

From the description, aff.
S.sarrachoides Sendtner.

S.subuniflorum Bitter in Reprium Spec. nov. Regni veg.10:
546 (1912). Type: Tanzania, Kilimanjaro, Volkens 2108
Affinity not known.

S.tarderemotum Bitter in Reprium Spec. nov. Regni veg. 10:
547 (1912). Type: Tanzania, Kilimanjaro, Winkler 3856
(WRSL?).
See Solanum sp. B above.

S.tetrachondrum Bitter in Bot. Jb. 49: 565 (1913).
Type: Tanzania, Marangu, Volkens 623.
From the description, aff.
S.sarrachoides Sendtner.

S.tinctorium Welwitsch in Annaes do Conselho
Ultramarina 1: 590 (1859). Type: Angola,
Welwitsch 6103 (BM).
A synonym of S.scabrum Miller
(Edmonds, 1979a).

Subgenus 3 **Potatoe** (G. Don) D'Arcy in Ann. Mo. bot. Gdn. 59(2): 262-278 (1972).

Type species: S.tuberosum L.

Herbs, vines or shrubs, unarmed, hairs (if any) simple or branched, never stellate; leaves often deeply lobed sometimes appearing compound; inflorescence generally paniculate, pedicels articulate at or shortly above their bases, corollas rotate to rotate-stellate, anthers stout; fruit usually a juicy berry, globose or ellipsoid.

Notes: D'Arcy (l.c. and 1973) combined nine sections of the genus into this subgenus on the basis of inflorescence and pubescence types. Most of the sections are South American though section Normania, whose inclusion in this subgenus is anomalous and will be discussed later, is endemic to the Canary Islands.

Evidence for the cohesion of this group of sections is given by a study of the leaf architecture as has been discussed in Chapter 3 of the present thesis.

Representatives of three sections of subgenus Potatoe have been introduced in Africa, namely: Petota, Basarthrum and Jasminosolanum. Section Normania is endemic to the Canary Islands.

Section 7 **Petota** Dumortier., Fl. belg.: 3ᵥ (1827).

Type species: S.tuberosum L.

Perennial herbs, vines or shrubs, usually with simple multicellular hairs, and often tuberiferous; leaves generally imparipinnate with interstitial leaflets; pedicels articulating well above the base; fruits globose.

Notes: A section of 157 South American species (Correll, 1962) one of which, the potato, has been introduced into Africa.

25. **Solanum tuberosum** L., Sp. Pl. : 185 (1753). Lectotype: LINN 248.12 labelled "8 S.tuberosum" (fide Hawkes, 1956) (LINN, ILC microf.! 138: II. 4).

Perennial tuberiferous herb, up to 1m high. Stem angular and with wings decurrent from leaf bases. Leaves usually imparipinnate; primary lateral leaflet pairs varying from 3-5 decreasing in size from apex to base, usually with interstitial leaflets; leaves with scattered simple hairs. Inflorescence with about 10 flowers borne on a bifurcate peduncle; corolla rotate, 2.5-3.5cm diam., colour varying from white to mauve. Fruit, when produced, up to 2cm diam., globose, becoming pale brown when ripe.

Chromosomes: 2n=48

Distribution: Quite widely introduced into Africa

Notes: The potato is a crop of temperate climates with its main centre of diversity in the South American Andes. It is rarely cultivated in the tropics below an altitude of 500m or above 2,500m (Hawkes, 1956). As one of the world's most important crops the potato has been the subject of extensive investigations; the taxonomy has been revised by Hawkes (1963, and Hawkes and Hjerting 1969) and the tetraploid species S.tuberosum is now considered to include two subspecies namely subsp. tuberosum, and subsp. andigena (Juz. and Buk.) Hawkes. There has been some debate as to the origin of polyploidy in S.tuberosum with arguments for the species being either an autotetraploid or an amphidiploid arising from a hybrid. Cribb (1972) has shown the latter to be more likely, and it appears that subsp. tuberosum is probably derived from subsp. andigena.

Correll (1962) raised the question of whether section Tuberarium (Dunal) Bitter (equivalent to the combination of sections Petota and Basarthrum) occurred naturally in Africa and mentioned evidence that potatoes were being grown in South Africa in 1833. He suggested that there may be an indigenous species and felt that it was conceivable that continental drift may have left some representatives of the section in Africa. This is most unlikely, see Chapter 4 of this thesis for a discussion of the distribution of the genus. There are no close relatives of section Petota

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indigenous in Africa.

Section 8 **Basarthrum** (Bitter) Bitter in Reprium Spec. nov.

Regni veg. 12: 1 (1913). Type species: S.suaveolens Kunth

& Bouche (fide Seithe, 1962).

Perennial herbs, vines or shrubs, non-tuberiferous; pedicels

usually articulate at the base; hairs acute, usually two-

celled, the basal cell longer with a thicker cell wall and

the apical cell shorter and tapering (=bayonet hairs); fruits

ellipsoid to ovoid.

Notes: A section accounting for 23 species of Solanum

(Anderson, 1979a) only one of which is represented in

Africa.

26. **Solanum muricatum** Aiton in Hort. kew ed.1, 1: 250

(1789). Type: Cult. L'Heritier s.n. (BM!)

As unarmed shrub, about 1m high. Leaves entire, usually

undulate and occasionally trifoliate, up to 15 X 5cm;

petioles 3-7cm long, articulate at the base. Inflorescence

a dense cluster of 10-12 flowers; corolla blue, up to 4cm

diam. Fruit white or pale green and purple variegated,

ovoid, 5-10cm long and often seedless.

Chromosomes: 2n=24 (Federov, 1969)

Distribution: Cultivated in North East Africa.

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Notes: S.muricatum, commonly known as the 'pepino', has been cultivated since pre-Columbian times in the temperate highlands of the Andes of Columbia, Ecuador and Peru (Patino, 1962). It is valued for its fruit, which is cooked when under-ripe or eaten raw when ripe. In common with many domesticates there are several distinct forms and these are distinguished largely on fruit characters. The pepino was first introduced to Europe by the French horticulturist Thouin in 1785 (Aiton, l.c.). Fairchild (cited by Schultes and Romero-Castaneda, 1962) reported it as being widespread in the Canary Islands at the beginning of this century. In Africa it is grown in Ethiopia, possibly introduced there by the Italians during their occupation, and it is also known in Kenya and the Sudan. Research into the origin of S.muricatum (Anderson, 1979a) has suggested several different species in the section as possible wild progenitors. Correll (1962) has discussed the species and its synonomy in detail.

Section 9 **Jasminosolanum** Bitter ex Seithe in Bot. Jb. 81: 291 (1962). Type species S.jasminoides Paxt.

Shrubs or vines, generally glabrescent; leaves simple, or compound, entire or lobed, often with haptotropic petioles; inflorescence terminal, many flowered, with pedicels articulated almost at the base; fruit globose.

Notes: A small section of species from Central and South America. Two species have been introduced to Africa as ornamental garden plants and have since escaped.

Key to the species:

1. Leaves generally entire, with a prominent tuft of hairs in the vein axils beneath; calyx repandly lobed, corolla up to 2cm diam., lobed less than half way down

.... 27. S.jasminoides

1'. Leaves pinnately lobed, sometimes to the extent of appearing compound, lacking tuft of hairs in the vein axils beneath; calyx sub-truncate, teeth minute, corolla 2-2.5cm diam., lobed more than half way down

.... 28. S.seaforthianum

27. **Solanum jasminoides** Paxton, Mag. Bot. 8: t.5 (1841).
Type: Probably the plate accompanying the original description.

Glabrescent vine. Leaves usually entire, though sometimes with basal lobes, sub-cordate, ovate, and acute, lower surface with tufts of hairs in the vein axils. Inflorescence a lax panicle with numerous flowers; calyx repandly lobed; corolla pale blue to white, 2cm diam., shallowly lobed. Fruits purple or black, 0.8cm diam.

Chromosomes: n=12 (D'Arcy, 1974a)

Distribution: Introduced to Africa as an ornamental. There is material at Kew collected from Kenya and South Africa.

Notes: An attractive climber originally from southern Brazil and neighbouring Paraguay (Harley, 1970). It is curious that there is no description of the fruits in the literature on this frequently cultivated species. It has fruited at Birmingham. Darwin became interested in the way in which the petioles were used by the plants for climbing, and discussed the phenomenon in a paper 'On the Movement and Habits of Climbing Plants' (Darwin, 1865, pp 41-43; see also Darwin, 1882, pp 72-75.)

28. **Solanum seaforthianum** Andrews, Bot. repos: pl.504 (1808). Type: Probably the plate in 'The Botanist's

Repository' since no herbarium specimens made by Andrews are known to exist (Stafleu and Cowan, 1976).

Glabrescent vine. Leaves pinnatisect, often appearing compound. Inflorescence a terminal, pendant panicle, 10-20cm long with numerous flowers; calyx sub-truncate with minute teeth; corolla deep blue to violet, 2-2.5cm diam., deeply lobed. Fruit globose, ca. 1cm diam., bright red. Chromosomes: n=12 (D'Arcy, 1974a)

Distribution: Introduced to tropical Africa as ornamental garden plants and now locally naturalised.

Notes: The species is native to the West Indies but is now well distributed in the tropics being valued for its showy, pendant inflorescence. It seems that most of the material from Afica belongs to the var. disjunctum O. Schulz which is distinguished from the type in that the upper leaves as well as the lower leaves are pinnate.

The plate by Andrews (l.c.) is of a rather different form to the plant commonly known as S.seaforthianum: the depiction shows an erect inflorescence arising from a leaf axil, having a lobed calyx and a pink corolla with shallow triangular lobes.

Section 10 **Normania** (Lowe) Bitter in Reprium Spec. nov.
Regni veg. 11: 251-255 (1912). Type species: S.trisectum
Dunal.

Herbs or sub-shrubs, with tomentum of unequal glandular
hairs; inflorescence racemose, pedicels articulated at the
base, corolla rotate-campanulate, anthers not connivent,
unequal with one much shorter than the other four, two of
which have a spur-like lobe towards the base.

Notes: A section of two species endemic to Macaronesia.
Their distinctive floral morphology sets them apart from
most of the species in this genus which is characterised by
regular flowers. Lowe (1872) placed both species in a
separate genus Normania (an arrangement which has not been
followed by subsequent authors), and discussed their
affinities as follows:-

'With the habit and aspect of Solanum tuberosum L.
and coming near to Lycopersicon, this very curious
and interesting plant has the racemose
inflorescence of Pionandra or Cyphomandra, the
leafy cal. of Atropa or Triguera, the angular cor.
of Physalis or Triguera, and the many-seeded juicy
berry of a Solanum.' (Lowe, 1872)

I have followed D'Arcy (1972) in placing these two species
in subgenus Potatoe, which is the most suitable of the
available subgenera of Solanum, but it is an unsatisfactory

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arrangement. Consideration should be given to erecting a separate subgenus for this anomalous section.

Key to species:

Leaves entire; Canary Islands species

.... 29. S.nava

Leaves pinnately trifoliolate; Madeira species

.... 30. S.trisectum

29. **Solanum nava** Webb & Berthelot in Phytogr. Canar. Sect. 3: 123, tab. 174 (1835). Type: Tenerife, Webb & Berthelot s.n. and Berthelot s.n.; Canaria, Webb & Berthelot s.n. and Despreaux s.n. (There are three isotypes at K!).

Herbaceous annual with glandular tomentum of unequal hairs. Leaves entire, or with the margin toothed. Inflorescence racemose with 5-10 flowers, congested in flower, elongated in fruit; calyx enlarged and leafy in fruit; corolla rotate-campanulate, up to 3cm diam., lilac; anthers unequal with one a quarter of the length of the others. Fruit red, juicy, up to 1cm diam., partially concealed by calyx.

Distribution: Canary Islands, Tenerife and Gran Canaria.

Notes: As the only apparent differences between this

species and S.trisectum are the division of the leaves and the islands on which they grow, it seems more likely that they are different forms of the same species. Thus, they might be treated as subspecies of the earliest name, S.nava.

30. **Solanum trisectum** Dunal in DC., Prodr. 13(1): 36 (1852). Type: Madeira, Leman s.n. (K!)

Similar to S.nava but with leaves pinnately trifoliolate, the two lateral leaflets smaller and more oblong than the terminal one.

Distribution: Madeira.

Subgenus 4 **Brevantherum** (Seithe) D'Arcy in Ann. Mo. bot.
Gdn. 59: 262-278 (1972). Type species: S.erianthum D. Don.

Shrubs, small trees or vines, unarmed, pubescence of
branched or stellate hairs; leaves entire; inflorescence
often appearing terminal, flowers small to medium sized,
anthers stout; fruit globose, often pubescent.

Notes: D'Arcy (l.c.) elevated the section Brevantherum
described by Seithe (1962) to subgeneric level in order to
embrace five South American sections whose placement
elsewhere was unsatisfactory. To this extent this subgenus
is more of a convenient grouping than a natural one.

Species from the sections Brevantherum and Pseudocapsicum
have been introduced to Africa.

Section 11 **Brevantherum** Seithe in Bot. Jb. 81: 297 (1962).

Type species: S.erianthum D. Don.

Shrubs or small trees, usually with stellate (or more complex) pubescence; leaves entire; inflorescence terminal becoming lateral, compound; pedicels often reflexed at anthesis; fruits yellow when ripe. Sclerotic granules sometimes present.

Notes: Some 27 species from tropical and subtropical areas of North and South America are included in this section (Roe, 1972). Two species, S.erianthum and S.mauritianum, are now widely distributed in the Old World; a third species, S.umbellatum, has also been found growing in West Africa. Roe (1979) has noted a correlation between the distribution in the Old World of these three species and the old Spanish and Portugese trade routes from the sixteenth century.

The species of the section are mostly plants of disturbed habitats having weedy tendencies, and the ability of S.erianthum and S.mauritianum to form large colonies has made them a serious problem in some parts of Africa.

Key to the species:

1.   Hairs of young stems, petioles and peduncles stellate with less than 12 rays; leaf bases long-attenuate,

decurrent along the length of the petiole; ovary with
scattered stellate hairs, fruit glabrous

.... 31. S.umbellatum

1'. Hairs of young stems, petioles and peduncles echinoid
with more than 12 rays; leaf bases not decurrent on
petiole; fruits and ovary tomentose

.... 2.

2. Axillary leaves generally present; flowers blue-purple,
calyx lobes glabrous inside at the base, pedicels
deciduous near the middle

.... 32. S.mauritianum

2'. Axillary leaves absent; flowers white, calyx lobes
completely tomentose inside, pedicels deciduous near
the base

.... 33. S.erianthum

31. **Solanum umbellatum** Miller, Gard. dict., ed. 8, art.
Solanum No. 27 (1768). Type: Mexico, "at Campeachy",
Houstoun (fide Roe, 1967).

Large shrub up to 4m high, with tomentum of stellate hairs.
Leaves lanceolate, 1-8cm wide, the bases long attenuate,
decurrent along the length of the petiole. Inflorescence
erect, peduncle often not branching for 12cm, with numerous
flowers in a compound cyme; corolla white; ovary sparsely

stellate. Fruits up to 1cm diam., yellow, glabrous.

Chromosomes: 2n=24 (Roe, 1967)

Distribution: Originally from Central America and the West
Indies, introduced and widely dispersed in West Africa.

Notes: This weedy colonizer of disturbed ground has often
been confused with S.erianthum but is easily distinguished
by its narrower leaves which are decurrent along the
petiole. D'Arcy (1974b) considered the material of this
species at MO from West Africa to be S.rugosum Dunal,
however the specimens were redetermined by Roe, who revised
the section (Roe, 1972), as S.umbellatum.

The earliest collection of this species from West Africa at
K was made in 1939 (F. C. Deighton 3827) in Sierra Leone. A
later specimen (F. C. Deighton 4142) also from Sierra Leone
and collected in 1945, is annotated as follows:

    "A shrub which is becoming a serious weed of

    cultivated land.   KONDOGBAI (Mende), meaning

    "locust droppings". Regarded as having first come

    in with locust swarms about 8 years ago (and

    certainly not seen by me till 1939, and apparently

    does not yet occur outside the area south and

    south-east of Kenema). Said to "poison the

    ground", since the rice will not grow properly

    where it has grown. Grows up immediately after

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the "brushing" of the farm, even before the rice."
Forest duikers are said to be responsible for its
distribution (Alexandre, 1982).

32. **Solanum mauritianum** Scopoli, Delic. fl. faun. insubr.
3: 16, t.8 (1788). Type: The illustration t.8 in Scopoli
(l.c.) (_fide_ Roe, 1972). Note: the plant illustrated has no
axillary leaflets and furthermore the laminas are shown as
being decurrent along the petiole.

Shrubs or small trees, up to 12m high with dense pubescence
of echinoid hairs. Leaves ovate with pairs of axillary
leaves curving round the stem. Inflorescence erect,
peduncle unbranched for 6-20cm, numerous flowers in a
compound cyme, corolla deep purple, ovary tomentose. Fruits
1cm diam., globose, yellow, tomentose.

Chromosomes: n=12 (D'Arcy, 1974a)

Distribution: Native to Uruguay and south eastern Brazil
this species is now widely introduced in the tropics. In
Africa it is growing in West, Central and East Tropical
Africa as well as South Africa, Madagascar, Mauritius and
the Atlantic Islands.

Notes: The widespread distribution of this species is in
part due to its exceptional ability to colonize disturbed
ground. Once established the plants rapidly form thickets

by adventitious shoots from their shallow roots. The most severe invasion in Africa of the species seems to be in South Africa where a survey by le Roux (1980) of encroaching plant species in state plantations indicated that the largest and densest infestations were those involving S.mauritianum. The species is also of some importance in South Africa as it is a host plant for the larval stage of the Natal fruit fly (Pterandrus rosa) (Phillips, 1938), hence the colloquial name 'Bug tree'.

The species has been widely known in the past as S.auriculatum Ait., but the publication of S.mauritianum antedates this name by one year.

33. **Solanum erianthum** D. Don, Prodr. fl. nepal.: 96 (1825). Type: "in Valle Nepalia propa Kalmanda, 1821", Wallich Herb. 2616c, (K!) (fide Roe, 1967).

Shrubs or small trees, up to 6-8m high, forming flat-topped spreading crowns, with pubescence of echinoid hairs. Leaves ovate, axillary leaves absent. Inflorescence erect, peduncle unbranched for 3-12cm, numerous flowers, corolla white, ovary tomentose. Fruits 1cm diam., globose, yellow, tomentose.

Chromosomes: 2n=24 (Roe, 1967).

Distribution: A native of Central America and the West

Indies, the species has been introduced along the coast of West Africa.

Notes: Previously, this species was known as S.verbascifolium L. The confusion, which dates back to Burman, has been discussed and the problem resolved by Urban (1920) and Roe (1968). The application of the name S.verbascifolium however is still in doubt since the type specimen (LINN 248.1) has not been identified. Roe (1968) suggested that it was possibly a member of section Torvaria, and it seems to me that it resembles S.giganteum Jacq. of that section. Obviously the application of the name needs further investigation.

Like S.mauritianum, this species uses adventitious shoots from its roots to form thickets. A note attached to a herbarium specimen at K from Ghana (Lloyd Williams 304) mentions that 440 seedlings 3-4 feet high of this species were found in one square yard. This is an equivalent density to two million plants per acre.

Roe (1979) cited a report (Tanaka, 1976) which claimed that the fruits of S.erianthum were edible.

Section 12 **Pseudocapsicum** Bitter in Bot. Jb. 54: 497 (1917).

Type species: S.pseudocapicum L.

Shrubs or small trees, glabrescent, or pubescent with simple or branched hairs; leaves entire or sinnuate; inflorescence few flowered, corolla mauve or white; fruits red, orange or yellow, sclerotic granules absent.

Notes: A small section with less than a dozen species from Mexico or extra-tropical South America (D'Arcy, 1973).   The ornamental species, S.pseudocapsicum L. has been introduced to many parts of the World and is now naturalised in some parts of Africa.

34.   **Solanum pseudocapicum** **L.,**   Sp. Pl.: 184 (1753)   Type: Madeira, LINN 248.4 labelled "3 Pseudo-Capsicum" (IDC microf! 137: III.6).

Shrub to 2m high, glabrescent.   Leaves entire or repand, narrowly elliptic or lanceolate, length up to five times the width, lamina decurrent along petiole, veins prominent beneath.   Inflorescence lateral, with up to five flowers, condensed into a fascicle; corolla white, rotate-stellate. Fruits, 1-2cm diam., globose, orange-red, shiny.

Chromosomes: 2n=24 (Federov, 1969).

Distribution: Introduced and naturalised on the Atlantic

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Islands and in East and South Africa and Madagascar.

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Notes: This species is cultivated as an ornamental and is commonly known as the "Christmas Cherry". It is sometimes confused with S.capsicastrum Link ex Schau which is densely pubescent and has yellow fruit.

Subgenus 5 **Leptostemonum** (Dunal) Bitter in Bot. Jb. 55: 68 (1919) Lectotype species : <u>S.mammosum</u> L. (<u>fide</u> D'Arcy, 1972).

Herbs, shrubs or small trees; prostrate, climbing or erect, usually armed with prickles but quite often unarmed; indumentum of stellate hairs or sometimes simple hairs (by reduction of the lateral rays of stellate hairs?); inflorescence sometimes andromonoecious; flowers pentamerous, but occasionally tetramerous; stamens sometimes unequal, anthers attenuate; fruits various, red, orange, yellow or dark violet to black.

<u>Notes</u>: It seems that Linnaeus (1753) was the first author to separate the prickly species of <u>Solanum</u> from the non-prickly ones. The assemblage of species which he put under the heading <u>aculeata</u> is the forerunner of subgenus <u>Leptostemonum</u>. Sendtner (1846) recognised a correlation between the attenuate anthers and prickliness, and Dunal (1852) made use of this combination to form the section <u>Leptostemonum</u>. Bitter (1919) raised Dunal's section to subgeneric status. Seithe (1962) demonstrated the value of study of the trichomes in <u>Solanum</u> taxonomy by revealing that stellate hairs, as opposed to simple or dendritic hairs, are confined to subgerus <u>Leptostemonum</u>.

Whalen (1984) has recently published a conspectus of the species groups in subgenus <u>Leptostemonum</u> as a starting point

for detailed, systematic investigations. The conspectus includes a review of the morphological features of the subgenus as well as a tentative discussion of the phylogeny and a description of the biogeography. The species groups themselves are discussed in some detail and it is thought that the subgenus comprises about 450 species.

For the present thesis I have followed the sectional classification of Bitter (1923) rather than the informal groupings recognised by Whalen (l.c.), but the two are not greatly different.

Section 13 **Aculeigerum** Seithe   in Bot. Jh. 81: 291-292

(1962).   Type species: S.wendlandii Hook.f.

Climbing shrubs with small recurved prickles, generally

glabrous; leaves entire, deeply lobed or pinnate (often all

on the same plant); inflorescence a large showy panicle of

rotate flowers with unequal stamens.

Notes: A small section of species from South and Central

America. The placement of this group of species within the

genus has posed problems to those authors who have

considered the infrageneric taxonomy of Solanum (e.g. Dunal

1852, Seithe 1962, D'Arcy 1972). The problem arises from

the unusual combination of characters in the plants such

that their leaves and flower shape place them in subgenus

Potatoe, while their spines and slender anthers suggest that

the affinities are to subgenus Leptostemonum. Since I am

following the infrageneric arrangement of D'Arcy's (1972)

conspectus of the genus I have maintained this section in

subgenus Leptostemonum, though I would suggest that there

are stronger affinities to section Jasminosolanum in

subgenus Potatoe. The section is anomalous in either

subgenus and to raise it to distinct subgeneric status

merely avoids the dilemma.

One species from this section has been introduced to Africa

as an ornamental.

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35. **Solanum wendlandii** Hook.f. in Curtis's bot. Mag. 113: t. 6914 (1887). Type: Cultivated at Kew from Costa Rican seed (K!).

Strong climber, glabrous, armed with small recurved spines. Leaves up to 15 x 12cm, broadly elliptic, entire or deeply lobed (as in section Jasminosolaum). Inflorescence a showy many-flowered panicle; flowers blue tinged purple, rotate, 3-5cm diam., stamens unequal. Fruits not seen.

Chromosomes: 2n=24 (Federov, 1969).

Distribution: Introduced as an ornamental to West and East Africa and occasionally established there.

Notes: Despite being widely cultivated as an ornamental, descriptions of the fruits are not only infrequent but also contradictory. Symon (1981) quoted three differing descriptions including one sent to him which referred to the fruits as red and 10-15mm in diameter.

Section 14 **Torva** Nees in Trans. Linn. Soc. Lond. 17: 51 (1834) sensu D'Arcy in Ann. Mo. bot. Gdn. 59(2): 262-278 (1978). Type species: **S.torvum** Sw.

Shrubs or small trees, unarmed or armed with either robust prickles or bristles, young parts usually with stellate hairs; leaves medium to large, 7-30 x 3-14cm, entire or lobed, diverse shapes; inflorescence corymbose or cymose, at first terminal, becoming lateral by subsequent growth of the stem; flowers white or violet, stellate; fruits yellow or red.

Notes: This section is used here for the group of species which Bitter included in section **Torvaria** (Dunal) Bitter in his **Solana africana** (1921, pp 250-286). It is an unsatisfactory grouping and further confusion has been caused by D'Arcy's (l.c.) proposal that the correct name for the group should be section **Torva** Nees.

Bitter derived section **Torvaria** from Dunal's homonymous subsection by restricting Dunal's taxon to exclude several species. Bitter divided the section into three series, namely **Eutorvum**, **Giganteiformia** and **Anomalum**, but he indicated his dissatisfaction with the group in commenting that further study would probably result in the separation of these series.

In his review of the subdivisions of **Solanum** D'Arcy (l.c.)

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suggested that the correct name for the section was _Torva_ Nees, presumably because it was an earlier name at equivalent rank which was also typified by _S.torvum_. However, comparison of the species composition of the sections _Torva_ and _Torvaria_ indicate that they cover rather different species and the confusion is compounded by D'Arcy's inclusion in section _Torva_ of the series which Bitter had erected within section _Torvaria_. Section _Torva_ Nees contains some species which Bitter considered to be in _Torvaria_, others in section _Oliganthes_ and others in section _Andromonoecum_ (this last now called section _Melongena_) and it is not surprising therefore, that D'Arcy also commented that section _Torva_ could be combined with section _Oliganthes_ into section _Melongena_.

Child (1979a) followed D'Arcy's nomenclature but applied it to Bitter's sections. He considered that series _Giganteiformia_ Bitter should be extracted from section _Torva_, raised to the rank of section and placed in subgenus _Brevantherum_ (Seithe) D'Arcy. This is nearer to the arrangement of the species by Nees since the type of series _Giganteiformia_ is _S.giganteum_ Jacq. which Nees had placed in section _Verbascifolia corymbiflora_ along with _S.verbascifolium_ L. (now _S.erianthum_ D. Don) which is the type of subgenus and section _Brevantherum_.

In consideration of all this confusion it is appropriate to maintain Bitter's concept of the section under D'Arcy's

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nomenclatural ruling, for the present thesis. However, the
section needs further study and amendment : firstly, the
lobed-leaved yellow-fruited New World species, should be
separated from the entire-leaved red-fruited African
species, and the affinities of both groups to other Solanum
species should be investigated. Secondly, more taxonomic
work is needed on the African members of this section as
there are still some species limits which are not clear, for
example, the S.renschii, S.kwebense and S.tettense groups of
species. Thirdly, the relationship of the African species
to other Old World species needs investigation since there
are some similarities to, for example, the Oceanian species
S.tetrandrum R. Br. and S.dunalianum DC.

Generally the native African species of this section are
inhabitants of forest or woodland and most of the species
are to be found in East Africa. S.giganteum is the only
species known to be distributed outside Africa although it
is possible that S.schimperianum from North East Africa is
conspecific with the Arabian species S.carense. As far as
is known, none of the species is cultivated although there
are reports on specimens and in the literature of certain
species being used either for food (e.g. the fruits of
S.torvum and the leaves of S.goetzei) or medicinally
(S.giganteum, S.torvum, S.goetzei).

Key to the species:

1. Leaves lobed or at least angular; flowers white, 2.5-3.5cm diam.; anthers 8 x 1mm, filaments longer than 1mm, clearly visible; mature fruits yellow to brown usually more than 1cm in diameter

    .... 2.

1'. Leaves entire or at most repand, lamina often decurrent along the petiole; flowers generally pale violet to mauve, up to 1.5cm diam.; anthers up to 6 x 1mm, filaments not longer than 1mm and not obvious; mature fruits bright red usually less than 1cm in diameter

    .... 3.

2. Indumentum of young parts off-white coloured; calyx lobes in flower 4mm long; corolla less than 2.5cm in diameter

    .... 36. S.torvum

2'. Indumentum of young parts rust coloured; calyx lobes in flower 7mm long; corolla 1.5-3.5cm in diameter

    .... 37. S.hispidum

3. Sympodia plurifoliate; corymbose inflorescence of 20-200 flowers; peduncle 3cm or longer

    .... 4.

3'. Sympodia 2-3-foliate; inflorescence of 5-20 flowers;

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peduncle less than 2cm long, pedicels congested

giving inflorescence a sub-umbellate appearance

.... 10.

4.   Young branches covered with bristles

.... 5.

4'.   Young branches unarmed or armed but without bristles

..........6.

5.   Bristles themselves pubescent with stellate hairs; the

leaves very large and oblong, up to 30 x 11cm;

peduncle branching dichotomously at its base and

several more times before the flowers

.... 41. S.schliebenii

5'.   Bristles glabrous; the leaves 6 x 2.5 - 13 x 4.5 (17 x

5.5) cm; peduncle not branching for at least 3cm

from its base

.... 40. S.schumannianum var.

schumannianum

6.   Leaves ovate, base rounded or obtuse, upper surface

coarse with small stellate hairs

.... 44. S.renschii

6'.   Leaves elliptic or lanceolate, base attenuate, upper

surface glabrescent

.... 7.

7. Hairs on the inflorescence with unequal rays, the
median ray much longer, giving a hirsute
appearance
.... 8.

7'. Hairs equal rayed throughout
.... 9.

8. Plant unarmed; mature leaves glabrous or with a few
inconspicuous hairs
.... 40. S.schumannianum var. 1

8'. Plant armed; mature leaves pubescent or tomentose at
least below
.... 39. S.kagehense group

9. Young branches and underside of the leaves white
floccose or pulverulent, the leaves sub-glabrous
above with scattered stellate hairs; inflorescence
of 40-200 flowers; leaves entire, elliptic-
lanceolate
.... 38. S.giganteum

9'. Young branches and underside of leaves not white
floccose or pulverulent; the leaves often repand,

broadly elliptic

.... 39. <u>S.kagehense</u> group

10. Leaves elliptic, bases attenuate; mature leaves always glabrous or glabrescent; fruiting pedicels up to 1.5cm long

.... 11.

10'. Leaves lanceolate to ovate, bases obtuse or rounded; mature leaves tomentose with stellate hairs, if glabrous (commonly in <u>S.schimperianum</u>) then with fruiting pedicels longer than 1.5cm

.... 12.

11. Plants usually armed; flowers tetramerous, sub-fasciculate on a short peduncle

.... 43. <u>S.anomalum</u>

11'. Plants unarmed; flowers pentamerous, peduncle usually about 1.5cm long

.... 42. <u>S.goetzei</u>

12. Inflorescence up to 10-flowered; shrub from southern Africa

.... 45. <u>S.kwebense</u>

12'. Inflorescence usually more than 10-flowered; shrub from N. E. Africa

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36. **Solanum torvum** <u>Swartz</u>, Prodr. 47 (1788). Type: "India Occidentalis" O. Swartz (S) - see Heine (1976, pp 167-168) for a discussion of the legitimacy of the name and its typification.

Shrub or small tree to 4m high, pubescent with stellate hairs, armed with large straight or recurved prickles. Leaves up to 17 x 11cm angular to deeply lobed. Inflorescence a branched corymb of about 50 flowers, the distal flowers often failing to set fruit; corolla white, stellate, about 2cm diam. Fruit yellow to brown, 1-1.5cm diam.

<u>Chromosomes</u>: 2n=24 (Federov, 1969) but Randell and Symon (1976) reported n=24.

<u>Distribution</u>: In forest areas of West Africa spreading inland from the coast, 0-1500m alt.

<u>Notes</u>: An introduced species, native to Meso-America, which is now widely distributed in the tropics. Its success as a colonizer is undoubtedly due to its weedy characteristics : it fruits heavily and produces large numbers of seeds per fruit. Under suitable conditions the seeds germinate rapidly and develop into vigorous shrubs. Hall and Swaine (1980) studied the seed bank in the soil from selected sites

in Ghana and found S.torvum seeds to he some of the most numerous in the forest soils. The seeds only germinated in sunlit conditions, indicating dormancy controlled by shade and the opportunistic nature of the species.

Hossain (1973) studied the characteristic incomplete fruit set of the inflorescences of this species and found that only the lower flowers in any inflorescence were hermaphrodite. The distal flowers have slightly reduced ovaries and much shortened styles, and so act as male flowers. Symon (1979b) considered this phenomenon to be an early stage in the development of andromonoecy.

As the species has become widely distributed so an extensive synonymy has accumulated. In Africa this has not created as great a problem as it has in other areas (for a review of synonymy see O. E. Schulz in Urhan, Symb. Antill. 6: 233 (1909)), but C. H. Wright (1894) described S.mannii as a new species, though the material is undoubtedly of S.torvum, and included a variety var. compactum which from the description seems to be S.anomalum Thonning.

Bitter (1921) accepted a variety of S.torvum, namely var. daturifolium (Dun. p.pte.) O. E. Schulz, to cover the deeply lobed material. This is unnecessary since the unlobed and lobed leaf-forms are age-dependent and occur on the same plant.

Gooding (1965) considered the name S.torvum Sw. to be an illegitimate substitute by Swartz for S.indicum L. and therefore he replaced it with the later name S.ficifolium Ortega. Heine (1976) and Hepper (1979) have discussed this and demonstrated that Swartz had realised that the Linnaean S.indicum encompassed too wide a range of material and therefore was justified in separating S.torvum.

37. **Solanum hispidum** Persoon, Syn. pl. I: 228 (1805). Type: Peru, Huanuco, Ruiz & Pavon (fide McBride, 1962).

Shrub or small tree up to 4m high, armed with straight or recurved prickles, young parts with rust-coloured pubescence of stipitate or subsessile stellate hairs. Leaves broadly ovate, deeply lobed, up to 35 x 25cm. Inflorescence corymbose with 30-50 flowers; corolla white, stellate, up to 3.5cm diam. filaments 2.5-4mm long. Fruits yellowish, about 1.5cm diam.

Chromosomes: 2n=24 (Federov, 1969).

Distribution: Introduced from Meso-America for its ornamental value; now escaped and found in open disturbed habitats in West and southern Africa.

Notes: C. T. White (1939) has reviewed the synonymy of this species. Two synonyms have been used for African material, namely S.warsewiczii Weick ex Lambertye and S.pynaertii De

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Wildemann.

38. **Solanum giganteum** Jacquin, Collectanea 4: 125 (1790) and Icon. pl. rar. 2: 11, t.328 (1792). Type: Collected near the Cape of Good Hope and cultivated in Vienna; in the absence of a specimen the type must be the illustration t.328!

Shrub or small tree up to 6m high, armed with stout prickles, the young branches with a floccose white tomentum. Leaves narrowly elliptic, entire, dark green glabrescent above, white floccose below, up to 28 x 8cm. Inflorescence terminal, a dense corymb of up to 200 flowers; pedicels reflexed in flower, erect in fruit, corolla violet, 1.5cm diam. Fruit red, globose, 5-7mm diam.

Chromosomes: 2n=24 (Federov, 1969).

Distribution: Widely distributed in Africa south of the Sahara, it is also found, after introduction, in India and Australia.

Notes: A distinctive species which has been reported to be of medicinal value. Pappe (1850) reported that the application of the woolly lower surface of the leaves of S.niveum (S.gigantum) to foul ulcers "cleanses them, and a cure is afterwards effected by applying the upper surface. Hence the Dutch name 'Geneesblaen'. The fresh juice of the

berries and leaves, when formed into an ointment with lard or fat, are also in use amongst the farmers for the same purpose".

39. **Solanum kagehense** group including:

Solanum kagehense Dammer in Bot. Jh. 38: 187 (1906). Type: Tanzania, Muansa, **Fischer 78** (Isotype LE?).

Solanum muansense Dammer in Bot. Jh. 48: 243 (1912). Type: Tanzania, Muansa, **Stuhlmann 4504** (Isotype HBG?).

Solanum sordidescens Bitter in Bot. Jh. 57: 260 (1921). Type: Mozambique, Tschumo, in the Matumbi Mts., **Busse iii 3097** (Isotype KA).

Solanum wittei Robyns in Bull. Jard. bot. Etat Brux. 17: 82 (1943). Type: Zaire, Kabasha, **de Witte 1142** (Holtype BR?).

Shrubs about 2m high, armed with broad-based prickles. Leaves elliptic, entire or often repand, up to 15 x 7cm, dark green above, pale beneath, stellately hairy or glabrous above and below. Inflorescence cymose, the flowers often sub-umbellate on the branched peduncle; corolla violet, 14mm diam. Fruits red, about 7mm diam.

Distribution: The material at K which is placed in this

group was collected in East Africa, typically growing in thickets and areas of light shade at altitudes between 600 and 1500m.

Notes: This group has been brought together for the convenience of dealing with the material which appears to belong to the four species named above. The close relationship of these species is implied by the number of specimens which conform to the description of more than one of the species. As the grouping is based solely on published descriptions, no new combinations can be made until the types have been studied.

Bitter included S.muansense and S.sordidescens in the species collectiva S.giganteum' and from their descriptions they are obviously similar to each other but it is not clear why they were considered to be closer to S.giganteum than to S.renschii. S.wittei apparently fits the description of S.muansense subsp. mildbraedii Bitter (in Bot. Jb. 57: 262 (1921) even though Robyns (l.c.) suggested that they differ in leaf shape.

S.kagehense seems to belong to this group and gives the group its name by being the first published, but it is perhaps the species which further study is most likely to separate from the others. It has an affinity with both S.anomalum and S.renschii, having the leaf shape and size of the former, the indumentum of the latter, and inflorescence

characters of both.

40. **Solanum schumannianum** Dammer in Engler, Pflanzenw. Ost-
Afrikas C: 352 (1895). Type: Tanzania, Usambara Mts.,
Holst 3841 (B?).

Shrub to 2m high, armed with pale brown bristles up to 6mm
long or unarmed (var 1). Leaves narrowly elliptic, entire,
up to 17 x 4cm, with stellate hairs when young, glabrous
when mature. Inflorescence corymbose, with up to 70
flowers; corolla white or pale violet, 1cm diam. Fruit red,
8mm diam.

Distribution: Upland forests of Kenya and Tanzania, between
1300 and 2500m alt.

Key to the varieties:

Young branches with bristles 3-7mm long; the inflorescence
        axes usually floccose or mealy tomentose, rarely
        hirsute

            .... var. schumannianum

Bristles absent; young branches and inflorescence axes
        hirsute with stellate hairs of which the median rays
        are much longer than the other rays

            .... var. 1

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notes: An easily recognised species, the branches being densely armed with numerous bristles. Although var. 1 from the Mbeya and Poroto Mts. in Tanzania is without bristles it is so similar to the species in leaf and inflorescence characters that it is best included in the species. Bitter's varieties however, (var. austerum almost glabrous and with purple tinged bristles, and var. stolzii more robust and with bristles on the midveins) are not sufficiently helpful to be worth maintaining .

From their descriptions the following seem to be synonyms of S.schumannianum: S.ulugurense Dammer, S.hirsuticaule Wedermann, S.lignosum Werdermann and S.ulugurense Holub. The nomenclatural combination S.lignosum published by Werdermann had unfortunately been used previously by Sloboda (Rostlinictvi: 358 (1852)) for an unidentified taxon in the S.dulcamara group. Holub (1974) recognised this as a homonym and gave the Werdermann taxon the new name S.ulugurense apparently without realising that this combination had already been published by Dammer. However, from their descriptions it seems that both the Dammer name and the Werdermann name are synonymous with S.schumannianum.

41. **Solanum schliebenii** Werdermann in Notizbl. bot. Gart. Mus. Berl. 12: 92 (1934). Type: Tanzania, N.W. side of the Uluguru Mts., Schlieben 3415 (location unknown).

Shrub or small tree, 4-6m high, armed with bristles, the

bristles themselves pubescent. Leaves large, up to 30 x 14cm, oblanceolate to elliptic, entire, at first stellate-tomentose later glabrescent above, somewhat pulverulent below: primary veins (12-14 on each side) prominent on both surfaces. Inflorescence a much branched, lax cyme with numerous flowers; corolla violet, 8-9mm diam. Mature fruits not seen.

Distribution: Endemic to the forests of the Uluguru Mts. having been collected at about 1500m.

Notes: A striking species easily recognised from the description; the whitish undersurface of the leaf is reminiscent of S.giganteum.

42. **Solanum goetzei** in Bot. Jb. 28: 473 (1901). Type: Tanzania, Khutu-Steppe, Goetze s.n. (Isotype K!).

Unarmed shrub, about 2m high, young branches densely pulverulent with stellate hairs. Leaves elliptic, entire, up to 16 x 7cm, glabrescent. Inflorescence compoundly cymose, 15-20 flowers; corolla violet, about 1.5cm diam., pentamerous. Fruit red, 6-9mm diam.

Distribution: Disturbed or open places in the forests of East Africa between a few metres above sea level and 1200m.

Notes: An East African shrub usually found at lower

altitudes than S.schumannianum. It is very similar in appearance to S.anomalum from West Africa but may be distinguished from that species by its lack of spines and its pentamerous flowers. Both of these two characters are often variable in other species of Solanum, and although the geographical disjunction might support the maintenance of two species, they are both recorded from Zambia and Angola.

The identity of S.pauperum C. H. Wright, a species with affinities to S.goetzei and S.anomalum, is not clear but the absence of spines and its pentamerous flowers suggest that it is more likely to be a synonym of S.goetzei than of S.anomalum. According to Bitter (1921, pp 269-270) S.muha Dammer and S.bagamojense Bitter & Dammer are both synonyms of S.goetzei.

In the material at Kew there are two reports of the use of this species : the notes with Tanner 3617 (collected in Kenya) indicate that the leaves are used s a vegetable and Magogo & Glover 1030 (collected in Tanzania) mention that the leaves are used in hot poultices to draw out abscesses.

43. **Solanum anomalum** Thonning in Schumacher, Beskr. Guin. pl.: 126 (1827). Type: "Guinea", Thonning 135 (Isotypes C! (IDC microf! 2203 101: I.4 II.2-7 III.1-2) and G-DC (IDC microf! 2081: II.8)).

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43. **Solanum anomalum** Thonning in Schumacher, Beskr. Guin. pl.: 126 (1827). Type: "Guinea", Thonning 135 (Isotypes C! (IDC microf! 2203 101: I.4 II.2-7 III.1-2) and G-DC (IDC microf! 2081: II.8)).

Shrub about 2m high, at first stellately hairy, later glabrescent, branches usually armed with straight, flattened pale brown prickles, sometimes unarmed. Leaves elliptic, often repand, up to 16 x 7cm, glabrous when mature. Inflorescence sub-fasciculate on a short peduncle, 15-20(-50)-flowered; flowers white, tetramerous, corolla 12mm diam. Fruit red, 5mm diam.

Distribution: Lowland forests of West Africa.

Notes: A West African species which was previously confused with S.indicum L. (now = S.anguivi Lam.) and considered to be a later synonym. The confusion was started by C. H. Wright in his account of Solanum for the Flora of Tropical Africa (4(2): 232 (1906)) and continued by Bullock in his account of Solanum for the Flora of West Tropical Africa (ed. 1, 2: 207 (1931)). Although the two species have a superficial vegetative similarity, the sub-fasciculate inflorescence S.anomalum is quite different from the racemose inflorescence of S.anguivi.

Later synonyms of of S.anomalum include S.warneckeanum Dammer, S.lescrauwaetii De Wildemann and S.marquesi Dammer. From the description of S.mannii C. H. Wright var. compactum C. H. Wright it seems as though this too is a synonym, but it should be noted that S.mannii C. H. Wright s.str. is a synonym of S.torvum. S.goetzei has a strong affinity to S.anomalum.

In his original description of S.anomalum Thonning (l.c.) recorded that the natives used juice from the berries for painting over sores on the ears.

44. **Solanum renschii** Vatke in Linnaea 43: 328 (1882). Type: Kenya, Ukamba, Hildebrandt 2735 (Isotype K!).

Shrub or subshrub, covered when young with ashy-white stellate hairs, armed with broad-based spines. Leaves, 7.5 x 3cm, ovate, entire, dark green above, paler beneath, stellately hairy on both surfaces, more densely on the lower. Inflorescence corymbose, 20-50 flowers; corolla pale violet, 13mm diam. Fruit about 5mm diam, red (turning black?).

Distribution: Widespread in East Africa, growing in open upland bushland and grassland between 900 and 2000m alt.

Notes: Within its range in East Africa this species is quite variable and it may be that other species such as S.kwebense N. E. Brown, S.munitum Bitter, S.tettense Klotzsch and the material included in this thesis in the S.kagehense group should be incorporated in a broad understanding of it.

S.kwebense is a recognisable taxon from southern Africa with obvious affinities to S.renschii but it may be distinguished by its smaller number of flowers per inflorescence and the

shorter peduncle. Such differences are not always clear, and perhaps subspecific status would be more appropriate. From the descriptions, S.munitum does not differ significantly from S.renschii, but its identity will not be known until a type is located. This also applies to S.tettense, but if this name should turn out to be synonymous it would take precedence having been published 21 years earlier than S.renschii. There is a specimen at K labelled S.renschii which was collected near Tete, Mozambique (the type locality of S.tettense) by Dr. Kirk (s.n.); C. H. Wright (in F.T.A. 4(2): 229 (1906)) considered it to be S.renschii but Bitter (in Bot. Jb. 57: 277 (1921)), without seeing the specimen, mentioned the possibility that it was S.tettense. If this is S.tettense then S.renschii should be sunk since the two species are indistinguishable.

S.diplocincinnum Dammer, S.kibweziense Dammer and S.koniortodes Dammer are all later synonyms of S.renschii.

45. **Solanum kwebense** N. E.Brown in F.T.A. 4(2): 225 (1906). Type: Botswana, Kwebe Hills, Lugard 50, Mrs. Lugard 62 (Syntypes K).

Shrub up to 2m high, at first densely covered with close white or pale yellow tomentum, then pruinose, finally glabrous, unarmed or with a few small prickles. Leaves lanceolate or ovate-lanceolate, entire, up to 7 x 3cm, with numerous minute stellate hairs above, more dense below,

later both surfaces glabrescent. Inflorescence corymbose, 2-7(-10)-flowered; corolla white or mauve, 17-20mm diam. Fruit red, about 5mm diam.

Distribution: Southern Africa in open, sandy or rocky ground between 300 and 100Cm alt.

Notes: S.kwebense bears a strong resemblance to S.renschii and it may be best to treat them as one species. Bitter erected four varieties for this species, none of which, from the descriptions, seem to be worth maintaining.

S.omitiomirense Dammer and S.chondropetalum Dammer may be synonyms of S.kwebense.

46. **Solanum schimperianum** Hochstetter ex A. Richard, Tent. fl. abyss. 2: 98 (1850). Type: Ethiopia, Adua, Schimper 202 (BM!).

Unarmed shrub up to 1.5m high, young parts pubescent with small stellate hairs. Leaves ovate, entire, 5-12 x 3-8cm. Inflorescence cymose to sub-umbellate, 10-30-flowered, tomentum of glandular hairs; calyx lobes acuminate, up to 8mm long; corolla pale mauve, 1.5cm diam. Fruit red (becoming black?), about 6mm diam.

Distribution: North East Africa, generally in thickets and shaded places on well-maintained soils between 1400-2500m

alt.

Notes: The relationship of this species to the Arabian species S.carense Dunal needs further investigation as the two are virtually indistinguishable. C. H. Wright (F.T.A. 4(2): 220 (1906)) mistakenly cited four specimens from Somalia as S.carense which is otherwise unknown outside Arabia. These have since been re-identified as S.somalense Franchet. Bitter (1921, p.284) maintained that S.carense did not occur in Africa, yet it is surprising that the Red Sea should present such a barrier. If the two names are synonymous, as they seem to be, then the epithet schimperianum will take precedence.

S.polyanthemum Hochst. ex A. Rich. is a synonym of this species and was given varietal status by Bitter (1921, p.283) to cover the many-flowered, densely pubescent material.

Species not sufficiently well known:-

Solanum tettense Klotzsch in Peters, Naturw. Reise Mossambique 6(1): 237 (1861). Type: Mozambique, Tete, Peters s.n. (Holotype B+).

Possibly a synonym of S.renschii in which case S.tettense should take precedence. An isotype must be found to confirm this.

Solanum munitum Bitter in Bot. Jb. 57: 284 (1921). Type:

Ethiopia, Sheikh Hussein, **Ellenbeck 1287** and var

javellense Lanza in Miss. Biol. Paeso Borana 4(4): 200

(1939). Type: Ethiopia, Javello, **Cufodontis 379** (FI?).

Species close to **S.renschii** or **S.schimperianum**.

Solanum chiovendae Lanza in Miss. Biol. Paeso Borana 4(4):

192 (1939). Type: Ethiopia, Moyale, **Cufodontis 734**

(FI?).

Apparently a synonym of **S.renschii**.

Solanum grewioides Lanza in Miss. Biol. Paeso Borana 4(4):

193 (1939). Type: Ethiopia, Javello, **Cufodontis 563**

(FI?).

Affinities to **S.schimperianum** and **S.renschii**.

Solanum nossibeense Vatke in Linnaea 43:329 (1882). Type:

Nossibe, Madagascar, **Hildebrandt 3147** (Isotypes K!).

From the two specimens at K it seems that this species

belongs to section **Torva** rather than section **Oliganthes**

series **Loafra** where Bitter had placed it. Its umbellate

inflorescence, with tetramerous flowers, and small red

fruits with quite large (3 x 1.5cm) brown reticulate

surfaced seeds, are more reminiscent of section **Torva**

species than those in section **Oliganthes**. Further study

may indicate a particular affinity to a mainland species

(cf. **S.kwebense**). Vatke (l.c.) mentioned a similarity

to **S.renschii**.

Section 15 **Anisantherum** _Bitter_ in Bot. Jb. 54: 503-506

(1917). Type species: <u>S.pubescens</u> Willdenow (<u>fide</u> Seithe,

1962).

Unarmed shrubs, young parts, at least, with stellate

tomentum; leaves entire; inflorescence up to 20-flowered,

peduncle short, branched; corolla violet, stellate, anthers

unequal; fruits red, without sclerotic granules.

<u>Notes</u>: A section of two closely allied species, <u>S.pubescens</u>

and <u>S.somalense</u> Franchet, which are characterised by their

distinctly unequal anthers. Bitter (l.c.) was unsure

whether to place this section in subgenus <u>Eusolanum</u> or

subgenus <u>Leptostemonum</u> but decided on the former on the

basis of anther shape and the absence of prickles. Seithe

(1962) moved the section to subgenus <u>Stellatipilum</u> (her name

for <u>Leptostemonum</u>) so that she grouped all the stellate-

haired species together. This seems to be a more

satisfactory arrangement especially because of the obvious

affinities between this section and section <u>Torva</u>.

<u>S.somalense</u> has a strong similarity to <u>S.schimperianum</u>/

<u>S.carense</u> and previously has been confused with this group

from which it may be distinguished by the leaf shape, flower

size, and of course, the anthers. The section could be

combined with the Old World species of section <u>Torva</u>.

The biological significance of the unequal anthers in these

species is unknown but the phenomenon is seen in other
sections in the genus, for example, sections <u>Androceras</u> and
<u>Nycterium</u>. <u>S.rostratum</u> (in section <u>Androceras</u>) is probably
the best documented case : it has been shown (Bowers, 1975)
that the longer anther and the style have two possible
orientations so that there are 'left-handed' and 'right-
handed' flowers which evidently leads to outbreeding. Such
arrangements have not been seen in section <u>Anisantherum</u>.

The section has a curious distribution : <u>S.somalense</u> occurs
in North East Africa and possibly on the Arabian peninsula.
<u>S.pubescens</u> grows mainly in India though there are two
records at K of it growing in the Hadhramaut region of the
Peoples Democratic Republic of Yemen. Perhaps this
signifies a distributional range which was once continuous
from North East Africa to India.

47. <u>Solanum somalense</u> <u>Franchet</u>, Sert. somal. 47 (1882).
Type: Somalia, <u>Revoil s.n.</u> (P?).

Shrub, 1-2m high, stem often with minute stellate tomentum.
Leaves elliptic, entire, up to 8 x 5cm, apex rounded.
Inflorescence at first terminal, becoming lateral, up to 20-
flowered though usually less, pedicels racemosely arranged;
calyx lobes acuminate, enlarged in fruit; corolla about
3.5cm diam., lobes abruptly acuminate, reflexed; four
anthers around 6-7mm long, fifth 11mm long with incurved
apex; style 12mm long, tip reflexed. Fruit orange, globose,

1.0-1.5cm diam.

Distribution: Ethiopia, Somalia and N. E. Kenya (possibly also in the People's Democratic Republic of Yemen), generally at an altitude between 500 and 2000m.

Notes: Bitter included S.anisantherum Dammer and S.withaniifolium Dammer as varieties of this species and he separated off one further variety, var. parvifrons. These varieties are of doubtful importance.

C. H. Wright (1906) confused S.somalense and S.carense Dunal by citing specimens of the former as representatives of the latter. However, his description of S.somalense is accurate, and of the two specimens he cited with it one is probably the type.

Section 16 **Somalanum** <u>Bitter</u> in Bot. Jb. 54: 500-503 (1917).

Type species: <u>S.jubae</u> Bitter (<u>fide</u> Seithe, 1962).

Unarmed shrubs with stellate tomentum; leaves entire or repand, ovate or elliptic; inflorescence few-flowered, peduncle short; corolla violet, stellate, anthers equal.

<u>Notes</u>: A section of four dry-country species from North East Africa. Bitter (l.c.) saw only the types of the three species and he wrote no notes to follow their descriptions. In his brief notes on the section he observed that the relationship of the constituent species to other African <u>Solanum</u> species needed further study on more plentiful material; it can be assumed that he placed this section in subgenus <u>Eusolanum</u> on the basis of the affinity he saw to section <u>Anisantherum</u>.

The section is a poor one lacking the defining characters which might be expected to maintain such a small section. The large flowered scrambling shrub <u>S.pampaninii</u> Chiov., which Bitter named <u>S.mesadenium</u>, is too distinct from the other two specimens to make this a coherent grouping. It may be best therefore to follow Polhill who in his unpublished key to the genus <u>Solanum</u> in eastern Africa (Polhill, 1961), included this section within section <u>Oliganthes</u>.

Key to the species:

1. Leaves and inflorescence glabrescent or with equal-rayed stellate tomentum

.... 2.

1'. Leaves and inflorescence hirsute with unequal-rayed stellate hairs, the median rays much longer than the laterals

.... 49. S.robecchii

2. Sturdy, much-branched bushy shrubs; leaf bases shortly angustate or truncate; corolla 2cm diam., lobes narrowly lanceolate; inland species

.... 48. S.jubae

2'. Scrambling shrubs, leaf bases slightly cordate; corolla 2.5-5cm diam., lobes obovate; coastal species

.... 50. S.pampaninii

48. **Solanum jubae** Bitter in Bot. Jb. 54: 501 (1917). Type: Somalia, Elmeged, Keller s.n., and Webi Suabeli, Keller s.n. (both cited by Bitter as in Z).

Unarmed shrub up to 3m high usually forming a much-branched open bush. Young branches with a dense off-white tomentum, older stems glabrescent with a red-brown, becoming grey-black, bark. Leaves crowed on the new branches, broadly ovate or elliptic, entire, up to 4 x 3cm, both surfaces tomentose with equal-rayed stellate hairs. Inflorescence few-flowered, terminal; calyx with triangular abruptly

acuminate lobes; corolla violet, 2cm diam, deeply lobed, lobes narrowly lanceolate. Fruit globose, yellow, 8mm diam.

Distribution: Common in N. E. Kenya, Somalia and Ethiopia, growing on rocky well-drained slopes around 400-1300m alt.

Notes: A common, distinctive species into which S.robecchii could possibly be sunk. Material of S.jubae is usually poor, having shed leaves, flowers and fruits. The young twigs and branches are thick and tough and the multi-angular branching habit makes material difficult to press.

49. **Solanum robecchii** Bitter and Dammer in Bot. Jb. 54: 5C2 (1917). Type: Somalia, Webi, Robecchi-bri⊖hetti s.n. (cited by Bitter as in RO).

Unarmed shrub 0.5m high, stem and branches glabrous and pale grey. Leaves ovate, entire, 2.5 x 1.5cm, densely villose with stellate hairs of which the median ray is glandular and much longer than the laterals, leaves crowded on branches. Flowers solitary; calyx with elliptic lobes; corolla 2.5cm diam., deeply lobed, lobes often reflexed. Fruit globose, 5-6mm diam. (Bitter l.c.).

Distribution: Ogaden region of Somalia and Ethiopia.

Notes A species represented at K by a single specimen,

Simmons 36, which was collected within 50 miles of the type locality and is a good match with the description. From the small piece available for study this species seems to have an affinity to S.juhae.

50. **Solanum pampaninii** Chiovenda, Collez, bot. Steph. e Paoli: 126 (1916). Type: Somalia, Giumbo, **Paoli 166**, and Mogadiscio, **Paoli 72** and **91** (syntypes FT).

Scrambling unarmed shrubs with flexuose branches, young branches with dense tomentum of minute stellate hairs. Leaves elliptic, entire, ca 4 x 2cm with scattered stellate hairs on both surfaces. Flowers solitary or in pairs at the ends of the new leafy branches; calyx with leafy obovate lobes up to 8mm long; corolla mauve, rotate or deeply lobed, lobes obovate, mucronate. Fruits red, globose, 1.5cm diam., possibly edible.

Distribution: Coastal sand dunes of N. E. Kenya and eastern Somalia.

Notes: A characteristic coastal species with a tendency to scramble or climb in the associated vegetation. The range in flower sizes is perplexing and the large deeply lobed flowers are reminiscent of **S.richardii** Dunal which is otherwise not closely related.

From the descriptions it seems that **S.benadirense** Chiov.,

<u>S.mesadenium</u> Bitter and <u>S.cicatricosum</u> Chiov. should be included in <u>S.pampaninii</u>.

Section 17 **Croatianum** D'Arcy & Keating in Phytologia 34: 282 (1976). Type species: S.croatii D'Arcy & Keating.

Shrubs, armed with straight broad-based prickles, indumentum of porrect-stellate hairs with lateral rays somewhat fused or peltate hairs; inflorescence solitary or many flowered, flowers white or lilac, pentamerous, corolla reflexed; fruits poorly known.

Notes: A little known section of three species confined to the deciduous thickets of the extreme south of Madagascar. The affinities of the section seem to be towards the African species of section Torva or perhaps, in view of the porrect-stellate hairs and the solitary flowers in S.heinianum, towards S.cordatum Forssk. in section Oliganthes. I have kept the section distinct following D'Arcy and Keating, pending further research.

Key to the species:

1. Leaves rarely longer than 5cm, crowded on short spurs and rarely with prickles; inflorescence few-flowered (less than 10); shrubs to 2m

.... 2.

1'. Leaves up to 15cm long, not crowded and usually with prickles; inflorescence with 10 or more flowers; small tree 3-6m tall

.... 51 S.croatii

2.   Leaves 3 x 0.5cm, pale green on both surfaces; leaf

epidermal hairs stalked

.... 52 <u>S.bumeliifolium</u>

2'. Leaves 2 x 0.5cm, distinctly paler on the under surface;

leaf epidermal hairs sessile; flowers solitary

.... 53 <u>S.heinianum</u>

51. **Solanum croatii** <u>D'Arcy & Keating</u> in Phytologia 34: 282
(1976). Type: Madagascar, locality not cited, <u>Croat 32021</u>
(Holotype MO, isotype P).

Small tree 3-6m high, well armed with red broad-based
prickles 0.5cm long or longer, young stems ash grey. Leaves
linear, 20 x 1.5cm or more, armed on both surfaces, upper
surface green, lower surface with dense tomentum, trichomes
minute appearing peltate. Inflorescence corymbose, with 15
or more flowers, peduncle 2cm usually branched; flowers
lilac, stellate, 2.5cm diam., held erect. Fruiting pedicel
pendulous, calyx enclosing fruit.

<u>Distribution</u>: In the extreme south of Madagascar, around
Tsihombe, 20-50m alt.

<u>Notes</u>: This species bears some resemblance to <u>S.giganteum</u>
Jacq. with its reddish broad-based prickles, white
indumentum on the young branches and leaf undersides, and
the corymbose inflorescence on a long peduncle.

52. **Solanum bumeliifolium** Dunal in DC, Prodr. 13(1): 292 (1852). Type: Madagascar, St. Augustin Bay, ~~~er s.n. (G-DC, IDC Microfiche 2084: I.7!).

Small shrub, armed with numerous straight brown prickles. Leaves linear, 2.5 - 3 x 0.5cm, crowded on short spurs, both surfaces covered in porrect-stellate hairs. Inflorescence and fruits not seen.

Distribution: Around St. Augustin Bay in south Madagascar.

Notes: This species is represented at K by two sterile specimens neither of which are accompanied by much field data. Bitter (1923) included this species within section Oligantles but did not place it within a series. He guessed from inadequate material that it might be close to subseries Parvifolia within series Eoafra. Its inclusion in an alliance with S.croatii and S.heinianum is doubtful. Unless flowering and fruiting material becomes available its taxonomic position will remain conjectural.

53. **Solanum heinianum** D'Arcy & Keating in Phytologia 34: 282 (1976). Type: Madagascar, locality not cited, Croat 31213 (holotype MO, isotypes P and ADW).

Shrub to 2m tall with scattered brown prickles. Leaves linear, 1.5-2 x 0.5cm, congested on short spurs, white below, darker green above; hairs on lower surface minute

with lateral rays partially fused so appearing peltate. Flowers solitary on ends of leafy spurs, white. Fruit 1cm diam., perhaps yellow when mature, partially enclosed by enlarged calyx.

Distribution: Endemic to the area around Tulear in the south west of Madagascar.

Notes: The indumentum on this species indicates an affinity to S.croatii while the leaf arrangement and habit are reminiscent of S.humeliifolium.

Section 18 __Oliganthes__ (Dunal) Bitter in Beih. Repert. nov. Spec. Regni veg. 16 : 4 (1923).

Lectotype species : __S.indicum__ auctt. non L. (= __S.anguivi__ Lam.) (__fide__ D'Arcy, Ann. Mo. bot. Gdn. 59: 266, 1972).

Small to medium shrubs; sometimes scandent; usually armed; indumentum of stalked or sessile stellate hairs with variation in the mid-rays (absent, reduced, equal to the laterals or prolonged); leaves entire or undulate; inflorescence usually with an unbranched axis, occasionally several-branched; flowers 4-5-parted, white or violet; berry globose, red or orange (or rarely yellow), juicy; seeds pale.

__Notes:__ For the present thesis I have recognised 35 species in section __Oliganthes.__ All the species are native to Africa or the adjacent islands; some of the species extend their range into India (e.g. __S.forskalii__); and some Asian species (e.g. __S.violaceum__) clearly belong in this section but do not occur in Africa. I agree with Whalen's (1984) assessment that the American and Australian species which have been included here by other authors (e.g. Dunal, 1852 and Symon, 1981) should be excluded . The juicy, often red, berries are quite characteristic of the African and Indian species of section __Torva__ (sensu Bitter) and may point to a related phylogeny. Furthermore, tetramerous flowers are seen both in __S.anomalum__ (sect. __Torva__) as well as in the __S.zanzibarense__ (sect. __Oliganthes__) alliance of species.

Section Oliganthes is a difficult group to define morphologically. The species have an overall similarity to one another, but they are quite variable as regards individual characters; indeed there are exceptions to almost every defining feature. It would therefore seem preferable to divide the section into recognisable groups, but as yet it is not clear how this division is to be made. Bitter (1923) managed to recognise eight series here, but none are entirely convincing, and three are monotypic. Whalen (1984) divided his Solanum anguivi Group (equivalent to sect. Oliganthes) into five clusters, leaving six 'miscellaneous species' unattached. Similarly, any attempt at producing a dichotomous key to the species results either in the same small groups of species keying out in several different places, or in a tedious key with single species being whittled off the group at each dichotomy.

A synoptic key to the species of section Oliganthes is given below. A dichotomous key has not been constructed since many of the species are very variable and there is a shortage of defining characters. The key should not be read as defining the species (e.g. as if all specimens of species 54 S.aethiopicum have no prickles), rather it should be inferred that the particularly character in question is only found in the listed species (i.e. absence of prickles is only seen in specimens of species 54, 59, 61, 69, 74 and 88, but some specimens of these species may have prickles).

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Synoptic Key to the Species:

Scandent/Climbing	62, 64, 65, 66, 67, 68, 70.
Low Shrubs (< 1m)	76, 77, 78, 79, 80, 81, 82.
Tall Shrubs (> 3m)	56, 75.
Cultivated	54
Stem bristles present	74
Stem prickles absent	54, 59, 61, 69, 74, 88.
Stem prickles ± straight	54-61, 71, 72, 73, 75, 76, 77.
Stem prickles hooked	59, 62-70, 78, 79, 80, 85.
Stem prickles completely straight	81, 82, 83, 84, 86, 87.
Prickles red	71, 84.
Stems glabrescent	54, 59, 77, 79.
Stem hairs long stalked	58, 60, 64, 65, 80.
Stem hairs with a long mid-ray	55, 56, 57, 59, 68, 82.
Leaf prickles absent	54, 59, 60, (67?), 69, 74, 75, 87, 88.
Leaf upper surface with a dense indumentum	56-63, 65, 71, 75, 76, 81, 84, 85, 87, 88.
Hairs on leaf upper surface with a long mid-ray	55, 56, 57, 59, 68, 82, 83.
Leaf upper surface glabrescent	54, 70, 77, 79.
Leaves 0-5cm long	60-64, 66, 69, 71-83, 85-88.
Leaves >15cm long	55, 56, 84.
Leaf margin deeply lobed	55, 59, 62, 70, 76-80, 84.
Leaf base decurrent on petiole	61, 63, 66, 70, 73, 74, 76, 77, 78, 80, 85, 86.
Leaf base acute	54, 55, 59, 62, 67, 69, 79, 83, 88.

Flowers ± sessile	54, 57, 68, 69, 70-74, 76-80, 83, 85.
Flowers solitary	69, 72, 73, 76, 78.
2-5 flowers/inflorescence	54, 59, 60, 62, 64, 66, 68-71, 74, 77-83, 85.
>15 flowers/inflorescence	56, 87.
Inflorescence branched	56, 65, 66, 87.
Flowers tetramerous	62, 64, 66, 67, 71, 72.
Flowers 6-10-partite	54.
Calyx enclosing fruit	75, 76.
Flowers <1.0cm diameter	55, 56, 58.
Flowers 1.5cm diameter or more	54, 57, 60, 61, 62, 64, 65, 66, 68, 71, 72, 83, 84, 86, 87.
Flowers white (perhaps tinged violet)	54-59, 63, 76, 79, 80, 83.
Fruit red	54, 56, 57, 58, 59, 60, 62-71, 74, 88.
Fruit yellow	76, 84.
Fruit >1.5cm diameter	54, 60.

54. **Solanum aethiopicum** Linnaeus, Cent. pl. II: 10 (1756).

Lectotype: 'Habitat in Aethiopia', Burser Vol. IX No. 17

(IDC Microf! 1064 51:2.1). Selected by Hepper & Jaeger

(1985).

Cultivated annual, biennial or perennial herbs, glabrous or

tomentose, unarmed or with scattered prickles. Leaves to 15

x 9cm, entire or repand. Inflorescence extra-axillary, 1-

10-flowered; flowers white, stellate, 1.5cm diam. Fruits

variable in colour, shape and size but usually scarlet and

globose; seeds straw coloured.

Chromosomes: 2n = 24 (Federov, 1969)

Distribution: Cultivated as a leaf and/or fruit vegetable in many parts of Africa and tropical South America.

Notes: Grouped here are all the species recognised by Bitter (1923) in his series Aethiopica. Biosystematic studies (Lester and Niakan, In press) have revealed that the species of series Aethiopica form a continuum of interfertile populations, within which is a wealth of land races and cultivars, domesticated from S.anguivi. Lester and Niakan reported that they were able to identify four groups within S.aethiopicum on the basis of morphological attributes that have been selected for according to human preferences. These cultivar groups have been named under the rules for nomenclature of horticultural plants to provide an infraspecific structure. (Lester, In press).

Key to the cultivar groups (based on Lester et al, 1985).:

1. Plants generally armed with prickles sometimes not; leaves tomentose with stellate hairs

.... 2.

1'. Plants lacking prickles; leaves usually glabrous apart

from minute glandular hairs

.... 3.

2. Plants mostly unarmed; peduncle and rachis

more or less condensed; perianth 5-lobed; ripe

fruit red tending to orange, with 2-6 locules

.... Gilo Group

2'. Plants armed; peduncle and rachis elongate; perianth

6-10 lobed; ripe fruit scarlet, with 4-10 locules

.... Aculeatum Group

3. Mature leaves usually 10-20cm long, entire; fruit

diameter ca 2cm, only slightly broader than long,

smooth, with 2-3(-5) locules

.... Shum Group

3'. Mature leaves 20-30cm long, lobed; fruit diameter at

least 5-10cm, sulcate, with 10-15 outer locules and

often several inner locules

.... Kumba Group

Gilo Group - Commonly cultivated throughout tropical
Africa and parts of South America for its fleshy fruits
which, when unripe, are eaten raw or stewed. S.gilo Raddi
and S.olivare Paill. & Bois belong in this group. Bitter
(l.c.) considered S.geminifolium Thonning, S.naumanii

Engler, S.poggei Dammer, S.pierreanum Paill. & Bois and S.monteiroi C. H. Wright to be synonymous with S.gilo.

Shum Group - a leaf vegetable, occasional throughout tropical Africa. S.zuccagnianum Dunal belongs here.

Kumba Group - cultivated for its very large fruits and for its leaves. It is particularly known in areas around the Niger River (Mali, Burkina Faso). The Burser lectotype of S.aethiopicum corresponds to this cultivar group.

Aculeatum Group - a cultivar which is apparently unknown in Africa but is grown in several European botanic gardens. Possibly it is of hybrid origin. S.aethiopicum var. aculeatum Dunal, S.integrifolium auctt. non Poir. and S.texanum Dunal should be included here.

55. **Solanum sp. nov.** = **Kerfoot 4721** (K!) Kenya, S.W. Mau Forest.

Shrub to 1m tall, densely armed with straight brown broad-based prickles, young stems with stellate indumentum. Leaves elliptic, 10-20 x 5-10cm, margin quite deeply cut, base cuneate, apex acute, with scattered simple hairs above and sessile stellate hairs on the mid-vein. Inflorescence racemose, 6-8-flowered; corolla white, 0.8cm diam. Fruits

0.8cm diam, colour when ripe not known, held below the rachis of the inflorescence.

Distribution: Scattered upland forest localities in northern Tanzania, southern Kenya and Uganda.

Notes: I have unable to trace a name for this species which has affinities to the S.anguivi complex of species. The simple hairs on the upper surface of the leaf are distinctive.

56. **Solanum usambarense** Bitter & Dammer in Beih. Repert. nov. Spec. Regni veg.16: 40 (1923). Type: Holst 380 (K!), 8921, 8925a (K!), 9091a; Lick 28a, 200, 273, 382; Volkens 616; Buchwald 380. All collected in northern Tanzania and all cited with the original description.

Bush to 3m tall, armed with numerous pale brown prickles, indumentum pilose. Leaves ovate, up to 20 x 15cm, margin angulate or more deeply cut, base usually truncate and unequal but may be shortly attenuate, upper surface with indumentum of stellate hairs with mid-ray very much longer than laterals. Inflorescence 8- to many-flowered, rachis simple or branched, pedicels arranged racemosely; corolla cream white, occasionally tinged with purple, stellate, 1.0cm diam. Fruits red or orange-red, 0.8cm diam., held below the rachis.

Distribution: In the shrub layer of the forests on the East African mountains. Tanzania, Kenya and Uganda. Apparently not reaching into Ethiopia. 1500-2000m alt.

Notes: A species which seems to intergrade with forms of S.adoense. It may be that I have taken too wide a view of S.usambarense but it is not clear how it might be subdivided. At K many collections which I would incorporate now in S.usambarense have been previously determined as S.indicum, and part of Bitter's S.indicum also belongs here. While there is an obvious relationship with S.anguivi these two species are easily distinguished by inflorescence and infructescence characters.

57. **Solanum adoense** Hochstetter ex Dunal in DC., Prodr. 13 (1) : 282 (1852). Type: Ethiopia, Adoa, Schimper 147, 1840, 1865 & 1844 (G-DC) (IDC microf.! 2083: I. 4, 5 = Nos. 147 & 1865).

Shrub to 1m tall, heavily armed with straight or slightly recurved prickles, indumentum of short-stalked stellate hairs. Leaves ovate, base cuneate or sub-cordate, apex acute, margin repand or sinuate, (5-)8(-12) x (3-)5(-7)cm, armed on primary and secondary veins, stellate hairs on upper surface often with elongate mid-ray. Inflorescence racemose, 8-12-flowered; corolla white or tinted violet, 1.5cm diam. Fruits red or orange, 0.8-1.0cm diam. held below the rachis by deflexed pedicels.

Distribution: Ethiopia, eastern Uganda and occasionally in Kenya, 1800-2600m alt., typically growing on open rocky ground but also in more shaded areas.

Notes: Bitter (1923) reduced S.adoense to a subspecies of S.indicum using it alongside subsp. mesodolichum Bitter to name specimens with 'nodding' fruiting pedicels. In this aspect, as well as habitat, habit and leaf characteristics, these two taxa seem to me to be distinct from S.anguivi (=S.indicum sensu Bitter). I would therefore return subsp. adoense to specific level, and include subsp. mesodolichum as a subspecies within it to account for the plants growing at slightly higher elevations.

The latter taxon comprises plants usually growing within the forest zone, having broadly ovate leaves with a villous indumentum of stellate hairs with elongate mid-rays. Bitter reduced S.rohrii C. F. Wright to a subspecies of S.indicum placing it in that portion of the species having erect fruiting pedicels. The holotype (K!) has 'nodding' fruiting pedicels and seems to belong to the same taxon as subsp. mesodolichum and so should be included here. The sundry varieties of subsp. rohrii recognised by Bitter are of little value.

The forest subspecies of S.adoense bears a strong resemblance to S.usambarense Bitter which occupies a similar but slightly more southern habitat.

58. **Solanum mauense** Bitter in Beih. Repert. nov. Spec. Regni. veg.16: 42 (1923). Type: Kenya, Mau Plateau, G. S. Baker 44 (Holotype B?).

Shrub to 1m tall, armed with straight and recurved prickles, indumentum of stalked stellate hairs. Leaves lanceolate, entire, base rounded, apex obtuse, 3 x 1 to 10 x 4cm, densely hairy, stellate hairs on upper surface on a thin stalk with the lateral rays spreading upwards and approximately the same length as the mid-ray. Inflorescence racemose with 8-12 flowers; corolla white or pale lilac, 1.5cm diam. Fruits red or orange-red, 0.8-1.0cm diam., hanging down below the horizontal rachis by reflexed pedicels.

Distribution: Montane bushland of southern Kenya and northern Tanzania, 1800-2100(-2700)m alt.

Notes: A pioneer species of forest edges, bushland and disturbed places, here identified from Bitter's description. Its lanceolate leaves with entire margins distinguish it from other closely related taxa in the S.anguivi complex. The species typically occurs within an altitudinal range of 1800-2100m alt. but there are a number of speciments at K collected from higher elevations from within the evergreen forests. These are distinguished from the bushland type by their larger leaves with slightly angular margins and an indumentum of stalked stellate hairs

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with greatly elongated mid-rays. They approach the S.adoense-S.usambarense group in appearance, but are not completely distinct from S.mauense.

An infusion of the roots of this species is said to be used to treat anthrax.

59. **Solanum anguivi** Lamarck, Tabl. encycl. 2: 23 (1794). Type: Madagascar, Commerson s.n. (Holotype MPU, syntype P fide Hepper, 1978).

Wild, weedy or cultivated shrubs, from 1 to 2m tall, armed with straight straw-coloured prickles or unarmed, indumentum of stalked stellate hairs. Leaves ovate or elliptic shapes, entire or dentate or deeply lobed, 6 x 4 to 20 x 10cm, both surfaces with stellate indumentum. Inflorescence racemose, 3-8-flowered; corolla white sometimes tinged violet, stellate, 0.9-1.3cm diam. Fruit red or orange, 0.5-1.0cm diam., held above or below the rachis.

Distribution: Throughout the forests and thickets of Africa and its neighbouring islands, often in association with human habitation.

Notes: S.anguivi is the correct name for the species known for a long time as S.indicum. Hepper (1978) reported that the name S.indicum L. had been misapplied almost since the

date of its publication and should have been used for the species known as S.sodomeum L. (now = S.linnaeanum). S.indicum and S.sodomeum have been rejected as confused names and the next available name for the S.indicum auctt. taxon was found to be S.anguivi Lam.

While Bitter has often been criticised as a splitter, he (Bitter, 1923) took quite an inclusive view of this particular species, including taxa which I believe should be given specific status. Bitter divided S.indicum into 14 subspecies and 35 varieties and he recognised S.usambarense and S.mauense as separate, but closely allied, species. I would maintain these two, and reinstate S.adoense to specific level from the subspecies of S.indicum into which Bitter had sunk it. Further, the Indian representatives of Bitter's S.indicum should be separated under the name S.violaceum Ortega : as far as I am aware S.anguivi sensu strictu does not occur on the Indian sub-continent.

Following the work of Lester and Niakan (In press) I have used the name S.aethiopicum for the domesticated plants which Bitter recognised as the species of series Aethiopica. Lester and Niakan have demonstrated that S.anguivi is most likely the wild progenitor of the red or orange fruited garden eggplants commonly cultivated in Central and West Africa.

Within S.anguivi there is considerable morphological

variation particularly in prickliness, pubescence and inflorescence characters. This may be the result of the influence of man imposing selection pressures in the course of domesticating the plants now known as S.aethiopicum, thereby deriving races which crossed amongst themselves and with the parental stock. A spectrum of morphological variants between S.anguivi and S.aethiopicum is known today. The supposedly wild S.anguivi sensu strictu often occurs near villages and other habitation and sometimes collecting notes refer to culinary uses; its widespread distribution may be a result of its association with man.

The following variants can be recognised. Subspecific names are from Bitter's treatment of S.indicum. No infraspecific combinations have been published for S.anguivi yet.

1. Plants armed with numerous well developed prickles
.... 2

1'. Plants unarmed or with occasional small prickles
.... 4

2. Hairs on upper leaf surface stalked and often with an elongated mid-ray
.... 3

2'. Scattered hairs on leaf upper surface sessile, stellate, with vestigial mid-ray and lateral rays appresses to

the leaf surface. From northern Tanzania and Kenya

.... subsp. <u>brevistellatum</u>

3. Leaves ovate, usually angulate or more deeply lobed, quite densely pubescent above; inflorescense 6-12-flowered; corolla 0.8cm diam.

.... subsp. <u>anguivi</u>

3'. Leaves narrowly elliptic or lanceolate, more or less entire, scattered pubescent above; inflorescence 2-6-flowered; corolla 1.0 - 1.5cm diam.

.... subsp. <u>keniense</u>

4. Fruiting pedicels spreading upwards holding the berries above the rachis of the inflorescence

.... subsp. <u>distichum</u>

4'. Fruiting pedicels strongly reflexed holding the berries below the rachis. Ugandan

.... subsp. <u>clinocarpum</u>

Tentative synonymy between the taxa in Bitter's series <u>Afroindica</u> and the system adopted here can be inferred from the chart overleaf.

Series Afroindica   Present Arrangement

57. S.heudelotii ———————————— 87. S.forskalii

58. S.piperiferum ——————————— 83. S.piperiferum

59. S.indicum ——————— ?—— S.violaceum

     subsp. erosum

     subsp. newtoni ———————— 59. S.anguivi

     subsp. brevistellatum

                    subsp. anguivi

     subsp. rohrii

                    subsp. brevistellatum

     subsp. olivaceum

                    subsp. keniense

     subsp. grandifrons

                    subsp. distichum

     subsp. adoense

                    subsp. clinocarpum

     subsp. mesodolichum

     subsp. zechii

                    57. S.adoense

     subs clinocarpum

     subsp. ambifarium

     subsp. pervilleanum

60. S.bellicosum ———— ?

61. S.usambarense ——————————— 56. S.usambarense

62. S.mauense ——————————— 58. S.mauense

60. **Solanum tomentosum** Linnaeus, Sp. Pl. ed. I: 188 (1753). Type: Two syntypes have been traced, the one is in Linnaeus' herbarium at S (IDC microf! 5075 92:II.6) the other is in the Clifford herbarium p.61 No. 13 (BM!).

Shrubs to 1m tall, armed with straight prickles and densely tomentose (less so in var.) with stalked stellate hairs giving a woolly appearance. Leaves ovate, to 8 x 6cm, base cordate. Inflorescence few-flowered; flowers violet, to 2cm diam. Fruits red or orange, 1-1.75cm diam.

Distribution: Shrub species of the fynbos in the southern parts of Cape Province, South Africa. Usually growing between 500-1500m alt.

var. **coccineum** (Jacquin) Willd., Sp. Pl. ed. V: 1046 (1797) including S.coccineum Jacquin, Misc. austriac. 2: 329 (1781). Type: Untypified but see illustration in Jacquin, Icon. pl. rar. 1 (2): tab. 43 (1782).

Leaves usually smaller than in strict sense of the species and indumentum much sparser. Flowers to 1cm diam. Fruits red or orange, up to 1cm diam.

Distribution: Shrubland of southeastern Cape Province, South Africa.

Notes: Known in Europe at least since the early eighteenth

century, this species is frequently cultivated in botanic gardens. With its thick woolly indumentum it is a distinctive species. Nevertheless Linnaeus found some confusion in his original treatment of S.tomentosum and subsequently renamed it S.pulverulentum in Systema Naturae ed.X. The confusion may have come about through the superficial similarity of some vegetative parts between S.incanum and S.tomentosum, but the name change was unnecessary and S.tomentosum continues in use.

I have included S.coccineum Jacq. here as a variety to cover the rather variable material collected at the eastern extreme of the range of S.tomentosum sensu strictu. I have been unable to separate two taxa with any certainty and therefore follow Bitter (1923) by including S.coccineum within S.tomentosum.

61. **Solanum burchellii** Dunal in DC., Prodr. 13(1): 291 (1852). Type: South Africa, Asbestos Mountains, Burchell 2045, 1 (Holotype G-DC, IDC microf.! 2084:I.5 and isotype K!)

Shrub to 1m tall, armed with straight prickles when young later unarmed, densely covered with sessile stellate indumentum. Leaves elliptic, up to 6 x 3cm, margin undulate, mid-vein raised on both surfaces. Inflorescence few-flowered, calyx lobes caudate, corolla violet, 1.5-2cm diam. Fruits orange, drying to black, 1cm diam.

Distribution: Confined to the Karoo shrublands of southern Namibia and north-western Cape Province.

Notes: According to Bitter (1923) S.rangei Dammer and S.schaeferi Dammer both belong here as synonyms of this dry country species.

62. **Solanum zanzibarense** Vatke in Linnaea 43: 326 (1882). Type: Tanzania, Zanzibar, Hildebrandt 988 (K!).

Shrub to 2m tall, armed with small brown recurved prickles; indumentum of short-stalked stellate hairs. Leaves narrowly elliptic, 5-8 x 2-5cm, variably lobed, almost entire to deeply lobed, especially the basal leaves. Inflorescence 4-7-flowered; flowers tetramerous or pentamerous, lilac, 2cm diam. Fruits red, 1.3cm diam.

Distribution: Coastal woodland and forest of Tanzania and southern Kenya, usually below 150m alt.

Notes: Part of an alliance of forest, woodland and thicket species of the East African coast. Within S.zanzibarense I include S.lamprocarpum Bitter (Busse 2498 - isotype EAH, photo K!) which seems improperly distinct though it might be given infraspecific rank.

63. **Solanum aldabrense** C. H. Wright in Bull. misc. Inf. R. bot. Gdn., Kew 1894: 149 (1894). Type: Aldabra,

<u>W. L. Abbott s.n.</u> (K!)

Shrub to 2m tall, with many small recurved prickles on stem. Leaves ovate, up to 5 x 3.5cm, entire to sinuate, stellate hairs on both surfaces, often armed with straight blue-black prickles which dry to pale yellow colour. Inflorescence cymose, 5-7 flowers; corolla white or pale lavender, stellate, 1.5-2cm diam. Fruits scarlet, globose, 1cm diam.; seeds straw coloured.

<u>Distribution</u>: Aldabra Atoll in mixed scrub on limestone.

<u>Notes</u>: Fosberg (1978) reduced this species to a variety of <u>S.indicum</u> (=<u>S.anguivi</u> Lam. or <u>S.violacaum</u> Ort.) arguing that it fell within the range of variation circumscribed by the contemporary understanding of <u>S.indicum</u>. He pointed out the anomaly between his inclusion of <u>S.aldabrense</u> within <u>S.indicum</u> and Bitter's (1923) separation of the two species into distant series within section <u>Oliganthes</u>. Fosberg's treatment of this species was repeated in the Flora of Aldabra (Fosberg & Renvoize, 1980).

More recently, it has become clear that the Indian component of <u>S.indicum/anguivi</u> is a quite distinct taxon from the African plants under that name, and the two should be separated. <u>S.anguivi</u> therefore appears to be a slightly more homogeneous species than previously recognised, and it seems to me that while <u>S.aldabrense</u> clearly has an affinity

to S.anguivi it is sufficiently removed to be given specific status. At the same time, with its white (or very pale lavender) flowers and scarlet fruits, it is distinct from the Asiatic taxon previously included in S.indicum and now known as S.violaceum Ortega.

Fosberg and Renvoize (1980) recorded that the fruits are eaten and the seed locally dispersed by the tortoise, blue pigeon, dove and bulbul.

64. **Solanum monotanthum** Dammer in Bot. Jb. 28: 474 (1901). Type: Tanzania, Khutu Steppe, Goetze 113 (B or possibly BR?).

Climbing shrub, armed with small recurved prickles, indumentum of stalked stellate hairs with mid-ray shorter than the laterals. Leaves ovate, 4-6 x 2-3cm, entire, dark green above, paler beneath. Inflorescence 3-6-flowered, racemose, the pedicel of the proximal flower emerging from the base of the inflorescence, pedicels and calyces very prickly; flowers 4 or 5 partite, corolla violet, 2.5cm diam. Fruit red, 0.8cm diam.

Distribution: Coastal region of Kenya and northern Tanzania.

Notes: Not definitely identified as no type material has been traced, but the description adequately matches a number

of specimens at K collected near the coast of East Africa.
The range of this species is slightly more northern than
S.zanzibarense and it appears to occupy a north-south belt
slightly further inland than that species.

65.   **Solanum kitivuense** Dammer in Engler, Pflanzenw. Ost-
Afrikas. C: 353 (1895).   Type: Tanzania - two specimens
cited - Usaramo, Stuhlmann 7026 and Kitivu, Holst 276.

Spreading shrub to 2m tall, armed with small brown prickles,
indumentum of brown, stalked stellate hairs. Leaves ovate or
narrowly ovate, 6-8(-12) x 3-4(-6)cm, entire or repand.
Inflorescence 8-12-flowered, rachis sometimes branched;
flowers pentamerous, calyx sometimes armed, corolla violet,
1.8-2cm diam. Fruits red, 0.8cm diam.

Distribution: In the shrub layer of the rain forest of the
Usambara Mountains in north-eastern Tanzania.

Notes: A member of the S.zanzibarense - S.cyaneo-purpureum
alliance of species only collected from the Usambara
Mountains. I suspect that S.inaequiradians from the Uluguru
Mountains might be included within S.kitivuense but for the
moment I maintain it as a separate species. Bitter's
S.kitivuense subsp. ukerewense I would remove to S.cyaneo-
purpureum in whose distributional range the type of Bitter's
subspecies was collected.

Bitter included S.scheffleri Dammer, S.englerianum Dammer and S.glochidiatum Dammer as infraspecific taxa which are hardly worth recognising. S.stipitato-stellatum Dammer should be included here : the isotype (Holst 9121) at K! merely seems to be a poorly grown form of S.kitivuense.

66. **Solanum cyaneo-purpureum** De Wildeman, Pl. bequaert. 1: 425 (1922). Type: Zaire, Kabare, Bequaert 5333 (BR).

Scrambling shrub to 2-3m tall, young stems and leaves with indumentum of stalked stellate hairs with lateral rays often missing or vestigial, armed with small brown recurved prickles. Leaves narrowly ovate, 1.5-5 x 0.6-2cm, entire, mid-rib and petiole armed with prickles. Inflorescence 2-5-flowered, flowers rarely tetramerous; corolla purple, 1.8cm diam. Fruits red, 0.8cm diam.

Distribution: Scrub forest in the plains of south-western Uganda, Ruanda, Burundi, and eastern Zaire; often growing on termite mounds.

Notes: Evidently Bitter (1923) had not seen De Wildeman's publication (t.c.) before he completed Solana africana where he named this species S.tanganikense based on Kassner 3160 (isotype K!) collected on the north shore of Lake Tanganyika. Although S.tanganikense was included in subseries Parvifolia of series Eoafra the affinity of this species is clearly to Bitter's subseries Subcontinentalia,

particularly to S.zanzibarense and S.kitivuense of which it may be an inland form. Under the present arrangement S.kitivuense subsp. ukerewense Bitter based on Conrad 380 (K!) from the Lake Victoria area should be included in S.cyaneo-purpureum.

67. **Solanum vagans** C. H. Wright in Bull. misc. Inf. R. bot. Gdn., Kew 1894: 128 (1894). Type: Tanzania, Dar es Salaam coast, Kirk s.n. (K!).

Shrub (sometimes scandent) to 2m tall, armed with small brown recurved prickles, indumentum of sessile (rarely short-stalked) stellate hairs with vestigial mid-rays. Leaves elliptic, 9 x 4cm, entire or repand. Inflorescence 12-15-flowered with unbranched rachis; flowers tetramerous, pale violet, 1.25cm diam. Fruits red, 1cm diam.

Distribution: In the moist evergreen forests of the scattered patches of highlands (400-1000m) along the coast of southern Kenya (Shimba Hills, Mrima Hill) and Tanzania (Pugu Hills and Rondo Plateau).

Notes: Bitter (1923) included this species as a variety of S.zanzibarense from which it is distinguished by its indumentum, leaf shape and inflorescence size. In several respects S.vagans resembles S.goetzei (section Torva) and may represent an intermediate branch between sections Torva and Oliganthes.

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68. **Solanum inaequiradians** Werderman in Notizbl. bot. Gart. Mus. Berl. 12: 90 (1934). Type: Tanzania, Uluguru Mountains, Schlieben 2707 (B?).

Scandent shrub, densely armed with small brown recurved prickles, pilose indumentum of sub-sessile stellate hairs with mid-rays greatly extended. Leaves lanceolate, 8-10 x 3-5cm, armed with straight prickles, repand to sub-sinuate, base cuneate. Inflorescence 2-5-flowered, sub-sessile with the pedicel of the proximal flower arising from the base of the inflorescence; flowers pentamerous, corolla pale violet, 2cm diam. Fruit red, 1cm diam.

Distribution: Confined to the rain forest of the Uluguru Mountains in eastern Tanzania, 1350-1500m alt.

Notes: An ally of the S.zanzibarense group of species which is readily identified by Werderman's description. It is represented at K by three specimens. The species has an indumentum characteristic of Solanum species growing in African rain forests.

69. **Solanum taitense** Vatke in Linnaea 43: 327 (1882). Type: Kenya, between Ndi and the River Tsavo, Hildebrandt 2605 (B?, Isotypes possibly at L, M, P). Slender stemmed scandent shrub to 1m tall, usually armed with small brown recurved prickles. Leaves lanceolate, entire or sub-repand, 2.5-3 x 0.8-1cm, both surfaces scabrous with stalked

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stellate hairs. Inflorescence 1-2-flowered, peduncle virtually absent; corolla violet, stellate, 1.5cm diam. Fruits red, 5mm diam.

Distribution: Bushland of northern Tanzania and Kenya, possibly extending into Ethiopia.

Notes: Often confused with S.hastifolium but distinguished by its inflorescence of one or two smaller flowers.

70. **Solanum hastifolium** Hochst. ex Dunal in DC., Prodr. 13 (1): 284 (1852). Type: Sudan, Kordofan, Kotschy 393 (Holotype MPU, Isotype K!).

Shrub, often scandent, to 2m tall, branches armed with small brown recurved prickles. Leaves ovate, entire or lobed, base shortly cuneate, generally 5 x 3cm. Inflorescence 2-4-flowered, peduncle virtually absent, pedicel of proximal flower arising close to stem, all other flowers borne at end of 1cm long rachis so appearing umbelliform; corolla violet, 1.5cm diam. Fruits red, 0.8cm diam.

Distribution: Deciduous bushland of North East Africa from northern Tanzania through Kenya and eastern Uganda to Ethiopia and Somalia.

Notes: Rather polymorphic shrub species of north-eastern Africa, often confused with S.sepicula Dunal and S.taitense

Vatke. From the description S.cynanchoides Chiovenda could probably be included in S.hastifolium. The Indian species S.trilobatum L. shows a close affinity and the two species may even be conspecific.

71. **Solanum erythracanthum** Dunal in DC., Prodr. 13(1): 201 (1852). Type: Madagascar, Emirna Province, Bojer s.n. (Holotype G-DC IDC microf.! 2078: I.4; Isotype K!).

Shrub to 2m tall with numerous small red or brown prickles, young branches with rust-red stellate tomentum. Leaves ovate, up to 9 x 4cm, entire or lobed, darker above than below, generally paired with a much smaller orbiculate leaf. Inflorescence sub-sessile with up to 5 flowers, pedicels to 2cm long; flowers stellate, tetramerous or pentamerous, violet, 2cm diam. Fruits red, 0.75cm diam.

Distribution: In the forests of Central and north-western Madagascar.

Notes: Within S.erythracanthum I would include S.myoxotrichum J. G. Baker and S.forsythii Dammer combined as a variety. The field notes on the specimens at K are insufficient and it is not possible to recognise a geographical separation between the two varieties.

Key to the varieties:

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Plants lacking bristles on the branches; leaves often repand
to sinuately lobed, apices acute

.... var. erythracanthum

Plants with dense bristles covering the branches; leaves
entire, apices acuminate

.... var. myoxotrichum

72. **Solanum flagelliferum** J. G. Baker in J. Linn. Soc. Bot.
20: 213 (1883). Type: Madagascar, Forest of Alamazaotra,
Baron 1482 (K!)

Shrub, with slender branches bearing scattered slightly
recurved prickles. Leaves ovate, entire, up to 6 x 2.5cm,
base unequal. Flowers solitary, sessile, arising from leaf
axils, stellate, tetramerous, 2cm diam. Fruits not seen.

Distribution: Central Madagascar.

Notes: The holotype alone represents this species at K.
Bitter did not cite Baron's specimen but recorded a
collection by Paulay from Diego Suarez on the northern tip
of Madagascar.

73. **Solanum cordatum** Forsskal, Fl. aegypt.-arab.: CVII & 47
(1775). Type: Yemen Arab Republic, Suq Ar Rubu', Forsskal
(C not traced) Neotype: Wood 2327 (K!) fide Wood (1984).

Shrub to 1m tall, usually armed with small brown prickles, idumentum of stellate sometimes porrect-stellate hairs. Leaves orbicular, 2.5 x 2cm, entire, usually bunched on short stalks. Flowers usually solitary, pedicels to 2.5cm long, flowers violet, 1.5cm diam. Only one dried fruit found (on 13 specimens) approx. 8mm diam., colour indeterminable.

Distribution: From North-East Africa through the Arabian Peninsular to India.

Notes: Wood (1984) reported that the species previously known as S.gracilipes Decne should correctly be called S.cordatum. Wood included S.hadaq Deflers in the synonymy to which I would add S.darassumense Dammer and S.numulifolium Chiovenda.

S.cordatum is often confused with S.forskalii Dunal but the many-flowered pedicellate inflorescence of that species is one obvious distinction. Bitter (1923) placed S.cordatum (as S.gracilipes) in a subseries and series of section Oliganthes with many other Solanum species of the African continent. It seems also to have affinities to the Madagascan species of section Croatii D'Arcy & Keating.

74. **Solanum setaceum** Dammer in Engler. Pflanzenw. Ost-Afrikas. C: 353 (1895). Type: Tanzania, Kilimanjaro District, Volkens 2202 (Holotype B?).

Shrub to 1.2m tall, slender branches densely covered with bristles up to 7mm long. Leaves ovate, base cordate, 2.5 x 1.5cm, both surfaces with indumentum of stalked stellate hairs. Inflorescence sub-sessile, 1-4-flowered, peduncle extending in fruit; flowers pale violet, 1.5cm diam. Fruits red, 0.8cm diam.

Distribution   In the deciduous bushlands of northern Tanzania and southern Kenya.

Notes: A local species recognisable by the bristles on the young branches.   Extracts from the roots are said to be useful for treating stomach ache and curing boils.

75.   **Solanum sp. nov.** = Lorence 1940 (K!).

Arcuate shrub to 3m tall with numerous small straight or slightly reflexed prickles. Leaves paired or often congested on short spurs, ovate, 1.25 x 1cm., entire, stellately tomentose. Inflorescence of 6 flowers; corolla pale blue, stellate, 1.5cm diam. Fruit enclosed in spiny calyx.

Distribution: Near Tulear in the south-west of Madagascar, in thorn scrub on sand dunes.   5m alt.

Notes: A distinctive plant only known from the one collection at K.

76. **Solanum supinum** Dunal in DC., Prodr. 13(1): 289 (1852). Type: South Africa, Cape of Good Hope, Drege 7861a (Holotype G-DC, IDC microf.! 2083: II.8 and Isotypes K!).

Small sprawling shrub to 40cm tall, well-armed with many straight prickles and bearing an indumentum of stellate hairs. Leaves elliptic, up to 6 x 2cm, sinuate lobed or pinnatifid . Flowers solitary, remote from the leaves, pale violet or white, 1.5cm diam. Fruits yellow, 1.5cm diam. half covered by prickly, accrescent calyx; seeds pale tan.

Distribution: In the wooded grasslands on the great Interior Plateau of southern Africa.

var. **leucophaeum** (Dunal) Bitter in Beih. Repert. Spec. nov. Regni veg. 16: 97 (1923) including S.leucophaeum Dunal in DC., Prodr. 13(1): 290 (1852). Type: South Africa, Cathcart Division, Drege 7859 (Holotype G-DC, IDC microf.! 2083: III.2 and Isotype K!).

Leaves less lobed and with a sparser indumentum than S.supinum sensu strictu.

Distribution: South-eastern Cape Province.

Notes: Bitter (1923) included S.aranoideum Dammer and S.lyratifolium Dammer as further varieties of S.supinum. With its large yellow fruits partially enclosed by a prickly

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calyx S.supinum seems rather remote from other species in section Oliganthes. There is some similarity to S.coagulans Forssk. and this possible affinity needs further investigation.

77. **Solanum sepicula** Dunal in DC., Prodr. 13(1): 283 (1852). Type: Yemen Arab Republic, Schimper 943 (1837) (Isotypes G-DC IDC microf.! 2003: I.7 and K!).

Shrubs to 0.6m tall, usually with a deep tap-root, branches armed with broad-based recurved prickles. Leaves linear or rectangular, entire or lobed, up to 11 x 5cm more usually about 4 x 1cm, lamina decurrent along petiole, both surfaces with sessile stellate hairs. Inflorescence 2-6-flowered, peduncle and rachis extending in fruit; corolla violet, 1.5cm diam., stellate becoming reflexed with age. Fruit orange (red sometimes ?), 0.8cm diam.

Distribution: On the dry slopes of upland areas in Ethiopia, Somalia and the Arabian Peninsular. Possibly extending into northern Kenya.

Notes: S.glabratum Dunal was based on the description of a plant identified in Forsskal's Flora Aegyptiaco-Arabica (1775) as 'S.bahamense?'. Dunal apparently never saw the specimens collected by Forsskal (YAR, Wadi Surdud, Forsskal 411 & 429 (C IDC microf.! 101: II.5, 6 & 7, 8)) since he used only Forsskal's own short description without

adding any of his own observations. He guessed from this that the species was similar to, if not the same as, S.sepicula. Although the microfiche is rather unclear, it seems that S.glabratum and S.sepicula are conspecific: if so, S.glabratum published in 1813 takes priority.

S.palmetorum Dunal is synonymous with S.sepicula/glabratum having been separated by Dunal on the basis of trivial leaf characters.

Although Bitter (1923) separated S.sepicula and S.hastifolium Hochst. ex Dunal into different series within section Oliganthes the two are easily confused. While the habit, leaf shape, indumentum and fruit colour can be used to distinguish them, hybridisation may have occurred where the ranges of the two species overlap.

78. **Solanum namaquense** Dammer in Bot. Jb. 53: 325 (1915). Type: Namibia, Engler 6636 (not traced but probably B or secondarily BRSL or CGE).

Rounded shrub to 80cm tall, armed with recurved, sometimes almost straight, prickles, indumentum of sessile stellate hairs. Leaves elliptic, up to 6 x 3cm, margin lobed sometimes deeply. Inflorescence few-flowered, corolla violet, 1-1.5cm diam. Fruit orange, 0.8cm diam.

Distribution: Karoo shrublands of southern Namibia and north-western Cape Province.

Notes: Although type material of S.namaquense has not been traced there is a Drege specimen without collecting number, but with the caption "S.capense Th.a", at K.   A duplicate of this specimen was cited by Bitter (1923) as being S.namaquense.   Taking this as true S.namaquense some 40 specimens at K, previously scattered throughout the South African collections by misidentification with a variety of names, can be brought together and named.

Confusion in identification has arisen from certain similarities between this species and, in particular, S.giftbergense Dunal and S.capense L.   Most other South African Solanum species names have also been used for this species. Bitter distinguished S.subrectemunitum Bitter (Type: Pearson 7955 isotype K!) as a separate species lacking the dense indumentum of S.namaquense; but I do not find this character sufficiently consistent to be able to identify even an infraspecific taxon.

S.moestum Dunal (Type: Drege 9355) is possibly an earlier synonym for this species.   It is not represented at K and the microfiche of the holotype at G-DC (IDC microf.! 2083:I.1) is insufficiently distinct to allow identification.

79. **Solanum capense** Linnaeus, Syst. nat. ed. 10: 935 (1759). Type: Sheet 248.46 in LINN! (IDC microf.! 140:II.2).

Semi-erect or prostrate shrub, armed with broad-based recurved prickles, indumentum of sessile stellate hairs. Leaves elliptic, often deeply lobed, up to 6 x 3cm, cuneate at the base but lamina not continuing along the petiole. Inflorescence 2-3-flowered sessile or sub-sessile; flowers white, 1cm diam. Fruits orange, 0.8cm diam.

Distribution: In the bushland of the east coast of South Africa, below the Drakensberg Mountains, 600-1200m above sea level.

Notes: I would take a more restricted view of this species than that held by Bitter (1923) and return S.capense var. sodomaeoides (O.K.) Bitter to specific status, taking with it S.capense var. wilmsii (Dammer) Bitter as a synonym and S.capense var. uniradiatum Bitter as a variety. S.capense is then left as a morphologically quite uniform species which occupies the lower lying bushlands to the south-east of the S.sodomaeodes range. The two species are clearly allied but easily distinguished.

S.millerii Jacquin and S.drezei Dunal are both synonymous with S.capense. Linnaeus combined S.capense with S.trilobatum L. in the second edition of Species plantarum

(1762) and subsequent publications, but these two are quite distinct.

80. **Solanum sodomaeodes** Kuntze in Revis. gen. pl. 3(2): 227 (1898). Type: South Africa, Natal, Glencoe, Kuntze s.n. (Isotype K!).

Small shrub to 50cm tall, heavily armed with broad-based recurved prickles, indumentum of long-stalked long-rayed stellate hairs. Leaves narrowly oblanceolate, deeply lobed, apex rounded, base narrowly cuneate decurrent along petiole, up to 7 x 2cm. Inflorescence 2-3-flowered, sub-sessile, peduncle and rachis extending in fruit; corolla white or very pale violet, to 1cm diam. Fruits orange, 0.8cm diam.

Distribution: On the slopes of the mountainous regions of the eastern side of South Africa. Generally in the range of 1500-2000m above sea level.

Notes: A small shrub of the high grasslands in eastern South Africa, S.sodomaeodes was placed by Bitter (1923) as a variety of S.capense L. These seem to me to be sufficiently distinct for each to be given specific status particularly as they grow in ecologically different regions.

S.wilmsii Dammer should be considered a synonym of S.sodomaeodes, and S.capense var. uniradiatum can be included here as a variety with a more sparse indumentum of

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stalked finger hairs (i.e. lacking the lateral rays of stellate hairs).

81. **Solanum giftbergense** aggregate.

Spreading shrubs to 40cm tall, armed with straight brown prickles 1cm or more long, indumentum of sessile or sub-sessile hairs at least when young, gland hairs sometimes present. Leaves elliptic, repand, up to 3 x 1cm (6 x 2cm in S.denudatum). Inflorescence 2-4-flowered, corolla violet. Fruits orange, 1cm diam.

Distribution: As an assemblage of taxa S.giftbergense agg. is distributed along a north-south belt on the western side of southern Africa, from Cape Province through western Namibia to Angola.

Included species:

S.giftbergense Dunal in DC., Prodr. 13(1): 288 (1852). Type: South Africa, Drakenstein or Giftberge Mts., Drege 7863 (Holotype G-DC not found on microfiche; isotype K!)

S.multiglandulosum Bitter in Beih. Repert. nov. Spec. Regni veg. 16: 74 (1923). Type: The following specimens from southern Africa cited with the original description: Baum 63, Rautanen 39, Liljeblad s.n., Kestita 54, Schinz 872 and Rautanen 713 (K!)

S.denudatum Bitter in Beih. Repert. nov. Spec. Regni veg. 16: 60 (1923). Type: Central Namibia, **Belek 6** (K!).

Notes: Each of the three species included is probably best treated as a subspecies of a single, widely distributed species. On the basis of a limited number of specimens each of the taxa seems to occupy a discrete area within the overall range of the aggregate, and although there are distinguishing characters to each taxon the appearance is of a series of populations which sometimes intergrade.

Bitter omitted **S.giftbergense** from his treatment of section **Oliganthes** : possibly he was unable to find type material in the De Candolle herbarium and so unable to identify the name. I have used the name **S.giftbergense** for this aggregate as the earliest name available amongst the three included species. However, it seems that **S.giftbergense** is a later synonym of **S.rigescens** Jacquin which I suspect has been misapplied almost since the date of its publication. **S.rigescens** was originally described in the **Plantarum** .... **Schoenbrunnensis** (Jacquin, 1797 I:19:42) and an accompanying plate depicts a plant more like the species now known as **S.giftbergense** than the eastern Cape species to which the name was subsequently applied. If this interpretation is correct **S.rigescens** should be rejected as a **nomen ambiguum**.

Typification of the Jacquin name and plate would help to

resolve this point, but Jacquin's specimens were distributed to many herbaria in Europe, and, as D'Arcy (1970) has pointed out, the search for Jacquin's type material is a major under-taking. The provenance of Jacquin's species was given as the Cape of Good Hope. Original material most likely was brought to Schoenbrunn by the Austrians Boos and Scholl who had been sent in 1786 to the Cape to collect plants for the royal garden. After almost two years collecting Boos returned to Austria with his collections and became keeper of the Schoenbrunn botanic garden. Scholl, meanwhile, remained at the Cape for a further 12 years. Little is known of the route followed by Boos and Scholl but it seems that together, or Scholl alone, they made collections as far north as Namaqualand and as far east as Transkei (Gunn & Codd, 1981). Such an itinerary would have taken the collectors into the range both of <u>S.giftbergense</u> on the west and of <u>S.rigescens</u> auctt. non Jacq. to the east.

82. **Solanum cymbalarifolium** Chiovenda, Flora somala: 241 (1929). Type: Somalia, Migiurtinia, <u>Chiovenda 1062</u> (FI?).

Shrub, branches well armed with straight yellow prickles and when young densely covered with simple hairs. Leaves reniform or orbicular, 1 x 1cm, both surfaces with simple and stellate hairs. Inflorescence 2-3-flowered; corolla violet, 1cm diam., stellate. Fruit (orange?), 0.7cm diam.

Distribution: North-eastern Somalia.

Notes: Identified from the original description and plate, one specimen (Collenette 208) represents this species at K. It resembles S.giftbergense Dunal from south-western Africa.

83. **Solanum piperiferum** A. Richard, Tent. fl. abyss. 2: 106 (1850). Type: Ethiopia, Tchelikote, Petit s.n.(fide Cufodontis (1963) Petit 226 at K! is an isotype).

Shrub, armed with narrow, straight prickles up to 1cm long, young stems stellate pubescent. Leaves elliptic, up to 3 x 1.5cm, entire or lobed, stellate hairs often with elongate mid-ray. Inflorescence 2-4-flowered; corolla white or pale violet 1.5cm diam. Fruits orange, 0.8cm diam.

Distribution: Ethiopian highlands, up to 2700m.

Notes: There seem to be two forms of this species : one with larger, entire leaves with elongate mid-rays to the stellate hairs, the other with smaller, lobed leaves with equal-rayed hairs. The latter form has been collected from lower altitudes than the former.

84. **Solanum pyracanthos** Lamarck, Tabl. encycl. 2(3) : 21 n.2364 (1794). Type: Madagascar, Joseph Martin s.n. (P-LA IDC microf.! series 6207 470:II.4).

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Shrub to 2m tall, with numerous straight orange-red prickles often over 1.5cm long. Leaves oblong, pinnatifid, 6-9 lobed, at least 5 x 4cm, stellately pubescent. Inflorescence 6-10-flowered, peduncle 1cm long; flowers pentagonal, violet, 2.5cm+ diam. Fruits globose, yellow; seeds pale yellow.

Distribution: Central Madagascar.

Chromosones: 2n=24 (Federov, 1969).

Notes: An attractive shrub with spectacular orange-red prickles. It is often cultivated in European botanic gardens.

85. **Solanum rautanenii** Schinz in Vjschr. naturf. Ges. Zurich 56: 265 (1912). Type: Namibia, Rautanen 726 (Isotype K!)

Shrub to 1m tall, armed with narrow often recurved prickles, indumentum of stalked stellate hairs. Leaves elliptic, up to 6 x 2.5cm, margins entire or repand. Inflorescence 2-3-flowered, sub-sessile, peduncle and rachis entending in fruit; flowers violet. Fruits orange, 0.5 - 1cm diam., enclosed while developing by prickly calyx.

Distribution: In the interior of southern Africa from Namibia across to Natal.

Notes: An unremarkable species with a wide distribution through the _Acacia_ bushlands of southern Africa. Bitter (1923) included _S.sparsiflorum_ Dammer as a synonym.

86. **Solanum rubetorum** _Dunal_ in DC., Prodr. 13(1): 304 (1852). Type: South Africa, Cape Province, _Drege 7858_ (Holotype G-DC IDC microf.! 2085:I.6 and Isotype K!).

Shrub to 2m tall, armed with straight, narrow prickles, indumentum of stalked stellate hairs. Leaves elliptic, sinuately lobed, 5 x 2cm (up to 8 x 3cm). Inflorescence racemose, 6-8-flowered, corolla 2-3cm diam., deep purple. Fruits orange, 1cm diam.

Distribution: Dried specimens studied have been collected from three quite widely separated regions of South Africa : the type and the bulk of the specimens were collected in eastern Cape Province, other collections were made in northern Transvaal and Natal.

Notes: Bitter included _S.rubetorum_ as a variety of _S.rigescens_ Jacquin. I believe that he misapplied the name _S.rigescens_ which should have been used for the taxon otherwise known as _S.giftbergense_ (see notes above under _S.giftbergense_). Bitter's understanding of _S.rigescens_ can be confirmed by the presence at K of duplicates of representative specimens which he cited as true _S.rigescens_. I include all of these in _S.rubetorum_.

The leaf surface indumentum of many of the specimens of S.rubetorum is distinctive, with hairs on multi-cellular conical stalks with lateral rays emerging from the apex. This feature is also seen in S.anguivi and associated species. The character state is not uniform within the concept of S.rubetorum presented here, and some specimens bear ordinary stalked stellate hairs. However, I can find no correlations, morphological or geographical, with either hair type within the species.

S.didymanthum Dunal should be included as a synonym.

87. **Solanum forskalii** Dunal, Hist. nat. Solanum: 237 (1813). Type: Yemen Arab Republic, Wadi Surdud, Forsskal 414 (Holotype C, IDC microf.! 102:II.7,8).

Shrub to 1m tall, densely armed with long reflexed prickles, indumentum of stellate hairs, young branches densely tomentose. Leaves ovate, to 6 x 4cm, entire or repand. Inflorescence cymose, often branched, up to 20 flowers; corolla violet, stellate, 2cm diam. Fruits orange, 0.7cm diam.

Distribution: Dry country shrub, occuring in a belt extending across Africa, from Senegal to Ethiopia and northern Kenya, and on through the Arabian Peninsular to India.

Notes: Hepper and Wood (1983) have shown that S.forskalii is the correct name for the species previously known as S.albicaule Kotschy ex Dunal. Other synonyms are S.villosum Forsskal non Miller, S.heudelotii Dunal and S.scindicum Prain.

In Dunal's (1852) classification of Solanum, S.albicaule, its synonym S.heudelotii and the Madagascan species S.erythracanthum Dunal were the only African species in his section Juripeba. Bitter (1923) subsequently removed them and combined them into section Oliganthes where S.albicaule was placed in its own series (Albicaule) reflecting its distinctness from the other African species. While S.forskalii has some affinities to the species of section Oliganthes its bifurcate cymose inflorescence structure is reminiscent of S.somalense (sect. Anisantherum), S.schimperianum (sect. Torva) and S.vespertilio (sect. Nycterium). The difficulty of its taxonomic placement may be a reflection of the possession of plesiomorphic characters, and its removal to another section must wait until the phylogeny of the African species is better understood.

86. **Solanum sp. nov.** = Thomas 3436 (K!) collected Karamoja, Uganda.

Virgately branched shrub to 1m tall, unarmed, indumentum of stalked stellate hairs with upward pointing lateral rays.

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Leaves very narrowly elliptic, to 8 x 1.5cm, dark green above, paler below. Inflorescence at first terminal, cymes lax, 5-8(-10)-flowered; flowers pale violet, 1cm diam. Fruit orange (or red) 0.7cm diam.

Distribution: Through the evergreen and semi-evergreen bushlands of north-eastern Africa (1500-1900m alt.). White (1983) records that extensive areas of this ecological unit have been degraded to wooded grasslands.

Notes: A widely collected species currently lacking a name. From the original description and accompanying plate (Lanza, 1939 pp.190-191) S.angustifolium Lanza seems to correspond to this species, but there are some discrepancies notably in characters of the inflorescence.

While the species has the overall appearance of belonging to section Oliganthes its inclusion here is uneasy; it has no obvious relationship to another African species in the section. The possibility that this is not a native plant should be considered (note its occurrence in secondary vegetation types) but I have been unable so far to match it to a known extra-African species.

Section 15 **Ischyracanthum** **Bitter** in Beih. Repert. nov. Spec.
Regni veg. 16: 142-147 (1923). Type species: S.ogadense
bitter (_fide_ Seithe, 1962 - nominated without having seen
material of S.ogadense or the section).

Shrubs or bushes to 4m tall, with dense stellate tomentum at
least when young, heavily armed with compressed recurved
prickles on the branches and straight prickles on the leaf
mid-ribs; inflorescence few-flowered, tending to
andromonoecy, flowers mauve; fruits yellow, with a tough
pericarp; seeds brown.

Notes: A section of two or perhaps three species from North
East Africa. The andromonoecious inflorescence and the
yellow fruits are reminiscent of section **Melongena** species
but the tough pericarp is quite distinctive and is not found
in other African species of **Solanum**. The occurrence of two
forms of prickles, being recurved on the stems and straight
on the leaves, is a useful character for recognising the
section.

Key to the species:

1. Tall shrub or bush; mature leaves elliptic, glabrous or
     with scattered stellate hairs, margins
     sinuate; leaf prickles 5-15mm long
     .... 89. S.arundo

1'. Medium shrub; mature leaves ovate, with dense tomentum

of stellate hairs, usually entire; leaf prickles

2-5mm long

.... 90. S.dennekense

89. **Solanum arundo** Mattei in Boll. R. Orto bot. Palermo 7:

188 (1908). Type: Somalia, Mogadiscio, <u>Macaluso 82</u> (PAL).

Much branched, bushy shrubs to 4m tall, heavily armed with

compressed recurved prickles on the stems and branches,

young branches tomentose with small pulverulent hairs,

becoming glabrous. Leaves generally elliptic, repand to

sinuate, up to 5 x 3cm, at first with scattered minute

stellate hairs later glabrous, armed with 2-4 acicular

prickles. Inflorescence 4-5-flowered, corolla stellate,

2.5-3cm diam., deeply lobed, lobes tomentose on both

surfaces. Fruits yellow, hard, 2.5cm diam., partially

enclosed in accrescent calyx.

<u>Distribution</u>: Tanzania, Kenya and Somalia.

<u>Notes</u>: Bitter (1923) only knew <u>S.arundo</u> from the

description by Mattei which he found to be inadequate for a

positive identification of the application of the name. The

species was not written up for <u>Solana africana</u> further than

being mentioned as possibly belonging to section

<u>Ischyracanthum</u>. From the description <u>S.arundo</u> is synonymous

with <u>S.diplacanthum</u> Dammer, <u>S.helleri</u> Standley and

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S.gillettii Hutch. & E. A. Bruce.

S.arundo is often used as a hedging plant on account of its dense bushy habit and its prickliness.

90. **Solanum dennekense** Dammer in Bot. Jb. 38: 57 (1905). Type: Ethiopia, Arussi-Galla, Ellenbeck 1965 (B+?).

Robust shrub 2-3m tall, densely tomentose with stellate hairs, stems armed with broad-based recurved prickles. Leaves ovate, entire or repand, 6 x 4cm, tomentose, armed on the mid-rib with 1-2 acicular prickles. Inflorescence 5-9-flowered; corolla 2.5-3cm dia., stellate, violet, lobes with hairs on both surfaces. Fruits yellow, hard, 2.5cm diam., partially enclosed in accrescent calyx.

Distribution: Ethiopia, Somalia, Kenya and Tanzania.

Notes: From the description S.ogadense Bitter is probably synonymous with this name. If differs only in having yellow stellate hairs, smaller leaves and larger prickles.

Section 20 **Melongena** Dunal, Hist. nat. Solanum: 208 (1813). Type species: S.melongena L. (fide D'Arcy, 1972).

Perennial herbs, shrubs or small trees, prickly or unarmed, usually with a stellate tomentum; leaves entire, repand or more deeply lobed, ovate or elliptic; inflorescence few-flowered, only the proximal, or lower 2-3, flowers hermaphrodite the rest male; corolla violet or white and violet tinged, stellate or pentagonal; fruit yellow, white or purple, with a fleshy pericarp.

Notes: Within Africa section Melongena is a recognisable group of species, delimited by andromonoecy and the combination of violet flowers with yellow (in wild species) fleshy fruits. The only controversy in Africa might be over the inclusion of section Ischyracanthum within Melongena; worldwide the extent of the section is more difficult to define.

The delimitation of the section has been in dispute since Bitter (1923) split Dunal's (1852) series Melongena placing some species into section Oliganthes while combining S.melongena and other allied species with Dunal's series Logenoplum to form section Andromonoecum. D'Arcy (1973) took an inclusive view of the section as one comprising many species in the New World and in Africa, and he believed it to be perhaps the largest section in the genus in terms of the number of species included. Symon (1981) however held a

narrower view and included species from Africa and Australia while expressing doubt as to whether there were any species native to the Ameriacas. Whalen (1984) has restricted the limits of his informal version of section _Melongena_ (called by him the "_Solanum incanum_ Group") to the African species some of which are represented in the Middle East and southern Asia.

I agree with Whalen's interpretation, but for the present treatment I have included one further species, the South American _S.wrightii_ Bentham. The species surely does not belong here but having been placed in the section by Bitter (p.180, 1923 as _S.grandiflorum_ Ruis & Pavon) it is convenient to leave it until its taxonomic affinities are better understood.

I have accepted six African species in the section as well as one domesticated species, the type species _S.melongena_, and one aggregate species, _S.incanum_ L. agg. The species occupy a diversity of habitats from the Cape shrubland and the bushland of north eastern Africa to the Afromontane forests.

Key to the species:

1. Cultivated annuals, biennials or shrubs; usually unarmed
       but sometimes with prickles on the fruiting calyx,
       fruits more than 5cm diam.

.... 2.

1'. Shrubs, bushes or small trees; not cultivated; generally
     armed; fruits rarely more than 5cm diam.

.... 3.

2. Plants glabrous or sparsely hairy; leaves broadly
    sinuate, the lamina continuing along the petiole;
    fruits globose, white or yellow; gynoecium with
    glandular hairs

.... 91. S.macrocarpon

ssp. macrocarpon

2'. Plants with an obvious indumentum of stellate hairs,
    leaves repand, the base round or obtuse; fruits
    globose or more often obovate or pyriform, purple or
    less often ivory white; gynoecium with stellate hairs

.... 92. S.melongena

3. Large shrubs or trees growing to more than 5m tall

.... 4.

3'. Smaller shrubs

.... 5.

4. Prickles recurved; leaves glabrescent above, lower
    surface with a thick white indumentum; inflorescence
    5-10-flowered, flowers ca 2cm diam.; fruit yellow

.... 93. S.aculeastrum

4'. Prickles straight; leaves with simple hairs on the upper
surface, stellate below; inflorescence with 20 or
more flowers, corolla 5-7cm diam.; fruit red

.... 99. S.wrightii

5. Plants of forest areas; leaves hirsute with sessile
stellate hairs, the median rays of which are very
long (to 1.5mm) giving a pilose appearance; gynoecium
with glandular hairs

.... 6.

5'. Plants of drier areas, leaf hairs not as above;
gynoecium with stellate hairs

.... 7.

6. Leaves elliptic to oblong, pinnatifid, base cuneate
continued along the petiole

.... 91. S.macrocarpon
ssp. dasyphyllum

6'. Leaves ovate, sinuate, base truncate

.... 94. S.sessilistellatum

7. Leaves coriaceous, becoming glabrous above with a
conspicuous white indumentum below

.... 95. S.marginatum

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7'. Leaves membranaceous, indumentum not as above

.... 8.

8. Leaves entire

.... 96. S.incanum agg.

groups A & D

8'. Leaves lobed or at least repand

.... 9.

9. Flower diameter 4-6 cm

.... 97. S.richardii

9'. Flower diameter up to 4cm

.... 10.

10. Leaves becoming glabrous; shrubs of south coast of South

Africa or the western Mediterranean region of North

Africa and southern Europe

.... 98. S.linnaeanum

10'. Leaves usually tomentose; shrubs or scrub or wooded

grassland and occasionally forest

.... 96. S.incanum agg.

groups B, C and E

91.   **Solanum macrocarpon** Linnaeus, Mant. pl. 2 : 205 (1771).
Lectotype: Sheet 248.11 in LINN (IDC microf. ! 138:II.3).
The selection of this lectotype is discussed in the notes
below.

Much branched subshrub, up to 1.5m high, glabrous to
hirsute, unarmed or armed (see subsps.). Leaves elliptic,
10 x 5 x 15cm, sinuate to pinnatifid, cuneate and
characteristically continued along the length of the
petiole.   Inflorescence ca 8-flowered, corolla white to
violet or bluish, up to 4cm diam., campanulate, lobed; style
only developed in the proximal flower.   Fruit yellow, white
or brown, globose, up to 8cm diam., fleshy; seeds brown.

Notes: This frequently cultivated species has been known in
Europe at least since the end of the seventeenth century.
The first publication of the name S.macrocarpon is found in
Linnaeus' Mantissa altera (1771) where unfortunately two
distinct species were included as synonyms.   This confusion
was soon understood and corrected and has since been the
subject of a detailed paper by Burkill (1925) who found that
in all, four species had been confused with each other.

It seems that the typification of S.macrocarpon, which
Burkill did not discuss, introduces further complications.
The problems arise from Linnaeus' confusion of a specimen of
this species with the South American species S.bonariense
which he described in the Species Plantarum (p.185 (1753)).

Morton (1976), in a revision of the Argentine species of Solanum, designated sheet 248.10 in the Linnean herbarium (LINN) of a plant grown at Uppsala as the lectotype of S.bonariense. He considered that the only paratype was a plate in Dillenius' Hortus Elthammensis (p.364 t.272 f.351 (1732)) which was cited by Linnaeus in the protologue, but Morton was apparently unaware of sheet 248.11 in LINN. This sheet bears a specimen, also grown at Uppsala, of S.macrocarpon but the original determination in Linnaeus' handwriting reads '7 bonariense'. Linnaeus subsequently deleted the epithet 'bonariense' and wrote 'macrocarpon' beside it. Several factors indicate that this sheet is a more likely type of S.bonariense than sheet 248.10.

Firstly, the numeral '7' preceeding the epithet 'bonariense' on sheet 248.11 refers to S.bonariense being the seventh species of the genus Solanum in Species Plantarum (ed 1, p.185) and implies that this specimen was used in the original description. If sheet 248.10 was the earlier specimen it would surely have been given this number instead of sheet 248.11.

Secondly, the sheets 248.10 and 248.11 display specimens which are so distinct that it is difficult to believe that Linnaeus could have considered them to be the same species if he had studied them together. Thus if sheet 248.10 was the earlier specimen it is unlikely that, with that sheet for comparison, Linnaeus would have identified sheet 248.11

as S.bonariense. It seems more probable that sheet 248.11 was the earlier specimen and the subsequent accession of the living material which is now represented on sheet 248.10 caused Linnaeus to change his mind about the identity of sheet 248.11. If this is so, sheet 248.10 cannot be used as a lectotype for S.bonariense.

Thirdly, the likelihood that sheet 248.11 preceeded sheet 248.10 is reinforced by the difference between Linnaeus' discussion of S.bonariense in Species Plantarum and that in the Mantissa Altera (p.205). In the Species Plantarum Linnaeus wrote in the diagnosis of S.bonariense '.... foliis cuneiformibus ....' but subsequently altered this in the Mantissa to '.... foliis ovato-oblongis ....'. The adjective 'cuneiformibus' could only apply to material on sheet 248.11 whereas 'ovato-oblongis' describes the material on sheet 248.10.

Finally, in the Mantissa Linnaeus wrote under his modified description of S.bonariense 'Obs. deleatur Sol. bonariense in Sp. plant. hoc restito'. The next species on the page is S.macrocarpon and the protologue to this species is concluded with the words 'Obs. distincte seperandum a Solano bonariensi'. Thus Linnaeus evidently realised that his original concept of S.bonariense, including the Dillenian plate and sheet 248.11, embraced two species . After seeing the growing plant now represented on sheet 248.10 he sought to rectify this situation in the Mantissa by redefining

S.bonariense and restricting it to the Dillenian plate and the sheet 248.10 after removing sheet 248.11 to the new species S.macrocarpon. As mentioned above, this did not fully resolve the problem as the protologue of S.macrocarpon included two further species (S.quitoense Lam. and the obscure S.plumieri Jacq.) as synonyms.

The implications of Linnaeus' confusion over the identity of sheet 248.11 depend on whether he based the Species Plantarum diagnosis of S.bonariense on sheet 248.11 or on the Dillenian plate cited in the protologue. If he used the former then the species hitherto known as S.macrocarpon should be known correctly as S.bonariense, but if the illustration typifies S.bonariense then no changes are involved. Unfortunately it is more likely that the diagnosis is based on 248.11 than on the illustration for two reasons. Firstly, Linnaeus changed the description of the leaves of S.bonariense between Species Plantarum and Mantissa as already discussed, and then described S.macrocarpon as '.... foliis cuneatis ....' using almost the same adjective as he had used for S.bonariense in Species Plantarum. This implies that the element on which the Species Plantarum diagnosis of S.bonariense is based is now being used to describe S.macrocarpon.

Secondly, that Linnaeus wrote under the Mantissa description of S.bonariense 'Obs. deleatur Sol. bonariense in Sp. plant. hoc restituto' but included the same reference to Dillenius

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as a synonym, strongly suggests that he had used sheet 248.11 for the original diagnosis of S.bonariense but derived the name from Dillenius' 'Solanum Bonariense arborescens, ...'. In realising that he had combined two species he elected to keep the epithet 'bonariense' with the Dillerian species, to which it was more appropriate, and to remove the plant on sheet 248.11 to a new species. Thus S.bonariense had to be redefined.

If S.bonariense is typified by sheet 248.11 then the species previously known as S.macrocarpon should be called S.bonariense. This would lead to confusion: S.bonariense has been used since Linnaeus' Mantissa for a good Argentine species and its use for the African species should be avoided. The next available name for the African species is fortunately Linnaeus' S.macrocarpon, which can be typified, therefore, by sheet 248.11 in LINN, but the species hitherto known as S.bonariense is now left without a name. This unnecessary name changing can be avoided by using the Dillenian plate to lectotypify S.bonariense on the grounds that it is impossible to be certain that Linnaus did not use the illustration as well as the specimen for the diagnosis in Species Plantarum. As the Dillerian plate is not in serious conflict with the protologue I would nominate it as lectotype of bonariense, in preference to sheet 248.10 in LINN.

Solanum macrocarpon is accepted for the present thesis as

including the armed, hirsute wild species previously known as S.dasyphyllum Schum. rather than being solely restricted to the usually prickleless and glabrous cultivated plants. The distinction of the two supposed species was never satisfactory as both are very variable, and the variation of one species is often found to overlap with that of the other species. It is increasingly apparent that the form known as S.macrocarpon is a cultivated modification of the wild plants previously known as S.dasyphyllum, and that in the process of domestication prickleless and glabrous forms have been selected. Such selection is to be expected as domesticated S.macrocarpon is grown as a leaf vegetable as well as for its fruits.

Bitter (1923) treated S.macrocarpon and S.dasyphyllum as separate species but was perplexed by their obvious affinity to one another. He attempted to impose order on all the variants by dividing the material available to him into eight varieties of S.dasyphyllum, and two subspecies, six varieties and two forms of S.macrocarpon. These infraspecific taxa were ignored by Heine (1963) in his account of Solanum in West Africa but he maintained the two species noting that S.macrocarpon might be a glabrous form of S.dasyphyllum.

Morphological and experimental studies by Bukenya (MSc. thesis, 1980; J. B. Hall pers. comm.), carried out on locally collected material in Ghana, indicated that

S.dasyphyllum and S.macrocarpon are not true and different species. Bukenya considered them to be synonymous under the earliest name and his arrangement is adopted here.

In order that the wild and the cultivated forms be distinguished within the one specific name it is necessary to give them taxonomic rank. It seems that subspecies status is appropriate as this may be used to group the cultivars which have been developed. Although the rank of subspecies is generally applied to discrete populations which are geographically separate, which subsp. macrocarpon and subsp. dasyphyllum are not, the continued cultivation of subsp. macrocarpon generally maintains its genetic integrity, though many variants must be the result of 'hybridizations'. There can be no definite morphological limits prescribed to distinguish the one subspecies from the other, but it seems practicable to apply the respective names according to whether the material is intentionally cultivated or not.

Key to the subspecies:

Plants generally glabrous and unarmed but sometimes sparsely
        hairy and/or with scattered prickles; leaves broadly
        sinuate; flowers sky blue; calyx rarely accrescent in
        fruit; fruits up to 8cm; cultivated
                .... subspecies macrocarpon

Plants generally hirsute and armed with numerous yellow

prickles; leaves deeply bi- or tri-pinnatifid; flowers

pale violet or white; calyx accrescent in fruit; fruits

generally 3-4cm diam; wild

.... subspecies <u>dasyphyllum</u>

Subsp. **macrocarpon.**

<u>Chromosomes</u>:   2n=24 (Omidiji, 1979) but Federov (1969)

citing Miege (1962) gives 2n=36.

<u>Distribution</u>:   Cultivated in many parts of tropical Africa

and Madagascar, generally in wetter areas; also grown in

Malaya, the West Indies and Brazil (Burkill, 1925).

<u>Notes</u>:   In view of the extent of the cultivation of this

species it is surprising how little information on the

taxonomy, biology or cultivation has been published.   The

work which has been reported has frequently been obscured by

incorrect identifications : the species has been confused

with, for example, <u>S.melongena</u> L., <u>S.aethiopicum</u> L. and

<u>S.incanum</u> L.   It is therefore important that the species is

the subject of taxonomic study so that a stable

nomenclatural framework can be established.   The work of

Bukenya (1980, MSc thesis) on Ghanaian material of this

species has initiated such a development which should be

continued on a wider scale.   Bukenya concluded from his

studies that <u>S.macrocarpon</u> and <u>S.dasyphyllum</u> should not be

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maintained as separate species and that when combined, subsp. macrocarpon in Ghana could be divided into six forms. He designated these forms as cultivars since each form was peculiar to a limited area within Ghana. The cutlivars are probably maintained as distinct forms by the cultural preferences of the local growers and their markets and by the rarity of any exchange of living material between the different areas where the species is grown.

Since the morphological characters which are said to distinguish subsp. macrocarpon from subsp. dasyphyllum are found in a continuous range of variation within the species, it seems likely that the two subspecies occasionally hybridize. Burkill (1925), in his paper on S.macrocarpon, quoted observations by the Belgian botanist de Wildeman on the cultivation of S.sapini de Wild., a synonym of subsp. macrocarpon. De Wildeman found that in the second generation "two forms were obtained, one being spinous and the other without spines; the first fertile, the second rarely so". He concluded that the species, S.sapini, was hybrid of S.duplosinuatum (a synonym of S.dasyphyllum) with "another species which may or may not be S.macrocarpon".

The thesis that hybridization with an unidentified species featured in the evolution of subsp. macrocarpon cannot be defended properly without further study, but since the cultivated subspecies is so similar to the wild one extensive backcrossing of an original hybrid to subsp.

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<u>dasyphyllum</u> would have to have occurred to lead to the present forms. However, the diagnostic characters of the subspecies are ones which would be selected for, consciously or unconsciously, in the process of domestication : prickles and hairiness are undesirable in a leaf vegetable while an increase in fruit size is appreciated by the fruit harvester. Thus gradual selection by human intervention may have altered these characters and the occasional backcross to the wild progenitor would account for the continuous range of variation. Unless another parent species can be identified, introgressive hybridization seems a less likely explanation for the evolution of the forms <u>S.macrocarpon.</u>

The following names have been applied to this subspecies:- <u>S.crassifolium</u> Salisb., <u>S.thonningianum</u> Jacq., <u>S.mors-elephantum</u> Dammann, <u>S.zanoni</u> Gouan, <u>S.dimorphum</u> Matsumura, <u>S.atropo</u> Schum. and <u>S.sapini</u> de Wild.

Subsp. <u>dasyphyllum</u> (Schum.) <u>ined.</u>

Type: "Guinea", <u>Thonning 144.</u> Three sheets of this collection are known:- two sheets are at C (IDC microf! 2203 102:I.1-4) and one at G-DC (IDC microf! 2085:III.7).

<u>Chromosomes</u>: 2n=24 (Omidiji, 1979).

<u>Distribution</u>: Many parts of tropical Africa as well as South Africa. Often found growing in or around settlements,

generally in forested areas.

Notes: Synonyms of S.macrocarpon subsp. dasyphyllum include S.dasyphyllum Schum., S.acanthoideum Dunal, S.afzelii Dunal, S.duplosinuatum Klotzsch, S.farini Dammann, S.kilimandschari Dammer and S.macinae A. Chev. The identity of S.eickii Dammer and S.crepidotrichum Bitter is no longer certain as the types were most likely destroyed in the bombing of the Berlin herbarium, but Bitter (1923) discussed both as being similar to S.dasyphyllum. Similarly, the type of the Kenyan species S.sessilistellatum Bitter is also missing, but the description leaves little doubt as to its identity, and, although it shows considerable affinity to subsp. dasyphyllum, it is distinct.

Although subsp. dasyphyllum is frequently found in the vicinity of native settlements it does not seem to be cultivated. Dalziel (1937) recorded that it was said to be used to cure ring worm and as an antidote to Strophanthus (Apocynaceae) poison.

92. **Solanum melongena** Linnaeus, Sp. Pl. ed. 1: 186 (1753). Type: lectotypified by D'Arcy (1974a) with LINN 248.28 (IDC Microf! 139:II.2!).

Shrub to 1m tall, usually unarmed but occasionally with scattered prickles, pubescent with dense stellate hairs. Leaves up to 15 x 10cm, elliptic, lobed. Inflorescence few-flowered, racemose, proximal flower hermaphrodite and much larger than subsequent female-sterile flowers; corolla violet, to 4cm diam. on hermaphrodite flower, less on others, campanulate, lobed; style only developed in proximal flower. Fruit variable in colour, shape and size, usually dark purple (but may be pale to ivory white) at commercial ripeness, but eventually becoming yellow or brown, obovate (but may be globose), up to 20cm long. Seeds brown.

Chromosomes: n=12,18,24 Federov (1969) most likely 12.

Distribution: Widely cultivated as a fruit vegetable in many tropical and warm temperate parts of the world.

Notes: A species well-known in Europe for over 200 years it is often known by the common names of Aubergine, Brinjal or Eggplant. **S.melongena** is cultivated for its fruits which when cooked are valued by some as a useful vegetable. It is quite widely grown in Africa but it is really only of significance in the southern African diet. Its origin is uncertain but Pearce (1975) and Pearce and Lester (1979)

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have discussed the close taxonomic relationship with S.incanum L. agg. It seems likely that S.melongena was domesticated from S.incanum in Indo-China.

Breeding work has led to a large number of cultivars with particular variation in fruit characteristics.

93. **Solanum aculeastrum** Dunal in DC., Prodr. 13(1): 366 (1852). Type: South Africa, Cape Province, Morleg, Drege (Vb, as S.sodomeum) (G-DC, IDC microf! 2091:III.4).

Shrub or small tree 1-6m high, usually heavily armed with large brown recurved prickles up to 1.5cm long, young branches with grey or pale brown tomentum. Leaves ovate up to 15 x 13cm, usually deeply lobed, upper surface glabrescent, lower surface thickly tomentose, white. Inflorescence 5-10-flowered, only the proximal one(s) female-fertile; corolla white or pale violet, rotate-stellate, 2cm diam. Fruits yellow, globose or ovoid, up to 6cm diam., surface often verrucose.

Chromosomes: 2n=24 (Gottschalk, 1954b).

Distribution: Occurs in the Cameroon Highlands, and in East Africa extends from the Imatong Mountains in Sudan to the Cape in South Africa. Scattered records are known from Angola and western Zaire. Generally found above 1200m alt. at forest margins and in grassland.

Notes: A rather variable species which is widely
distributed on African upland grasslands.   The species is
largely confined to the archipelago-like Afromontane Region
discussed in Chapter 4 of this thesis.   The occurrence of
the species at scattered localities in Angola adds evidence
to the hypothesis (White, 1981) that tree migration between
the Cameroon Highlands and the East African mountains
followed a southern route.

Several uses have been recorded for this species but most
commonly S.aculeastrum is reported in use as a hedge or as
living fencing material for retaining livestock.   It is well
suited to this purpose on account of the speed of its growth
and its eventual size and in particular its large, hooked
prickles.   In consequence, it is often collected growing in
thickets close to villages. Watt and Breyer-Brandwijk (1962)
noted that the fruits are used as a remedy for ringworm in
cattle and horses though both the immature and the mature
fruit are recorded as poisonous, and they also reported that
the ash of the fruit has been used to relieve rheumatism.
The notes accompanying Gover, Gwynne & Samuel 935 (at K)
observe that the Masai use the roasted fruit in a tonic for
babies, and an infusion of the root is taken as a cure for
gonorrhoea.   Bitter (1923, p.170) mentioned that the fruits
were sometimes used as a soap substitute while the notes
with Hendricks 1410 (at K) suggest that the fruit can be
used to kill fish.   Both these last two uses imply that the
fruit has a high saponin content.

Bitter (1923, pp.165-175) placed S.aculeastrum in series Aculeastrum together with a species which he named S.protodasypogon. Although he numbered and described the two species separately he considered them to be components of a single "Grossart", S.aculeastrum (Dun.) sens. ampl. Bitter. From the description it seems that S.protodasypogon is synonymous with the earlier named S.thomsoni, the holotype of which is at K.

Bitter divided S.aculeastrum itself into three subspecies mainly on the basis of indumentum characters. Since these characters are particularly variable the subspecies are not worth maintaining. The five varieties into which he divided subspecies aculeastrum again serve little purpose, though some apparently prickleless material from localities near Lake Kivu in Zaire might belong to var. albifolium (C. H. Wright) Bitter or var. conraui (Dammer) Bitter. Although the large recurved prickles are very characteristic of this species, prickliness is variable in subgenus Leptostemonum and the absence of prickles from a specimen need not imply absence from the whole plant.

For the present thesis I would include the following as synonyms of S.aculeastrum: S.saponaceum Welwitsch, S.albifolium C. H. Wright, S.thomsoni C. H. Wright, S.sepiaceum Dammer, S.conraui Dammer, S.protodasypogon Bitter and S.subhastatum De Wildeman and I would divide the species into two further subspecies according to the key

below. These subspecies account for the diversification in the East African material of this species.

Key to the subspecies:

1. Fruits ovoid; leaves elliptic, repand; prickles scarce

.... subsp. 1

1'. Fruits globose; leaves ovate, sinuate lobed; prickles generally numerous

.... 2.

2. Young parts tomentose with white hairs; one or two fruits per infructescence, fruits more than 2cm diam.

.... subsp. aculeastrum

2'. Young parts hirsute, hairs brownish, if stellate then with long rays; more than two fruits per infructescence, fruits 1.5-2cm diam.

.... subsp. thomsoni

subsp. thomsoni (C. H. Wright) comb nov.

This subspecies includes the hirsute, multiple fruiting material from southern Tanzania though there is a record at K, Thomas 3812, from Uganda. From the description S.proto-dasypogor Bitter belongs here but type material must be found for this to be confirmed.

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subsp. **1**.

This subspecies covers the distinctive, scarcely armed specimens with ovoid fruits collected from central Kenya and northern Tanzania.

54. **Solanum sessilistellatum** Litter in Beih. Repert. nov. Spec. Regni veg. 16: 187 (1923). Type: Kenya, G. S. Baker 39. Baker's collection went to the Berlin herbarium and Lanjouw & Stafleu's (1954) index of collectors does not record duplicates having been sent elsewhere. If the holotype was destroyed during the bombing of Berlin it seems that a neotype must be designated.

Armed shrub to 1m high, stems often purple, pubescent throughout with sessile stellate hairs, the lateral rays short, median rays very long (to 1.5mm) giving a pilose appearance, hairs on young stems tinged purple, prickles yellow, straight, numerous. Leaves ovate, sinuate, about 6 x 4cm, armed, base truncate and not decurrent on petiole. Inflorescence with 6 flowers, racemose, only proximal flower female-fertile; corolla showy, stellate, up to 5cm diam., bright purple. Fruits yellow, 2-3cm diam.

Distribution: Endemic to Kenya, generally found growing in the bushland at forest edges at 2000-2900 alt.

Notes: Despite the absence of type material for this

distinctive species Bitter's (l.c.) description leaves little doubt as to its identity. However, I have found a specimen at K, Scheffler 279, collected in Limuru (Kenya) which is an isosyntype of S.nigriviolaceum Bitter but which had not been recognised as type material at K but included within S.sessilistellatum. This type is certainly the same species as the plants previously named S.sessilistellatum, though Bitter placed the two species in separate series of section Andromonoecum (=Melongena). The name S.nigriviolaceum has been ignored at K and probably elsewhere, partly because the type has gone unrecognised until now but also because Bitter's description of the species as having long decumbent branches is rather misleading. It seems therefore that S.nigriviolaceum and S.sessilistellatum are synonymous, though type material of the latter must be studied to confirm this.

Since both names were first published in the same publication neither can be given automatic precedence, but as S.sessilistellatum is in current use it is maintained here with S.nigriviolaceum as a synonym.

Glover, Gwynne & Samuel 1093 (at K) recorded that the charred roots of this species were chewed by the Masai tribe as a cough remedy.

55. **Solanum marginatum** L.f., Suppl. pl. 147 (1782). Type: The sheet 248.45 in LINN (IDC microf! 140:II:1) displays a

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specimen of <u>S.marginatum</u> and has been annotated "HU" (for Hortus Uppsaliensi) probably by the hand of the son of Linnaeus (Savage, 1945). The only traveller known to have collected in Ethiopia, where the species is native, prior to the publication of this species was the explorer James Bruce who journeyed through the country during the years 1768-1773 and whose collection was sent to Paris on his return. In the course of his travels he collected a certain amount of seed material including, apparently, seeds of <u>S.marginatum</u> for there is a specimen at BM which is annotated on the reverse side of the sheet "Hort. Kew. 1777 Sem. ex Abyssinia Bruce". Bruce may well have sent seed to Uppsala where the younger Linnaeus would have seen the living plant. The sheet 248.45 in LINN therefore probably represents the holotype; it does not conflict with the protologue and is designated lectotype.

Much branched shrub to 1.5m high, well armed with straight yellow prickles, stems and lower surface of leaves white with very dense sessile stellate tomentum. Leaves ovate, sinuate, 15 x 10cm, armed, the upper surface dark green. Inflorescence branched with 10-15 flowers, only the proximal one female-fertile; corolla white, tinged violet, sub-rotate, 2cm diam. Fruit yellow, 4cm diam; calyx lobes enlarged, well armed and reflexed at maturity.

<u>Chromosomes</u>: n=12 Randell & Symon (1976).

<u>Distribution</u>:　Native to Ethiopia, but also found in the Canary Islands, Ecuador and Mexico, growing above 2000m alt. in grassland. Also naturalised in the southern states of Australia (Symon, 1981).

<u>Notes</u>:　An easily recognised species with a characteristic white tomentum of dense stellate hairs on the young stems and the undersides of the leaves. The species has a wide and scattered distribution outside its native Ethiopia and man seems to have been the vector in this dispersal. A few uses of the species in Ethiopia have been reported (Bitter, 1923 and on <u>Bally 3051</u> at K) including the use of the fruits as a soap substitute, or for tanning hides or of the seeds for making loaves with barley flour. The plant was known in the European botanic gardens of the nineteenth century (it was figured in <u>Curtis's Botanical Magazine 44:1928</u> (1817)) and may have been transported to Central America and Australia as a curiosity for the garden which has since escaped.

Recently the potential economic importance of the fruits of this species as a source of solasodine was reported by Cruz and Proano (1970). The alkaloid, solasodine, can be used as a starting material for the synthesis of steroidal compounds of pharmaceutical interest. Trials have been conducted in Ecuador to assess the commercial viability of the cultivation of <u>S.marginatum</u> for solasodine production (Coppen, 1979).

series _Incaniformia_ but these are widely recognised species and are not confused within the range of material to be aggregated in _S.incanum_ agg.

Bitter divided series _Incaniformia_ into three subseries (_Campylacantha_, _Euincana_ and _Melongena_) although he acknowledged that all three were closely related. The species of subseries _Campylacantha_ were grouped into two _species collectivae_ which Bitter believed provided order to the species as well as some geographical clarification. However, the distinction between these two _species collectivae_ is hard to follow, and in the key to the series there is no dichotomy which separates these two groups.

Bitter's system for series _Incaniformia_ has to be rejected as unworkable : with the increase in number of collected specimens there are more and more specimens which cannot be identified with the species so narrowly defined by himself or Dammer. To avoid multiplying the number of names indefinitely or forcing a decision over which specific limits should be widened and which not, the _species aggregate_ is used here as a helpful device to indicate a close relationship without making any premature nomenclatural or taxonomic decisions. I believe that several species make up this aggregate but their taxonomic limits are far from clear and they are best treated as informal groups, perhaps recognised in the following

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descriptions.

A.   S.incanum group (typus speciei)

Shrubs, usually heavily armed with recurved prickles on the
stem and straight prickles on the leaves, densely tomentose.
Leaves ovate, more or less entire, base cordate or rounded
and often unequal.

Distribution: Dry country shrub of North East Africa and
the Middle East, perhaps extending through the Sahel region
of northern Africa.

Notes: The typification of S.incanum L. is discussed in a
paper by Hepper and Jaeger (1965).   A neotype (Herb. J.
Burser Vol. IX No. 20 UPS IDC microf.! series No. 1064
51:1.4) has been selected and now further studies must be
directed towards an understanding of the specific limits.
S.sanctum L. was described by Linnaeus after some confusion
over the application of S.incanum, but this substitution was
illegitimate and should be ignored.

The name S.coagulans Auctt. non Forssk. has often been used
for this taxon.

B.   S.lichtensteinii group

Shrubs, armed with recurved prickles, tomentose.   Leaves

ovate or elliptic, repand or sinuately lobed, dark leathery green above, pale beneath, base rounded or acute often unequal.

Distribution: Wooded grasslands of southern Africa.

Notes: Rather distinct from the type of S.incanum L. but some of the entire leaved material resembles specimens from the incanum group above. The separation is largely geographical.

C. S.panduriforme group

Small shrub, often densely armed, tomentose. Leaves very narrowly elliptic, not more than 10 x 1.5cm, repand, dark green above, pale beneath, base narrowly cuneate.

Distribution: Eastern South Africa.

D. S.campylacanthum group

Shrubs to 1.5m tall, armed or unarmed, coarsely pubescent. Leaves narrowly ovate or lanceolate or elliptic, more or less entire, dark green above, pale below, base obtuse or acute.

Distribution: Common shrub of disturbed ground in the grasslands of Central, East and Southern Africa.

Notes: A very common ruderal shrub, growing particularly in overgrazed areas. The fruits are used in tanning, healing sores and as fish poison, while extract of the roots is used to treat stomach ache. The name S.panduriforme has been used for this taxon but its type (South Africa, Transkei, Drege s.n. K!) suggests that this name is better applied to the shrubs included in group C above.

E. S.cerasiferum group

Shrub or small tree, usually armed with flattened glabrous prickles, tomentose or glabrescent. Leaves elliptic, repand or deeply lobed.

Distribution: North East Africa extending across to northern Nigeria.

Notes: A group of shrubs growing in forest margins. The range overlaps with the S.campylacanthum group and the two groups integrade morphologically. There seem to be two forms of this group : the one with leaves which are scarcely lobed and pubescent and the other with leaves which are deeply lobed and glabrous.

Synonymy: the following is a list of published species names which seem to belong to the S.incanum aggregate. For the most part I have not seen type material but from the descriptions they can be divided into the above five groups as follows:

A. S.incanum group

    S.sanctum L.

    S.unguiculatum A. Rich.

    S.hierochunticum Dunal

    S.floccosistellatum Bitter

B. S.lichtensteinii group

    S.subexarmatum Dammer

    S.lichtensteinii Willd.

C. S.panduriforme group

    S.panduriforme E. Meyer

D. S.campylacanthum group

    S.campylacanthum Dunal

    S.antidotum Dammer

    S.malacochlanys Bitter

    S.neumanii Dammer

    S.repandifrons Bitter

    S.merkeri Dammer

    S.stellativillosum Bitter

    S.lachneion Dammer

    S.macrosepalum Dammer

    S.tabacicolor Dammer

    S.maranguense Bitter

    S.magdalanae Dammer

    S.verbascifrons Bitter

    S.bojeri Dunal

    S.suaveolens Bojer

E. S.cerasiferum group

    S.cerasiferum Dunal

    S.duchartei Heckel

    S.yolense Hutch. & Dalz.

D. <u>S.deckenii</u> Dammer

    <u>S.ukerewense</u> Bitter

    <u>S.urbanianum</u> Dammer

    <u>S.jembaɔ</u> Bitter

    <u>S.iodes</u> Dammer

    <u>S.mesomorphum</u> Bitter

    <u>S.volkensii</u> Dammer

    <u>S.secedens</u> Dammer

    <u>S.endlichii</u> Dammer

    <u>S.himatacanthum</u> Dammer

    <u>S.psilostylum</u> Dammer

    <u>S.delagoense</u> Dammer

    <u>S.pharmacum</u> Klotzsch

    <u>S.picricum</u> Klotzsch

    <u>S.mossambicense</u> Klotzsch

    <u>S.trepidans</u> C. H. Wright

    <u>S.tomentellum</u> Klotzsch

    <u>S.obliquum</u> Dammer

    <u>S.astrochlaenoides</u> Dammer

    <u>S.fischeri</u> Dammer

    <u>S.benguelense</u> Peyritsch

    <u>S.baumii</u> Dammer

    <u>S.omahekense</u> Dammer

    <u>S.owitiomirense</u> Dammer

    <u>S.beniense</u> De Wild.

    <u>S.aureitomentosum</u> Bitter

    <u>S.chrysotrichum</u> C.H.Wright

    <u>S.bussei</u> Dammer

97. **Solanum richardii** <u>Dunal</u>, Solan. syn. : 45 (1816).

Type: Seen by Dunal in Richard's herbarium now at P.

Shrub to 2m high, well armed with flattened reflexed prickles, tomentose with small stellate hairs. Leaves ovate, 11 x 8 - 20 x 14cm, usually deeply lobed with three lobes on each side, base cordate. Cymes simple, 6-7-flowered, pedicels and calyces armed on proximal flowers with fully developed styles; corolla bluish-mauve, stellate, lobes abruptly acuminate, 4-6cm diam. Fruits yellow or orange, globose, 4-5cm diam.

<u>Distribution</u>: Tanzania, the Zambesi basin and south to Natal, Madagascar and the Comoro Islands; in forest or woodland, between sea level and 700m alt.

<u>Notes</u>: Dunal's original description (l.c.) of this species is vague and the type specimen in P should be found in order that the identity of the name may be confirmed. If a specimen is not available, an unpublished illustration of the species by Dunal is cited with the diagnosis and is probably to be found at MPU. Dunal's subsequent description of the species for de Candolle's <u>Prodromus</u> (Dunal, 1852) is more complete and the existence of further specimens in de Candolle's herbarium is mentioned. The three sheets at G-DC (IDC microf.! 2086:III.3.5) all bear specimens which comply with the current concept of <u>S.richardii</u>.

Bitter (1923) placed this species in series _Acanthocalyx_ with only one other species, S.acutilobatum Dammer. He considered them to be sufficiently similar to be combined into one "Grossart" or superspecies (_S.richardi_ (Dun.) sp. coll. sens. ampl. Bitt.) though they were still treated as two separate species. The described distinguishing characters of the two species are trivial, being concerned with the extent of the tomentum on the ovary and style, and it seems that the two names can be considered synonymous. Type material of S.acutilobatum must be located to confirm this.

Other synonyms of _S.richardii_ include _S.acanthocalyx_ Klotzsch, S.magnusianum Dammer and S.bathocladon Dammer. Bitter (p.176, 1923) also included _S.acanthodes_ J. D. Hooker, cultivated at Kew, as a possible synonym on the basis of the illustration accompanying the original description in _Curtis's Botanical Magazine_ 103: tʃ (1877). He wrote that he was uncertain of this inclusion and had not seen the specimen on which Hooker based the species. I have been unable to find type material of S.acanthodes at K but the illustration shows the lobes of the leaves to be deeper and more numerous in S.acanthodes and the prickles to be generally straight; furthermore the corolla lobes have a broad, wavy margin not seen in S.richardii. S.acanthodes should be omitted from the synonymy until a type is located.

98. **Solanum linnaeanum** Hepper & Jaeger in Kew Bull. (In press). Type: South Africa, Somerset Division, Burchell 3238 (Holotype K!)

Shrub to 1.5m tall, armed with straight yellow prickles, young branches violet and with scattered stellate hairs. Leaves elliptic, up to 15 x 10cm, armed, pinnatifid with rounded lobes, sometimes glabrous sometimes with scattered stellate hairs. Inflorescence 10-flowered, corolla violet, stellate, 2cm diam., only proximal flowers female-fertile. Fruit yellow, 2.5cm diam.

Chromosomes: n=12 Randell & Symon (1976, as *S.sodomeum*)

Distribution: Western Mediterranean areas, Macaronesia and the Cape Province of South Africa; in dry areas on well-drained soils below 200m alt. The species has also been introduced to scattered localities in Australia (Symon, 1981 as *S.hermannii*).

Notes: *S.linnaeanum* has been proposed as a new name for the species known for a long time as *S.sodomeum* and more recently as *S.hermannii* Dunal. Hepper (1978) having seen the type specimen of *S.sodomeum* L., recommended that the name *S.sodomeum* be rejected on the grounds that it was ambiguous having been misapplied consistently since it was first described. A formal proposal for the rejection of the name was accepted by the Nomenclatural Committee for

Spermatophyta (Taxon 32: 279, 1983).

In place of S.sodomeum Hepper proposed that the later name,
S.hermannii Dunal, be used. However, in the introduction to
his thesis Dunal (1813, p.17) wrote that he was changing the
name S.sodomeum because he considered that the epithet
'sodomeum' referring to the Biblical city of Sodom in Judea,
was unsuitable for a species which he believed to be South
African. According to Art. 62 of ICBN (1978) such a
substitution is not allowed and under Art. 63 S.hermanni(i)
is illegitimate and cannot be used.

Although Dunal (1813, 1816) at first believed this species
to be South African in origin, with introductions in
Mediterannean areas, he later reversed his opinion (Dunal,
1852). He reduced S.hermanni to a variety of S.sodomeum to
represent the more pubescent plants as distinct from the
glabrous ones of var. mediterraneu . Since pubescence tends
to be dependent on age this distinction is unnecessary.

An extensive search of the literature has failed to reveal
any other synonyms for this species. A new name is
therefore required. In view of Linnaeus' connection with
this species it has been renamed in his honour (Hepper &
Jaeger, In press).

I believe that it is more likely that the species is native
to South Africa rather than the western Mediterranean areas

where there are no other native species of <u>Solanum</u>.
<u>S.linnaeanum</u> is so well established in both regions that it
is not possible to be certain.

99.   <u>Solanum wrightii</u> <u>Bentham</u>, Fl. Hongk.: 243 (1861).
Type: Hong Kong, <u>C. Wright 489</u> (K!).

Large shrub or tree up to 9m high, young branches and
petioles with scattered prickles and hispid with stellate
hairs. Leaves ovate, up to 30 x 20cm, repand when young,
deeply lobed later, upper surface scabrid with simple hairs,
lower surface with stellate tomentum. Inflorescence with 20
or more flowers, calyx deeply lobed, corolla violet,
pentagonal, with five stripes of indumentum on the outside,
5-7cm diam. Fruit globose, about 5cm diam., red.

<u>Chromosomes</u>: Federov (1969) lists both <u>S.macranthum</u> Dun.
and <u>S.grandiflorum</u> Ruiz & Pav. as 2n=24. These may be
misidentifications of <u>S.wrightii</u>.

<u>Distribution</u>: Originally from South America this species is
often cultivated as an ornamental tree in the tropics and
may occasionally have escaped.

<u>Notes</u>: In his notes on <u>S.wrightii</u> Bentham (l.c.) wrote that
it appeared to belong to Dunal's section <u>Melongena</u>. He
presented no justification for this suggestion though many
characters indicate that the species is quite clearly

distinct from the African species of the section. In his
Solana africana Bitter (p.180, 1923) treated S.wrightii (as
S.grandiflorum Ruiz & Pavon) together with S.robustum Wendl.
within his section Andromonoecum (=Melongena) but he did not
assign them to a series : he commented briefly that they
were neither closely related to one another nor to any of
the African species. For the present thesis I have
maintained this species within section Melongena as a
convenience though it should be removed to a section of
allied New World species when its taxonomic affinities are
better known.

Subsequent to Bentham's description of S.wrightii the names
S.grandiflorum Ruiz & Pav. and S.macranthum Dunal were
frequently misapplied to this species. Heine (1960)
unravelled the resulting confusion showing that neither name
was synonymous with S.wrightii.

Section 21 **Monodolichopus** Bitter in Feih. Repert. nov. Spec.
Regni veg. 16: 257-307 (1923). Type species: S.coagulans
Forssk. (fide Seithe, 1962 as S.dubium Fresen.).

Armed subshrubs or perennial herbs, with stellate tomentum;
leaves repand to sinuate; flowers blue-violet, rotate or
rotate-stellate, stamens unequal, fifth filament longer than
the rest; fruits yellow, dry, sometimes enclosed in an
accrescent prickly calyx; seeds black.

Notes: A distinctive section from North East Africa which
apparently comprises only two species. Bitter's (l.c.)
treatment of the section accepted five species : the
material is better treated as one variable and quite widely
distributed species, S.coagulans Forssk. (previously
S.dubium Fresen.), and another more constant species,
S.melastomoides C. H. Wright, which is restricted to
Somalia. The other three species distinguished by Bitter
should be sunk into S.coagulans.

The characteristic unequal stamens, dry yellow fruits and
black seeds suggest that the section is taxonomically remote
from other African species and indicate an affinity to
Macaronesian and Central American species. In a revisionary
paper, Whalen (1979a) discussed the sectional relationships
and phylogeny of the Central American section Androceras and
he concluded from his studies that section Nycterium of the
Canary Islands was the most likely nearest relative of

section <u>Androceras</u>. He then added that plants resembling the common ancestral group of sections <u>Androceras</u> and <u>Nycterium</u> would be :

> "prickly, stellate woolly, herbaceous or suffrutescent perennials with weakly lobed leaves, extra-axillary, reduced, raceme-like inflorescence, dry berries and somewhat accrescent, prickly calyces".

These characters are all seen in section <u>Monodolichopus</u>, and in particular in <u>S.coagulans</u>, suggesting that perhaps this section represents the hypothetical ancestral group. It should be noted that <u>S.coagulans</u> was originally placed in section <u>Nycterium</u> (as <u>S.dubium</u>) by Dunal (1852, p.332) until Bitter described section <u>Monodolichopus</u>.

A proposed relationship between section <u>Monodolichopus</u> and the <u>Nycterium/Androceras</u> alliance might be doubted on the basis of the large discontinuities in the geographical distributions of these sections. However, similarly disjunct distributions between Macaronesia and North East Africa have been documented (Sunding, 1979; Thulin, 1981) in, for example, <u>Drusa glandulosa</u> (Poir.) Bornn.; <u>Adiantum reniforme</u> L., <u>Myrsine africana</u> L. and <u>Carex peregrina</u> Link and the genera <u>Canarina</u>, <u>Aeonium</u> and <u>Campylanthus</u>.

If there is a relationship between the sections <u>Monodolichopus</u>, <u>Nycterium</u> and <u>Androceras</u> then it may be

assumed that the ancestral group of species resembling section Monodolichopus was once distributed across northern Africa to North America, and subsequent extinction has left North-East Africa as a refuge.

It is interesting to note that all three sections Androceras, Nycterium and Monodolichopus exhibit unequal stamens, but in the first two sections the difference in length arises from a difference in anther lengths while in section Monodolichopus it is the filaments which are unequal. The adaptive advantage of unequal stamens in section Monodolichopus has not been studied and it is not known whether the feature promotes outcrossing as has been demonstrated by Bowers (1975) in section Androceras.

Key to the species:

Prickles yellow, straight, glabrous; stamens unequal, the long filament only slightly longer than the others, about 2.5mm long; fruiting calyx armed, tube accrescent, enclosing the fruit

.... 100. S. coagulans

Prickles dark brown, slightly recurved, with stellate hairs covering up to 3/4 of their length; stamens unequal, the long filament much longer than the rest, about 5mm long; fruiting calyx unarmed, not markedly accrescent

100. **<u>Solanum coagulans</u>** <u>Forsskal</u>, Flora aegypt.-arab.: CVII
and 47, CENT. II 55 (1775). Type: Yemen, <u>Forsskal s.n.</u>
(C!).

Perennial herb, often with several stems, up to 0.7m high,
stems with white stellate tomentum, usually densely armed
with straight yellow prickles. Leaves very variable, up to
10 x 5cm or more, ovate-lanceolate, armed and pubescent.
Inflorescence racemose with 6-10 flowers; corolla blue-
violet, rotate-stellate, reflexed, 1-1.5cm diam., stamens
unequal, one filament slightly longer than the rest. Fruit
yellow, globose, 1cm diam., dry, usually completely enclosed
by heavily armed accrescent calyx tube; seeds shiny black.

<u>Distribution</u>: North-East Africa and Egypt, common in over-
grazed areas on sandy soils particularly those which are
irrigated or regularly flooded.

<u>Notes</u>: A common species which inhabits the open woodland
and savannah of North-East Africa. It is a feature of
overgrazed areas and its fiercely armed habit and creeping
perennial roots must contribute to its tolerance of grazing
pressure.

In Bitter's (1923, pp.297-306) account of sections
<u>Monodolichopus</u> he accepted <u>S.dubium</u> Fresen., <u>S.thruppii</u> C.

i. Wright, S.depressum Bitter and S.ellenbeckii Dammer as separate species and within this framework he included several varieties. The characters on which Bitter claimed to be able to distinguish these species, in particular using leaf characters and prickliness, are notoriously variable in the genus, and it is difficult to find any consistent correlation between these characters in the material that I have seen. Thus I recommend that a broad understanding of a single species be adopted to include all such material. The correct name for this species is S.coagulans since this epithet antedates the more commonly applied S.dubium by 59 years. In the past, S.coagulans has frequently been misapplied to material with affinity to S.incanum L.

Bitter (1923, p.301) wrote that the fruits of S.coagulans were used in tanning; notes accompanying the specimen Mathew 6610 at K record that an infusion of the stem is used for stomach ache and the fruits are used for coagulating milk.

101. **Solanum melastomoides** C. H. Wright in Bull. misc. Inf. R. bot. Gdn. Kew 1894: 128 (1894). Type: Somalia, Bwobi, James & Thrupp s.n. (K!).

Armed, much branched shrub, up to 1m high, bark dark grey to red brown, young stems pubescent with white stellate tomentum. Leaves ovate, 3 x 2.25cm, entire to sinuate, stellate hairs on both surfaces, midrib often armed.

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Inflorescence a congested cyme of 5-7 flowers, corolla blue-
violet, rotate, 2-2.5cm diam. stamens unequal, four
filaments 1mm long, fifth 5mm long, anthers all 6mm long,
long stamen arcuate as is style.   Fruits 1-3 per
infructescence, yellow, globose, 1.5cm diam., dry; seeds
shiny black.

Distribution: Somalia, and occasionally in Ethiopia and
northern Kenya, in open bush on well-drained soils generally
above 750m alt.

Notes: An easily recognised and fairly abundant species
which is distinguished from _S.coagulans_ by its very long
fifth filament and the absence of an accrescent calyx.
Three specimens at K (_Peck 238_, _Ball 3793_ and _Bally 11160_)
all from northern Somalia seem to be a local variety with
irregularly lobed leaves.

The fruits of this species have been reported as being used
in powdered form for the treatment of wounds on livestock
and people.

Section 22 **Nycterium** (Ventenat) Dunal, Solan. Syn.: 35 (1816). Type species: S.vespertilio L'Heritier ex Aiton.

Erect or procumbent shrubs, pubescent with stellate hairs, often armed; leaves ovate or lanceolate, entire; inflorescence few- to many-flowered, buds curved, corolla lobes unequal, one anther double the length of the others, style and long anther arcuate.

Notes: A small section including two species endemic to the Canary Islands and a few others native to Central America. The sectional limits are poorly defined and different authors have shown sundry opinions on the number of New World species to be included.

Ventenat (1805) considered S.vespertilio to be sufficiently distinct from other Solanum species to merit its own genus, Nycterium, but Dunal returned the species to the genus Solanum eleven years later. The epithet, vespertilio, and generic name, Nycterium, are the latin and greek words, respectively, for a bat, the authors finding a resemblance between the flowers of these species and that mammal.

The flowers of S.vespertilio and S.lidii are distinctive in having one anther much longer than the rest suggesting an affinity to the Central American section Androceras Marzell in which the specialised floral morphology is understood to

promote outcrossing (Bowers, 1975). Little is known of the reproductive biology of section Nycterium.

Key to the species:

Plant heavily armed with numerous red-brown prickles; leaves

ovate, base unequally cordate; numerous flowers per

inflorescence; calyx up to 12mm diameter

.... 102. S. vespertilio

Plant unarmed or scarcely armed; leaves lanceolate, base

unequal attenuate to rounded; 6-8 flowers per

inflorescence; calyx 20mm diameter

.... 103. S. lidii

102. **Solanum vespertilio** L'Heritier ex Aiton, Hortus kew. Ed.1, 1: 252 (1789). Type: The Hortus kewensis description of this species cites L'Heritier's unpublished study Solana aliquot rariora implying that L'Heritier was the author. The type should therefore be found in L'Heritier's herbarium which, following his death, became the basis of de Candolle's collection. However, although there are four sheets in G-DC of S.vespertilio (IDC microf.! 2067:III.2-5) none seems to be L'Heritier's. Other L'Heritier material is to be found at CP, NEU and P (Stafleu & Cowan, 1981).

Erect shrub to 1.5m high, densely spiny with short, robust,

red-brown prickles, tomentose at first with stellate hairs. Leaves ovate, entire to repand, 5-15 x 3-8cm, rarely armed. Inflorescence complex, 10- to numerous-flowered; floral parts often in 4's; corolla deeply and irregularly lobed, bluish-purple, 3-3.5cm diam. Fruits red, globose, 1.5cm diam.

Distribution: Moist, shady valleys in Gran Canaria and Tenerife, 0-400m alt.

Notes: A heavily armed species often with a very dense inflorescence of showy flowers. It is certainly allied to S.lidii but the two species are easily distinguished .

103. **Solanum lidii** Sunding in Blyttia 24: 368 (1966). Type: Canary Islands, Gran Canaria, Lomo de la Cruz, Sunding s.n. (Holotype O).

Procumbent shrub to 0.7m high, young branches stellate tomentose, later glabrescent, occasionally armed with a few prickles. Leaves oblong-lanceolate, entire, 5 x 2cm. Inflorescence 6-8-flowered; corolla stellate, violet, zygomorphic, 2-2.5cm diam. Fruit orange, globose, 1cm diam.

Distribution: Very local in Central Gran Canaria, above 600m alt.

Notes: A species of rather drier habitats than S.vespertilio, it is only known from a hillside on the island of Gran Canaria.   Sunding (l.c.) has described the ecology and phytosociological behaviour of this rare species.

Section 23 **Leprophora** Dunal, Hist. nat. Solanum: 181 (1813).

Type species: S.elaeagnifolium Cav. (fide D'Arcy, 1972).

Shrubs, armed with needle-like prickles, stellately pubescent; leaves entire or sinuate-angulate; inflorescence racemose, unbranched, up to 15-flowered, flowers blue-violet, rotate, pentagonal or stellatiform; berries globose, 0.7-2cm diam., green or yellow at maturity and rather dry.

Notes: Dunal erected section Leprophora and subsequently (Dunal, 1852) combined it with section Oliganthes. Whalen (1984) considered that S.elaeagnifolium belonged to a taxon of Australian species which he called the 'S.ellipticum Group' being distinct from Section Oliganthes into which Symon (1981) had previously placed them. For the purposes of a taxonomic account of the African species of Solanum it seems appropriate to maintain section Leprophora while the relationships of S.elaeagnifolium remain uncertain.

104. **Solanum elaeagnifolium** Cavanilles, Icon. 3: 22, t.243 (1795). Type: Cavanilles s.n. (C, MA, P-JUSS).

Erect shrub to 60cm tall, often armed with red acicular prickles 2-5mm long, densely pubescent; long propagating rhizomes. Leaves narrow, 1-10cm long, often prickly, entire or sinuate, densely pubescent with short-stalked porrect stellate hairs. Inflorescence 3-6-flowered; calyx with filiform apices; corolla blue (rarely white), 3cm diam.,

stellate, lobes deltoid.   Fruits yellow, 1-1.5cm diam.

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Chromosomes: n=12 Averett & Powell (1972).

Distribution: Native to south western United States, North Mexico and possibly temperate South America; now growing in many parts of South Africa and Australia.

Notes: A pernicious weed of cultivated and disturbed land. It is poisonous to livestock and propagates easily from its spreading rhizomes.   The species has become a serious pest in South Africa, but as yet has not been recorded elsewhere on the continent.

Section 24 Androceras (Nuttall) Marzell in Hegi, Ill. Fl.
Mitt.-Eur.: 2585 (1927). Type species: S.rostratum Dunal.

Herbs, sometimes perennial, densely armed with pale yellow
spines, indumentum of stellate and glandular hairs; leaves
ovate, deeply lobed; inflorescence up to 10-flowered,
apparently racemose, corolla faintly zygomorphic, anthers
unequal; fruiting calyx densely armed, accrescent,
completely surrounding the fruit.

Notes: A section of twelve prickly species native to
central Mexico and the south western United States.   One
species, S.rostratum Dunal, is now widely distributed
outside the New World.   The section has a superficial
similarity to section Cryptocarpum Dunal but appears to be
more closely related to section Nycterium (Ventenat) Bitter.
It has recently been revised by Whalen (1979a).

105. **Solanum rostratum** Dunal, Hist. nat. Solanum: 234 t.24
(1813).   Type: ex Hort. Monsp. (G, G-DC, MPU, P) (fide
D'Arcy, 1974a p.858).

Spiny herb, 0.3-1m high, with scattered stellate and
glandular hairs; prickles numerous, pale yellow, up to 1cm
long.   Leaves ovate, pinnatifid, to 15cm long, armed,
pubescent.   Inflorescence, 6-10-flowered, apparently
racemose; calyx armed, lobed; corolla yellow, rotate
slightly lobed, lobes unequal, 3cm diam; anthers unequal,

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the one 2-3mm longer than the other four and incurved.
Fruit 0.6cm diam., completely enclosed by spiny, accrescent
calyx tube.

Chromosomes: n = 12 (Whalen, 1979a)

Distribution: Introduced in South Africa; two specimens at
K, one collected in 1925 growing round Queenstown, Cape
Province the other collected from Bloemfontein, Orange Free
State.

Notes: A vigorous weed which is a serious pest in its
native Mexico.   It is listed in the 'Geographical Atlas of
World Weeds' (Holm et al, 1979) as common in South Africa.

The specialised floral morphology has been shown to promote
outcrossing (Bowers, 1975).

Section 25 **Cryptocarpum** Dunal, Hist. nat. Solanum 134, 232 (1813). Type species: S.halbisii Dunal (fide Coles in D'Arcy, 1972) (= S.sisymbriifolium Lamarck, see Morton, 1976, p.194).

Herbs or subshrubs, viscid-villous, densely spiny; leaves ovate, deeply lobed; inflorescence appearing racemose, often only proximal flowers setting fruit, stamens equal; fruiting calyx accrescent, viscid and very spiny, fruit globose, red.

Notes: A small section of South American species. There is a resemblance to section Androceras (Nuttall) Marzell but the two sections are distinct. One species from section Cryptocarpum, namely S.sisymbriifolium, has become widely distributed around the world and is established in South Africa.

106. **Solanum sisymbriifolium** Lamarck, Tabl. encycl. 2: 25 (1794). Type: Argentina, Buenos Aires, Commerson s.n. (holotype P-LA, fide Morton, l.c.).

Subshrub up to 1.5m high, viscid-villous with simple glandular hairs as well as stellate hairs, densely spiny, spines yellow-orange, straight. Leaves ovate, pinnatifid or bipinnatifid, up to 15 x 10cm, armed as stem. Inflorescence 6-12-flowered, apparently racemose; corolla white or lilac tinted, rotate, ca 4cm diam. Fruit red, ovoid, 1.5cm diam., partly enclosed by enlarged calyx lobes.

<u>Chromosomes</u>: 2n=24 (Federov, 1969).

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<u>Distribution</u>: Material at K collected in South Africa from localities around Johannesburg, Durban and Port Elizabeth.

<u>Notes</u>: The widespread introduction of this species and its morphological variability, particularly in leaf characters, have resulted in several synonyms being used. There seems to be only one superfluous name which has been applied to African material, namely <u>S.rogersii</u> S. Moore (Journ. Bot. 58: 78 (1920).

Section 26 **Acanthophora** Dunal, Hist. nat. Solanum: 131, 218 (1813). Type species: S.mammosum L. (fide D'Arcy, 1972).

Subshrubs armed with numerous acicular straight or broad recurved spines, and pubescent with apparently simple hairs (reduced from stellate hairs) or with small stellate hairs; leaves ovate, deeply or shallowly lobed, membranaceous, usually much armed and hirsute; inflorescence a few-flowered simple cyme, often only proximal flowers hermphrodite, calyx not or scarcely accrescent in fruit, corolla stellate, ovary glabrous; fruit yellow to vermillion or blackish; seeds sometimes with a winged margin.

Notes: A section of 15 or more species from tropical Central and South America. Some of the species, in particular the ornamental S.capsicoides Allioni, are now widely distributed and naturalised in the tropics. The long, uniseriate, multi-celled, simple hairs of mature plants in this section are distinctive, and are generally considered to be the elongated median rays of sessile stellate hairs on which the lateral rays are undeveloped. Stellate hairs are found on the species but often only on juvenile plants or the emerging leaves of adult ones. Simple, single-celled hairs, often gland-tipped, also appear in the section.

Bitter used the characteristic hairs of the section to name it Simplicipilum (Bitter, 1923 pp.147-156) but 110 years

previously Dunal (l.c.) had named the same group of species, equally appropriately, Acanthophora. The Dunalian name takes precedence, but D'Arcy has since elevated subsection Lasiocarpa from within Dunal's section to sectional status. Section Lasiocarpa represents a group of species closely allied to section Acanthophora, but the species of section Acanthophora may be distinguished by their lack of stellate hairs on the ovaries, their more general coverage with multi-celled simple hairs and their less substantial habit.

Nee (1979) suggested that section Acanthophora might be separable into two subsections based on seed morphology. This arose from the observation that some species (e.g. S.capsicoides and S.atropurpureum Schrank) produce seeds with the margin flattened to become a wing while other species (e.g. S.mammosum L., S.aculeatissimum Jacq. and S.viarum Dunal) bear seeds which are wingless and resemble those of most other Solanum species. The biological significance of the winged margins is not understood but Nee suggested that the flattened margins might assist the local dispersal of the seeds by wind and water. In support, he pointed out that S.capsicoides with winged seeds has fruits which are dry and at maturity split to release the seeds, whereas other species have smaller fruits which are juicy and probably rely on animal (bird?) dispersal. The winged margins are unusual in the genus and their function deserves further study.

Four species from the section are known in Africa, namely
S.capsicoides, S.aculeatissimum, S.mammosum and S.viarum and
a further two, S.atropurpureum and S.stuhlmannii, have at
one time been recorded there.

Key to the species:

1. Margin of seed-coat flattened forming a prominent wing;
    seed 4-6mm diam.; leaves and branches sparsely
    pubescent or almost glabrous; ripe fruit vermillion
    .... 107. S.capsicoides

1'. Seed not winged; seeds ca 2-5mm diam.; leaves, at least
    on lower surface, and branches hirsute; ripe fruit
    yellow
    .... 2.

2. Stem aculeate with compressed recurved prickles mixed
    with long acicular straight prickles; branches
    hirsute with simple hairs
    .... 3.

2'. Stem aculeate with only acicular prickles; branches with
    scattered simple hairs
    .... 108. S.aculeatissimum

3. Hairs on stem variable, 2-4mm long; calyx without
    spines; corolla violet; fruit globose usually with an

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apical nipple and several basal protruberances; seeds 5mm diam.

.... 109.   S.mammosum

3'. Hairs on stem uniform, 0-5mm long; calyx aculeate; corolla white; fruit globose; seeds ca 2mm diam.

.... 110.   S.viarum

107.   **Solanum capsicoides** Allioni, Auctuarium ad synopsim methodicam stirpium horti Regii Taurinensis: 64 (1773). Type: Cultivated at Turin, Allioni s.n. (TO).

Shrub to 1m high, with scattered multi-celled simple hairs, well armed with straight acicular spines. Leaves broadly ovate, deeply lobed, lobes entire or repand, 10 x 10cm, glabrescent or with scattered simple hairs, armed on the veins, upper surface often shiny. Inflorescence 1-3-flowered, calyx triangular, aculeate; corolla white, stellate, 2-3cm diam. Fruit globose, vermillion, 3.5cm diam. Seeds winged up to 5mm diam.

Chromosomes: n=12 (Randell and Symon, 1976)

Distribution: Introduced in West and South Africa.

Notes: A species which has been widely introduced in the tropics as an ornamental. It was previously known by a later synomym, S.ciliatum Lamarck, and there has been some

confusion with the quite distinct species S.aculeatissimum Jacquin. The combination S.macowani Fourcade has been used for this species in South Africa.

108. **Solanum aculeatissimum** Jacquin, Collectanea 1: 100 (1787); Icon. pl. rar. 1(5): tab 41 (1787). Type: Cultivated plant at Vienna, Jacquin s... (W).

Woody herb up to 1m high, stems tinged purple and green, hirsute with simple hairs sometimes dense often not, heavily armed with many straight acicular spines. Leaves ovate, deeply lobed, lobes acutely lobed themselves, 12 x 12cm, hirsute, spiny, base truncate or slightly cordate. Inflorescence 3-5-flowered, corolla white, sometimes with a purple tint, stellate, 2.5-3cm diam. Fruits globose, 1.5-2cm diam., white with a green reticulation, yellow when ripe.

Chromosomes: 2n=24 (Federov, 1969, possibly a misidentification of S.capsicoides.)

Distribution: Widely distributed throughout Africa, generally growing in forest clearings.

Notes: The wide distribution of this species in Africa, and its scarcity or even absence from the New World, together suggest that S.aculeatissimum is native to Africa. This gives section Acanthophora an inexplicably disjunct

distribution. However, S.aculeatissimum grows as a weed of secondary vegetation indicating that it is more likely to be an introduction to Africa; and when it is considered that trade routes between the New World and Africa have been established for over 400 years (Roe, 1979) an early introduction of this species would allow time for its subsequent dispersal. Its hideously spiny habit must deter grazing and contribute to its success.

From the description and an isosyntype at K (Seret 1099!) it seems that S.angustispinosum De Wildeman is a synonym of S.aculeatissimum despite De Wildeman's comments to the contrary (De Wildeman, 1914 pp.397-398). De Wildeman followed C. H. Wright's account of Solanum in the Flora of Tropical Africa (Wright, 1906) in which S.aculeatissimum sensu Wright is in fact S.capsicoides Allioni.

109. **Solanum mammosum** Linnaeus, Sp. Pl. 1: 187 (1753). Lectotype: Plate 226 Fig. 1 in Plukenet, Phytographia London 1696 (!). (Typotype: Herb. Sloane Vol. 38 fol. 59 (BM!).

I have selected this plate to act as type in preference to available specimens for the following reasons:

1. The two sheets of this species in LINN, 248.32 and 248.33, are ineligible to serve as type material as although they were named S.mammosum, they were collected

by Brown and Dahlberg respectively and would not have reached Linnaeus before 1753 (Savage, 1945).

2. The main part of the phrase name of S.mammosum is taken from Linnaeus' Hortus Cliffortianus (1738) and a specimen referable to this entry is found in the Clifford herbarium but is without flowers or fruits.

3. In the protologue of S.mammosum Linnaeus referred to a description and figure in Plukenet's Almagestum and Phytographia. He mistakenly cited 't225 fig1' as the illustration but it is clear that this should read 't226 fig1' which depicts a branch of S.mammosum bearing the characteristic obpyriform fruits.

4. The specimen on which the Phytographia illustration is based is found in Vol. 98 fol. 59 of the Sloane Herbarium at BM in which Plukenet's herbarium was incorporated. This specimen lacks flowers and fruits, the latter presumably being too large to mount on a herbarium sheet, and it cannot be used as a type since it is doubtful if Linnaeus ever studied Plukenet's collection.

5. The illustration in the Phytographia is selected as lectotype in preference to the only alternative candidate, the specimen in the Clifford herbarium, since it clearly depicts the fruits whereas the specimen is

sterile.

Herb up to 1.5m high, hirsute with viscid hairs, armed with scattered acicular prickles as well as compressed often recurved prickles. Leaves broadly ovate, deeply lobed, lobes themselves slightly lobed, up to 15 x 15cm, base cordate. Inflorescence 4-5-flowered, calyx lobes lanceolate; corolla violet, stellate, up to 3cm diam. Fruit orange or yellow, ovoid, 4-10cm long, often with apical and basal nipple-shaped outgrowths.

Chromosomes: n=11, 12 (Heiser, 1971)

Distribution: Occasionally cultivated in Africa, there are specimens at K from Kenya and Burundi.

Notes: A species from the Caribbean region of Central America which is cultivated principally for its curious fruits. Nee (1979) cited various references to its use in South America for poisoning cockroaches, catching fish, extracting maggots, curing common colds and as a fetish to increase fertility. In Africa it has been introduced as an ornamental garden plant.

The morphology of the fruits has been discussed by Miller (1969) and by Martin (1972).

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110. **Solanum viarum** Dunal in DC., *Prodr.* 13(1): 240 (1852).
Type: Brazil, Lund 759 (G-DC, IDC microf! 2080:I.1).

Straggling subshrub up to 1m high, hirsute with predominantly multi-celled simple hairs, heavily armed with acicular and compressed spines. Leaves broadly ovate, lobed, sinuses reaching up to 1/3 of the way to the midrib, lobes themselves lobed, up to 15 x 15cm, hirsute, armed on the veins with acicular spines, base cordate. Inflorescence 4-5-flowered; calyx lobes triangular; corolla white or greenish, stellate, up to 2cm diam. Fruit green and white striped when unripe, yellow when ripe, globose, ca 3cm diam.

Distribution: Recorded in Zaire and in South Africa in Natal and possibly in Cameroon.

Notes: A South American species which has become a reasonably important source of the steroid alkaloid Solasodine in India. Its occurrence in Africa is presumably due to accidental introduction.

Hepper 1549 (K!) collected in Cameroon is of interest as it appears to be intermediate between **S.viarum** and **S.myriacanthum** Dunal also of this section.

Babu and Hepper (1979) have shown that **S.viarum** is the correct name for the taxon previously known as **S.khasianum** C. B. Clarke var. **chatterjeanum** Sen Gupta.

In his account of the representatives of this section in Africa, Bitter (1923, pp.147-157) included two further species, namely S.atropurpureum Schrank and S.stuhlmannii Dammer. The former is a common shrub in south-eastern South America which is characterised by its winged seeds, almost glabrous, violet branches and deeply lobed leaves; it was apparently growing at Amani in northern Tanzania. The latter is an unarmed shrub with deeply lobed leaves only known from the type locality at Bukoba in Tanzania. There is no material from Africa of either species at K.

Section 27 **Lasiocarpa** (Dunal) D'Arcy in Ann. Mo. bot. Gdn. 59: 270 (1972). Type species: S.lasiocarpum Dunal.

Shrubs from 1-6m tall, generally armed, tomentose with stellate hairs; leaves up to 50cm long, ovate, repand; cyme with only the proximal few flowers hermaphrodite, corolla stellate; pericarp of fruit with persistent stellate indumentum.

Notes: A section of 13 species concentrated in the northern Andes and western Amazon Basin of South America. The section has recently been revised by Whalen et al (1981) and two species which belong to their concept of the section have been recorded in Tanzania. For convenience, I have included here a third species, S.robustum Wendl., even though Whalen et al consider it to be phylogenetically isolated. As yet there is no named section to cover this species but Dunal (1852) and Morton (1976) both accepted it as a member of the group now referred to as section Lasiocarpa. Bitter (1923) included it in section Andromonoecum Bitter (= Melongena Dunal).

Key to the species:

1. Leaves decurrent along the petiole to give a broad wing; hairs on fruit simple

   .... 111. S.robustum

1'. Leaves not decurrent along petiole; hairs on fruits

   stellate
                        .... 2.

2. Stems hairs simple

                .... 112.   S.pectinatum

2'. Stem hairs predominantly stellate

                .... 113.   S.sessiliflorum

111.   **Solanum robustum** Wendland in Flora 27: 784 (1844).
Type: "A renaming of S.alatum Seem. & Schum., non Moench,
which was based on a cultivated plant originally from
Brazil.   Although not indicated, it may have been sent by
Clausen."   (Morton,   1976).

Bushy shrub to 3m high, young branches and leaves with rust-
brown stipitate stellate indumentum, armed with laterally
compressed spines.   Petioles winged, the wing up to 1.5cm
wide;   leaves elliptic, sinuate, 25 x 15cm or larger,
tomentose and armed.   Inflorescence racemose, 10-20-
flowered; corolla white, stellate, ca 2.5cm diam.   Fruits,
3-4 per infructescence, globose, dark green (?), 1.5cm
diam., persistently hirsute with simple hairs.

Chromosomes: 2n=24 (Federov, 1969).

Distribution: Locally common in the vicinity of the

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Usambara and Uluguru mountain ranges in north-eastern Tanzania.

Notes: A distinctive species from Paraguay, southern Brazil and Argentina, which is often cultivated as an ornamental. It has escaped in Tanzania where, according to collection notes, it is becoming a troublesome weed.

112. **Solanum pectinatum** Dunal in DC., Prodr. 13(1): 250 (1852). Type: Peru, Maynas, Poeppi 2224 (holotype G-DC, isotype F) (fide Whalen et al, 1981).

Shrub to 2m high, hirsute with long simple hairs 3-7mm long, armed with laterally compressed spines. Leaves ovate, repand, 25 x 13cm, hirsute and armed as stem. Inflorescence 2-6-flowered; corolla white, stellate, 3-4cm diam. Fruit, 1-2 per infructescence, ovoid globose, orange, ca 3.5cm long, hirsute with deciduous stellate hairs with elongated median rays.

Chromosomes: n=12 (Whalen et al, 1981)

Distribution: Cultivated at Amani, northern Tanzania.

Notes: A species described by Whalen et al (l.c.) as showing agricultural promise on account of its pleasantly flavoured fruits. There is only one specimen from Africa at K, though if its potential for cultivation is developed it

might become more widespread. The species is often known by the later synonym, <u>S.hirsutissimum</u> Standley.

113. <u>**Solanum sessiliflorum**</u> <u>Dunal</u> in Poiret, Encycl. Meth. Bot. Suppl. 3: 775 (1814). Type: Brazil, "Para", "<u>R.E. 7907</u>" (lectotype P, <u>fide</u> Whalen <u>et al</u>, 1981).

Spreading shrub about 1m high, usually unarmed, stem with stellate tomentum. Leaves broadly ovate, coarsely sinuate, up to 45cm long, densely pubescent with stellate hairs, hairs on upper surface apparently simple. Inflorescence 6-16-flowered, sub-sessile; corolla greenish-white, stellate, 2-3cm diam. Fruits 1-3 per infructescence, more or less globose, ca 6cm diam., orange-yellow, with deciduous stellate hairs.

<u>Chromosomes</u>: n=12 (Whalen <u>et al</u>, 1981).

<u>Distribution</u>: Cultivated at Amani, northern Tanzania.

<u>Notes</u>: Originally from the upper Amazon Basin this species is locally cultivated in South America for its fruit, and like <u>S.pectinatum</u> Dunal it is described by Whalen <u>et al</u> (1981) as having unrealised potential as a tropical fruit crop. It is known in Peru as the 'Cocona' and has been widely referred to as <u>S.topiro</u> Humb. & Bonpl., a later synonym. African material is represented at K by a single specimen from the original East African Research Institute

at Amani.

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S.erianthum              324,325,326,327,329,338
S.erythracanthum         398,415
S.exasperatum            265

S.farini                 435
S.ficifolium             346
S.fischeri               451
S.fistqsulosum           307
S.flagelliferum          399
S.floccosistellatum      450
S.florulentum            303,307
S.foliosum               307
S.forskalii              372,387,400,414
S.forsythii              398

S.geminifolium           377
S.geniculatum            265
S.gifthergense           405,408,411,413
S.giganteum              330,338,339,342,347,349,352,369
S.gillettii              418
S.gilo                   377
S.glabratum              403,404
S.glochidiatum           394
S.goetzei                339,343,352,354,395
S.gracilipes             400
S.grandiflorum           421,456,457
S.grewioides             359
S.grossedentatum         293,297,301,309
S.guineense              261,267,269,307

S.hadaq                  400
S.hastifolium            397,404
S.heinianum              368,369,370
S.helleri                418
S.hemisymphyes           278
S.hermannii              454,455
S.heudelotii             387,415
S.hierochunticum         450
S.hildehrandtii          307
S.himatacanthum          451
S.hirsuticaule           351
S.hirsutissimum          487
S.hirsutum               306,308,309
S.hirtulum               293,302
S.hispidum               340,346
S.holtzii                278
S.humhlotii              268,269
S.humile                 308
S.hypopsilum             308

S.imamense               267,268,270
S.imerinense             308
S.inaequiradians         393,396
S.incanum                389,421,424,432,437,445,462
S.incertum               308
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REFERENCES

ADAMSON, R. S. and T. M. SALTER,
        (1950)   Flora of the Cape Peninsula.
        Juta & Co. Ltd., Cape Town.

AGNEW, A. D. Q. (1974)   Upland Kenya wild flowers.
        Oxford University Press, London.

AHMAD, K. J.   (1964a)   Cuticular studies in solanaceae.
        Can.J.Bot. 42(7): 793-803.

        (1964b)   Epidermal studies in Solanum.
        Lloydia 27(3): 243-250

AHMAD, V., SYED FASAHAT ALI and R. AHMAD,
        (1980)   Isolation of Solamargine from
        Solanum albicaule.
        Planta med. 39: 186-191.

ALEXANDRE, D. Y. (1982)   La dispersion de Solanum
        verbascifolium en Cote d'Ivoire :
        role des Cephalophes.
        Terre Vie 36(2): 293-295.

ANDERSON, G. J. (1975)   Variation and evolution in selected
        species of Solanum section
        Basarthrum. Brittonia 27: 209-222.

ANDERSON, G. J. (1979a)   Systematic and evolutionary
        consideration of species of
        Solanum section Basarthrum.
        In : Hawkes et al., 1979.
        pp.549-562.

ANDERSON, G. J. (1979b)   Dioecious Solanum species of
                          hermaphroditic origin is an
                          example of a broad convergance.
                          Nature,Lond. 282: 836-838.

ANDERSON, G. J. and P. G. GENSEL,
          (1976)   Pollen morphology and the
                   systematics of Solanum section
                   Basarthrum. Pollen Spores 18:
                   533-552.

ANDERSON, G. J. and D. A. LEVIN,
          (1982)   Three taxa constitute the sexes of
                   a single dioecious species of
                   Solanum. Taxon 31(4): 667-672.

ANDREWS, F. W. (1956)   The Flowering Plants of the Sudan
                         Vol. 3 pp.95-102.
                         T. Buncle, Arbroath, Scotland.

ARTSCHWAGER, E. F. (1918) Anatomy of the potato plant with
                         special reference to the ontogeny
                         of the vascular system.
                         J.agric.Res. 14: 221-252.

ATTAVIAN, B. N., G. JELENKOVIC and B. L. POLLACK
          (1983)   Cytogenetical and fertility studies
                   of selected nontuberous Solanum
                   species and their hybrid derivatives.
                   J. Am. Soc. hort. Sci. 108 : 10-15.

AVERETT, J. E. and A. M. POWELL,
          (1972)   Chromosome numbers in Physalis
                   and Solanum (Solanaceae).
                   Sida 5 : 3-7.

BABU, C. R. and F. N. HEPPER.
          (1979)   Taxonomy and nomenclature of Solanum
                   khasianum and some of its relatives.
                   Kew Bull. 34(2): 407-411.

498

BAKER, J. G.   (1883)   Contributions to the Flora of
                          Madagascar. Part II Monopetalae.
                          Bot. J. Linn. Soc. 20: 159-236.

                (1885)   Further contributions to the Flora
                         of Madagascar. Second and first
                         part. Bot.J.Linn.Soc. 21 : 426.

BAKSH, S. and M. IQBAL,
                (1978)   Floral features of Solanum macran-
                         thum Dun. with special reference to
                         stylar heteromorphism and intercross-
                         ability.
                         Flora, Jena 167 : 423-431.

BARTLETT, H. H. (1940)   History of the generic concept in
                         botany Bull.Torrey bot.Club 67 :
                         349-362.

BAUHIN, C.   (1623)   Pinax Theatri Botanici ... Basel.

BAYLIS, G. T. S. (1958) A cytogenetical study of New
                         Zealand forms of Solanum nigrum
                         L., S.nodiflorum Jacq. and
                         S.gracile Otto. Trans. R. Soc. N.Z.
                         86: 379-385.

BELL, E. A.   (1981) Non-Protein Amino Acids in the
                         Leguminosae. In :   Polhill and
                         Raven, 1981   pp. 489-499.

BENDICH, A. J. and B. J. McCARTHY
                (1970)   DNA comparisons among barley, oats,
                         rye and wheat. Genetics 65: 545-565.

BENDZ, G. and J. SANTESSON
                (1973)   eds. Chemistry in Botanical
                         Classification. Nobel Foundation,
                         Sweden.

BENTHAM, G. and J. D. HOOKER
        (1862-1883) Genera plantarum.
                     A.Black,London.
                     Solanaceae in Vol 2(2) pp 882-913
                     contributed by Bentham,
                     published 1876.

BERHAUT, J.   (1967)   Flore du Senegal. 2nd Edition.
                            Editions Clairafrique, Dakar.

BESSIS, J. and M. GUYOT
        (1979)   An attempt to use stomatal
                     characters in systematic and
                     phylogenetic studies of the
                     Solanaceae. In : Hawkes et al.,
                     1979 pp.321-326 + 2 plates.

BISBY, F. A., J. G. VAUGHAN and C. A. WRIGHT
        (1980)   eds. Chemosystematics : Principles
                     and Practice.
                     Academic Press, London.

BITTER, G.   (1911)   Steinzellkonkretionen in Frucht-
                            fleisch beerentragender Solanaceen
                            und deren systematische Bedeutung.
                            Bot. Jb. 45 : 483-507.

                   (1912)   Solana nova vel minus cognita.
                            1. Reprium Spec.nov.Regni veg.
                            10: 542-548.

                   (1913)   Solana africana I.
                            (Morellae novae vel minus
                            cognitae) Bot. Jb. 49: 560-569.

                   (1915)   Weitere Untersuchungen uber das
                            Vorkommen von Steinzellkronkre-
                            tionen in Fruchtfleisch beerentragen
                            der Solanaceen.
                            Abh. naturw. Ver. Bremen 23 :
                            114-163.

BITTER, G. (1917) Solana africana II.
 Bot. Jb. 54 : 416-506.

 (1919) Die papuasischen Arten von Solanum
 Bot. Jb. 55 : 55-113.

 (1921) Solana africana III.
 Bot. Jb. 57 : 248-286.

 (1922) Solana nova vel minus cognita 21.
 Reprium Spec.nov. Regni veg. 18 :
 301-307

 (1923) Solana africana IV.
 Beih. Repert. nov. Spec. Regni veg.
 16 : 1-320.

BOULTER, D. (1980) The evaluation of present results
 and future possibilities of the use
 of amino acid sequence data in
 phylogenetic studies with specific
 reference to plant proteins.
 In : Bisby et al., 1980
 pp.235-240.

BOULTER, D., D. PEACOCK, A. GUISE, J. T. GLEAVES
and G. ESTABROOK
 (1979) Relationships between the partial
 amino acid sequences of plasto-
 cyanin from members of ten families
 of flowering plants.
 Phytochemistry 18 : 603-608.

BOWERS, K. A. W. (1975) The pollination ecology of Solanum
 rostratum (Solanaceae).
 Am. J. Bot. 62 : 633-638.

BRADLEY, V., D. J. COLLINS, P. G. CRABBE, F. W. EASTWOOD,
M. C. IRVING, J. M. SWAN and D. E. SYMON.
(1978)   A survey of Australian Solanum
plants for potentially useful
sources of solasodine.
Aust. J. Bot. 26 : 723-754.

BRIGGS, B. G. and L. A. S. JOHNSON
(1979)   Evolution in the Myrtaceae -
evidence from inflorescence
structure.
Proc. Linn. Soc. N.S.W. 102(4) :
157-256.

BRUNFELS, O.   (1530)   Herbarum vivae icones.
Strasbourg.

BUKENYA, Z. R.   (1980)   Studies in the taxonomy of Solanum
L. in Southern Ghana.
M.Sc. Thesis, University of Ghana,
Legon.

BULLOCK, A. A.   (1931)   Solanaceae.   In : J. Hutchinson
and J. M. Dalziel (eds.)
Flora of West Tropical Africa 2 :
pp.201-208.   Crown Agents, London.

BURKILL, I. H.   (1925)   Solanum macrocarpon.
Bull. misc. Inf. R. bot. Gdn., Kew
1925 : 333-341.

CARLE, R.   (1981)   Investigations on the content of
steroidal alkaloids and sapogenins
within Solanum sect. Solanun
(= sect. Morella) (Solanaceae).
Pl. Syst. Evol. 138(1-2) : 61-71.

CESALPINO, A.   (1563)   De plantis libri XVI.
Georgium Marescottum, Florence.

CHAUDRI, M. N., I. H. VEGTER and C. M. DE WAL
        (1972)   Index herbariorum. Part II(3)
                    Collectors I - L. IAPT, Utrecht.

CHENERY, E. M. (1948)   Aluminium in the plant world. I.
                    General survey in dicotyledons.
                    Kew Bull. 1948(2) : 173-183.

CHILD, A.   (1979a)   A review of branching patterns in
                    the Solanaceae. In : Hawkes
                    et al., 1979 pp.345-356.

        (1979b)   Branching as an infrageneric group
                    character in the genus Solanum.
                    A translation of Danert (1967).
                    Solanac.newsl. 6 : 16-34.

        (1983)   Taxonomic studies in Solanum L.
                    1. Section Nemorense Child,
                    sectio nova. Feddes Reprium 94:
                    35-42.

CHIOVENDA, E.
        (1929-1932)   Flora somala.
                    Sindicato Italiano Arti Grafiche,
                    Rome.

CLAUSEN, J.   (1951)   Evolution of plant species.
                    Cornell University Press.

COMPTON, R. H. (1976)   The flora of Swaziland.
                    J.S.Afr.Bot.
                    Supplementary Volume II :
                    pp.516-518.

COPPEN, J. J. W. (1979) Steroids : from plants to pills -
                    the changing picture.
                    Trop. Sci. 21(3) : 125-141.

CORRELL, D. S.   (1962)   The Potato and its Wild Relatives.
Renner, Texas.

CORTESAO, A.   (1961)   The Portuguese discovery and
exploration of Africa. Comptes
Rendus de la IVe Renunion
Pleniere de l'AETFAT : pp.21-39.

COUNE, C. and A. DENOEL.
(1975)   Etude phytochimique des Solanaceae
d'Afrique Centrale. I Les
alcaloides de Solanum dasyphyllum.
Planta med. 28 : 168-171.

CRIBB, P.   (1972)   Studies on the Origin of Solanum
tuberosum L. subsp. andigena (Juz.
& Buk.) Hawkes - the Cultivated
Tetraploid Potato. PhD Thesis,
University of Birmingham, England.

CRISTOFOLINI, G. (1980)   Interpretation and analysis of
serological data. In : Bisby
et al., 1980 pp.269-288.

CRONQUIST, A.   (1976)   The taxonomic significance of the
structure of plant proteins : a
classical taxonomist's view.
Brittonia 28 : 1-27.

(1977)   On the taxonomic significance of
secondary metabolites in angio-
sperms. Pl. Syst. Evol.,
Supp. 1 : 179-189.

(1980)   Chemistry in plant taxonomy : an
assessment of where we stand.
In : Bisby et al., 1980
pp.1-27.

CRUZ, W., and O. PROANO
          (1970)   Obtencion de solasodina a partir
                    del fruto de Solanum marginatum.
                    Politecnica 2 : 155-248.

CUFODONTIS, G. (1961)   A preliminary contribution to the
                    knowledge of the botanical explor-
                    ation of north eastern tropical
                    Africa. Comptes Rendus de la IV$^{\underline{e}}$
                    de l'AETFAT : pp.233-248.

          (1963)   Solanum in Enumeratio Plantarum
                    Aethiopiae Spermatophyta.
                    Bull. Jard. bot. Etat Brux. 33(3) :
                    861-880.

DAHLGREN, R.   (1975)   A system of classification of the
                    angiosperms to be used to demon-
                    strate the distribution of charac-
                    ters. Bot. Notiser 128 : 119-147.

DALZIEL, J. M. (1937)   The Useful Plants of West Tropical
                    Africa. Crown Agents, London.

DAMMER, U.   (1905)   Solanaceae africanae.
                    Bot. Jb. 38(1) : 57-60.

          (1906)   Solanaceae africanae I.
                    Bot. Jb. 38(2) : 176-195.

          (1912)   Solanaceae africanae II.
                    Bot. Jb. 48(1/2) : 236-260.

          (1915)   Solanaceae africanae III.
                    Bot. Jb. 53(3) : 325-352.

DANERT, S.   (1958)   Die Verzweigung der Solanaceen im reproduktiven Bereich. Abh.dt.Akad. Wiss.Berlin, math-naturwiss. Kl. Chem. Nr 6 : 1-183.

(1967)   Die Verzweigung als infragener-isches Gruppenmerkmal in der Gattung Solanum L. Kulturpflanze 15 : 275-292.

(1969)   Uber die entwicklung der stein-zellkonkretionen in der gattung Solanum. Kulturpflanze 17 : 299-311.

(1970)   Infragenerische Taxa Der Gattung Solanum L. Kulturpflanze 18 : 253-297.

D'ARCY, W. G.   (1970)   Jacquin names, some notes on their typification. Taxon 19 : 554-560.

(1972)   Solanaceae studies II : typificat-ion of subdivisions of Solanum. Ann. Mo. bot. Gdn. 262-278.

(1973)   Flora of Panama, Family 170 Solanaceae. Ann. Mo. bot. Gdn.60 : 573-780.

(1974a)   Solanum and its close relatives in Florida. Ann. Mo. bot. Gdn. 61 : 819-867.

(1974b)   Solanum rugosum Dun., une troisieme espece de Solanum section Brevan-therum en Afrique. Bull. Inst. fond. Afr. noire Serie A, 36(2) : 392-393.

D'ARCY, W. G.   (1979)   The classification of the
                           Solanaceae.
                           In: Hawkes et al., 1979 pp.3-47.

DARWIN, C.   (1865)   On the Movements and Habits of
                          Climbing Plants J. Linn. Soc.,
                          Botany 9 : 1-118.

                (1877)   The Different Forms of Flowers on
                          Plants of the Same Species.
                          John Murray, London.

                (1882)   The Movements and Habits of
                          Climbing Plants.
                          John Murray, London.

DAVIS, B. J.   (1964)   Disc electrophoresis. II Methods
                          and application to human serum.
                          Annals of the N.Y. Academy of
                          Sciences 121 : 404-407.

DAVIS, G. L.   (1966)   Systematic Embryology of the
                          Angiosperms.
                          John Wiley & Sons Inc., New York.

DAVIS, P. H. and V. H. HEYWOOD,
                (1973)   Principles of Angiosperm Taxonomy.
                          Oliver & Boyd, Edinburgh & London.

DESBOROUGH, S. and S. J. PELOQUIN
                (1968)   Acid gel electrophoresis of tuber
                          proteins from Solanum species.
                          Phytochemistry 8 : 425-429.

DILLENIUS, J. J. (1732)   Hortus Elthamensis 2 : pp.360-368,
                          London.

DIOSCORIDES   (AD 60)   Materia medica. Codex vindobonensis.
                                Facsimile   A.W. Sijthoff, Leiden 190

DODOENS, R.   (1583)   Stirpium historiae pemptades sex.
                                Christophori Plantini, Antwerp.

DRAY, S. and G. O. YOUNG
                (1959)   Two antigenically different γ
                                - globulins in domestic rabbits
                                revealed by isoprecipitins.
                                Science, N.Y. 129 : 1023-1025.

DREGE. J. F.   (1843)   Zwei pflanzengeografische Dokumente.

DULBERGER, R., A. LEVY and D. PALEVITCH
                (1951)   Andromonoecy in Solanum Marginatum,
                                Bot. Gaz. 142(2) : 259-266.

DUNAL, M. F.   (1813)   Histoire Naturelle Medicinale et
                                Economique des Solanum.   Paris,
                                Strasbourg, Montpellier.

                (1816)   Solanorum generumque affinium
                                synopsis seu Solanorum Historiae,
                                Montpellier.

                (1852)   Solanaceae. In: A. P. de Candolle
                                (ed), Prodromus Systematis
                                naturalis Regni vegetabilis 13(1) :
                                1690. Paris.

DUNKLEY. H.   (1937)   New Trees And Shrubs From Tropical
                                Africa V.
                                Bull. misc. Inf. R. bot. Gdn.,
                                Kew 9 III : 466-471.

508

EDMONDS, J. M. (1971) <u>Solanum</u> L. In: W.T. Stearn,
Taxonomic and nomenclatural notes
on Jamaican gamopetalous plants.
<u>J. Arnold Arbor.</u> <u>52</u> : 634-635.

(1972) A synopsis of the taxonomy of
<u>Solanum</u> section <u>Solanum</u>(<u>Maurella</u>)
in South America. <u>Kew Bull.</u>
<u>27</u>(1): 95-114.

(1977) Taxonomic studies on <u>Solanum</u> L.,
section <u>Solanum</u> (<u>Maurella</u>).
<u>Bot. J. Linn. Soc.</u> <u>75</u> : 141-178.

(1978) Numerical taxonomic studies on
<u>Solanum</u> L., section <u>Solanum</u>
(<u>Maurella</u>).
<u>Bot. J. Linn. Soc.</u> <u>76</u> : 27-52.

(1979a) Biosystematics of <u>Solanum</u> L.,
section <u>Solanum</u> (<u>Maurella</u>).
In: Hawkes <u>et al.</u>, 1979 pp.529-548.

(1979b) Nomenclatural notes on some species
of <u>Solanum</u> L. found in Europe.
<u>Bot. J. Linn. Soc.</u> <u>78</u> : 213-233.

(1982) Epidermal hair morphology in
<u>Solanum</u> L., section <u>Solanum</u>.
<u>Bot. J. Linn. Soc.</u> <u>85</u> : 153-167.

EDMONDS, J. M. and S. M. GLIDEWELL
(1977) Acrylamide gel electrophoresis of
seed proteins from some <u>Solanum</u>
(section <u>Solanum</u>) species.
<u>Pl. Syst. Evol.</u> <u>127</u> : 277-291.

EHLERINGER, J. (1982) The influence of water stress and
temperature on leaf pubescence
development in Encelia farinosa.
Am.J. Bot. 69(5) : 670-675.

EHRLICH, P. R. and P. h. RAVEN
(1969) Differentiation of populations.
Science, N.Y. 165: 1228-1232.

ESAU, K. (1977) Anatomy of seed plants. 2nd Edition.
John Wiley, New York.

EVANS, W. C. (1979) Tropane alkaloids of the Solanaceae.
Hawkes et al.,1979 pp.241-254.

FAIRBROTHERS, D. E. and F. P. PETERSEN
(1983) Serological investigation of the
Annoniflorae (Magnoliiflorae,
Magnolidae). In: Proteins and
nucleic acids in plant systematics.
(Jensen, U. and D. E. Fairbrothers,
eds.) pp.301-310
Springer-Verlag, Berlin.

FEDEROV, A. A. (1969) Chromosome numbers of flowering
plants. 926 pp.
Academy Sciences U.S.S.R., Moscow.

FORSSKAL, P. (1775) Flora aegyptiaco-arabica.
Moller, Copenhagen.

FOSBERG, F. R. (1978) Miscellaneous notes on the flora
of Aldabra and neighbouring
islands : IX. The native
Aldabra Solanum.
Kew Bull. 33 : 141-142.

FOSBERG, F. R. and S. A. RENVOIZE
  (1980) The Flora of Aldabra and
       neighbouring islands.
       Kew Bull. Additional Series VII.

FRESENIUS, J. B. G. W.
  (1833-1834) Beitrage zur Flora von Aegypten
       und-Arabien.
       Museum Senckenbergianum I
       pp.166-167

FRIDAY, A. E. (1980) The Status of Immunological
       Distance Data in the Construction
       of Phylogenetic Classifications :
       a Critique.
       In : Bisby et al., 1980 pp.289-304

FUCHS, L. (1542) De historia stirpium.
       Basel.

GBILE, Z. O. (1979) Solanum in Nigeria.
       In : Hawkes et al., 1979
       pp.113-120.

GBILE, Z. O. and M. A. SOWUNMI
  (1979) The pollen morphology of Nigerian
       Solanum species.
       In : Hawkes et al., 1979
       pp.335-344.

GELL, P. G., J. G. HAWKES and S. T. C. WRIGHT
  (1960) The application of immunological
       methods to the taxonomy of species
       within the genus Solanum.
       Proc. R. Soc., B. 151 : 364-383.

GERSHENZON, J. and T. J. MABRY
       (1983)   Secondary metbolites and the higher
                  classification of angiosperms. In :
                  New evidence of relationships and
                  modern systems of classifications
                  of the angiosperms. Proc.Symp. XIII
                  IBC, Sydney.
                  Nordic. J. Bot. 3 : 5-34.

GIBBS, R. D.   (1974)   Chemotaxonomy of Flowering Plants,
                  Vols. 1-4.
                  McGill-Queen's Universities Press,
                  Montreal and London.

GILLET, J. B.   (1961)   The history of the botanical
                  exploration of the area of 'The
                  Flora of Tropical East Africa
                  (Uganda, Kenya, and Tanganyika and
                  Zanzibar).
                  Comptes Rendus de la IV$^{\underline{e}}$ Reunion
                  Pleniere de l'AETFAT : pp.205-229.

GOEBEL, K.   (1931)   Blutenbildung und Sprossgestaltung.
                  Jena.

GOODING, E. G. B.
       (1965)   Flora of Barbados, 91, Solanaceae.
                  H.M.S.O. (London) pp.373-382.

GORNALL, R. J., B. A. BOHM and R. DAHLGREN
       (1979)   The distribution of flavonoids in
                  the angiosperms.
                  Bot. Notiser 132 :1-30.

GOTTLIEB, O. R. (1980)   Micromolecular Systematics :
                  Principles and Practice.
                  In : Bisby et al., 1980 pp.329-352.

GOTTSCHALK. W. (1954)   Die Grundzahl der Gattung Solanum
                  und einiger Nicotiana - Arten.
                  Ber. dt. bot. Ges. 67(9) : 369-376.

512

GRANT, V.   (1981)   Plant Speciation (Ed.2)
                             Columbia University Press, New York.

GRAY, J. C.   (1977)   Serological relationships of
                             Fraction I proteins from species
                             in the genus Nicotiana.
                             Pl. Syst. Evol. 128 : 53-69.

                   (1980)   FractionI protein and plant phylogeny.
                             In : Bisby et al., 1980 pp.167-193.

GRUND, C. and U. JENSEN
                   (1981)   Systematic relationships of the
                             Saxifragales revealed by
                             serological characteristics of
                             seed proteins.
                             Pl. Syst. Evol. 137 : 1-22.

GUNN, M. and L. E. CODD
                   (1981)   Botanical exploration of southern
                             Africa. Balkema, Cape Town.

hALL, J. B. and M. D. SWAINE
                   (1980)   Seed stocks in Ghanaian forest
                             soils.
                             Biotropica 12(4) : 256-263.

HARBORNE, J. B. (1973)   Flavonoids as systematic markers
                             in the Angiosperms.
                             In : Bendz and Santesson, 1973
                             pp.103-115.

                   (1975)   Biochemical systematics of
                             flavonoids.
                             In : Harborne et al., 1975
                             pp.1056-1095.

HARBORNE, J. B. (1980)   New experimental approaches to
                          plant chemosystematics.
                          In : Bisby et al. 1980 pp.39-70.

HARBORNE, J. B., T. J. MABRY and H. MABRY,
            (1975)   eds. The Flavonoids
                      Chapman and Hall, London.

HARBORNE, J. B. and T. SWAIN
            (1979)   Flavonoids of the Solanaceae.
                      In : Hawkes et al. 1979 pp.257-268.

HARBORNE, J. B. and B. L. TURNER
            (1984)   Plant Chemosystematics.
                      Academic Press, London.

HARLEY, R. M. (1970)   Solanum jasminoides.
                        Curtis's bot. Mag. 117 : t.568.

HASLAM, E.   (1981)   Vegetable tannins. In : The
                            Biochemistry of Plants :
                            A Comprehensive Treatise.
                            Volume 7 Secondary Plant Products
                            (E. E. Conn, ed.) pp. 527-556.
                            Academic Press, London.

HAWKES, J. G.   (1956)   Taxonomic studies on the tuber-
                             bearing Solanums : 1.
                             Solanum tuberosum and the
                             tetraploid species complex.
                             Proc. Linn. Soc. London, Session
                             166 : 97-144.

                   (1963)   A revision of the tuber-bearing
                             Solanums II.
                             Rec. Scott. Pl. Breed. Stn. 71-181.

                   (1979)   Evolution and polyploidy in potato
                             species. In : Hawkes et al. 1979
                             pp.637-646.

HAWKES, J. G. and J. M. EDMONDS
      (1972)   Solanum L. in T.G. Tutin,et
              al (eds.), Flora Europaea 3 :
              pp.197-199. Cambridge University
              Press, Cambridge.

HAWKES, J. G. and J. P. HJERTING
      (1969)   The Potatoes of Argentina, Brazil,
              Paraguay and Uruguay,
              A Biosystematic Study.
              Clarendon Press, Oxford.

HAWKES, J. G. and R. N. LESTER
      (1966)   Immunological studies on the tuber-
              bearing Solanums II. Relationships
              of North American Species. Ann.
              Bot. 30 : 270-290.

HAWKES, J. G. and R. N. LESTER
      (1968)   Immunological studies on the tuber-
              bearing Solanums III. Variability
              within S.bulbocastanum.
              Ann. Bot. 32: 165-186.

HAWKES, J. G., R. N. LESTER and A. D. SKELDING
      (1979)   eds. The Biology and Taxonomy of
              the Solanaceae
              Academic Press, London.

HAWKES, J. G. and P. M. SMITH
      (1965)   Continental drift and the age of
              angiosperm genera.
              Nature, Lond. 207 : 48-50.

HAWKES, J. G. and W. G. TUCKER
      (1968)   Serological assessment of relation-
              ships in a flowering plant family
              (Solanaceae). In : Chemotaxonomy
              and Serotaxonomy (Hawkes, J.G.,
              Ed.) pp. 77-88. Systematics
              Association Special Volume No. 2,
              Academic Press, London.

HEGNAUER, R. (1973) Chemotaxonomie der pflanzen VI.
Solanaceae: 403-452; nachtrage
750-754; 788-790.

HEINE, H. H. (1960) Notes on Solanum. Kew Bull. 14 :
245-249.

(1963) Solanaceae. In : Hepper, F. N. (ed.)
Flora of West Tropical Africa.
2nd ed. 2 : 325-335.
Crown Agents, London.

(1976) Solanaceae. In : Flore de la
Nouvelle Caledonie et Dependances 7
119-205.

HEISER, C. B. (1969) Nightshades, The Paradoxical Plants.
W.H. Freeman, San Francisco.

(1971) Notes on some species of Solanum
(sect.Leptostemonum) inLatin
America. Baileyas 18 : 59-65.

HENDERSON, R. J. F.
(1974) Solanum nigrum L. (Solanaceae) and
related species in Australia.
Contr. Qd.Herb. 16: 1-80.

(1977) Notes on Solanum (Solanaceae) in
Australia. Austrobaileya 1 : 13-22.

HEPPER, F. N. (1963) ed. Flora of West Tropical Africa.
Second Edition.
Crown Agents, London.

516

HEPPER, F. N. (1968) A standard citation of microfiches.
Taxon 17 : 604.

(1978) Typification and name changes of
some Old World Solanum species.
Bot. J. Linn. Soc. 76 : 287-292.

(1979) African Solanum species of actual
and potential importance.
In : G.Kunkel (ed.) Taxonomic
Aspects of African Economic Botany.
Proceedings of the IX Plenary
Meeting of AETFAT. Excmo, Las Palmas.

HEPPER, F. N. and P-M. L. JAEGER
(1985) The typification of six Linnaean
names of Solanum.
Kew Bull. 40(2) : 387-391.

(In Press) Name changes for two Old World Solanu
species. Kew Bull. 41.

HEPPER, F. N. and J. R. I. WOOL
(1983) New combinations and notes based on
Forsskal's Arabian collection.
Kew Bull. 38(1) : 83-86.

HICKEY, L. J. (1973) Classification of the architecture
of dicotyledonous leaves.
Am. J. Bot. 60 : 17-33.

(1979) A revised classification of the
architecture of dicotyledonous
leaves.
In : Anatomy of the Dicotyledons
Ed. 2 Vol. 1 Metcalfe, C. R. and
L. Chalk (eds.) pp.25-39.
Clarendon Press, Oxford.

517

HILLEBRAND, G. R. and D. E. FAIRBROTHERS
    (1970) Phytoserological systematic survey
       of the Caprifoliaceae.
       Brittonia 22 : 125-133.

HITCHCOCK, A. S. and M. L. GREEN
    (1929) Int. Bot. Congr. Cambridge 1930.
       Nom. Prop. 111-199.

HOGENBOOM, N. G. (1979) Incompatibility and incongruity in
       Lycopersicon. In: Hawkes et al.,
       1979 pp.435-444.

HOLM, L., J. V. PANCHO, J. P. HERBERGER and D. L. PLUCKNETT
    (1979) A Geographical Atlas of World Weeds.
       Wiley-Interscience.

HOLM, T. (1910) Medicinal plants of North America.
       No. 43. Solanum carolinense L.
       (Abstract) Bot. Zbl. 114 : 606.

HOLMGREN, P. K., W. KEUKEN and E. K. SCHOFIELD
    (1981) Index Herbariorum. Part I The
       herbaria of the world. Ed. 7.
       Regnum Vegetabile Vol. 106.
       Junk, The Hague.

HOLUB, J. (1974) Neglected plant names from the book
       'Rostlinictvi' by D. Sloboda.
       Preslia 46(2) : 169.

HORT, A. (1916) Theophrastus Eresios, enquiry into
       plants,.....etc. Translation by
       Sir Arthur Hort. Heinemann, London.

HOSSAIN, M. (1973) Observations on the stylar
       heteromorphism in Solanum torvum
       Sw. (Solanaceae).
       Bot.J.Linn.Soc. 66 : 291-301.

HUMPHRIES, C. J.
        (1981)   Biogeographical methods and the
                    southern beeches.
                    In : The Evolving Biosphere.
                    (Forey, P.L. ed.) pp.283-297.
                    British Museum (NH) & Cambridge
                    University Press, England.

HUMPHRIES, C. J. and P. M. RICHARDSON
        (1980)   Hennig's Methods and Phytochemistry.
                    In : Bisby et al., 1980 pp.353-378.

HUNZIKER, A. T. (1979a)   The Solanaceae in the Neotropics :
                    a critical appraisal.
                    In : Tropical Botany
                    (K. Larsen and L. B. Holm-Nielsen,
                    eds.) pp. 355-364.
                    Academic Press, London.

        (1979b)   South American Solanaceae: a synoptic
                    survey. In : Hawkes et al. 1979
                    pp.49-85.

INAMDAR, J. A. and G. S. R. MURTHY
        (1978)   Leaf architecture in some
                    Solanaceae.Flora 167(3/4) :
                    265-272.

INGHAM, J. L.   (1981)   Phytoalexin induction and its
                    taxonomic significance in the
                    Leguminosae (subfamily Papilion-
                    oideae). In : Polhill & Raven, 1981
                    pp.599-626.

JACOT GUILLARMOD, A.
        (1971)   Flora of Lesotho. J. Cramer, Lehre.

JACQUIN, N. J.   (1789)   Collecteana ad botanicam..... 2:
                    284-288. Vienna.

JACQUIN, N. J.   (1792)   Icones plantarum rariorum.....
                            Vienna.

                  (1797-1804)
                            Planatarum rariorum horti caesarei
                            schoenbrunnensis.....

JAEGER, P-M. L. and F. N. HEPPER
          (In Press) A review of the genus Solanum in
                     Africa. In : W.G. D'Arcy (ed.)
                     Solanaceae : biology and systematics.
                     Columbia University Press, New York.

JENSEN, U.   (1968)   Serologische beitrage zur systematik
                            der Ranunculaceae.
                            Bot. Jb. 88 : 204-268.

                  (1973)   The interpretation of comparative
                            serological results. In : Bendz and
                            Santesson, 1973 pp.217-227.

JENSEN, U. and B. GREVEN
          (1984)   Serological aspects and phylogenetic
                    relationships of the Magnoliidae.
                    Taxon 33(4) : 563-577.

JENSEN, U. and K. PENNER.
          (1980)   Investigation of serological
                    determinants from single storage
                    plant proteins. Biochem. Syst.
                    Ecol. 8(2) : 161-170.

JOHNSON, A. G. (1971)   Factors affecting the degree of
                          self incompatibility in inbred
                          lines of Brussels sprouts.
                          Euphytica 20 : 561-573.

KEAY, R. W. J.   (1961)   Botanical collectors in West Africa
                           prior to 1860. Comptes Rendus de
                           la IV Reunion Pleniere de l'AETFAT:
                           55-68.

EL KHEIR, Y. M. and M. H. SALIH
                 (1979)   Investigation of the alkaloidal
                           content of Solanum dubium L.
                           growing in Sudan.
                           Fitoterapia 50(6) : 255-258.

KIRSCH, J. A. W.
                 (1967)   Comparative Serology of Marsupials.
                           Ph.D. Thesis, University of Western
                           Australia.

KRAUS, R.   (1897)   Uber specifische reactionen in
                         keimfreien filtraten aus Cholera,
                         Typhus und pestbouillon culturen
                         erzeugt durch homologes serum.
                         Wien. klin. Wschr. 10 : 736-738.
                         (cited by Smith, P.S., (1976).

LAMARCK, J. B. A. P. MONNET DE
                 (1794)   Tableau enclyclopedique et
                           methodique des trois Regnes de
                           la Nature.
                           Botanique 2 : 13-25 Paris.

LAMBERTYE, CTE. L. de

                 (1865)   Solanum warscewiczii.
                           Solanum warscewicizii Hortul.
                           Catal. D'Alph. Weick. -
                           Morelle De Warscewicz.
                           In : Revue Horticole pp.429-431.

LANJOUW, J. and F. A. STAFLEU,
                 (1954)   Index herbariorum. Part II(1,2)
                           Collectors A-H.
                           IAPT, Utrecht.

LANZA,. D.   (1939)   Solanaceae in Cufodontis,
                              Missione Biologica nel paese dei
                              Borana .4 : Raccolte botaniche. Rome.
                              pp.190-206.

LEE, Y. S. and D. E. FAIRBROTHERS
                   (1978)   Serological approaches to the
                              systematics of the Rubiaceae and
                              related families.
                              Taxon 27 : 159-185.

LEEUWENBERG, A. J. M.
                   (1965)   Isotypes of which holotypes were
                              destroyed in Berlin.Webbia 19(2) :
                              861-863.

LESTER, R. N.   (1965)   Immunological studies on the tuber-
                              bearing Solanums I. Techniques and
                              South American species.
                              Ann. Bot. 29 : 609-624.

LESTER, R. N.   (1979a)   Patterns of proteins in potato
                              cultivars. Review of some recent
                              publications by H. Stegemann and
                              V. Loeschke. Solanaceae Newsl. 6 :
                              41-43.

                   (1979b)   The use of protein characters in the
                              taxonomy of Solanum and other
                              Solanaceae. In : Hawkes et al. 1979
                              pp.285-304.

                   (In Press) Taxonomy of scarlet eggplants,
                              Solanum aethiopicum L.
                              Acta hort.

LESTER, R. N. and P. DURRANDS.
                   (1983)   Enzyme treatment as an aid in the
                              study of seed surface structures
                              of Solanum species. Ann. Bot.

LESTER, R. N., J. J. H. HAKIZA,
    N. STAVROPOULOS and M. M. TEIXIERA.
        (1985)   Variation patterns in the African
                Scarlet Eggplant, Solanum aethiop-
                icum L.
                In : Infraspecific classification
                of wild and cultivated plants.
                (Styles, B. ed.) Oxford University
                Press, Oxford.

LESTER, R. N. and L. NIAKAN
        (In Press) Origin and domestication of the
                Scarlet Eggplant, Solanum
                aethiopicum L., from S. anguivi
                Lam. In : Solanaceae : biology
                and systematics.(D'Arcy, W. G. ed.)
                ColumbiaUniversityPress,New York.

LESTER, R. N. and P. A. ROBERTS
        (In Press) Serotaxonomy of Solanum,
                Capsicum, Dunalia and other
                selected Solanaceae.
                Ann.Mo.bot.Gdn. 73(1).

LESTER, R. N., P. A. ROBERTS and C. LESTER
        (1983)   Analysis of immunotaxonomic data
                obtained from spur identification
                and absorption techniques.
                In : Proteins and Nucleic Acids
                in Plant Systematics
                (Jensen, U., ed.). Springer, Berlin
                pp.275-300.

LEVIN, D. A.   (1979)   The nature of plant species.
                        Science, N.Y. 204 : 381-384.

LEVIN, D. A. and H. W. KERSTER
        (1974)   Gene flow in seed plants. Evolut.
                Biol. 7 : 139-220.

LINDER, P. H. (In Press) Gene flow, speciation, and species
diversity patterns in a species-
rich area : the Cape flora.
In : Species and speciation
(Vrba, E.S., ed.) Transvaal Museum
Monograph No. 4, Pretoria.

LINNAEUS, C.   (1738a)   Classes plantarum.
                              Wishoff, Leiden.

                   (1738b)   Hortus cliffortianus, Amsterdam.

                   (1751)   Philosophica botanica, Stockholm.

                   (1753)   Species plantarum Ed.1: 184-188.
                              Stockholm.

                   (1762)   Species plantarum Ed.2
                              Stockholm.

                   (1771)   Mantissa plantarum altera
                              Laurentii Salvii, Stockholm.

LOBEL, M. de   (1576)   Plantarum seu stirpium historia.
                              Christophori Plantini, Antwerp.

LOWE, R. T.   (1872)   A Manual Flora of Madeira. 2(1) :
                              87-89. London.

MABRY, T. J.   (1974)   Chemistry of disjunct taxa.
                              In : Bendz and Santesson, 1974
                              pp.63-66.

McBRIDE, J. F.   (1962)   Flora of Peru, Solanaceae.
                              Publ. Field Mus. Nat. Hist., Bot.
                              Ser. 13 Part V-B(1) : 267pp.

McCLURE, J. W.   (1975)   Physiology and function of
                           flavonoids.
                           In : Harborne et al. 1975
                           pp.970-1055.

MAGNOL, P.   (1689)   Prodromus historiae generalis
                           plantarum.
                           Gabrielis & Honorati, Pech,
                           Montpellier.

MAITI, P. C., SIPRA MOOKHERJEA, R. MATHEW and S. S. DAN
                  (1979)   Studies on Indian Solanum. I
                           Alkaloid content and detection of
                           Solasodine.
                           Econ.Bot. 33(1) : 75-77.

MANGENOT, S. and G. MANGENOT
                  (1962)   Enquete sur les nombres chromo-
                           somiques dans une collection
                           d'especes tropicales
                           Rev. Cytol. Biol. veg. 25(3/4) :
                           411-447.

MARKHAM, K. R.   (1982)   Techniques of Flavonoid
                           Idenification.
                           Academic Press, London.

MARTIN, F. W.   (1972)   Sterile styles in Solanum mammosum.
                           Phyton 29: 127.

MARZELL, H.   (1927)   Solanum In : Hegi (ed.) Illustrierte
                           Flora von Mitteleuropa pp.2582-2611.

MAYR, E.   (1942)   Systematics and the origin of
                           species.
                           Colombia University Press, New York.

MAYR, E.   (1965)   The biological meaning of species.
                             Biol. J. Linn. Soc. 1 : 311-320.

MERXMULLER, H.   (1969)   ed. Prodromus einer Flora von
                             Sudwestafrika. 124.

MICHENER, C. D. (1962)   An interesting method of pollen
                             collecting by bees from flowers
                             with tubular anthers.
                             Rev. Biol. trop. 10 : 167-175.

MIEGE, J.   (1962)   Quatrieme liste de nombres
                             chromosomiques d'especes d'Afrique
                             Occidentale. Rev. Cytol. et Biol.
                             Veg. 24(3/4): 149-164.

MILLER, R. H.   (1969)   A morphological study of Solanum
                             mammosum and its mammiform fruit.
                             Bot. Gaz. 130 : 230.

MILLER, P.   (1768)   The Gardeners Dictionary. Ed. 8
                             London.

MOORE, G. W. and M. GOODMAN.
                 (1968)   A set theoretical approach to immuno-
                             taxonomy : analysis of species
                             comparisons in modified ouchterlony
                             plates. Bulletin of Mathematics and
                             Biophysics 30 : 279-389.

MORITZ, O. and U. JENSEN
                 (1961)   An attempt at a formular description
                             of procedures and results in
                             comparative serology.
                             Serol.Mus 25 : 1-5.

MORTON, A. G.   (1981)   History of Botanical Science.
                             Academic Press, London.

MORTON, C. V.   (1976)   A Revision of the Argentine Species
                            of Solanum.
                            Academia Nacional de Ciencias,
                            Cordoba, Argentina.

MURPHY, T. M.   (1978)   Immunochemical comparisons of
                            ribulose bisphosphate carboxylases
                            using antisera to tobacco and
                            spinach enzymes. Phytochemistry
                            17 : 439-443.

MURTY, U. R. and K. ABRAHAM,
                  (1975)   Heterostyly in Solanum khasianum
                            Clarke. Current Sci. 44 : 525.

NEE, M.   (1979)   Patterns in biogeography in
                            Solanum, section Acanthophora.
                            In : Hawkes et al. 1979 pp.569-580.

NEES von ESENBECK, C. G.
                  (1837)   Monograph of the East Indian Solaneae.
                            Trans. Linn. Soc. Lond. 17 : 37-82.

NETTANCOURT, D.de
                  (1977)   Incompatibility in Angiosperms.
                            Springer, Berlin.

NIAKAN, L.   (1980)   Biosystematics of the Scarlet
                            Eggplant (Solanum aethiopicum L.)
                            and Related Species. Ph.D Thesis,
                            University of Birmingham, England.

NIELSEN, M. S.   (1965)   Introduction to the Flowering Plants
                            of West Africa.
                            University of London Press, London.

NUTTALL, G. H. F.
(1901) The new biological test for blood in relation to zoological classification.
Proc. Roy. Soc., B 69 : 150-153.

OMIDIJI, M. O. (1975) Interspecific hybridization in the cultivated, non-tuberous Solanum species. Euphytica 24 : 341-353.

(1979) Crossability relationships between some species of Solanum, Lycopersicon and Capsicum cultivated in Nigeria.
In : Hawkes et al., 1979 pp.599-604.

(1982) Interrelationships of Solanum species in different series of the subgenus Leptostemonum (Dun.)Bitt. Crop Res (Hort. Res.) 22: 3-12.

OUCHTERLONY, O.
(1948) In vitro method for testing the toxin-producing capacity of diphtheria bacteria. Acta path. microbiol. scand. 25 : 169-191.
(cited by Smith, 1976)

PANDEY, K. K. (1979) The genus Nicotiana : evolution of incompatibility in flowering plants.
In : Hawkes et al., 1979 pp.421-434.

PAPPE, L. (1850) Florae capensis medicae prodromus......
Ed. 1 : 21. A. S. Robertson, Cape Town.

PASTEUR, L. (1876) Etudes sur la Biere. Gauthiers-Villars, Paris.

PATIÑO, V. M.   (1962)   Edible fruits of <u>Solanum</u> in South
                          American historic and geographic
                          references. <u>Bot. Mus. Leafl. 19</u> :
                          215-234.

PAYNE, J. W.   (1976)   Electrophoresis of proteins on
                          sodium dodecyl sulphate polyacry-
                          lamide gels.
                          In : <u>Chromatographic and Electropho-</u>
                          <u>retic Techniques.</u> (Smith, I., ed.)
                          Wm. Heinemann Medical Books, London.
                          2 : 321-346.

PEARCE, K. G.   (1975)   <u>Solanum melongena L. and related</u>
                          <u>species.</u> Ph.D Thesis, University of
                          Birmingham, England.

PEARCE, K. G. and R. N. LESTER.
                (1979)   Chemotaxonomy of the cultivated
                          eggplant - a new look at the
                          taxonomic relationships of
                          <u>Solanum melongena</u> L.
                          In : Hawkes <u>et al.</u>, 1979 pp.615-628.

PHILLIPS, E. P. (1938)   The weeds of South Africa. In:
                          <u>Dept. of Agriculture, Division of</u>
                          <u>Botany. Series No. 41</u> : 48-49.

PLINY   (AD 77)   <u>Natural history.</u>
                          with an English translation.
                          Loeb Classical Library, Heinemann,
                          London. Publ'd 1958-1962.

POLHILL, R. M. (1961)   <u>The Genus Solanum in East and</u>
                          <u>North East Africa.</u> (Unpublished
                          typescript at R. B. G., Kew.

POLHILL, R. M. and P. A. RAVEN
                (1981)   <u>Advances in Legume Systematics.</u>
                          Royal Botanic Gardens, Kew.

QUAGLIOTTI, L.   (1979)   Floral biology of Capsicum and
                         Solanum melongena.
                         In : Hawkes et al.   1979 pp.399-420.

RADDI, G.   (1820)   Di alcune piante esculenti del
                         Brasile..... Atti Dell' I. e R.
                         Accademia Dei Georgofili di Firenze
                         2 : 537-548.

RANDELL, B. R. and D. E. SYMON
                 (1976)   Chromosome numbers in Australian
                         Solanum species.
                         Aust. J. Bot. 24: 369.

RAO, N. N.   (1979)   The barriers to hybridization
                         between Solanum melongena and some
                         other species of Solanum.
                         In : Hawkes et al. 1979 pp.605-614.

RAO, N. N. and B. W. X. PONNAIYA,
                 (1970)   A note on the hybridization tech-
                         niques in Solanum species. Anhadra
                         Agricultural Journal 17(3) : 95-96.
                         (cited by Pearce, 1975).

RAVEN, P. H. and D. I. AXELROD.
                 (1974)   Angiosperm biogeography and past
                         continental movements. Ann. Mo.
                         bot. Gdn. 61 : 539-673.

RAY, J.   (1686-1704)
                         Historia plantarum.
                         London.

REDDY, N. P. and BIK BAHADUR
                 (1977)   Flower morphism and sterile styles
                         in Solanum surattense Burm.
                         Geobios (Jodphur) 4 : 103-107.

530

RICHARD, A. (1850) <u>Tentamen Florae Abyssinicae</u>.....
         2 : 97-107. Paris.

ROBERTS, P. A. (1978) <u>Interrelations of Globodera a</u>...
         <u>some Solanum (Leptostemonum)</u>
         <u>species.</u> Ph.D Thesis,
         University of Birmingham, England.

RODDICK, J. G. (1979) Distribution of steroidal
         glycoalkaloids in cells of <u>Solanum</u>
         and <u>Lycopersicon</u>.
         In : Hawkes <u>et al</u>., 1979
         pp.223-229.

ROE, K. E. (1967) A revision of <u>Solanum</u> sect.
         <u>Brevantherum</u> (Solanaceae) in north
         and central America. <u>Brittonia</u> <u>19</u> :
         353-373.

      (1968) <u>Solanum verbascifolium</u> L.
         misidentification and mis-
         application. <u>Taxon</u> <u>17</u> : 176-179.

      (1971) Terminology of hairs in the genus
         Solanum. <u>Taxon</u> <u>20</u> : 501-508.

      (1972) A revision of <u>Solanum</u> sect.
         <u>Brevantherum</u> (Solanaceae).
         <u>Brittonia</u> <u>24</u> : 239-278.

      (1979) Dispersal and speciation in <u>Solanum</u>
         section <u>Brevantherum</u>. In : Hawkes
         <u>et al</u>., 1979 pp.563-568.

ROMEIKE, A. (1978) Tropane alkaloids - occurrence and
         systematic importance in angiosperms.
         <u>Bot. Notiser</u> <u>131</u>(1) : 85-96.

le ROUX, P. J.   (1980)   Encroaching plant species in state
plantations in South Africa.
In : <u>Proc. 3rd nat. Weed Conf.</u>
<u>S.Africa.</u>
(Neser, S. and A. L. P. Cairns, eds.)
pp.181-186. Balkema, Cape Town.

SANDER, H.   (1963)   Zur chemotaxonomie der gattung <u>Solanum</u>
(sensu ampl.) <u>Bot. Jb.</u> <u>82</u> : 404-428.

SANGAR, V. K., R. W. LICHTWARDT, J. A. W. KIRSCH
        and R. N. LESTER
            (1972)   Immunological studies on the fungal
genus <u>Smittium</u> (Trichomycetes).
<u>Mycologia</u> <u>64</u> : 342-358.

SAVAGE, S.   (1936)   Studies in Linnaean synonymy.
1 Caspar Bauhin's 'Pinax' and
Burser's herbarium.
<u>Proc. Linn. Soc. Lond.</u> <u>148</u> : 16-26.

            (1945)   <u>A Catalogue of the Linnaean herbarium.</u>
Linnaean Society, London.

SCHREIBER, K.   (1956)   Neure Untersuchungen auf dem Gebiet der
<u>Solanum</u>-Alkaloide. <u>Abh. dt. Akad.</u>
<u>Wiss. Berl.</u> <u>1956</u> : 143-156.

            (1968)   Steroid alkaloids: the <u>Solanum</u> group.
In : <u>The Alkaloids</u> (Manske,
R. H. F., ed.)
Academic Press, New York, 10 : 1-178.

            (1979)   The steroid alkaloids of <u>Solanum.</u>
In : Hawkes <u>et al.</u>, 1979 pp.193-202.

SCHULTES, R. E and R. ROMERO-CASTANEDA
            (1962)   Edible fruits of <u>Solanum</u> in Columbia.
<u>Bot. Mus. Leafl.</u> <u>19</u> : 235-286.

SCHULZ, O. E.   (1909)   VI Solanacearum genera nonnulla.
In : <u>Symbolae Antillanae seu
Fundamenta Florae Indiae Occident-
alis</u>. (Urban, I., ed.) pp.140-279.

SEITHE, A.   (1962)   Die Haararten der Gattung <u>Solanum</u> L.
und ihre taxomische verwertung.
<u>Bot. Jh.</u> <u>81</u> : 261-336.

          (1979)   Hair types as taxonomic characters in
<u>Solanum</u>. In Hawkes <u>et al.</u>, 1979
pp.307-320.

SEITHE, A. and G. J. ANDERSON.
          (1982)   Hair morphology and the relationships of
species in <u>Solanum</u> sect.<u>Basarthrum</u>.
<u>Pl. Syst. Evol.</u> : 229-256.

SENDTNER, O.   (1846)   <u>Solanum</u>. In <u>Flora brasiliensis</u>
(Martius, C. F. P. von, ed.) <u>10</u> :
10-111. Munich.

SHARMA, B. D.   (1974)   Contribution to the palynotaxonomy
of genus <u>Solanum</u> Linn.
<u>J. Palynology</u> <u>10</u>(1) : 51-68.

SLOBODA, D.   (1852)   <u>Rostlinictvi</u>, Prague.

SMITH, P. M.   (1976)   <u>The Chemotaxonomy of Plants</u>
Edward Arnold, London.

SMITH, W. K. and P. S. NOBEL
          (1977)   Influence of seasonal changes in
leaf morphology on water-use-
efficiency for three desert broad-
leaf shrubs.
<u>Ecology</u> <u>58</u> : 1033-1043.

SNEATH, P. H. A. and R. R. SOKAL.
        (1973)   Numerical Taxonomy.
                 W. H. Freeman, San Francisco.

SOKAL, R. R.   (1973)   The species problem reconsidered.
                            Syst. Zool. 22 : 360-374.

SOKAL, R. R. and T. J. CROVELLO.
        (1970)   The biological species concept.
                 Am. Nat. 14 : 127-153.

STAFLEU, F. A. and R. S. COWAN
               Taxonomic literature :

(1976)	Volume I :	A-G	Reg. veg.	94.
(1979)	Volume II :	H-Le	Reg. veg.	98
(1981)	Volume III :	Lh-O	Reg. veg.	105
(1983)	Volume IV :	P-Sak	Reg. veg.	110
(1985)	Volume V :	Sal-Ste	Reg. veg.	112

STEBBINS, G. L. (1950)   Variation and Evolution in Plants.
                          Columbia Universiy Press, New York.

STEBBINS, G. L. and E. P. PADDOCK.
        (1949)   The Solanum nigrum complex in
                 pacific North America.
                 Madrono 10(3) : 70-81.

STEGEMANN, H.   (1975)   Properties of and physiological
                     changes in storage proteins.
                     In : The Chemistry and Biochemistry
                     of Plant Proteins.
                     (Harborne, J. B.and C. F. van Sumere,
                     eds.) pp.71-78
                     Academic Press, London.

SUNDING, P.   (1979)   Origins of the Macaronesian flora.
                     In : Plants and Islands.
                     (Bramwell, D. ed.)
                     Academic Press, London.

SWAIN, T.   (1975)   Evolution of flavonoid compounds.
                             In : The Flavonoids. (Harborne,
                             et al., 1975, pp.1096-1129.

SYMON, D. E.   (1979a)   Fruit diversity and dispersal in
                             Solanum in Australia.
                             J. Adelaide bot. Gdns. 1 : 321-332.

SYMON, D. E.   (1979b)   Sex forms in Solanum (Solanaceae)
                             and the role of pollen collecting
                             insects.
                             In : Hawkes et al., 1979 pp.385-398.

                  (1981)   A revision of the genus Solanum in
                             Australia. J. Adelaide bot. Gdns.
                             4 : 1-367.

TAKHTJAN, A.   (1980)   Outline of the classification of
                             flowering plants. (Magnoliophyta).
                             Bot. Rev. 46 : 225-359.

TANAKA, T.(1976)   Tanaka's Cyclopedia of Edible
                             Plants of the World.
                             Keigaku, Tokyo.

TANDON, S. L. AND G. R. RAO.
                  (1964)   Cytogenetical investigations in
                             relation to the mechanisms of evol-
                             ution in hexaploid Solanum nigrum.
                             Nature, Lond. 201 : 1340.

                  (1966a)   Genome analysis in Solanum nigrum.
                             J. Cytol. & Genetics 1 : 41-47.

                  (1966b)   Interrelationships within the
                             Solanum nigrum complex.
                             Indian J. Genet. Pl. Breed. 26 :
                             130-141.

THAINIKAIMONI, G.   Index bibliographique sur la
                                     morphologie des pollens.
                                     Trav. Sect. scient. tech. Inst.
                                     fr. Pondichery
                    (1972)   12(1) : 1-337.
                    (1973)   12(2) : 1-162.
                    (1976)   13   : 1-385.
                    (1980)   17   : 1-336.

THEOPHRASTUS   Enquiry into plants. Translated by
                                     A. Hort (1916) Heinemann, London.

THIEL, A. F.   (1931)   Anatomy of the primary axis of
                             Solanum melongena.
                             Bot. Gaz. 92 : 407-419.

THULIN, M.   (1981)   The disjunct distribution of Carex
                             peregrina confirmed. Nord. J. Bot.
                             1 : 521-522.

TOURNEFORT, J. P. de
                   (1700)   Institutiones Rei Herbariae, Editio
                             Altera.   Paris.

TROLL, W.   (1964)   Die infloreszenzen. Typologie und
                             Stellung im Aufbau des Vegetations-
                             korpers. Vol 1. Gustav Fischer,
                             Jena.

                   (1969)   Die infloreszenzen.....etc   Vol 2
                             Gustav Fischer, Jena.

TUCKER, W. G.   (1969)   Serotaxonomy of the Solanaceae: a
                             preliminary survey. Ann. Bot. 33 :
                             1-23.

URBAN, I.   (1920)   Sertum Antillarum VIII.
                             Reprium. Spec. nov. Regni veg. 16 :
                             40-41.

VEGTER, I. H.   (1976)   Index herbariorum Part II(4) Collectors M. IAPT, Utrecht.

VENTENAT, E. P.   (1803-5)
                            Jardin de la Malmaison.   Paris.

VICKERY, B.   (1964)   Barriers to gene exchange between members of the Mimulus guttatus complex(Scropulariaceae). Evolution 18 : 52-69.

VICKERY, M. L. and B. VICKERY.
                (1981)   Secondary Plant Metabolism. MacMillan Press, London.

WEBB, L. J.   (1954)   Aluminium accumulation in the Australian-New Guinea flora. Austral. J. Bot. 2 : 176-196.

WEBERLING, F.   (1981)   Morphologie der Bluten und der Blutenstande. Ulmer, Stuttgart.

WEILER, E. W., H. KRUGER and M. H. ZENK.
                (1980)   Radioimmunoassay for the determination of the steroidal alkaloid Solasodine and related compounds in living plants and herbarium specimens. Planta. med. 39 : 112-124.

WETTSTEIN, R. V. von
                (1895)   Solanaceae. In: Die Naturlichen Pflanzenfamilien. (Engler, A. and Prantl, K. eds.) 4(3) : 4-38. Leipzig.

WHALEN, M. D.   (1978a)   Reproductive character displacement and floral diversity in Solanum section Androceras. Syst. Bot. 3 : 77-86.

WHALEN, M. D.   (1978b)   Foliar flavonoids of Solanum section
                          Androceras : a systematic survey.
                          Syst. Bot. 3 : 257-276.

                 (1979a)   Taxonomy of Solanum section
                          Androceras. Gentes Herb. 11 :
                          359-426.

                 (1979b)   Speciation in Solanum, section
                          Androceras.
                          In : Hawkes et al., 1979
                          pp.581-596.

                 (1984)   Conspectus of species groups in
                          Solanum subgenus Leptostemonum.
                          Gentes Herb. 12(4) : 179-282.

WHALEN, M. D. and G. J. ANDERSON.
                 (1981)   Distribution of gametophytic self-
                          incompatibility and infrageneric
                          classification in Solanum.
                          Taxon 30(4) : 761-767.

WHALEN, M. D., D. E. COSTICH and C. B. HEISER.
                 (1981)   Taxonomy of Solanum section
                          Lasiocarpa.
                          Gentes Herb. 12(2) : 41-129.

WHITE, C. T.   (1939)   71 - Solanum hispidum Pers. :
                          Its distribution and synonymy.
                          Bull. misc. Inf. R. bot. Gdn., Kew
                          1939 : 666-668.

WHITE, F.   (1976)   The vegetation map of Africa - the
                          history of a completed project.
                          Boissiera 24b: 659-666.

WHITE, F.   (1978)   The taxonomy, ecology and chorology
                          of African Ebenaceae.
                          I.   The Guineo-Congolian species.
                          Bull. Jard. bot. nat. Belg. 48 :
                          245-358.

                 (1979)   The Guineo-Congolian Region and its
                          relationships to other phytochoria.
                          Bull. Jard. bot. nat. Belg. 49 :
                          11-55.

                 (1981)   The history of the Afromontane
                          archipelago and the scientific need
                          for its conservation.
                          Afr. J. Ecol. 19 : 33-54.

                 (1983)   The vegetation of Africa.
                          UNESCO, Paris.

WIJNANDS, D. O. (1983)   The botany of the Commelins :
                          Balkema, Rotterdam.

WILEY, E. O.   (1981)   Phylogenetics: the theory and
                          practice of phylogenetic systematics.
                          John Wiley, New York.

WILEY, E. O. and D. R. BROOKS
                 (1982)   Victims of history - a nonequilib-
                          rium approach to evolution.
                          Syst. Zool. 31 : 1-24.

WOOD, J. R. I.   (1984)   Eight new species and taxonomic
                          notes on the flora of Yemen.
                          Kew Bull. 39(1) : 123-139.

WILLDENOW, C. L. (1798)   ed. Fifth edition Species plantanum
                          Vol. I part 2. Berlin.

WILLDENOW, C. L.
       (1809)   Enumeratio plantarum horti regii
                  botanici Berolinensis,......
                  Berlin.

WRIGHT, C. H.   (1894)   Solanaceae.
                  Bull. misc. Inf. R. bot.Gdn.,Kew 1894:
                  127-129.

           (1904)   Solanaceae. In : Flora Capensis
                  (Thistleton-Dyer, W. T. ed.)
                  4(2) : 87-121.
                  Lovell Reeve, London.

           (1906)   Solanaceae. In : Flora of Tropical
                  Africa. (Thistleton-Dyer, W. T.
                  ed.) 4(2) : 207-261.
                  Lovell Reeve, London.

ZUCKER, W. V.   (1983)   Tannins : does structure determine
                  function? An ecological perspect-
                  ive. Am. Nat. 121 : 335-365.

ZUCKERKANDL, E. and L. PAULING
       (1965)   Molecules as documents of evolution-
                  ary history.
                  J. theor. Biol. 8 : 357-366.