STUDIES IN THE
SOUTH AFRICAN
BULBOUS LILIACEAE

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JOHN PETER JESSOP

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ABSTRACT

The work comprises two principal sections; an attempt at ellucidating generic relationships in the South African bulbous Liliaceae, and a revision of the species of selected genera.

In the first section the approaches investigated were:

1) A re-evaluation of the nature of the bulb apex, showing a likelihood that certain groups possess axillary and other groups terminal inflorescences.

2) An investigation of leaf anatomy, showing that most genera have very similar leaf structure, but that a few genera do differ from this norm. Scilla (Euscilla) generally possesses a distinctly lignified bundle sheath and the Urginea-Drimia group show a great range in structures - including a palisade.

3) An impression technique to determine patterns in the surface of the leaf cuticle. A close correlation appears to exist between these patterns and leaf shape.

4) Scanning Electron Microscope pictures of pollen revealed a considerable uniformity within the group and between this group and most other members of the Liliaceae.

5) Scanning Electron Microscope pictures of seeds revealed two main groups in the bulbous Liliaceae determined on the appearance of the cell walls of the testa.

6) A simple chromatographic technique was not found to

be useful.

7) An investigation of chromosome numbers of 44 samples of 15 species supplemented published data in allowing an analysis to be made of the application of chromosome numbers to generic concepts. Many genera of the Liliaceae - especially in the bulbous group - have extremely variable chromosome numbers. It is considered that numbers are more applicable to tribal than to generic concepts. Few indications of meiotic abnormalities were detected.

Phylogenetic and taxonomic aspects of the genera of the bulbous Liliaceae are discussed and a key to the South African bulbous Liliaceae genera constructed.

The following generic alterations are proposed: *Ledebouria* to be split off *Scilla*. *Schizocarphus* to be placed in *Scilla*. *Resnova* to be placed in *Drimiopsis*. The *Astemma* section (= *Neobakeria*) to be removed from *Polyxena* and placed in *Massonia*. The Cape species of *Hyacinthus* to be placed in *Polyxena*. *Thuranthos*, *Urgineopsis* and *Urginea* to be placed in *Drimia*.

It is suggested that *Schizobasis* and *Bowiea* are of great importance in explaining the origin of *Asparagus* - possibly even directly from this group.

In the generic revisions, thirteen genera are dealt with including typification, synonymy, distribution, field notes, species descriptions and

keys.

67 species are dealt with, of which three are new (all in <u>Ledebouria</u>), and 31 new combinations are proposed.

PART 1

INTRODUCTION

1.1 History

The first South African plants known to have reached Europe were Haemanthus bulbs, collected at the Cape towards the end of the sixteenth century by a Dutch expedition under Cornelis Houtman. These were illustrated by De L'Obel (1605). Plants with bulbs and other similarly durable perennating organs were to dominate the lists of early plants introduced into horticulture from South Africa.

By 1612, when Emanuel Sweert published his "Florilegium", the first Iridaceae and Liliaceae had appeared in European gardens. His figure of the plant, which was later to be known as Urginea altissima, was the first of a member of the Liliaceae. Several other pre-Linnaean authors dealt with members of the bulbous Liliaceae, among them Cornut (1635) and Breyne (1739). It is, therefore, remarkable that Linnaeus (1753) recorded only two species of this group from South Africa - Albuca canadensis and Lachenalia orchioides (as species of Ornithogalum and Hyacinthus respectively). Other species were, however, known through paintings and herbarium collections. For example there are a further four species in the pre-Linnaean volume of water-colours in the library of the Botanical Research Institute, Pretoria (Jessop, 1965).

It was not until the collections of Masson, Sparrman and Thunberg reached Europe at the end of the eighteenth century that considerable advances in knowledge of the group were made. These collections were used to typify most of the species described by Linnaeus (fil.) (1781). This work, usually attributed to the younger Linnaeus, but reflecting rather Thunberg's work, included a further eleven species in Ornithogalum and Hyacinthus (including species now regarded as species of Scilla, Rhadamanthus, Urginea and Ornithogalum) and in Albuca and Massonia, which two genera were described for South African species. An important contemporary was Jacquin whose collectors, Boos and Scholl, sent back several bulbs for the Schönbrunn Gardens. But it was Thunberg who summed up the rapidly expanding knowledge of the South African flora, by publishing his "Prodromus" in 1794-1800. In this work he recognised the following genera (the numbers of species indicated are now placed in the bulbous Liliaceae):- Massonia (4 spp), Mauhlia (1 sp in Polyxena), Ornithogalum (14 spp, including species of Eucomis, Ornithogalum and Urginea), Hyacinthus (5 spp all but one of which have been transferred to Dipcadi, Scilla or Rhadamanthus), Lachenalia (8 spp) and Albuca (5 spp). It is important to note that although the majority were placed in European genera, it was early appreciated that not all the South African species could be satisfactorily treated in this way. The identification of South African with European genera has remained a controversial matter up to the present.

For almost a century knowledge of the South African flora increased, with collectors such as Drége, Ecklon and Zeyher to the fore, before a comprehensive treatment of the South African species was again undertaken. Authors of particular importance during this period were Willdenow (1797-1810), De Candolle (1824-73), Redouté (1802-16), Roemer and Schultes (1817-30), Kunth (1833-50) and Salisbury (1866). An important summary of generic concepts was that of Harvey (1838). Harvey recognised many of the presently accepted genera, which he placed in the Asphodeleae. These were:- Bowiea (which was not, however, the genus now known by this name, but applied to species now placed in Aloe), Veltheimia (3 or 4 spp), Ornithogalum (a large genus of unspecified number of species), Massonia (several species), Hyacinthus (4 or 5 spp, but doubt was expressed about the correct placing of all except H. corymbosus), Scilla ("few, and if we may judge by the descriptions, congenerous with our Hyacinths, whether or not they be true species of that genus"), Albuca (numerous species), Uropetalum (several species, now in Dipcadi), Lachenalia ("there are several species worthy of cultivation").

Harvey's work was revised and published posthumously in 1868, but Baker's studies on the world's Liliaceae (1873) in the section Scilleae constituted the major landmark in the second half of the nineteenth century, only to be exceeded, so far as the South African species are concerned, by Baker's contribution to the "Flora Capensis" (1896/7).

The "Flora Capensis" remains the most comprehensive work on the South African species, although individual groups have been dealt with more recently. In it Baker used most of the presently accepted generic names although his species concepts have been questioned on many occasions. In evaluating Baker's work it is important to bear in mind that many of the species he recognised were known to him from single specimens, often from unrecorded localities, and often only from figures. For example, in Massonia (in which he recognised 33 species) ten species were known to him only from an illustration or description and a further fourteen known from a single specimen - that is fewer than a third were known from more than a single collection. In addition, Baker did not visit South Africa and what he knew of the living plant was based on plants grown in hothouses in Britain. Although, in the present author's opinion, few botanists could have bettered Baker's work under the circumstances, it is possible that some subsequent workers in South Africa, with first hand field knowledge, may have been unjustifiably anxious to accept the reliability of Baker's work. This is thought to have led to the adoption of Baker's rather narrow species concepts. While this is speculation, it is agreed by all South African taxonomists that the identification of South African Liliaceae has generally given more trouble than is the case for almost any other families. Baker recognised the following:- Bowiea (1 sp), Schizobasis (4 spp of which 2 may have been regarded as species of Asparagus by Harvey), Massonia (33 spp), Daubenya (3 spp), Whiteheadia (1 sp, probably regarded as a species of Eucomis by Harvey), Polyxena (10 spp, probably regarded as species of Massonia by Harvey), Lachenalia (42 spp), Drimia (22 spp), Litanthus (1 sp), Dipcadi (16 spp), Galtonia (3 spp), Albuca (34 spp), Urginea

(27 spp), *Veltheimia* (3 spp), *Hyacinthus* (2 spp), *Drimiopsis* (7 spp), *Eucomis* (9 spp), *Scilla* (56 spp), *Ornithogalum* (75 spp); making 19 genera and 349 species.

Although there have been no comprehensive evaluations of generic concepts in the bulbous Liliaceae as a whole or, even, of the South African members, there have been several surveys in which some opinion has been expressed on which genera should be recognised. The most important of these have been Krause (1930) in "Die Pflanzenfamilien", Hutchinson (1959) and Phillips (1951). Phillips (perhaps the most important of these) recognised:- *Schizobasis* (9 spp), *Bowiea* (1 sp), *Albuca* (77 spp), *Thuranthos* (1-3 spp), *Urginea* (57 spp), *Urgineopsis* (1 sp), *Galtonia* (3 spp), *Drimia* (26 spp), *Rhadamanthus* (2 or 3 spp), *Dipcadi* (36 spp), *Litanthus* (1 sp), *Scilla* (79 spp), *Eucomis* (13 spp), *Ornithogalum* (120 spp), *Drimiopsis* (9 spp), *Hyacinthus* (2 spp), *Pseudogaltonia* (1 sp), *Veltheimia* (6 spp), *Lachenalia* (65 spp), *Polyxena* (10 spp), *Neobakeria* (8 spp), *Whiteheadia* (1 sp), *Neopatersonia* (1 sp), *Massonia* (45 spp) and *Androsiphon* (2 spp), making a total of 25 genera and almost 580 species.

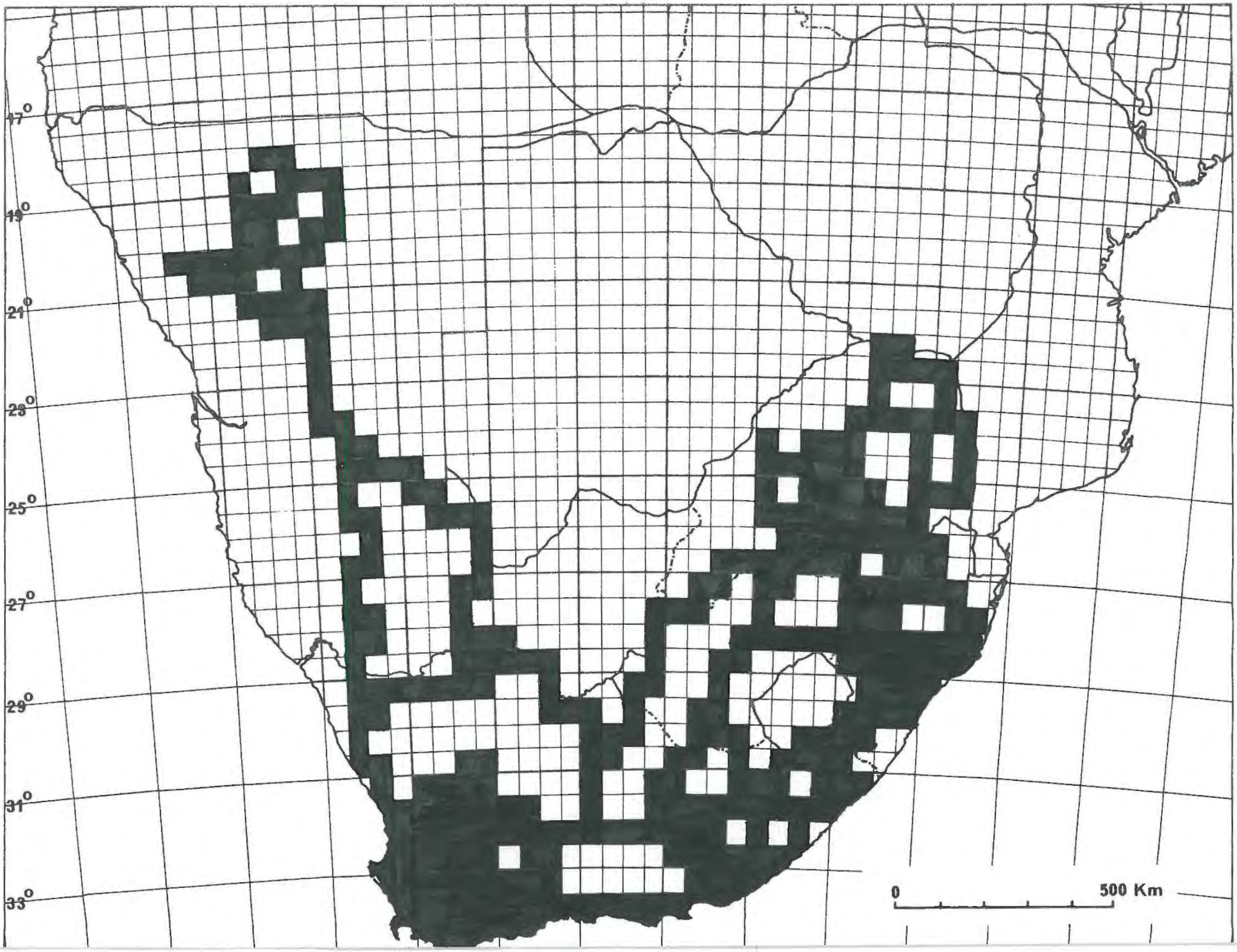
Of the more recent floras the most important have probably been the "Flora of the Cape Peninsula" (Adamson and Salter, 1950), contributed to by Adamson, Barker and Leighton, and the "Prodromus einer Flora von Südwestafrika" by Sölch, Roessler and Merxmüller (Merxmüller, 1970).

Several genera, or groups of genera, have received detailed study. Some of the more important of these investigations have been:- Adamson (1942, 1944 and 1946) and Duthie (1928) on the south-western Cape species of *Urginea*, Nordenstam (1970) on *Rhadamanthus*, Obermeyer (1964) on *Dipcadi*, Van der Merwe (1946) and many papers in "Flowering Plants of Africa" on the *Scilla*-*Drimiopsis* group, Leighton (1944 and 1945) on *Ornithogalum*, and Barker (several contributions (e.g. 1966, 1969 and 1972) on *Lachenalia*. Recent monographs account for *Rhadamanthus*, and *Dipcadi*, while *Ornithogalum*, *Albuca*, *Eucomis* and *Lachenalia* are being studied by Obermeyer, Archibald, Reyneke and Barker respectively. No comprehensive work has appeared since Baker on the large *Urginea*-*Drimia*, *Scilla*-*Drimiopsis* or *Massonia*-*Polyxena* groups.

The definition of generic limits requires attention in relation to separating *Ornithogalum* and *Albuca* and possibly in other areas within this group, but it is believed that the most urgent problems occur in the groups mentioned above as being in need of revision at the species level. It is, therefore, with the intention of elucidating some of the problems both at species and at generic level in these specific groups that this study has been undertaken.

1.2 Concepts

A detailed discussion of the background to the problems encountered is included in later chapters of this work. A number of general points must, however, be made about problems encountered in defining taxa at various levels in the work as a whole.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1.2.1 Populations

It was important to ascertain the extent of the variation occurring in morphological characters within populations. Collecting trips were undertaken over a period of about ten years, covering most of South West Africa and South Africa, especially those areas for which records indicate a particularly high number of species.

Map 1 indicates half-degree blocks traversed during these trips, although plants were not examined in all of the areas designated. Many of the plants have variable flowering seasons depending on the prevailing weather conditions. In many cases flowering occurs particularly during spring when the author was generally not free to make extended collecting trips. Locating members of the bulbous Liliaceae not in flower is difficult on trips with rather restricted time available. For these reasons, despite the area covered, several species were not examined in the living state.

These plants often do not occur in sufficiently large numbers in a definite area to enable detailed studies to be made of variation in morphology, but measurements were taken for important characters, especially leaf measurements, in populations of a few species and these are recorded in this work in the form of scatter diagrams.

In addition, the collections of both the National Botanic Gardens, Kirstenbosch, and the Botanic Garden of the Botanical Research Institute, Pretoria, were a source

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Opposite- Map 1. Half degree blocks traversed by the author on collecting trips.

of valuable living material. Collections were also made for the present author by Col. R.D.A. Bayliss, Miss E. Esterhuysen, Mr R.G. Strey and Mr H.R. Tölken.

1.2.2 Species

The historical background has been given as a reason for believing that the species concepts in this group have developed along rather narrow lines. There is a further important reason why this may have happened. Within the genera under discussion there is often rather little variation in floral characters. Vegetatively, the species have been distinguished on characters of their simple leaves and less often of their bulbs. There is, however, limited scope for morphological variation and what variation there is is largely quantitative and susceptible to environmental influences. The size and to some extent shape of the leaves is, for example, a character often used in the past in distinguishing between species. Probably considerably fewer than 10% of all leads used by Baker (1896/7) in his keys to the groups dealt with here could be regarded as qualitative. But quantitative characters may be affected by the age of the plant and season when collected, edaphic and climatic factors, fire, grazing, and the inclination of collectors to collect exceptionally large specimens or possibly to collect larger numbers of smaller specimens.

It has, therefore, been decided that existing concepts should be completely re-examined and, where necessary, to adopt a very much broader species concept. It is hoped that by recognising very much smaller numbers of species a greater stability may be brought about in the taxonomy of the group. An attempt has been made to employ qualitative characters where possible, although this is not always practical and in many cases quantitative characters are entirely satisfactory. But quantitative characters have only been used where there is a distinct break in the continuity of the measurements made or where two or more characters appear to be sufficiently strongly linked. In the genus *Ledebouria*, where particular difficulty was encountered in defining subgeneric groups, it was decided, as is explained in the treatment of that genus, to recognise a few species on rather less well defined grounds than is the case elsewhere.

1.2.3 Genera

While the general level of generic concepts has been found to be both logical and convenient, there are several apparently artificial groupings as the genera are at present defined. Generic limits were largely established when very much less was known about the group. This situation has been maintained as a result of a desire on the part of taxonomists to retain the status quo rather than to look for natural groupings. However, it is of interest that most workers in this field have recognised this problem. Baker (1896/7) mentioned in his treatment of *Polyxena*: "Here, as throughout, I have followed Mr Bentham in classification, but my own view would be to unite, at any rate, the subgenus *Astemma* with *Massonia*." In the *Massonia* group, Phillips (1951) mentioned: "It is probable that further study would reduce the species to one or two well-defined genera." Nordenstam (1970) recognised a possibility that Rhadamanthus might prove to be an artificial genus.

While morphological characters are considered to be the only ones suitable for the final definition and recognition of generic limits, it is believed that the largest number of characters possible must be used in establishing these limits if a relatively stable generic concept is to be developed. With this in mind, and in the absence of large numbers of qualitative morphological characters, a number of approaches have been attempted to add to the taxonomic characters provided by conventional morphological techniques.

1.3 Presentation of data

The approaches to elucidating taxonomic concepts - especially at generic level - as mentioned in the previous section are dealt with first (section 2). This data is then used in a discussion of generic concepts and the allied topic of the phylogeny of the group, leading to the definition of the genera in the form of a key and to a suggested scheme of relationships. The discussion of generic concepts includes the historical development of these concepts and a commentary on the morphological characters employed previously in defining genera.

Although a detailed discussion of the relationships of the bulbous Liliaceae to other members of the Liliaceae is not included, the group does appear to offer rather important evidence for the evolution of certain other genera. Section 3 deals with this topic.

The presentation of the taxonomic sections follows the patterns established for the Journal of South African Botany. Citation of specimens examined follows the method proposed by Edwards and Jessop (1967), and since approved by both the Journal of South African Botany and Bothalia.

Names used in the chapters of this thesis, preceeding the taxonomic section, are, for ease of reference, in many cases those introduced for the first time in the taxonomic section of this thesis.

1.4 Prior publication of parts of this thesis

As work on this thesis has taken eight years it was decided to publish parts of it to make the results available without excessive delay.

Four papers have been submitted. Jessop (1970) dealt with the taxonomy of the Scilla group. Jessop (1972a) dealt with the taxonomy of Drimiopsis and Resnova. Jessop (1972b) dealt with the meiotic chromosomes of Ledebouria. (Copies of these papers are attached.) A description of a new species of Ledebouria (L. scabrida), which was not known to the author at the time of publication of the paper on the Scilla group has been submitted to the Journal of South African Botany.

This thesis has been prepared without reference to these papers and all the material included in them is repeated as though it had not already appeared. For example, Latin diagnoses are included for species described in these papers.

1.5 Acknowledgements

A great deal of the material of this thesis stems from ideas suggested by Mrs A.A. Mauve who has always been prepared to pass on her remarkable knowledge of the South African Liliaceae. A particular debt is also owed to Miss W.F. Barker who, too, has helped immensely with her wide knowledge of the family both in the field and in the herbarium.

Numerous others have provided living or preserved material or invaluable advice and encouragement. Among these must be mentioned Mr R.G. Strey, Col. R.D.A. Bayliss, Miss E. Esterhuysen, Mr H.R. Tölken and Dr K.D. Gordon-Gray. Professor Twyman has always been available for assistance in many ways including assistance with obtaining the necessary equipment for the work. His wide botanical knowledge has been greatly appreciated on a large number of subjects.

The Curators of many herbaria have provided a great deal of material. Sheets have been borrowed from:- Trinity College, Dublin; the Royal Botanic Gardens, Kew; the Botany School, Cambridge; Botanisches Museum, Berlin; Rijksherbarium, Leiden; Conservatoire et Jardin botaniques, Geneva; Botanischer Garten und Institut für Systematische Botanik der Universität, Zürich; Botanische Staatssammlung, Munich; Institut für Systematische Botanik und Pflanzen-

geographie der Martin-Luther-Universität, Halle; the National Herbarium, Pretoria; the South African Museum, Kirstenbosch; the National Botanic Gardens Herbarium, Kirstenbosch; the Bolus Herbarium, University of Cape Town; the State Herbarium, Stellenbosch; the Albany Museum Herbarium, Grahamstown; the Botany Department Herbarium, University of Natal, Pietermaritzburg; the State Herbarium, Durban. Photographs have been provided by the Keeper of Botany, British Museum (Natural History).

The C.S.I.R. has subsidised the field work.

PART 2

TECHNIQUES FOR INVESTIGATING AFFINITIES

2.1 Bulb morphology

2.1.1 Introduction

Very little work has been done on the morphology and structure of the bulbs of the Liliaceae. Probably the most important studies have been those of Chouard (1931 and 1934) and Chouard and Galap (1933). More recently, the form of secondary thickening in the bulb axis of Drimia delagoensis (sub Urginea lydenburgensis) has been investigated by Coetzee and Van der Schijff (1969).

The particular aim of the present investigation was to attempt to determine whether the development of bulbs of the genera under investigation is monopodial or sympodial. This appears to be of interest as superficial observation suggests that in most species of Scilla (section Ledebouria) the inflorescence is axillary and development therefore monopodial. In Scilla (section Euscilla), on the other hand, the inflorescence appears terminal and development, therefore, sympodial. In section Ledebouria there are often several (usually three) inflorescences produced in succession, but maturing almost simultaneously. They all first become visible in a position lateral to the vegetative axis. In section Euscilla there is usually a single inflorescence produced during the annual cycle and this appears from the centre of the rosette of leaves. Although species of most genera of the bulbous Liliaceae can be readily allocated to one of these groups, there are some in which individual plants appear to produce both types of inflorescence - for example Ornithogalum longibracteatum.

The difficulty in interpreting the development of the bulb arises from the extremely compact arrangement of the organs in the apical region. Tomlinson (1970) has expressed a further problem thus: "The most striking examples of apical dominance are found in arborescent monocotyledons of the Agavaceae, Liliaceae and Pandanaceae. These plants with exclusively terminal inflorescences may be contrasted with the Palmae in which inflorescences are predominantly lateral." This suggests that Tomlinson considers the apex type to be of fundamental importance and possibly fairly readily determined, but he concluded: "In Aloe, as a further example, it may not be at all obvious that inflorescences are always terminal, because eviction is very precocious and is repeated rapidly". And, admitting the problem in recognising the type, he then suggests that the differences may not in fact be fundamental at all: "The distribution of hapaxanthic and pleonanthic shoots in monocotyledonous families is such as to suggest that the difference between them, although quite clear, is not a fundamental one". (Hapaxanthic flowering is that type producing a terminal inflorescence - i.e. sympodial growth; pleonanthic flowering produces lateral inflorescences.)

Tomlinson's point that eviction may be very precocious is of the utmost importance. Assuming that in the dormant bulb both vegetative axis bud and inflorescence axis bud have developed at or very close to the apex of the bulb, remaining enclosed well within the leaf rosette, it will be the order of further development of the two buds which leads to the appearance of an axillary or terminal inflorescence. In other words, although the inflorescence may be initiated from the apical bud it may appear lateral if its further development is delayed until the vegetative (lateral) bud has formed the foliage leaves (figs 1 & 2).

2.1.2 Method, material and observations

Because of the difficulty in determining the growth pattern from an external examination of the plant it was decided to look at the anatomy of the apical region of the bulb axis.

Both transverse and longitudinal serial sections were cut, using paraffin-wax embedded material from which leaves and the greater part of the bulb-stock were removed. The species investigated in this way were *Scilla* (*Euscilla*) *firmifolia*, *S*. (*Euscilla*) *nervosa* (fig. 3a) and *S*. (*Ledebouria*) *revoluta* (fig. 3b).

It was found that there was a distinct difference between the members of the two sections of *Scilla*. In section *Euscilla* the vascular strands to the inflorescence were collected together in the centre of the stock and passed vertically into the peduncle. However, the vascular tissue to the vegetative axis, although arising from the same region of the bulb, showed a distinct deflexion before entering the vegetative axis. The opposite appeared to be the case in section *Ledebouria*. The deflexion occurred in the vascular tissue to the inflorescence(s).

These observations suggested that members of the section *Euscilla* should be regarded as sympodial while members of the section *Ledebouria* were monopodial - as appeared from their external morphology.

Further investigations showed that if serial sections were used there was more information to be gained from the use of longitudinal than transverse sections. But it proved to be more convenient to dissect out the apex of the bulb under a low power (less than 100x) stereo-microscope than to cut sections.

Scilla (*Ledebouria*) *concolor* is one of the less typical species of the *Ledebouria* section in having an apparently terminal inflorescence, as determined by external observation of the plant. Dissection of the bulb showed, however, exactly the same form of vascular strands as in *S. revoluta*. Similarly, *S.* (*Ledebouria*) *floribunda*, both externally and on the basis of dissection, agrees with these species.

Both of the other species of the *Euscilla* section of *Scilla* from South Africa (*S. natalensis* and *S. plumbea*) were found by dissection to have apparently terminal inflorescences.

Drimiopsis maculata (fig. 3c) and *Lachenalia glaucina* (fig. 3d) appeared to agree with *Scilla* (*Ledebouria*).

Material of Massonia, Urginea and Drimia did not show a distinct deflexion of the traces to either vegetative or inflorescence axis. Members of these genera appear, externally, to have terminal inflorescences, but Massonia appears to be rather closely related to Lachenalia and Scilla section Ledebouria and it would have been particularly interesting to have been able to demonstrate whether or not the apparently terminal inflorescence could be derived from the Lachenalia and Scilla (Ledebouria) type.

2.1.3 Discussion

Chouard (1931) studied several species of Scilla section Euscilla, Hyacinthus, Muscari and possibly other members of what are considered by the present author to be likely to be fairly closely related European genera and came to the conclusion that they all had terminal inflorescences. Unfortunately he did not specify the species examined, but based his conclusions on dissections of the bulbs.

It is generally agreed that the inflorescence in Liliaceae is terminal, for example McLean and Ivimey-Cook (1958), Priestley and Scott (1938), Brook (1964), Rendle (1963) and Bower (1947). While it would not be justified on the basis of the single characteristic of these bulbs, namely the deflexion of the vascular tissue to the inflorescences, to claim proof of an axillary inflorescence, it does seem possible that this is in fact the case. It is of interest that this characteristic has so far only been reported for the two groups of spotted-leafed species both of which are largely or entirely restricted to South Africa. It is thought possible that even if the significance of this observation is morphologically questionable, its value to the taxonomy of the group may prove to be considerable.

2.2 Leaf anatomy and morphology

2.2.1 Material and methods

Material was selected to investigate variation in the arrangement of leaf tissue in transverse section.

Hand-cut and freezing-microtome sections were used for some material, but did not provide entirely satisfactory results, partly because of large quantities of mucilage and partly because of the removable spiral thickening on the walls of the tracheary elements (cf. Badenhuizen, 1954). The removal of the spirals both interferes with observation of tissues and damages the tracheary elements themselves. The numerous crystals are also a cause for tearing of sections.

Wax-embedded sections were also prepared. In all cases N-butyl was used as a solvent and embedding was in 55^{o} melting point paraffin wax. Sections were satisfactorily stained in safranin and fast green although, because of the limited quantities of lignin, the safranin tended to stain somewhat lightly.

The following specimens were examined:-

<u>Scilla</u> (<u>Ledebouria</u>) <u>undulata</u> (=<u>L. undulata</u>) <u>Bayliss</u>
<u>BS/3469</u>, Nsoko, Swaziland (2731B).

Scilla (*Ledebouria*) *lanceaefolia* (= *L. revoluta*) *Christensen* s.n., Highlands Road, Grahamstown (3326A).

Scilla (*Ledebouria*) *megaphylla* (=*L. floribunda*) *Jessop 1063*, Woest Hill, Grahamstown (3326B).

Scilla (*Ledebouria*) *marginata* (=*L. marginata*) *Jessop* s.n., north of Pretoria (2528C).

Scilla (*Ledebouria*) *ovatifolia* (=*L. ovatifolia*) *Jessop* s.n., near Pretoria (2528C).

Scilla (*Ledebouria*) sp (=*L. scabrida*) *Tölken* s.n., Gobabis, South West Africa (2119).

Scilla (*Euscilla*) *firmifolia* Ex hort., Rhodes University.

Schizocarphus gerrardii (=*Scilla* (*Euscilla*) *nervosa*) *Jessop 883*, Rabbits Wood, Grahamstown (3326B).

Scilla natalensis Ex hort., Rhodes University.

Scilla plumbea *Jessop* s.n., Bain's Kloof, Worcester (3319C).

Scilla peruviana Ex hort., Grahamstown (European).

Endymion non-scriptus Ex hort., Grahamstown (European).

Drimiopsis maculata *Strey 9031*, Manteka, Lusikisiki (3129B).

Massonia depressa *Tölken* s.n., near Stinkfontein, Namaqualand (2817C).

Massonia pustulata Ex hort., Kirstenbosch, NBG 395/71.

Urginea pusilla (=*Drimia pusilla*) *Jessop* s.n., north of Sutherland (3220B).

Drimia elata Ex hort., Rhodes University.

Urginea altissima (*Drimia altissima*) *Jessop* s.n., near Arniston, Bredasdorp (3420C).

Drimia anomala Jessop 722, Table Hill Farm, Grahamstown (3226B).

The binomials in brackets in the above list refer to names adopted in the taxonomic part of this thesis.

Figures 4 - 12 illustrate the distribution of the tissues in more or less median sections through fully-developed laminae.

2.2.2 Observations

Species of Scilla (section Ledebouria) (fig. 4), Drimiopsis (fig. 5) and Massonia (fig. 6) are extremely similar. The most obvious differences lie in the structure of epidermal trichomes, but as these are readily observable in surface view, their presence does not provide any additional characters. The vascular bundles are arranged in a single row, all with their xylem uppermost, with no lignification of the bundle sheath. Lignification is entirely restricted to the tracheary elements. There is usually no significant development of a palisade layer, although in the specimen of S. floribunda the two adaxial rows of mesophyll cells are almost twice as long as broad. Crystals, especially raphides, are common.

In Scilla (section Euscilla) (fig. 7) the arrangement of tissues is similar to that in the species described above. The only significant difference appears to be that in three of the four South African species the bundle sheath is strongly lignified. However, this is not the case in S. plumbea, which closely resembles members of the section

Ledebouria of *Scilla*, nor in the European species *S. peruviana* and *Endymion non-scriptus* (=*S. nutans*). These three species could not be distinguished from species of *Massonia*, *Drimiopsis* or *Scilla* (section *Ledebouria*).

Drimia and *Urginea* show a very much more interesting variation in structure.

Drimia elata (figs 8 & 9) possesses a dorsi-ventrally flattened leaf, rich in raphides (which are present, but generally in smaller numbers, in most, if not all, species examined). No significant differences between this and the previously mentioned species were observed.

Urginea altissima is rather similar to *D. elata*, but a very distinct midrib is developed. In the midrib (fig. 10) vascular bundles are scattered at various levels between the upper and lower epidermis, but the xylem is uppermost in all bundles.

U. pusilla has a single row of bundles in the lamina, but scattered bundles in the bulb scale. Furthermore, unlike *D. elata* and *U. altissima*, there is a well-developed palisade (fig. 11) adjoining both upper and lower epidermis.

A further development takes place in *D. anomala* which has a terete leaf. Here there are six large bundles arranged in a ring, partly interrupted on the adaxial surface, and several times this number of small bundles to the outside. Again there is a well-developed palisade.

2.2.3 Discussion

Arber (1925) developed a theory, first proposed by De Candolle (1827), that the monocotyledonous leaf was "equivalent to the leaf-base and petiole of the dicotyledon - the blade being unrepresented". This type of leaf was claimed by Arber to be recognisable in some species of, for example, Triglochin and Allium in which there is a basal sheath and an "awl-like radial limb". She considered that the primitive type of monocotyledonous leaf was one with a leaf-base terminating in a simple petiole. From this type it was common for a flattening, or loss, of the petiolar portion to lead to an isobilateral or dorsi-ventral leaf as in most Liliaceae. This theory has found recent support by, for example, Cronquist (1968) and Eames (1961).

If Arber's "phyllode theory" is correct, D. anomala should probably be regarded as showing a primitive leaf type from which the other types occurring in Drimia and Urginea were derived. It would suggest, too, that in Drimia and Urginea possession of a distinct palisade may be a primitive character.

2.2.4 Conclusions

At the generic level leaf anatomy does not appear entirely to support current concepts. The type found in all species examined of Scilla (section Ledebouria), Drimiopsis and Massonia occurs also in some species of Scilla (section Euscilla) and in Drimia and Urginea.

Within Scilla (section Euscilla) there is evidence for two groups within the South African flora. S. plumbea is clearly separated from the other species in the absence of a lignified bundle sheath.

In Drimia and Urginea there is evidence of a well-defined evolutionary sequence from the D. anomala type, in which there is a petiole-like arrangement of vascular bundles in the lamina and a well-defined palisade, to the D. elata type which shows a typical dorsi-ventral arrangement and no palisade. The D. elata type is similar to that in Scilla (section Ledebouria), Drimiopsis and Massonia.

2.3 Leaf surface characters

2.3.1 Introduction

No work on the epidermal characters of the bulbous Liliaceae has been found. Papers have, however, been published on light microscope and scanning electron microscope studies on the genus Aloe (Liliaceae) and on other families, for example Newton (1972) on Aloe and Baranova (1972) on the Magnoliaceae and some related families. Most studies have concentrated on outer surface characters and have employed cuticular or epidermal strips or electron microscope studies of the intact leaf. The method used in the present study provides data only on the shape of the leaf surface.

2.3.2 Method

"Xantopren" precision impression material, with "soft" hardener, was applied to the leaf surface, allowed to set and peeled off. An impression of this mold was then taken by applying a thin layer of colourless nail varnish which, when dry, was easily peeled off the mold.

The colourless films of nail varnish were examined and photographed dry. They readily adhere to microscope slides and cover-slips were unnecessary.

Bright field illumination was used for photography. Phase contrast was tried but both definition and contrast was inferior. Despite the lack of variation in either density or pigmentation of the preparations, the photographs, taken on Kodak Pan-X film, are considered to possess a satisfactory degree of contrast. All prints were made at a magnification of 160x.

Camera lucida drawings were also made, using a Wild microscope, and the photographs compared with these. However, there appeared to be no information which could be more clearly demonstrated by means of the drawings.

2.3.3 Observations

Fifteen preparations of abaxial surfaces were examined and 28 of the adaxial surface. Both surfaces of the majority of specimens showed cell-like patterns. While it is very likely that these reflect the shapes of the underlying epidermal cells, it cannot be assumed that they did in all cases. They will, however, be referred to here as cells.

The abaxial surface preparations showed relatively little variation, with longer epidermal cells and fewer stomata than did the adaxial surface. However, there was considerable variation in the shapes and sizes of epidermal cells in the adaxial surface. As there did not appear to be sufficient characters no further work has been undertaken on the abaxial surface preparations.

Although even the adaxial surface did not provide many characters for comparing the various preparations, eight characters were scored for 29 preparations. These are indicated in table 1. All data was recorded from the photographs without reference to the original preparations. The quantitative data represents the mean of five measurements where possible.

Stomatal measurements (L = length; B = breadth) were taken (in mm) from the photographs and not corrected to absolute measurements of the original material. They were grouped as follows:- lengths - A = 0-5,9 mm

B = 6-7,9 mm

C = 8-12 mm

breadths - A = 0-4,9 mm

B = 5-8 mm.

Epidermal measurements were treated the same way, but with a different scale as follows:-

lengths - A = 0-39 mm

B = 40-69 mm

SPECIES	COLLECTOR	LOCALITY	FIG NO	STOMATA		EPIDERMAL CELLS		RADIATING STRIATIONS FROM STOMATA	CELLS TRUNCATE AT STOMATA	MAIN STRIATIONS LONGITUDINAL	NO OF STOMATA IN FIELD
				L	B	L	B				
Trachyandra sp	Jessop s.n.	Struisbaai (3420C)	13	A	A	A	A	–	–	–	B
Bulbine asphodeloides	Jessop s.n.	Sir Lowrys Pass (3418B)	14	B	B	C	A	+	–	–	A
Albuca setosa	Black s.n.	Alicedale (3326A)	15	C	B	B	A	–	–	–	A
Drimia elata	Ex hort., Rhodes University		16	C	B	B	A	–	–	+	A
Drimia elata	Jessop s.n.	Sir Lowrys Pass (3418B)	17	C	B	B	A	–	–	+	B
Drimia elata	Jessop s.n.	Struisbaai (3420C)	18	C	B	C	A	–	–	+	B
Urginea altissima	Jessop s.n.	Struisbaai (3420C)	19	C	B	B	A	–	–	–	B
?Rhadamanthus sp	Jessop s.n.	Wilton, near Alicedale (3326A)	20	C	B	C	A	–	–	+	A

TABLE 1

ANALYSIS OF ADAXIAL LEAF SURFACE DATA

Scilla natalensis	Ex hort., Rhodes University		21	C	B	A	A	–	+	–	A
Scilla firmifolia	Ex hort., Rhodes University		22	C	B	B	A	–	–	–	A
Scilla megaphylla (=*Ledebouria floribunda*)	*Strey 9029*	Port Grosvenor (3129B)									
	(near margin of leaf)		23	C	B	B	A	–	–	–	A
ditto	(centre of leaf)		24	B	B	B	A	–	–	–	A
Scilla lanceaefolia (=*Ledebouria revoluta*)	Ex hort., Rhodes University		25	B	A	A	A	+	+	–	B
Scilla ovatifolia (=*Ledebouria ovatifolia*)	*Jessop* s.n.	24 miles N. of Pretoria (2528A)	26	B	A	A	A	–	–	–	B
Scilla socialis (=*Ledebouria socialis*)	*Jessop* s.n.	Kaffir Drift (3327A)	27	B	A	A	A	–	+	–	A
Drimiopsis maculata	*Strey 9031*	Mateka, Lusikisiki (3129B)	28	B	A	A	A	+	+	–	A
Drimiopsis maculata	*Jessop* s.n.	20 miles W of Potgietersrust (2428B)	29	B	A	A	A	+	+	–	A

TABLE 1 Continued

Ornithogalum maculatum	Ex hort., Kirstenbosch NBG 1267/70		30	B	A	B	A	–	–	–	B
Ornithogalum sp nr fimbrimarginatum	Ex hort., Kirstenbosch NBG 718/60		31	A	A	A	A	–	–	–	B
Ornithogalum longibracteatum	Ex hort., Rhodes University		32	B	A	A	A	+	+	–	A
Veltheimia viridifolia	Ex hort., Rhodes University		33	B	B	B	A	–	–	–	A
Lachenalia pendula	Jessop s.n.	Arniston (3420C)	34	B	A	B	A	+	–	–	B
ditto	ditto	ditto	35	B	A	A	A	+	–	–	B
Massonia depressa	Tölken s.n.	5 miles S.W. of Stinkfontein (2817C)	36	A	A	A	B	–	+	–	B
Massonia depressa	Bayliss BS/5090	Vaalkrans (3326B)	37	A	A	A	A	–	+	–	B
Massonia echinata	Bayliss BS/4868	near Klipplaats (3324A)	38	A	A	A	B	–	+	–	B
Massonia pustulata	Muller 684	Cradock (3225B)	39	A	A	A	B	–	+	–	B

TABLE 1 Continued

Massonia jasminiflora	*Jessop* s.n.	near Winburg (2826D)	40	B	A	A	B	-	+	-	B
Neobakeria sp (=*Massonia angustifolia*)	*Rourke 754*	Donkergat (3318A)	41	A	A	A	A	+	+	-	B

TABLE 1 Concluded

C = 70— mm
breadths – A = 0–12 mm
B = 13–20 mm.

The remaining characters were recorded as present (+), if they were present in the majority of cells – although they were selected for being as consistent as possible and were, therefore, usually present in all cells or absent from all cells in any preparation.

Despite the small number of characters scored, a similarity table has been drawn up. In table 2 a score of '8' indicates a 100% similarity. In comparing two samples, the two samples were regarded as being identical for a particular character if they both had a similar scoring – whether they were both '+' or both '–'.

The following pairs of preparations have a similarity value of 8 (100%) in table 2:–

Trachyandra sp : *Ornithogalum* sp nr *fimbrimarginatum*
Albuca setosa : *Scilla firmifolia*
Albuca setosa : *Scilla megaphylla* (marginal)
Scilla firmifolia : *Scilla megaphylla* (marginal)
Veltheimia viridifolia : *Scilla megaphylla* (median)
Drimiopsis maculata (both samples) : *Ornithogalum longibracteatum*
Massonia depressa (both samples) : *Massonia echinata*
Massonia depressa (both samples) : *Massonia pustulata*
Massonia echinata : *Massonia pustulata*.

Using the method of Sokal & Sneath (1963) for the

	Trachyandra sp	Bulbine asphod.	Albuca setosa	Drimia elata	Drimia elata	Drimia elata	Urginea altissima	?Rhadamanthus sp	Scilla natalensis	Scilla firmifolia	Scilla megaphylla (marg.)	Scilla megaphylla (med.)	Scilla lanceaefolia	Scilla ovatifolia	Scilla socialis	Drimiopsis maculata	Drimiopsis maculata	Ornithog. maculatum	O. sp nr fimbrimarg.	O. longibracteatum	Veltheimia viridifol.	Lachenalia pendula	Lachenalia pendula	Massonia depressa	Massonia depressa	Massonia echinata	Massonia pustulata	Massonia jasminiflora
Trachyandra sp																												
Bulb. asphod.	3																											
Albuca setosa	4	4																										
Drimia elata	3	4	7																									
Drimia elata	4	3	6	7																								
Drimia elata	4	4	5	6	7																							
Urginea altissima	5	4	7	6	7	6																						
?Rhadamanthus sp	3	5	6	7	6	7	4																					
Scilla natalensis	4	4	6	5	4	4	5	5																				
Scilla firmifolia	4	5	8	7	6	5	7	6	6																			
Scilla megaphylla (margin)	4	5	6	7	6	5	7	6	6	8																		
ditto (median)	4	6	7	6	5	4	6	5	5	7	7																	
Scilla lanceaefolia	5	4	2	1	2	2	3	1	4	2	2	3																
Scilla ovatifolia	7	4	4	2	4	4	5	3	4	4	4	5	6															
Scilla socialis	5	4	4	3	2	2	3	3	6	4	4	5	6	6														
Drimiopsis maculata	4	5	3	2	1	1	2	2	5	3	3	4	7	5	6													
Drimiopsis maculata	4	5	3	2	1	1	2	2	4	3	3	4	7	5	6	8												
Ornithog. maculatum	7	4	5	4	5	4	6	3	3	5	5	6	5	7	5	4	4											
O. sp nr fimbrimarg.	8	3	4	3	4	4	5	3	3	4	4	3	5	7	5	4	4	6										
O. longibracteatum	4	5	3	2	1	1	2	2	4	3	3	4	7	5	7	8	8	4	4									
Veltheimia viridi.	4	6	7	6	5	4	6	5	5	7	7	8	3	5	5	4	4	6	4	4								
Lachenalia pendula	5	5	4	3	5	3	5	2	2	4	4	5	6	7	4	5	5	7	5	5	5							
Lachenalia pendula	6	5	3	2	3	3	4	2	2	3	3	4	7	5	5	6	6	6	6	6	4	7						
Massonia depressa	6	1	2	1	2	2	3	1	3	2	2	2	5	6	5	4	4	4	6	4	2	3	4					
Massonia depressa	7	2	3	2	3	3	4	2	4	3	2	3	6	5	6	5	5	5	7	5	3	4	5	7				
Massonia echinata	6	1	2	1	2	2	3	1	3	2	2	2	5	5	5	4	4	4	6	4	2	3	4	8	7			
Massonia pustulata	6	1	2	1	2	2	3	1	3	2	2	2	5	5	5	4	4	4	6	4	2	3	4	8	8	8		
Massonia jasmini.	5	2	2	1	2	2	3	1	3	2	2	3	6	6	6	4	5	5	5	5	3	4	5	7	5	7	7	
Neobakeria sp	6	2	2	1	2	2	3	1	3	2	2	2	7	5	5	6	6	4	6	6	2	5	6	6	7	6	6	5

TABLE 2

Similarity table for leaf surface data derived from data in table 1. 100% similarity is designated '8'.

construction of a dendrogram, it was attempted to form groups. At the 100% level (8 in table 2) there was slight grouping, as indicated in the list of pairs of samples with 100% similarities. However, at the 87,5% level (7 in table 2) all groups combine if it is assumed that in linking two groups (as defined at the previous similarity level) only a single member of each group need have a similarity value of 87,5%. This is the assumption made by Sokal and Sneath.

2.3.4 Conclusions

There is only a single group (two samples of *Massonia depressa*, *M. echinata* and *M. pustulata*) as defined at the 100% similarity level in which there is an apparently natural grouping of samples. The next level (87,5%) is not sensitive enough to detect groupings and a larger number of characters is certainly required to provide any meaningful system.

There is a distinct correlation between the shape and size of the epidermal cells and the shape and size of the leaves themselves. This suggests that epidermal cell shape and size does not provide any characteristics useful to supplement gross leaf measurements. Striations, the finer points of cell shapes and stomatal characters are not considered to be correlated with other taxonomically useful characters at the generic level.

It is, therefore, not likely that further work on these lines will prove taxonomically justified.

2.4 Pollen characters

2.4.1 Introduction

Little work has been published on the morphology of the pollen of South African species of the Scilleae. Erdtman (1952) dealt with the main groups of the Liliaceae, including the "Scilloideae". The majority of the Liliaceae have monosulcate pollen. Erdtman mentioned this characteristic for the following genera represented in the South African flora:- *Iphigenia*, *Wurmbea*, *Gloriosa*, *Anthericum*, *Aloe*, *Gasteria*, *Kniphofia*, *Agapanthus*, *Dracaena*, *Sansevieria*, *Asparagus* and *Smilax* and for the only genera of the Scilloideae mentioned, namely "ten species of *Dipcadi*, *Massonia*, *Muscari*, *Ornithogalum*, *Scilla* and *Veltheimia*". Of the genera of the Scilloideae, it is possible that all except *Massonia* and *Veltheimia* were exemplified by European species. The only liliaceous genus represented in the South African flora not complying with this characteristic is *Androcymbium*, which is described as being (2-) 3-aperturate in *A. capense* and 2-porate in *A. punctatum*. The only other information provided on the Scilloideae was that the grains, in their longest axis, measured 33µm (*Massonia echinata*) to 88µm (*Ornithogalum nutans*).

In his survey of South African pollen, Van Zinderen Bakker (1953) described Liliaceae grains as "mostly monosulcate, sometimes anaperturate or trichotosulcate" and the exine as "psilate, pitted, granulate or reticulate, subechinate or echinate".

2.4.2 Method

To determine the likelihood that pollen morphology would provide useful taxonomic characters, twenty species of Scilleae (in ten genera) and a single representative of each of four other genera of Liliaceae were examined.

Material, either fresh or from herbarium material, was examined under a J.E.O.L. JSM U3 scanning electron microscope. A thin layer of gold palladium alloy was evaporated onto the surface of the samples. The magnification used varied with the sample and was selected to give maximum information from the negatives. All prints were made at a 2x magnification from the negatives. Measurements were made directly off the photographs.

2.4.3 Observations

The following generic desciptions are taken from the photographs. They cannot be considered as more than very preliminary in view of the small samples employed. Despite the choice of the least distorted grains for photography only the greatest measurement was taken as the other principal dimensions can either not be determined in equatorial view or are more susceptible to contraction during drying.

Massonia (three species):- Grains 37,5 µm long, monosulcate. Exine with a few rounded lumina up to 0,2 µm in diameter in M. echinata; with many irregularly-shaped lumina up to 1,2-1,4 µm in M. angustifolia; and with similar lumina, but the whole wall apparently greatly fissured in M. depressa (it is possible that this is an artefact or that the grains were damaged, but light microscope study of material from the same source suggested that the fissures are always present although possibly exaggerated by drying); the lumina decreasing in size towards the poles (figs 42-47).

Daubenya (monotypic):- Grains 51 µm long, monosulcate. Exine reticulate, with the lumina irregular and up to 3 µm long, decreasing in size towards the poles. Very similar to M. angustifolia, but with larger lumina (figs 48 & 49).

Whiteheadia (monotypic):- Grains 25-29 µm long, monosulcate. Exine with very few rounded lumina up to 0,3 µm diameter. Resembles M. echinata in surface characteristics (figs 50-52).

Lachenalia (four species):- Grains 37,5-48 µm long, monosulcate. Exine reticulate, with the lumina irregular, up to 1,3-1,7 µm long in a specimen of an unidentified species (from near Calvinia, Jessop s.n.), and up to 2,5-3 µm in another unidentified specimen (Barker 10656); the lumina decreasing in size towards the poles. Very similar to M. angustifolia (figs 53-60).

Ledebouria (three specimens of L. revoluta):- The following data was prepared under a light microscope;

measurements being made by means of a camera lucida attachment. Grains 37,7-61,5 µm long, monosulcate. Exine smooth or reticulate with lumina less than 0,1 µm long and decreasing in size towards the poles.

Eucomis (one species):- Grains 35-42 µm long, monosulcate. Exine reticulate, with the lumina irregular and the larger somewhat elongate, up to 0,8-1,0 µm long, but decreasing in size towards the poles (figs 61 & 62).

Veltheimia (one species):- Grains 54-70 µm long, monosulcate. Exine reticulate, with lumina irregular, up to 2,0 µm long, but decreasing in size towards the poles (figs 63 & 64).

Drimia (including *Urginea*)(five species):- Grains 39-70 µm long, monosulcate. Exine reticulate (smooth in a minority of grains of *D. hyacinthoides*), with lumina up to less than 0,5 µm in *U. delagoensis* and up to 1,3-1,85 µm in *U. fragrans*, but in all species decreasing in size towards the poles (figs 65-75).

Scilla (*Euscilla*) (two species):- Grains 46,25-50,6 µm long, monosulcate. Exine reticulate, with irregularly-shaped lumina up to 1,3-1,85 µm long, decreasing in size towards the poles (figs 76-79).

Ornithogalum (one species):- Grains 92 µm long, monosulcate. Exine reticulate, with irregularly-shaped lumina up to 2,1 µm long, decreasing in size towards the poles (figs 80 & 81).

Bulbine (Asphodeleae - one species):- Grains 40,0-53,3 µm long, monosulcate. Exine reticulate, with oblong, only slightly irregularly-shaped lumina up to 2 µm long, decreasing in size towards the poles (figs 82 & 83).

Chlorophytum (Asphodeleae - one species):- Grains 44,0-47,5 µm long, monosulcate. Exine reticulate, with irregularly-shaped lumina up to 0,5-0,6 µm long, decreasing in size towards the poles (figs 84-86).

Androcymbium (Iphigenieae - one species):- Grains 14,5-18,0 µm long, nonaperturate. Exine reticulate, with irregularly-shaped lumina up to 0,7 µm long, decreasing in size towards the poles. The sulcus is not as distinct as in the other species described above owing to the failure of the grain to collapse to the same extent on drying. Note that Erdtman (1952) described two species as being (2-) 3-aperturate or 2-porate. (Figs 87 & 88).

Asparagus (Asparageae - one species):- Grains 50,7-59,3 µm long, monosulcate. Exine reticulate, with irregularly-shaped lumina up to 0,7 µm diameter, decreasing in size towards the poles (fig. 89).

The source of the material used in drawing up the above descriptions and the numerical data is summarised in table 3.

2.4.4 Discussion

The Scilleae appear to be characterised by being monosulcate and usually with a reticulate exine. Length varies from 25 to 90 µm, but the majority fall within a range of 42-60 µm. The lumina always decrease in size towards the poles. The presence of a few grains with a very small number of very small lumina, or none at all, does not appear taxonomically significant as these have been found in both *Massonia* and *Drimia*, which have a majority of species with a reticulate pattern. In *Scilla* (*Ledebouria*) *revoluta* some specimens produce grains with a reticulation of exine, while others do not.

The only genus in the South African Liliaceae which does appear to be distinguishable on pollen morphology is *Androcymbium* (Iphigenieae) which has exceptionally small grains - up to 18 µm long - which are nonaperturate, (2-) 3-aperturate or 2-porate. *Ornithogalum* has been found to have exceptionally large grains, 92 µm long in *O. longibracteatum* and 88 µm in *O. nutans* (Erdtman, 1952).

It is, therefore, concluded that the Scilleae cannot generally be separated from other tribes of the Liliaceae by their pollen characteristics. The limited data available does not suggest that the genera of the Scilleae are separable from one another on pollen characters either.

SPECIES	LOCALITY AND COLLECTOR	GRAIN LENGTH µm	STANDARD DEVIATION ±	LARGEST LUMEN LENGTH µm
Massonia				
echinata	Farm Vaalkrans (3326B) Bayliss BS/5090	37,5		0,2
angustifolia	8 miles E. of Molteno (3126A) Acocks 22097 (PRE)	51,9		1,2-1,4
depressa	2 miles along Sutherland road from Calvinia (3120C) Jessop s.n.	41,0		not applicable
Daubenya				
aurea	Fransplaas (3220A) Marloth 10415 (PRE)	51,0		2,8-3,0
Whiteheadia				
bifolia	Bokkeveld near Nieuwoudtville (3129A)	25,0-29,0		0,3
Lachenalia				
sp (short tubed group)	S. of Calvinia (3120C) Jessop s.n.	37,5		1,3-1,7
pendula	Arniston (3420C) Jessop s.n.	43,5		2,1
sp	Nooitgedacht near Vredenburg (3218C) Barker 10228 (NBG)	48,0		2,5-3,0

TABLE 3

Table of measurements of Liliaceae pollen.

Lachenalia contd				
aloides var *quadricolor*	Swartwater Farm near Darling (3318A) *Barker 10656* (NBG)	44,0		1,6-1,8
Scilla (sect. *Ledebouria*)				
revoluta	Hendersons Farm, Zuurberg (3325B) *Bayliss BS/3296*	44,5 (range: 37,7-49,2)	4,17	0,1
revoluta	Willowmore (3323A) *Bayliss BS/3887*	42,7 (range: 37,7-47,7)	3,81	none
revoluta	Martindale (3326B) *Jessop 1054* (RUH)	53,3 (range: 46,2-61,5)	4,75	0,1
Eucomis				
autumnalis var *clavata*	Gwaliweni Forest Ubombo (2732A) *Moll 4503* (PRE)	35,0-42,0		0,8-1,0
Veltheimia				
viridifolia	Ex hort., Rhodes University	62,5 (range: 54,0-70,0)	3,86	2,0
Drimia				
hyacinthoides	Gletwyn Farm Grahamstown (3326B) *Dyer 3306* (PRE)	64,12 (range: 53,0-70,0	4,90	0,2-0,8
Urginea				
altissima	Worcester Vald Reserve (3319C) *Olivier 67* (PRE)	39,5		1,25

TABLE 3 continued

Urginea contd				
capitata	Oribi, Aerodrome, Pietermaritzburg (2930C) *Moll 1877* (PRE)	73,0		0,6-1,2
delagoensis	Kruger National Park *Codd 5717* (PRE)	39,0-46,5		0,5
fragrans	Saldanha Bay (3317B) *Marloth 8028* (PRE)	66,0-67,0		1,0-1,5
Scilla (sect. *Euscilla*)				
natalensis	Cathedral Peak Forest Research Station (2929A) *Killick 963* (PRE)	46,25		1,3-1,85
nervosa	Barberton (2531C) *Thorncroft* sub *Tvl Mus 3960* (PRE)	50,6		1,3-1,4
Ornithogalum				
longibracteatum	Ex hort, Rhodes University	92,0		2,1
Bulbine				
frutescens	Ex hort., Rhodes University	48,7 (range: 40,0-53,3)	3,7	2,0
Chlorophytum comosum	Ex hort., Rhodes University	44,0-47,5		0,5-0,6
Androcymbium				
sp.	S. of Calvinia (3120C) *Jessop* s.n.	14,5-18,0		0,7
Asparagus asparagoides	Ex hort., Rhodes University	50,7-59,3		0,7

TABLE 3 continued

2.5 Seed surface characters

2.5.1 Introduction

The seed of 49 plants belonging to 43 species in 21 genera of Liliaceae were examined by means of a stereoscan electron microscope. Most of the material used was taken from herbarium specimens, but some fresh material was used. No differences in the seeds appeared to result from the use of dried material. Preparation of the material was by the same method as described for the pollen.

No previous work on Liliaceae testa fine detail has been discovered.

2.5.2 Observations

The following brief descriptions are based on the photographs. Because of the limited material examined it was not considered justified to draw up more detailed descriptions.

Bulbine

B. frutescens (Ex hort., Rhodes University)
Cells 4- or 5-angled with raised, somewhat papillose, margins, 160-240 µm diameter. Surface papillose.
(Figs 80 & 91.)

A single species was examined. The concave, more or less isodiametric, cells with several papillae are not similar to those in any other material examined.

Schizobasis

S. intricata (Klaasvoogds, Robertson (3319D), Esterhuysen 22711, BOL)

Cells rectangular, with more or less straight walls, concave. Surface smooth. (Figs 92 & 93.)

A single species was examined. Sub-rectangular ridges probably represent cell margins, but their irregular arrangement suggests that they may be wrinkling, perhaps as a result of drying. There is some similarity with several species of Drimia and Urginea.

Bowiea

B. volubilis (Byrne, Richmond, Natal (2930C), Galpin s.n., BOL)

Cells rectangular, with undulate margins, convex, 120-130 x 40-50 µm. Surface smooth. (Figs 94 & 95.)

Monotypic. Rectangular convex cells with slightly wavy margins and a smooth surface are characteristic, but it is somewhat intermediate in form between Urginea modesta and Urginea marginata. It is also similar to Galtonia princeps.

Albuca

A. canadensis (Huguenot College, Wellington, without collector, sub RUH 4473, RUH)

Cells with wavy margins, 130-180 x 20-30 µm. Surface smooth. (Figs 96 & 97.)

A. patersonii (Without locality, Martin s.n. sub RUH 9548, RUH)

Cells with wavy margins, c.90-120 x c.30 µm, more deeply indented than in *Neopatersonia uitenhagensis* or *Galtonia princeps*. Surface smooth. (Figs 98 & 99.)

Two species were examined. The deeply wavy margined, almost flat and smooth-surfaced cells are very similar in both species. The cell outline is similar to that in some species of Urginea which, however, have an undulating surface. *Ornithogalum* also has similar-shaped cells but these are very considerably convex. There is a strong similarity with *Neopatersonia uitenhagensis*, which has pits however, and to *Galtonia princeps*, which has more rectangularly shaped cells.

Galtonia

G. princeps (Port Edward (3130A), *Strey 4516*, PRE)

Cells with wavy margins, c.120-150 x c.30 µm. Surface smooth. (Figs 100 & 101.)

A single species was examined. The sub-rectangular cells are more deeply wavy than in *Bowiea volubilis*.

Drimia and *Urginea* (These genera are treated together because of the difficulty experienced in separating them.)

D. anomala (Uniondale, near Joubertina (3323D), *Esterhuysen 18343*, PRE)

Cells 5- or 6-angled, 40-60 x 20-30 µm. Surface contorted, minutely rough; the protuberances less than 1 µm diameter. (Figs 102 & 103.)

U. delagoensis (Nelspruit (2530B), Buitendag 118, PRE)
Cells rectangular, 300-400 x 40-60 µm. Surface pitted, with the pits up to 1-1,3 µm diameter; otherwise smooth. (Figs 104 & 105.)

U. basutica (Willow Glen, Pretoria (2528C), Strey 3128, PRE)
Cells irregular in outline, convex, 80-230 x 70-120 µm. Surface with numerous curled hairs and pits c. 1-2 µm diameter. (Figs 106 & 107.)

U. fragrans (7 miles S. of Klaver (3118D), Godfrey VH-1254, PRE)
Cells concave, with distinct ridges, with wavy margins, 230-300 x 30-50 µm. Surface with a reticulation of ridges 1-1,5 µm thick. (Figs 108 & 109.)

D. media (Great Drakenstein (3418B), Esterhuysen 21348, BOL)
Cells more or less rectangular, 80-200 x 40-50 µm. Surface more or less smooth. (Figs 110 & 111.)

U. pusilla (Bultfontein, Kimberley (2824D), Marloth 857, PRE)
Cells irregular in outline, 110-240 x 40-70 µm. Surface more or less smooth. (Figs 112 & 113.)

U. sanguinea (Without locality, Marloth 7686, PRE)
Cells with deeply wavy margin, 200-300 x 30-50 µm. Surface pitted; pits 1-1,5 µm diameter. (Figs 114 & 115.)

U. modesta (Near Premier Mine (2528C), Young s.n. sub Tvl. Mus. 32493, PRE)
Cells rectangular, c.65 x 20-25 µm. Surface almost smooth. (Figs 116 & 117.)

U. modesta (Albany district above Rabbits Wood (3326B), Jessop 853, RUH)
Cells not distinguishable. Surface irregular. (Figs 118-120.)

U. multisetosa (A) (Willow Park, Pretoria (2528C) Strey 3054, PRE)
Cells with wavy margins, 100-130 x 50-60 µm. Surface smooth. (Figs 121 & 122.)

U. multisetosa (B) Duiwelskloof (2330C), Scheepers 686, PRE)
Cells with wavy margins, 150-210 x 40-100 µm. Surface smooth. (Figs 123 & 124.)

U. marginata (Richtersveld, Pillans 5780, BOL)
Cells with wavy margins, 120-150 x c.50 µm. Surface smooth. (Figs 125 & 126.)

Twelve specimens of ten species were examined. There is considerable variation in cell shape. In one specimen of U. modesta they are subrectangular, but in the other they are difficult to make out but may be constricted in the centre. Several specimens have rather deeply undulate margins (e.g. U. fragrans). In a few specimens (e.g. U. delagoensis) the boundaries of cells are poorly defined, but generally the cells are fairly to very distinct. In surface characters there is also considerable variation from smooth (e.g. U. pusilla) to pitted (e.g. U. delagoensis). In U. fragrans the pitting is reticulate. Because of the variation it is not possible to compare the genus (or genera) as a whole with other genera. There does not appear to be any correlation with the normal division of this group into two genera in the sense of, for example, Phillips (1951).

Litanthus

L. pusillus (Lesotho, Mamathes (2927B), Jacot Guillarmod 3233, RUH)
Cells mostly not distinguishable, 5-or 6-angled, c.20-25 μm diameter. Surface considerably folded, rough, with ridges up to 1 μm thick. (Figs 127 - 129.)

The single species was examined. The rather poorly defined cells are somewhat similar to those of one specimen of Urginea modesta, but the rugulose surface is unique amongst the samples examined.

Rhadamanthus

R. platyphyllus (Strandfontein, Vredendal (3118C), Hall 3473, NBG)
Cells 4- to 7-angled, isodiametric to oblong, depressed, 80-240 µm diameter. Underlying cells forming convexities in the surface. Otherwise smooth.
(Figs 130 & 131.)

R. sp (Ex hort., Rhodes University)
Cells more or less rectangular, 5- or 6-angled, depressed, 70-150 x 50-70 µm. Underlying cells forming convexities in the surface. Otherwise smooth.
(Figs 132 & 133.)

Two specimens of Rhadamanthus were examined. In both the cells are exceptionally clearly delimited by prominent marginal ridges. The underlying cells are also distinct. It is possible that the gold palladium may not have been thick enough to prevent a large number of electrons from passing through the surface of the seed. But as this phenomenon was not observed in samples of other genera it is believed to be due to a characteristic in the seed surface. However it was not established whether the electrons were passing through the surface or whether collapse of the epidermis had allowed the pattern of the underlying cells to be reflected in the form of the seed surface.

Dipcadi

D. ciliare (Bushman's River Mouth (3326D), Noel s.n. sub RUH 12089, RUH)
Cells 5- or 6-angled, 60-130 x 30-45 µm, with numerous shallow pits c.1 µm diameter. Some cells appeared raised, but this may be an artefact. (Figs 134 & 135.)

D. viride Burnt Kraal, near Grahamstown (3326B), Martin s.n. sub RUH 9271, RUH)
Cells 5- to 7-angled, 40-50 µm diameter. Surface smooth. (Figs 136 & 137.)

Two species of Dipcadi were examined. The cells are 5- or 6-angled (rarely 7-angled), not often more than twice as long as broad. In D. ciliare a few cells appear to have separated from, and become raised above, the surrounding cells. In D. viride the cells are smooth, but in D. ciliare they are minutely pitted. The most similar species examined are in the Drimia-Urginea group (in which they are not as distinctly angled, however), and in Rhadamanthus (in which the margins are raised and the underlying cells visible).

Scilla section Euscilla

S. firmifolia (Ex hort., Rhodes University)
Cells 5- or 6-angled, 25-35 µm diameter, each distinctly papillose - the papillae rather flattened with 3 grooves. (Figs 138 & 139.)

S. nervosa (Warmbaths (2428C), Leendertz s.n. sub Tvl. Mus. 28064, PRE)
Cells indistinct, probably 5- or 6-angled, 30-40 µm diameter; structures resembling thin-walled papillae present. (Figs 140 & 141.)

S. natalensis (Pietermaritzburg (2930C), Mogg 2238, PRE)
Cells indistinct, probably 5- or 6-angled, 30-40 µm diameter, with structures resembling thin-walled papillae. (Figs 142 & 143.)

Three species of Scilla (sect. Euscilla) were examined. In both S. nervosa and S. natalensis there is a wrinkling of the surface which may be caused by the collapse of the convex outer walls. In S. firmifolia, however, there are large papillae each with 1-3 (usually 3) furrows. If the appearance of the former two species is caused by the collapse of thin-walled papillae, the differences between them and S. firmifolia may not be as great as the first impression of the photographs may suggest. Although the cells of S. nervosa and S. natalensis are indistinct it is thought likely that all species have 5- or 6-angled cells. Note that S. nervosa has been treated as belonging to a distinct genus - Schizocarphus (Van der Merwe, 1943).

Scilla section Ledebouria

S. megaphylla (Happy Rest, Soutpansberg, N. Tvl., Van der Merwe 2240, PRE)
Cell-like convexities more or less 4-angled, 15-25 µm diameter, arranged in regular rows. Surface very irregular; the outermost layer or layers apparently damaged. (Figs 144-146.)

A single species of Scilla (Ledebouria) was examined. It is not certain that the cell-like patterns are in fact cells as the larger cell-like shapes are subdivided by shallower grooves. There is a close similarity with the Massonia group and possibly Lachenalia. In parts there is a rugulose covering which may be a cuticle, but which is damaged in parts. The structure shown in fig. 146 is probably also a result of damage.

Eucomis

E. autumnalis var clavata (Tabamhlope, Estcourt (2929B), Downing 53A, PRE)
Shallow depressions over whole surface c.20-40 µm diameter. Minute more or less reticulate ridges c.0,1 µm wide over both raised and depressed portions, but otherwise smooth. (Figs 147 & 148.)

A single specimen of *Eucomis* was examined. The surface shows no evidence of cells although there is a reticulate pattern of ridges, similar in appearance to those of some members of the *Massonia* group.

Ornithogalum

O. thyrsoides (A) (Table Mountain above Kirstenbosch, (3418A), *Bolus 4919*, PRE)
Cells with wavy margins, 110-150 x c.50 µm, smooth but separated by deep grooves. (Figs 149 & 150.)

O. thyrsoides (B) (Bought at Houtbay Nek, PRE)
Cells with wavy margins, 110-150 x c.40 µm, smooth but separated by deep grooves. (Figs 151 & 152.)

O. conicum (Clanwilliam (3218B), *Leipoldt 4374*, PRE)
Cells with wavy margins, 90-140 x 30-40 µm, papillose; the papillae verrucose. (Figs 153 & 154.)

O. ceresianum (Ceres (3319A), *Goatcher* s.n. sub BOL 13726, PRE).
Cells with wavy margins, 90-130 x 40 µm. Surface smooth. (Figs 155 & 156.)

O. maculatum (Sandberg near Clanwilliam (3218B), *Leighton* s.n. sub BOL 2161, PRE)
Cells with wavy margins, ?65 x 20 µm, minutely verrucose, deeply grooved between the cells. (Figs

157 & 158.)

O. miniatum (A) (Near Riversdale (3421A), Muir 2988, PRE)
Cells with wavy margins, c.70 x 20 µm; each cell produced into a papilla up to 70 µm long. Surface with numerous shallow depressions c.1,0 µm diameter. (Figs 159 & 160.)

O. miniatum (B) (Kommaggas (2917D), without collector sub Stellenbosch Garden no. 3983, PRE)
Cells with wavy margins, 70-80 x c.20 µm; each cell produced into a papilla up to 80 µm long. Surface with numerous shallow depressions c.1,0 µm diameter. (Figs 161 & 162.)

Seven specimens of five species were examined. They were all very similar with deep grooves between the cells and the outer tangential walls strongly convex or produced into papillae. There is a similarity with Galtonia princeps and to a limited extent with Albuca and the Drimia -Urginea group, but these genera have flatter cells.

Pseudogaltonia

P. clavata (Sturmveld, Gobabis (2119), Tölken s.n.)
Cells sub-isodiametric, 5- to 7-angled, 65 - 100 µm diameter. Surface reticulately patterned with shallow depressions c.20 µm diameter. (Figs 163 &

164.)

The only species in the genus was examined. The cell pattern is similar to that in Scilla (Euscilla) and Dipcadi. But the surface is reticulate in a form more similar to that of a few species of the Drimia-Urginea group.

Lachenalia

L. monophylla (storms River (3323D), Seagrief s.n. sub RUH 22228, RUH)
Cell-like pattern more or less rectangular, c.30-40 x 30 µm. Surface wrinkled but otherwise smooth. (Figs 165 & 166.)

The absence of surface details allies this specimen with the Massonia group.

Whiteheadia

W. bifolia (Ratelpoort between Springbok and Steinkopf (2917D), Hardy 542, PRE)
Wrinkled with rows of more or less 4-angled cell-like convexities 10-23 um diameter. Otherwise smooth. (Figs 167-169.)

The only species in the genus was examined. It is thought possible that the lonitudinal furrows indicate the positions of cell walls, but that the less regular transverse grooves may not do so. This seed belongs to the Massonia group.

Massonia (including Neobakeria)

M. depressa (Without locality, Marloth 10367, PRE)
Cell-like convexities arranged in rows, 7-10 µm diameter. Otherwise smooth. (Figs 170 & 171.)

M. echinata (Near the Redhouse turnoff (3325D), Bayliss BS/4868)
Cells not distinguishable. Surface coarsely verrucose, with papillae and ridges down to less than 1 µm diameter. (Figs 172-174.)

M. echinata (Near Klipplaats Village (3324A), Bayliss BS/4890)
Cells not distinguishable. Surface coarsely verrucose, with ridges down to less than 1 µm diameter. (Figs 175 & 176.)

M. pustulata (Locality not recorded, Acocks 21339, PRE)
Cell-like convexities more or less square, c.10-15 µm diameter. Otherwise smooth. (Figs 177 & 178.)

M. angustifolia (De Aar (3024C), Friedlander s.n., GRA)
Cell-like convexities 5- or 6-angled, 20-30 x c.10 µm. Otherwise smooth. (Figs 179 & 180.)

Five specimens of four species were examined. Epidermal cells are either not recognisable or (as in Whiteheadia) there are rectangular or triangular cell-like structures which, because of their small size and irregular shape, are thought likely not to be cells.

Daubenya

D. aurea (Sutherland (3220A), Marloth 7106, PRE)
Cell-like convexities 4- to 6-angled, 18-23 µm diameter. Otherwise smooth. (Figs 181 & 182.)

The only species in the genus was examined. The cell (or cell-like) pattern is similar to that in Whiteheadia and in some specimens of Massonia.

Androsiphon

A. capense (Farm Plaatberg S.W. of Calvinia (3119B), Acocks 18606, PRE)
Cell-like convexities 4- to 6-angled, 13-23 µm diameter. Surface densely lepidote; the scales irregular in form and arrangement and up to c.3 µm broad. (Figs 183-185.)

The only species in the genus was examined. At low magnification (x 100) the surface appears indistinguishable from other members of the Massonia group. However, the higher magnifications show a unique scaly covering which may be produced by the cuticle.

Polyxena (including the Cape species of Hyacinthus)

P. ensifolia (Oudtshoorn (3322C), Dyer 99a, GRA)
Cells not distinguishable. Surface more or less smooth with shallow pits up to c.10 µm diameter. (Figs 186 & 187.)

P. (Hyacinthus) corymbosa (Witklip Farm, Vredenburg, without collector sub NBG 374/64, NBG)
Cells not distinguishable. Surface more or less smooth with shallow pits up to c.10 µm diameter. (Figs 188 & 189.)

Both species of the genus were examined. The surface is more or less smooth with broad shallow pits. It is not very different from Massonia angustifolia.

Neopatersonia

N. uitenhagensis (Bethelsdorp (3325D), Long 135, GRA)
Cells with wavy margins, c.130-170 x 60-70 µm, pitted; the pits c.1-1,5 µm diameter. (Figs 190 & 191.)

One species of Neopatersonia was examined. The shape of the cells is similar to that of Albuca and some species of the Drimia-Urginea group. The pits are reminiscent of the Drimia-Urginea group or Pseudogaltonia.

Asparagus

A. virgatus (Ex hort., Rhodes University)
Cells isodiametric, 5- or 6-angled, 30-40 µm diameter, smooth, slightly concave, separated from one another by grooves with almost vertical sides c. 5-6 µm deep. (Figs 192-194.)

The raised tabular cells are quite unlike any others in the material examined.

2.5.3 Discussion and conclusions

Several essentially different types of seed surfaces were observed in the bulbous Liliaceae.

1) The Massonia group (Whiteheadia, Lachenalia, Scilla section Ledebouria, Massonia, Eucomis, Daubenya, Androsiphon and Polyxena) possess either no indication of cells or rectangular or triangular shapes (generally about 15 µm diameter) which are thought not to represent cells.

2) The Ornithogalum type (Ornithogalum) possesses deeply divided cells.

3) Cells with deeply wavy outlines, but flatter in the vertical plane than in Ornithogalum (Albuca, Galtonia and Neopatersonia).

4) Angular cells (Scilla section Euscilla, Dipcadi, Rhadamanthus and Pseudogaltonia).

5) Drimia, Urginea, Litanthus, Schizobasis and Bowiea do

not fit exactly into any of the above types although certain species of the Drimia-Urginea group could be allocated to types 3 or 4. Other species have less deeply wavy outlines than in the previous types or more or less rectangular cells.

It does appear, therefore, that cell characters of the testa epidermis may show a reasonable correlation with the morphological characters that have been used in defining generic concepts.

2.6 Chromatography

2.6.1 Introduction

Simple paper chromatographic techniques are considered as a source for taxonomic characters. Ideally, the compounds separated on the paper should be identified. It is, however, considered that any characteristic, such as the position of spots on controlled runs, could be used, provided a set of spots which can be objectively correlated between different sources of material is obtained.

The methods employed here were developed from work by Riley and Bryant (1959 and 1961) on South African Iridaceae and by Riley and Isbell (1963) on Haworthia (section Coarctatae).

2.6.2 Methods

2.6.2.1 Extraction method

Two extraction methods were attempted:-

1) Extraction of bulb scales of Scilla (Ledebouria) revoluta, in 80% methanol, using a homogeniser, was tried. But large quantities of mucilage, which was insoluble in methanol, were encountered and the method was not further developed.

2) Extraction in distilled water, using a homogeniser, resulted in the mucilage being brought into solution. Solid material was removed by centrifugation at 3 000 r.p.s. for 10 minutes. The mucilage was precipitated by the addition of 95% ethanol and removed by centrifugation at 3 000 r.p.s. for 10 minutes.

The clear supernatant was concentrated on a rotary concentrator. 80% ethanol was used to dissolve the concentrate.

A micro-syringe was used to produce c.10 mm diameter spots on the chromatographic paper. These were air dried.

The solvent used to run the chromatograph consisted of:

Ethyl acetate	18 pts by vol.
Acetic acid	12 pts by vol.
Formic acid	4 pts by vol.
Distilled H_2O	16 pts by vol.

The descending chromatogram was run on a single axis for 24 hours.

The air-dried chromatograms were sprayed with para-anisedene hydrochloride, again dried and heated at 106°C for 10-20 minutes in an oven.

This method produced only four (yellow) spots, which it was considered inadequate to justify continuing with this technique.

2.6.2.2 Smear method

Fresh samples were crushed onto the chromatographic paper with the rounded end of a test tube. Two sets of trial runs were made as follows:-

1) *Scilla* (*Ledebouria*) *revoluta* and *Allium cepa* bulb scale and root material were run separately on a descending chromatogram in the following solvent:

Ethyl acetate	18 pts by vol.
Acetic acid	3 pts by vol.
Formic acid	1 pt by vol.
Distilled H_2O	4 pts by vol.

This method produced six or seven spots and appeared, therefore, to be preferable to the extraction methods.

2) Similar material was run using a different solvent:

Butanol	4 pts by vol.
Acetic acid	1 pt by vol.
Distilled H_2O	5 pts by vol.

Again about six or seven spots were usually found. These were examined with ultra-violet light and they were found to fluoresce.

The spots moved further and separated better than in the previous solvent and for this reason this solvent was preferred.

In both cases the chromatograms were heated at 106°C in an oven for up to 24 hours, and examined under an ultra-violet lamp with 95% emission at 3650 A.

The following procedure was used with a set of eleven specimens:-
Approximately 5 mm cubes of bulb scale material were used. They were smeared at intervals of 25 mm along a line 75 mm from one end of 6" x 24" sheets of Watman's (no. 1) filter paper. Six smears could, in this way, be run simultaneously. The paper rested on a clean glass plate during smearing to prevent contamination. After smearing, crushed material was scraped from the paper with a clean blade.

After air-drying for 24 hours a descending run was made for 18 hours in the second solution described above. After a further 24 hours of air-drying the chromatogram was baked in an oven at 106°C for 24 hours.

The spots were examined under an ultra-violet lamp with 95% emission at 3650 A, outlined in pencil and the colour noted.

2.6.3 Materials

The following specimens were used (with number of runs):
1) Scilla (Euscilla) natalensis (Ex hort,, Rhodes

University) (18).

2) Scilla (Ledebouria) revoluta (Ex hort., Rhodes University) (24).

3) Scilla (Ledebouria) revoluta (Near Airport, Grahamstown - 3326B - Easton s.n. (12).

4) Scilla (Ledebouria) undulata (Wooldridge - 3327A - Bayliss BS/3224) (2).

5) Scilla (Ledebouria) sp. (Mbabane, Swaziland - 2631A - Bayliss BS/3469) (2).

6) Scilla (Ledebouria) sp. (Riebeek East - 3326A - Bayliss BS/3590) (2).

7) Albuca sp. (Pluto's Vale - 3326B - Jessop s.n.) (18).

8) Veltheimia viridifolia (Ex hort., Rhodes University) (18).

9) Ornithogalum longibracteatum (Ex hort., Rhodes University) (6).

10) Massonia echinata (Table Hill Farm - 3326B - Jessop s.n.) (6).

11) Drimia anomala (Table Hill Farm - 3326B - Jessop s.n.) (6).

2.6.4 Results

From four to nine spots were obtained for each sample, varying in colour from blue or brown to yellow. The colours were, however, apparently to at least some extent, dependent on the concentration of the substance isolated.

They have, therefore, not been used in the identification of spots.

R.f. values were obtained by measuring the distances from the base line to the centre of each spot. As, however, the spots did not have sharply defined boundaries, and generally exceeded 10 mm in diameter, their centres could only be established very approximately. The maximum R.f. value obtained was 16,5 cm for Scilla natalensis. The data is shown in table 4.

The data thus obtained was examined to determine the likely value in running sufficient series to conduct a statistical test on the data, or the prospects for refinements in the technique.

The correlation table (table 5) was drawn up by expressing the number of R.f. values common to each pair of samples as a percentage of the total number of R.f. values occurring in one or both members of each pair. This involved a subjective estimate of whether or not a particular R.f. value in one sample should be treated as the same as a slightly different R.f. value for the other sample. It was considered putting this decision onto an objective basis by treating each R.f. value as a range covering its arithmetic mean plus and minus its standard deviation. Because of the small number of runs and the subjective element involved in obtaining a R.f. value for each replication this method was not, however, considered helpful.

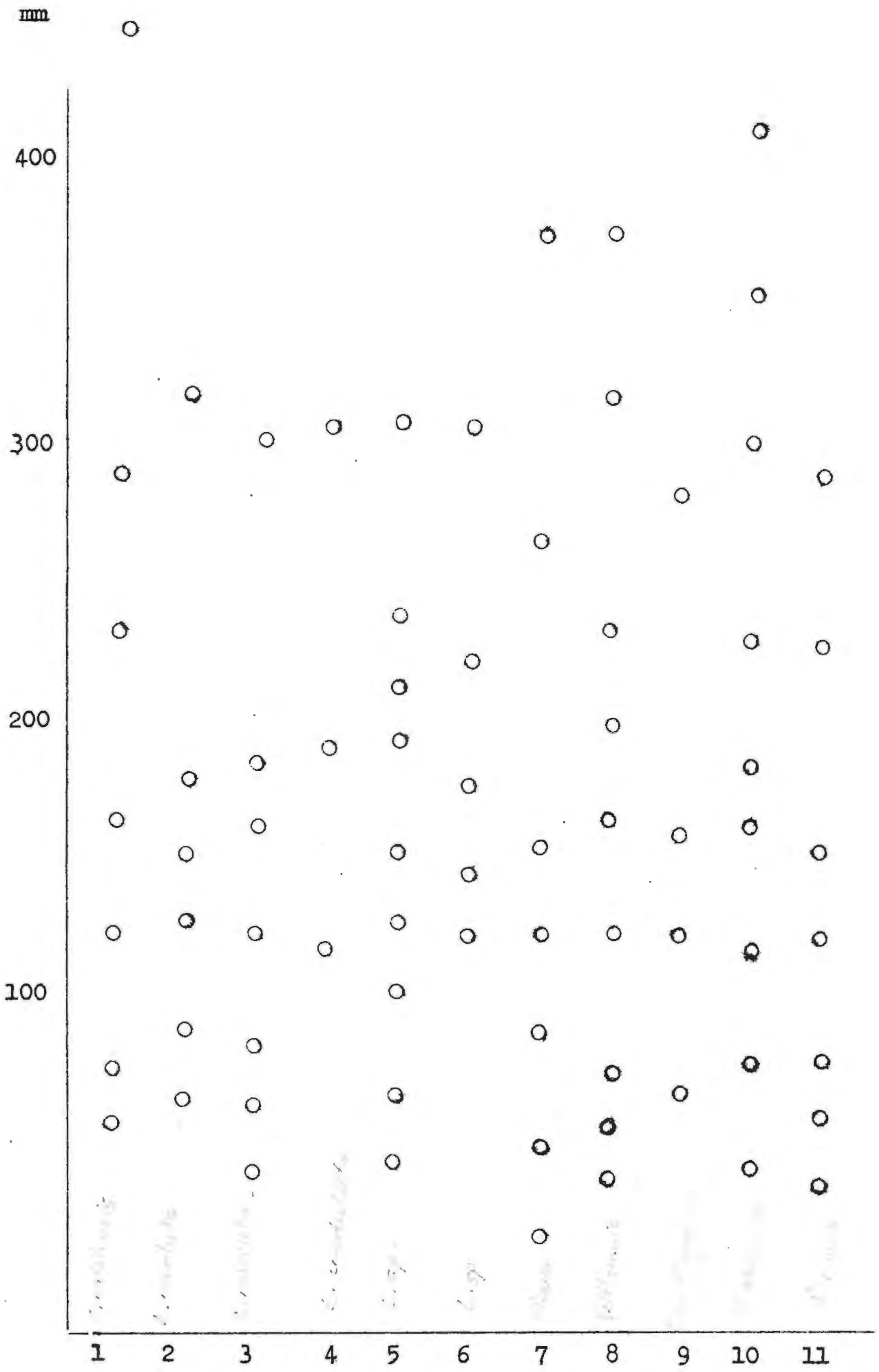


TABLE 4

Positions of spots for species 1-11 (numbered according to list on pages 64 and 65).

Scilla natalensis	S. natalensis	S. revoluta	S. revoluta	S. undulata	S. sp.	S. sp.	Albuca sp.	V. viridifolia	O. longibract.	M. echinata
Scilla revoluta	71									
Scilla revoluta	63	63								
Scilla undulata	10	37	43							
Scilla sp	32	63	50	33						
Scilla sp	37	57	33	60	56					
Albuca sp	40	63	50	25	45	33				
Veltheimia viridi.	55	45	78	33	64	80	37			
Ornithog. longibract.	37	43	37	40	80	50	37	27		
Massonia echinata	32	63	60	33	42	30	23	64	44	
Drimia anomala	75	44	56	27	25	50	17	42	33	40

TABLE 5

Similarity table for chromatographic data derived from data in Table 4. Each figure has been expressed in the form a percentage.

2.6.5 Discussion

An examination of the correlation table shows a high (above 75%) correlation value between the following pairs of samples:-

1) *Veltheimia viridifolia* : *Scilla revoluta* (sp. 3)
2) *Veltheimia viridifolia* : *Scilla* sp. (sp. 6)
3) *Scilla* sp. (sp. 5) : *Ornithogalum longibracteatum*
4) *Scilla revoluta* (sp. 2) : *Scilla natalensis*
5) *Scilla natalensis* : *Drimia anomala*.

Low values (below 25%) were obtained for correlation values between the following pairs:-

1) *Scilla undulata* : *Albuca* sp.
2) *Scilla* sp.(sp. 5) : *Drimia anomala*
3) *Scilla undulata* : *Scilla natalensis*
4) *Albuca* sp. : *Massonia echinata*
5) *Albuca* sp. : *Drimia anomala*.

These lists of low and high values do not suggest any indication of taxonomic significance in the method described here. The two specimens of *Scilla revoluta* only have a value of 63%. Only one other pair of samples from the *Ledebouria* section of *Scilla* has a correlation value of more than 60% (also 63%).

The original chromatograms for the *Scilla* (*Ledebouria*) spp were re-examined to evaluate the likelihood of the subjective element being responsible for the seemingly low values for the intra-generic correlations. The conclusion reached, however, is that there is in fact less similarity between these patterns than in several intergeneric correlations.

It is considered that considerable improvement would have to be made to the method for it to offer any taxonomically usable data. Two possible lines of development might justify consideration:-

1) Larger numbers of replications, possibly run on a two-dimensional chromatogram, including a control on each chromatogram. This would enable statistical tests to be applied and could eliminate the subjective element, to a large extent.

2) Identification, or partial identification, of the compounds present in each spot or, as a minimal requirement, the adoption of colour tests which could identify more accurately some of the spots.

2.7 Cytology

2.7.1 Introduction

Studies were undertaken to investigate:-

1) the possibility of using chromosome number and/or morphology as taxonomic characters;
2) the possibility of chromosomes' assisting in determining phylogenetic lines, and
3) the possible occurrence of meiotic abnormalities,

which may indicate particular reproductive systems.

The extent to which the studies assisted will be discussed towards the end of this paper.

It was decided to spend as much time as possible on a single genus as it was felt that an equivalent amount of data spread over several genera might not be as useful. Scilla (section Ledebouria) was chosen because, for its size, it was cytologically comparatively little known, because a wide range of plants were readily procurable and because it had been found that they grew well in cultivation. Taxonomically, it is also considered to be one of the most difficult groups within the South African bulbous Liliaceae.

2.7.2 Methods

2.7.2.1 Germinating pollen

Attempts were made to germinate Scilla (Ledebouria) pollen on semi-permeable cellophane over a cavity slide. A sucrose solution varying from 2,5 - 15 %, with and without the addition of 0,001% boric acid, was tried. In the samples from some plants germination occurred. But growth was limited and nuclear division was never detected.

2.7.2.2 Pollen mother cells

Pollen mother cells were, however, found to be satisfactory and were used throughout the investigation where suitable material was available.

Root tip mitotic chromosomes were considered (see sect. 2.7.2.3) but difficulty was experienced in obtaining growth of the roots and it was doubted whether sufficient counts or other types of data could be obtained in the time available to provide useful data. At the same time, despite their deficiencies as material for morphological studies (mainly because of excessive contraction), meiotic chromosomes might be expected to provide information on certain abnormal behaviour patterns, especially during pairing. These abnormalities might be of value, especially, in determining possible hybrid origins.

No fixation or other pre-staining treatments were employed. Anthers were dissected out of buds and squashed in lacto-propiono-orcein, prepared as described by Haskell and Wills (1968).

Material was either photographed with a Zeiss Photomicroscope on Kodak Pan-X film or drawn under a Wild (M11) Camera Lucida. Measurements were taken from the photographs (employing where necessary photographs taken in different planes) or from camera-lucida drawings. The drawings accompanying the photographs were drawn from the photographs, using sketches made from the original preparations as a guide to interpretation. The quality of the negatives was found, after this work had been completed, to be better if a high contrast film (e.g. Kodak Copy Film or Ilford Micro-neg Pan) were used.

2.7.2.3 Bulb roots, radicles, cotyledons and plumule material from germinating seeds

The material was fixed in 1 : 3 acetic-alcohol for three to 24 hours and stored in 70% ethyl alcohol. Hydrolysis was in 10% HCl at 60°C for 5 - 15 minutes. After rinsing in distilled water, it was macerated and squashed in lacto-propiono-orcein.

This method gave satisfactory results, but several problems were encountered:-

1) It was not always possible to stimulate bulbs to produce roots.
2) Difficulty was experienced with germinating seeds.
3) The diploid number of chromosomes is more difficult to examine than the haploid. Colchicine was used, but the affect was slight.

2.7.3 Application of methods

2.7.3.1 The meiotic chromosomes of *Scilla* section *Ledebouria*

2.7.3.1.1 Introduction

Prior to the present author's work on *Scilla* (sect. *Ledebouria*) cytology, only two papers dealing with the chromosomes of South African members of the group had been published (Giménez-Martin, 1959, and Fernandes and Neves, 1962). Giménez-Martin reported a somatic number of twelve for *S. graminifolia* Bak. (sub *Scilla stenophylla*) and Fernandes and Neves reported a somatic number of 24 for *S. apertiflora* Bak. (sub *Scilla linearifolia*). Three papers on S. hyacinthina (sub Scilla indica), which is an Indian species (also occurring in East Africa), give somatic numbers of 30, 44, 45, 46, 58 and 60 (Rao, 1953 and 1956, and Sheriff and Murthy, 1946).

The present study was undertaken to provide information which might be of value in determining relationships between Scilla section Ledebouria and section Euscilla and other genera in the bulbous Liliaceae, to assist in the subdivision of the section, and also to obtain information on the occurrence of abnormalities during meiosis.

2.7.3.1.2 Results

Satellites and heterochromatic regions were not detected and centromeres were usually not identifiable. But these structures are usually not visible in meiotic material.

It was found that the chromosomes did not fall into natural size categories. In calculating the average sizes the measurements for each complement were placed in descending order of size and it was assumed that the chromosomes in equivalent positions in the order in different complements were homologous. Drawings of leaves were made from herbarium material of the actual specimens employed in the cytological investigations. In a few cases suitable material for making these drawings was not available.

Tables 6-14 summarise the specimens employed in the studies, the haploid chromosome numbers and the number of

Specimen	Fig. nos	Haploid number	Number of cells counted
Jessop 1061, GRA - Bakkerspas, Thabazimbi (2427)	196	10	10
Strey 9291, GRA - Mgongongo tributary to Tsotsha River, Wickman's Farm (3030)	197-200	13	10
Strey 9203, GRA - Hella Hella (2930)	201-203	15	8

TABLE 6

Chromosome data for Scilla cooperi.

Specimens	Fig. nos	Haploid number	Number of cells counted
Bayliss BS/3920, GRA - Basson's Kloof, Zuurberg (3325)	205	10	8
Jessop 1062, GRA - 1 mile S. of Nkandla (2831)	206	11	10
Jessop 1063, GRA - Woest Hill Grahamstown (3326)	207	17	16
Strey 9234, GRA - along road near Pietermaritzburg (2930)	208-210	30	9

TABLE 7

Chromosome data for Scilla floribunda.

Specimen	Fig. nos	Haploid number	Number of cells counted
Tim s.n., GRA - kariega (3326)	212-214	13	7
Bayliss BS/3806, GRA - Andrieskraal, Baviaans Kloof (3324)	215-217	13	4
Bayliss BS/3224, RUH - Wooldridge, Peddie (3327)	218-220	15	6

TABLE 8

Chromosome data for *Scilla socialis*.

Specimen	Fig. nos	Haploid number	Number of cells counted
Bayliss BS/3377, GRA - Brooklands (3326)	222	18	6

TABLE 9

Chromosome data for *Scilla concolor*.

Specimen	Fig. nos	Haploid number	Number of cells counted
Jessop 1064, GRA - Rhodes University Garden	224	9	11
Jessop 1064 as above	225	10	8
Jessop 1064 as above	226	10	12
Bayliss BS/3296, GRA - Henderson's Farm, Zuurberg (3325)	227	10	14
Strey 9292, GRA - Mgongongo tributary to Tsotsha River Wickman's Farm (3030)	228	10	11
Jessop 1065, GRA - 34 miles W. of Potgietersrust (2428)	229	11	7
Jessop 1065 as above	230	22	10
Jessop 1066 - 5 miles W. of Colenso (2829)	232	12	15
Jacot Guillarmod s.n., GRA - Kroomie, Fort Beaufort (3226)	233	13	14
Jessop 1067, GRA - 7 miles S. of Nkandla (2831)	234	13	8
Bayliss BS/3910, GRA - Graaff Reinet (3224)		15 ± 1	5

<u>TABLE 10</u> (continued on p. 78)

Chromosome data for <u>Scilla revoluta</u>.

Specimen	Fig. nos	Haploid number	Number of cells counted
Easton s.n., RUH - 2 miles N.W. of Grahamstown (3326)	235	15	12
Bayliss BS/3887, GRA - Willowmore (3323)	236	16	12
Bayliss BS/3744, GRA - Ngwavuma, Swaziland (2731)	237	17	14

TABLE 10 (concluded)

Chromosome data for Scilla revoluta.

Specimen	Fig. nos	Haploid number	Number of cells counted
Bayliss BS/3224, GRA - Wooldridge Peddie (3327)	239	10	10
Bayliss BS/3558, GRA - Willowmore (3323)	240	10	15
Jessop 1068, GRA - 18 miles west of Cala (3127)	241-243	13	8
Bayliss s.n., GRA - Queenstown (3126)	244-248	14	15

TABLE 11 (continued on p.79)

Chromosome data for Scilla undulata.

Specimen	Fig. nos	Haploid number	Number of cells counted
Jessop 1053, GRA - Martindale (3326)	249-251	15	14
Bayliss s.n., GRA - Addo (3325)		c. 20-30	

TABLE 11 (concluded)

Chromosome data for Scilla undulata.

Specimen	Fig. nos	Haploid number	Number of cells counted
Bayliss BS/3931, GRA - Dordrecht (3127)	253-256	13	5
Jessop s.n. - 14 miles N. of Pretoria (2528)	257	15	10

TABLE 12

Chromosome data for Scilla marginata.

Specimen	Fig. nos	Haploid number	Number of cells counted
Jessop 1057, GRA - 25 miles north of Pretoria (2528)	258	?46	4

TABLE 13

Chromosome data for Scilla sp. nov.

(= Ledebouria luteola)

Specimen	Fig. nos	Haploid number	Number of cells counted
Jessop 1069, GRA - near Howick (2930)	259-261	27	7

TABLE 14

Chromosome data for Scilla ovatifolia.

complements measured in preparing the idiograms.

Scilla cooperi.

Three specimens were examined from the Cape, Natal and the Transvaal. They were found to have numbers of 10, 13 and 15 (Table 6). Figures 196, 200 and 203 show the range in size of the chromosomes. It may be of interest that one specimen (Jessop 1061)has the smallest number, but the largest - almost twice the size of the other two specimens.

No evidence for abnormalities during meiosis was detected in S. cooperi during this survey, although apparently reliable counts of 12 and 14 had previously, in a preliminary study, been obtained for one of the specimens (Strey 9291). If this is accepted as evidence for variable numbers in different flowers, or at least different inflorescences, it is likely that there are abnormalities in mitotic divisions.

Scilla floribunda.

Four specimens were examined from the Cape and Natal.

The specimens were found to have haploid numbers of 10, 11, 17 and 30. Although it is possible that the numbers were derived from a polyploid series a certain amount of aneuploidy would also have to be taken into account with probably both the addition to and loss from the basic number. If the basic number for the series is 10, the hexaploid (3N in the haploid stage) shows no morphological features which could be explained by the increase in chromosome number (fig. 211). The specimen with N = 17 (Jessop 1063) is problematical. The plants making up the population from which this count was made are somewhat intermediate between S. floribunda and S. revoluta. In general morphology they are closer to S. revoluta, but they have been placed in S. floribunda because of the large size of the bulbs (up to 100 mm or more long) and leaves (often 150-200 mm long; although smaller leaves are shown in fig. 211). Evidence for polyploidy is inconclusive although the presence of multivalents was suspected. It is possible that this population is of hybrid origin with S. floribunda and S. revoluta as parents.

Scilla socialis.

This is a particularly sharply defined species, morphologically, showing less variation than do most species of Scilla. No meiotic abnormalities were detected, but it is of interest that of the three specimens examined one (from the most easterly locality) should have 15 chromosomes while the other two have 13.

<u>Scilla concolor</u>.

This is also a well-defined species, restricted in distribution and lacking in variation. A single count of N = 18 was obtained and no abnormalities detected.

<u>Scilla revoluta</u>.

Fourteen counts were made on specimens from the Cape, Natal, the Transvaal and Swaziland. The lowest numbers were 9 and 10. One specimen (from an unknown locality, grown in the Rhodes Botany Department Garden) was examined in particular detail. Three clonal bulbs were selected and flowers from each bulb were examined. In one there was a haploid number of 9 (11 identical counts being made) and the other two of 10. Plants from the Cape and Natal also had numbers of 10, but other numbers encountered were 11, 12, 13, 15, 16, 17 and 22. The counts of 11 and 22 were made from different flowers from the same inflorescence of a Transvaal specimen which had been established in cultivation in Grahamstown. There were other flowers on the same inflorescence with around 22 (not accurately counted), but no others were found with around 11. The material did not enable a thorough investigation of the whole inflorescence as only a narrow band of flowers was at the right stage for examining the chromosomes, but it is suggested that the best explanation is that part of the inflorescence had been produced from a tetraploid cell. No other abnormalities were detected.

No correlation was found between numbers and distribution or morphology (figs 231 and 238) or chromosome size.

An additional count of N = 15 was made during the preliminary survey for a specimen from a locality ten miles north of Pretoria (not included in table).

Scilla undulata.

Six specimens were examined from the Cape (although the species does also occur in the other provinces and South West Africa). Numbers counted were 10 (two specimens), 13, 14, 15 and probably between 20 and 30. The specimen which was not accurately counted (Bayliss s.n. from Addo) is of particular interest. Pairing was irregular and laggards frequent. It is possible that this specimen is a hybrid between S. undulata and S. revoluta, both of which are common and widespread in the area where it was collected. The leaves are rather narrow for the latter (up to about 8 mm broad) and rather linear. These characters suggest affinities with S. cooperi which is, however, very much less common. The bulb is distinctly of the S. undulata or S. revoluta type.

Again no correlation was found between numbers or distribution or leaf morphology (fig. 252) or chromosome size.

Scilla marginata.

Two specimens were examined from the Cape and the Transvaal. Numbers of 13 and 15 were found with no abnormalities detected. Again this is a rather homogeneous species, morphologically, despite its wide distribution.

Scilla sp. nov. (Ledebouria luteola).

A single specimen of this rather well-defined species was examined and found to have N = approximately 46. Counts of sixteen cells varied from 39 to 56. Whether the difficulty in obtaining an accurate count only reflects the difficulties in counting a fairly large number or whether several haploid numbers existed could not be determined.

Scilla ovatifolia.

A single specimen (from Natal) was found to have a haploid number of 27. No abnormalities were detected.

2.7.3.1.2 Discussion

Table 15 summarises the numbers reported for Scilla (section Ledebouria), including those previously reported, all expressed as haploid numbers. The number under the heading "number of specimens" refers to the total number of specimens counted and not to the number of species.

No basic number or numbers are suggested by the data presented in this table. This is apparently a feature shared with Scilla (section Eusoilla). Darlington and Wylie (1955) reported basic numbers of 4, 6, 7, 8, 9, 10 and 11 from Scilla (Euscilla). Similarly, the South African genus Lachenalia, which resembles Scilla (Ledebouria) to some extent in vegetative and floral characters, is reported as having basic numbers of 7, 8, 11 and 13. Drimiopsis, which is also a related genus

Haploid number	Number of specimens
6	1
9	1
10	8
11	2
12	2
13	7
14	1
15	6
16	1
17	2
18	1
20	1
22	2
23	2 and one with 2n=45
27	1
29	1
30	2
46	1

TABLE 15

Number of specimens for which chromosome numbers have been recorded.

occurring in southern Africa, has not been studied in detail, but does appear (see section 2.6.3.4) to have similar chromosome features. On the other hand, Muscari, which is a northern hemisphere member of the Scilleae, appears to be very consistent, with a bsaic number of 9 indicated for all fifteen species recorded by Darlington and Wylie.

Whether this great variability of number in Scilla (section Ledebouria) is as a result of the frequent occurrence of B-chromosomes or whether the chromosomes tend to fragment and perhaps rejoin has not been established. There is, however, very little evidence of abnormalities in pairing in meiosis. An examination of the idiograms shows that the sum of the lengths of the chromosomes in a complement is not inversely proportional to the number of chromosomes as might occur if the greater numbers were produced by fragmentation.

Diagrams of leaf shape and size are included to enable a correlation to be made between leaf size or shape and chromosomal number. The sample examined does not suggest that there is any relationship between these features of the plant such as is usually the case with polyploidy. However, this does not necessarily rule out the possibility of polyploidy's playing a major role in the origin of many of the number differences.

The lack of chromosomal number consistancy in the species of Scilla (Ledebouria)examined, and the lack of obvious basic numbers or simple polyploid series, reduces the potential value of these studies in determining relationships or evolutionary sequences within the genus or between it and other genera. There appears on the data so far available to be no correlation, either, between numbers of chromosomes and distribution.

The identification of individual chromosomes or of arms of individual chromosomes is probably not possible in meiotic chromosomes because of the extreme contraction and difficulty in recognising centromeres and satellites.

For this reason the idiograms should only be taken as approximations. Further discrepancies in comparing different complements are caused by not having the material all at the same stage of division, despite every effort to ensure that data employed was as similar as possible. The use of mitotic chromosomes, in which contraction is generally not so great, is preferable for the study of both morphology and size.

The behaviour of the chromosomes is to some extent parallelled in the problems of defining the species of this group. Both morphological and cytological characters appear to vary almost continuously without producing well-defined groupings. It is possible that the chromosomal variation is linked with a reduced fertility. Seeds are set in a very small percentage (perhaps about 1%) of flowers. Studies of embryo sac development are needed to establish whether or not development follows on fertilization in the few fertile flowers. Hand pollination (both self and crossed) have failed to produce increased numbers of seeds.

2.7.3.2 The mitotic chromosomes of *Scilla* sp nov (= *Ledebouria scabrida*)

Roots from bulbs (*Tölken* s.n., Sturmveld, Gobabis, South West Africa; 2119) growing in the soil in cultivation in Grahamstown were used.

A diploid number of 40 is based on accurate counts of three cells (fig. 263).

The largest chromosomes were 7,0 µm long. The longest meiotic chromosomes recorded for this section were 6,2 µm, which is appreciably shorter. The longest chromosomes of the majority of samples of section *Ledebouria* lay between 3,0 and 4,5 µm. This difference in size is, however, almost certainly entirely due to the difference to be expected between mitotic and meiotic chromosomes and cannot be accorded any taxonomic significance.

2.7.3.3 The mitotic chromosomes of *Scilla* (section *Euscilla*) including *Schizocarphus*.

2.7.3.3.1 Introduction

De Wet (1957) examined the chromosomes of *Scilla firmifolia* and *S. natalensis* and of three specimens of *S.* (*Schizocarphus*) *nervosus* (identified as one specimen of *Schizocarphus gerrardii* and two specimens of *S. nervosus*). No other work has been published on the South African species, but there are many studies on species from North Africa, Europe and Asia. These indicate great variety in chromosome number, with basic numbers of 4, 6, 7, 8, 9, 10 and 11 being reported. Among the more recent of these papers there is a series by Giménez-Martin (1959a, b, c). He worked on sixteen species, with diploid numbers of 12, 16, 20, 22, 24 and 30. No adequate explanation for the variability in number has been offerred, although there have been a few reports of B-chromosomes (cf. Battaglia, 1964).

2.7.3.3.2 Materials and methods.

In the present study specimens of S. nervosa, S. firmifolia and S. plumbea were examined.

Germinating seeds were used to provide radicle, cotyledon and plumule material of S. nervosa and S. firmifolia. Roots formed by mature bulbs were used for S. plumbea.

Colchicine was used in an attempt to shorten the chromosomes, but the effect was not significant. Most slides were discarded after examination. But one slide of S. plumbea was made permanent by inverting the slide in absolute ethyl alcohol until the coverslip dropped off and then mounting in euparal.

2.7.3.3.3 Results

Table 16 summarises the information obtained from the study and figures 264-271 illustrate the morphology and size of the chromosomes. Table 17 summarises previous work on the South African species of this section.

Centromeres and satellites were not detected. Idiograms are, therefore, not based on definite identifications of individual chromosomes as only the measurements (based on camera-lucida drawings) could be

Specimen	Fig. nos	Diploid number	Number of cells counted
Scilla firmifolia			
Jessop s.n., ex hort., Rhodes University	264-266	18	10
Scilla nervosa			
Jessop 883, Rabbits Wood, Grahamstown (3326)	267-269	42	4
Scilla plumbea			
Jessop s.n., Bains Kloof, Worcester (3319)	270-271	14	8

TABLE 16

Chromosome data for species of Scilla (Euscilla) examined during the present project.

Species	Number	Reference
Scilla firmifolia	2N = 18	De Wet (1957)
Scilla nervosa	2N = 28, 28 and 56	De Wet (1957)
Scilla natalensis	2N = 32	De Wet (1957)
Scilla natalensis	2N = 40	Giménez-Martin (1959d)

TABLE 17

Previously published data on the chromosome numbers of Scilla (Euscilla).

used in placing the chromosomes of each complement in the correct sequence. Note that because of the large size of the longest chromosomes of S. plumbea it was not practical to use the same scale for the idiograms of the Scilla (Euscilla) chromosomes as for the other groups discussed.

2.7.3.3.4 Discussion

The idiograms are of a similar shape to those for meiotic chromosomes of the other groups studied. The size of the chromosomes tends, especially in S. plumbea, to be larger than in section Ledebouria but, as mitotic instead of meiotic chromosomes were used, valid comparison is difficult.

Again, considering also the published data, there is no evidence for a bssic number for the genus. S. nervosa is the only South African species of Scilla (Euscilla) for which there is more than two counts. These are 2N = 28, 28, 42 and 56 (additional count of 40 was determined by Jong, 1961, but remains unpublished) and suggest a very considerable degree of instability in the diploid number. An even greater range of numbers has been reported for certain European species, notably S. peruviana.

The remarkable size of the largest chromosomes of S. plumbea (over 0,03 mm) is worth investigation. Only one plant was available for this study, but similar chromosomes in a second specimen would be of interest. It is not known if any allied genera have any examples of chromosomes of this order of size. So far as is known no other species of Scilla has chromosomes of similar size and it is possible that this cytological feature reflects the genetic separation of this species whose geographical distribution also separates it to a very marked extent from other species of Scilla. Other species of Scilla generally do not have chromosomes as much as one third of this length.

2.7.3.4 The meiotic chromosomes of Drimiopsis

2.7.3.4.1 Introduction

Four papers dealing with Drimiopsis chromosomes have been published. Sato (1942) recorded 2N= 64 for D. maculata, while Fernandes and Neves (1962) reported 2N = 60 for the same species. Diploid numbers of 20 have been reported for D. burkei (sub D. crenata) and D. maxima (sub D. saundersiae) by De Wet (1957). Matsuura and Suto (1935) found 2N = 80 in D. botryoides, which is a tropical African species.

2.7.3.4.2 Results

Table 18 summarises the data obtained in the present study.

Two specimens of D. maculata were examined by the present author. In both, laggards (fig. 275) and micronuclei (fig. 276) were observed. For Strey 9031 a haploid number of 15 was obtained. The average length of the largest chromosome in each of five cells was 7,8 µm and the average for the shortest in each of these cells was 2,5 µm. The standard deviations are 0,91 and 0,38 respectively. For Jacot Guillarmod s.n. it was not possible to determine a number, probably because irregularities in meiotic divisions produced varying numbers, but a haploid number of approximately 26 was estimated.

Specimen	Fig. nos	Haploid number	Number of cells counted
Drimiopsis maculata Strey 9031, GRA - Manteka Lusikisiki (3129)	272-274	15	5
Drimiopsis maculata Jacot Guillarmod s.n., GRA - Port St Johns (3129)	275-276	c.26	-
Drimiopsis burkei Jessop s.n., GRA - 30 miles S. of Louis Trichardt	277	10	10

TABLE 18

Chromosome data for Drimiopsis.

2.7.3.4.3 Discussion

There appears, as in Scilla (Ledebouria), to be little significance in chromosome numbers. A basic number of 5 (or possibly 10) for the genus is suggested, but it does not seem likely that chromosome numbers would be any more relevant to the separation of taxa than in Scilla (Ledebouria).

The occurrence of abnormalities in Drimiopsis may indicate reproductive abnormalities and may be related to the difficulties in defining subgeneric taxa in the genus. The range of size of the chromosomes and the size of the largest are greater than in Scilla (Ledebouria), as Scilla (Ledebouria) meiotic chromosomes rarely exceed 5-6 µm.

2.7.3.5 The meiotic chromosomes of Drimia, Urginea and Thuranthos

2.7.3.5.1 Introduction

The majority of reports for Drimia, Urginea and Thuranthos indicate a basic number of 5. In Urginea maritima, disregarding B-chromosomes, diploid numbers form a polyploid series: 10, 20, 30 and 40 having been reported.

Table 19 summarises the published work on the chromosomes of the South African members of this group.

2.7.3.5.2 results

Pollen mother cells were used to determine the haploid chromosome numbers in two specimens of D. anomala from the

Name	Reference	2N
Drimia elata	De Wet (1957)	18
Drimia haworthioides	De Wet (1957)	20
Thuranthos macranthum	De Wet (1957)	20
Urginea altissima	De Wet (1957)	20
Urginea altissima	Miege (1960)	20
Urginea burkei	De Wet (1957)	20, 20
Urginea lydenburgensis	De Wet (1957)	32
Urginea depressa	De Wet (1957)	40
Urginea epigea	De Wet (1957)	32
Urginea multisetosa	De Wet (1957)	20
Urginea pretoriensis	De Wet (1957)	20
Urginea rubella	De Wet (1957)	42
Urginea tenella	De Wet (1957)	20
Urginea indica	Raghavan (1935)	20
Urginea indica	Battaglia (1957)	20

TABLE 19

Summary of published data on the chromosomes of *Drimia*, *Urginea* and *Thuranthos*.

3326 (Grahamstown) degree square. The numbers were 17 from Graskop near Fort Brown (fig. 279) and 8 from Kaffir Drift (fig. 278). A considerable difference in size was also found; the average for the largest in each complement being 7,8 and 4,9 µm respectively, and for the shortest 2,6 and 1,2 µm.

2.7.4 Application of cytological data to the definition of taxa above the rank of species

2.7.4.1 Introduction

The first data published on the chromosomes of a South African member of the Liliaceae was on Galtonia candicans in 1924. There are now over 600 published counts, dealing with fewer than 350 species. This amounts to only about one third of all species currently recognised, estimated by the present author (checklist to be published by the Botanical Research Institute, Pretoria) at about 1000. The distribution of these counts by tribe is very unequal. The Aloineae have counts for about 150 species - or a third of the total species in the tribe. The Kniphofieae have 22 (nearly half) and the Asphodeleae 17 (a tenth) with none at all for Anthericum or Trachyandra, and the Massonieae none. This absence of data for major genera reduces greatly the value of the present information in determining tribal limits. Nevertheless, it is worth examining the numbers available in relation to possible groupings of the genera.

2.7.4.2 Family level

Cytological data as indicators of affinities at the family level will be dealt with first as this may help to evaluate the available data at lower taxonomic levels. It is to be hoped that it may become possible to determine the most primitive number in the Liliaceae, if this is in fact a monophyletic family.

One of the most-discussed problems is the question of whether to place the Allieae in the Liliaceae or the Amaryllidaceae. Most South African publications have retained these genera in the Liliaceae, but the "Prodromus einer Flora von Südwestafrika" (Sölch, et al, 1969) transferred them to the Amaryllidaceae. Airy-Shaw (Willis, 1966) recognises a distinct family, the Alliaceae, but states that it lies in an intermediate position between the Amaryllidaceae and the Liliaceae. Among attempts at solving the problem, Maia (1941) studied pollen grains, Anderson (1940) studied floral anatomy and Cheadle (1942) also worked on the anatomy. These three all favoured placing them in the Amaryllidaceae. Bose (1962) has reviewed the cytological data, although he concentrated on a study of the Amaryllidaceae without apparently examining the data necessary for a comparison with the Liliaceae. Among the aspects he took into consideration were the supposed methods of evolution of existing chromosome numbers. In Agapanthus (Allieae) the somatic number is 30 or 32. These may be derived from ancestors with N = 15 or 16 or even with x = 6 or 8. ('x' is the basic haploid number for a group, from which it is believed all others are derived by polyploidy and aneuploidy.) Without adequate data on meiotic pairing patterns, which might provide information on the history of the present complements, these numbers are pure speculation based on the assumption that existing numbers were produced by the formation of simple polyploid series -

which is not at all certain. *Tulbaghia* almost certainly has a basic number of 6. Twelve South African species have been recorded with 2N = 12 and there have been a few isolated records of 24 and 36 - which are likely to represent straight polyploid series. A single figure of 2N = 14 may represent an inaccurate observation or an aneuploid produced by fragmentation or an abnormal division. It is believed that the primitive chromosome number for *Allium* is 7. There is a euploid series based on this and also on N = 8. The derivation of N = 8 is believed to have taken place by the loss of an arm of a V-shaped chromosome according to Bose. However, modern opinion is (e.g. Stebbins, 1971) that fragmentation of a chromosome in this way, leading as it must to acentric fragments, will rarely if ever produce additional permanent chromosomes. In fact there is a tendency to define aneuploidy as the loss or gain of one or more centromeres rather than of chromosomes (e.g. Solbrig, 1970). If it is more frequent for chromosomes to be entirely lost or for the major part of one to be joined to another with the loss of the remaining fragment, then it must be regarded as being more likely that the basic number for *Allium* is 8 - as with *Agapanthus*. The relationship between these two genera and *Tulbaghia* is less evident. *Nothoscordum* (morphologically similar to *Allium*) has N = 8, but also N = 9.

In other genera of the Amaryllidaceae 8 is not a common basic number. Although lower numbers occur as well, N = 9, 10, 11 and 12 are common. The number of rods and V chromosomes are not recorded by Bose, but these two main types apparently occur throughout the family.

A second phenomenon common to the Amaryllidaceae is the presence of B-chromosomes. In these plants they take the form of very small fragments of variable number in the nuclei.

While Bose has shown no reason for separating Allium, Agapanthus and Tulbaghia from the Amaryllidaceae, he did not deal adequately with their affinity with the more complex Liliaceae at all. No further work on defining the Liliaceae in terms of its cytology has been found.

2.7.4.3 Tribal level

The numbers of chromosomes in each of the tribes (as defined by Hutchinson, 1959) will now be examined to try to determine the likelihood that these will have any bearing on the acceptance or rejection of any of his taxa. Table 20 summarises the chromosome numbers reported for the genera of Liliaceae. Only South African species have been included in the table, although non-South African data is included in the discussions. All available sources have been consulted in drawing up the South African lists, but additional information on other species is taken entirely from Darlington (1955).

Taxa	Number of species	2N
Asphodeleae		
Bulbine	10	14
Bulbinella	2	14
Chlorophytum capense	1	14 & 28
C. comosum	1	28
C. krookianum	1	14 & 46
C. sternbergianum	1	28 & 32
Trachyandra giffenii (Jessop ined.)	1	14
Kniphofieae		
Kniphofia	22	12
Aloineae		
Aloe	55	14
A. ciliaris	1	35 & 42
Chamaealoe	1	14
Astroloba	4	14
A. bicarinata	1	21
A. pentagona	1	28
Poellnitzia	1	14
Haworthia	30	14
	4	28
	2	35

TABLE 20

Published chromosome numbers for South African Liliaceae

Haworthia contd	3	42
	3	14 & 28
H. glauca	1	28 & 29
H. greenii	1	28 & 30
H. herrei	1	14 & 42
H. reinwardtii	1	14, 21, 26, 28 and 42
H. sampiana	1	35 & 36
H. tesselata	1	14, 28, 35, 40, 42, 56, c.58, c.61 & 63
Gasteria	36	14
	3	14 & 28
Uvularieae		
Littonia	1	18 & 22
Gloriosa	1	22, 88 & 90
Anguillarieae		
Dipidax	1	20
Asparageae		
Asparagus	7	20
	2	40
	1	80
A. setaceus	1	20 & 40
A. densiflorus	1	20 & 60

TABLE 20 (continued)

Scilleae		
Albuca	1	16
	4	18
	1	20
	1	18, 20 & 36
	1	18 & 20
	1	20 & 40
Dipcadi	1	12
	1	18
	1	38
Drimia	1	16 & 34
	1	50
	3	60
	1	30 & 32
	2	30 & 60
Drimiopsis	2	20
	1	60 & 64
Eucomis	1	20
	1	50
	1	50
	3	60
	1	30 & 32
	2	30 & 60
Galtonia	3	16

TABLE 20 (continued)

<u>Scilleae</u> contd		
<u>Lachenalia</u>	2	14
	8	16
	1	14 & 16
	1	28 & 56
	1	18 & 28
	1	14 & 56
	1	16 & 17
	1	14 & 21
	1	21, 22, 24 & 26
<u>Scilla</u> (<u>Ledebouria</u>)	1	12
	1	24
	1	26
	1	54
	1	c.92
	1	10, 26, 30, 32 & 54
	1	20, 22, 34 & 60
	1	18, 20, 22, 24, 26, 30, 32, 34, 44
	1	26 & 30
	1	20, 26, 28, 30, 36, c.44 & c.60
<u>Ornithogalum</u>	14	12
	1	12 & 16
	4	10

<u>TABLE 20</u> (continued)

Ornithogalum contd	2	10 & 12
	3	20
	1	10, 12 & 32
	1	18 & 54
	4	12 & 14
	1	24
	1	12 & 24
	1	36
	1	12 & 18
	1	6, 12 & 50
Pseudogaltonia	1	24
Rhadamanthus	1	20
Scilla (*Euscilla*)	1	18
	1	32 & 40
	1	28, 42 & 56
	1	14
Thuranthos	1	20
Urginea	5	20
	2	32
	1	40
	1	42
Veltheimia	2	40
Bowieae		
Bowiea	1	20
Schizobasis	1	20
Eriospermum	1	24
Iphigenieae		
Androcymbium	1	16
	1	18

TABLE 20 (concluded)

Tribe Asphodeleae

All species counted appear to have a basic number of 7, except that in each of two species of Chlorophytum there are both counts of multiples of 7 and anomalous numbers as well. It is also of interest that polyploidy has not been recorded in two genera for which there is data but that diploid numbers are not as common as higher ploids in Chlorophytum.

Basic numbers of from 8 to 13 have been recorded for non-South African genera, including 7 and 8 for Anthericum (for which no South African species have been counted), and 7 and 8 for non-South African species of Chlorophytum. In most non-South African genera the commonest basic number is, however, also 7.

Tribe Kniphofieae

For both South African and non-South African species of the single genus (Kniphofia) the basic number is 6. In only one species (from Uganda) has polyploidy been reported.

Tribe Aloineae

The basic number is 7, with polyploids and aneuploids rather infrequent. Polyploidy does not appear to have been recorded for any non-South African species.

Tribe Uvularieae

For the South African species the most likely basic number is 11, but there is a possibility of 9 in Littonia. For non-South African species (of Uvularia and Oakesiella) basic numbers of 7 and 8 have been suggested. These are both North American genera.

Tribe Anguillarieae

Basic numbers of 5 (or 10) and 11 are suggested for the South African material. *Anguillaria* (from Australia) is considered to have a basic number of 10. *Baeometra* (2N = 22) might repay more careful investigation.

Tribe Asparageae

A basic number of 10 (or perhaps 5) is indicated. This number is also constant for non-South African species of the only genus.

Tribe Scilleae

Basic numbers for this tribe are either very variable or indeterminate. Basic numbers of 10 (or 5) occur in species of *Drimiopsis*, *Eucomis*, *Rhadamanthus*, *Thuranthos*, *Urginea*, *Veltheimia* and less frequently in *Albuca*, *Scilla* (*Ledebouria*), *Drimia*, *Ornithogalum* and possibly *Scilla* (*Euscilla*). Numbers of 6 (or 12) sometimes occur in *Dipcadi*, *Scilla* (*Ledebouria*), *Ornithogalum* and *Pseudogaltonia*. A basic number of 9 occurs in *Albuca* and *Drimia*, of 8 in *Galtonia*, *Lachenalia* and possibly *Drimia*, *Urginea* and *Scilla* (*Euscilla*); and of 7, possibly in *Lachenalia* and *Scilla* (*Euscilla*).

Other infrequent basic numbers might also be determined.

It does, therefore, appear that no useful purpose can be achieved by discussing any further the determination of a basic number for the tribe. Non-South African groups show a similar range in chromosome numbers.

Tribe Bowieae

There appear to be two distinct basic numbers - 10 (or possibly 5) in Bowiea and Schizobasis, and 12 (or possibly 6) in Eriospermum.

Tribe Iphigenieae

With only two records it is difficult to assign a basic number but 8 and/or 9 are possible.

Tribe Massonieae

No species have been examined.

What sort of groupings do these numbers suggest in isolation from other characters?

A basic number of 7 appears to be a very consistent feature of both the Asphodeleae and Aloineae and a possibly basic number for Lachenalia. This tends to confirm the grouping of Chamaealoe, Astroloba, Gasteria, Poellnitzia, Haworthia and Aloe together and the separation of Kniphofia ($x = 6$), which to some extent appears on morphological grounds to be fairly close to Aloe. At the same time it suggests the validity of the grouping of the rather diverse members of the Asphodeleae together. It is desirable to investigate other possible approaches to try to elucidate possible affinities between the Asphodeleae and the Aloineae.

The position of Lachenalia will be discussed later.

A basic number of 10 (or 5) also appears to be consistent in one tribe - the Asparageae. This tribe has not been regarded as particularly closely allied to any others in the South African Liliaceae. Cytological, however, there appears to be a possible association with Bowiea and Schizobasis (Bowieae) and with several of the Scilleae - notably Drimiopsis, Eucomis, Rhadamanthus, Thuranthos, Urginea and Veltheimia. This alliance appears improbable, but further information is discussed later, in the sections on phylogeny, which makes this an extremely important idea.

Of the remaining tribes, the Scilleae is the only one for which there is sufficient data to justify further discussion. Beside the group with a basic number of 10 (or 5) there are several groups which could be recognised on the basis of their numbers. This suggests that either:
1) the Scilleae are, or have been, cytologically unstable;
2) or the Scilleae have a polyphyletic origin.

If the latter is the case, it is possible that some, or all, of the genera with a basic number of 10 (or 5) may be allied to the Bowiea-Asparagus group. If these genera with a basic number of 10 (or 5) are removed from the Scilleae, Drimia would have to be associated with them on morphological grounds although a single count of 20 does not provide cytological support for this arrangement. On the other hand, Drimiopsis, Eucomis and Veltheimia cannot, on morphological grounds, be regarded as closer to the Urginea group than to other members of the Scilleae.

In general, chromosome numbers support or at least do not seriously conflict with the existing tribal arrangement, However, in the Scilleae, owing to the great range of basic numbers within most of the genera, little correlation between chromosome numbers and tribes has been found.

2.7.4.4 Generic level

Distinguishing genera has not been attempted to any extent in the South African Liliaceae. De Wet (1957) published the most extensive work, correlating numbers with morphological data in relation to generic limits. At that time *Schizocarphus* and *Scilla* were regarded as distinct genera of the Scilleae. On the basis of measurements of his drawings of *Scilla* chromosomes, and in the absence of measurements in the paper, the conclusion was reached that there was a distinct possibility that one could distinguish these two genera on the length of the chromosomes. *Schizocarphus* chromosomes appeared to range in length between 1,2 and 2,5 µm; while *Scilla* chromosomes ranged between 1,2 and 4,3 µm. On repeating this work on specimens from other localities it was found that the *Scilla* and *Schizocarphus* chromosomes measured approximately 2-6 µm. De Wet's original diagrams were examined and it was found that they were reduced in publication and incorrectly labelled. The corrected measurement, moreover, compared closely with measurements recorded for *Scilla* in the northern hemisphere and suggested that the South African species cannot be distinguished on overall chromosome length.

Although De Wet did not comment on this point, his drawings of *Albuca* and *Ornithogalum* chromosomes show considerable similarity in size. He did, however, point out a correlation between his counts and the subdivision of *Albuca* into subgenera. He found that *Eualbuca* had a diploid number of 18 and *Falconera* a diploid number of 20 or 40. Further data is now available which contradicts this conclusion. Two species have been investigated in which the diploid number is sometimes 18 and sometimes 20, and *A. fastigiata* (*Falconera*) has 18. It would be of interest to follow this up as, if there is any tendency for *Falconera* to have 20 more frequently, it might point to this being a more primitive number. *Falconera* shows morphological characters closer to those of *Ornithogalum* than does *Eualbuca*. Again the suggestion is that a plant loses a pair of chromosomes more readily than it gains a pair - but this does not imply a necessary loss of a significant amount of genetic material as translocation may occur. In *Ornithogalum*, De Wet stressed the frequency of 2N = 12 and implied that the three species he looked at with 2N = 10, 20 or 50 differ from other members of the genus morphologically as well as cytologically. Several other species have been found to have a basic number of 10 (or 5), but Pienaar (1963) and Roos and Pienaar (1966) found that in two of the three on which De Wet worked 2N = 12 also occurred. One is tempted to suggest that the species of *Ornithogalum* with 2N = 20 might belong to a group linking the genus with *Albuca*. This does not, however, appear to be the case. In fact the occurrence, in four species, of numbers based on both 5 and 6 suggests that loss of chromosomes has occurred several times within the genus Ornithogalum. Pienaar has worked out the details of the loss of one chromosome pair in O. lacteum. Pienaar worked on mitotic chromosomes of this species and was able to measure overall lengths, lengths of arms, and presence or absence of a satellite (SAT-chromosome). He found that the most useful characteristics were in fact the ratio of length of a particular chromosome to the total length for the whole complement and the ratio of the lengths of the two arms. In O. lacteum there were 12 chromosomes in eight populations from the western Cape to Grahamstown and 10 in one from Sutherland. He found that in the Sutherland plants two pairs of chromosomes present in all the other populations were missing but instead the SAT-chromosome was much larger than in the other populations. Using his accurate measurements he showed that it was chromosomes II and III that were missing because they had recombined to form the new one in the Sutherland plant. II had lost most of its short arm and III had lost its shorter arm and its centromere. The translocation of one arm to replace the short arm of II at the same time may have produced a very small chromosome possessing most of the material formerly present in the two short arms. This fragment had, however, become lost. These conclusions agree with the suggestion that aneuploidy resulting from a loss of a chromosome may involve loss of a centromere, but not of the majority of the genetic material.

PART 3

PHYLOGENY
OF THE FRUTESCENT HABIT

3.1 Introduction

Few genera in the South African Liliaceae have aerial vegetative stems. Of these, two - Schizobasis and Bowiea - have bulbs. These bulbous genera are not generally placed with the Scilleae. Hutchinson (1959) regarded them as being allied to Eriospermum - a tuberous genus of plants which produce well-developed photosynthetic leaves and do not appear to share any important features with Schizobasis and Bowiea. Hutchinson, in his key to the tribes of the Liliaceae, stated for the Bowieae: "Leaves soon disappearing; inflorescence scandent". Neither of these features is true of Eriospermum and the latter is only partly true of Schizobasis.

3.2 Affinities of Schizobasis and Bowiea

It is considered that the two bulbous genera with aerial vegetative axis should be placed with the Scilleae. This decision is based on the following points:-

1) The bulb is of the normal type found in the Scilleae. It resembles very closely that found in Urginea and Drimia, even to the absence of starch from the bulb scales, unlike probably all other members of the Scilleae.
2) In the seedling stage they produce strap-shaped leaves

similar to those in both the *Urginea-Drimia* group and in *Ornithogalum*.

3) The bracts are spurred as in *Urginea*, *Drimia*, *Litanthus*, *Thuranthos* and *Rhadamanthus* - all members of the Scilleae. This characteristic is known from only one other genus in the Liliaceae, namely *Asparagus* (Asparageae).
4) The flowers are similar to those of several of the Scilleae, for example *Ornithogalum* and, more especially, *Urginea*.
5) The flowers are marscecent as in the *Urginea-Drimia* group.
6) The seeds are flattened and, as in the *Urginea-Drimia* group, the testa is loosely associated with the rest of the seed (principally endosperm). This characteristic seed type is not known in any other group of the Liliaceae.

In view of the above considerations there is a very high probabibility that *Schizobasis* and *Bowiea* are very closely related to *Urginea*, *Drimia* and certain other lesser genera of the Scilleae. It is considered that the *Schizobasis-Bowiea* group should only be separated from the Scilleae if *Urginea* and *Drimia* are likewise separated from the Scilleae.

It is suggested that evolution of these genera (i.e. *Schizobasis* and *Bowiea*) proceeded from a member of the *Urginea-Drimia* group by the development of a persistent branched inflorescence, taking over the photosynthetic function of the vegetative leaves, which became reduced to perform a purely storage function as bulb scales (fig. 280).

3.3 Affinities of other frutescent Liliaceae

An interesting point arises out of the reference to Asparagus as being the only other genus with spurred bracts. Arber (1925) believed that the spur represented the main axis of the leaf in Asparagus, with the adaxial structure (more often regarded as the main part of the leaf axis by morphologists) representing a structure homologous with the ligule of grasses. The suggestion of a link between the Liliaceae and the Gramineae is taken by the present author to infer that this is a primitive character. It is, therefore, of particular interest to note its presence in members of the bulbous Liliaceae, especially as the Urginea-Drimia group also appears to possess species with exceptionally primitive vegetative leaves (page 24).

The question must be asked as to whether the presence of spurred bracts in Asparagus and the frutescent bulbous Liliaceae is a result of convergent evolution or whether it indicates a relationship. The answer to this question may depend to some extent on the nature of the primitive Liliaceae - or even of the earliest Monocotyledoneae. There appear to be two opposing schools of thought on this problem.

Tomlinson (1970) wrote: "Even though one cannot derive existing monocotyledons from the Palmae as we know the family today, it is clearly quite reasonable to look upon ancestral monocotyledons as palm-like plants .... they (Palmae) certainly should not be accorded derivative status as in all modern systems of angiosperm classification".

Cronquist (1968) and probably the majority of phylogenists (e.g. Hutchinson, 1959) disagree and believe that monocotyledons derive from herbaceous, possibly aquatic, forms. Hutchinson also regarded the ancestral Liliaceae as herbaceous.

The next question which arises is whether the Bowiea-Schizobasis habit is a primitive one, whether derived from a more robust aerial stem, or whether derived from a more herbaceous form. The great majority of the members of the Liliaceae are perennial herbs, most frequently with subterranean perennating stems or bulbs. Substantial aerial stems occur in a few members, but especially Dracaena (if this is regarded as a member of the Liliaceae), Aloe and Asparagus. Aloe and Asparagus appear to differ from one another in at least one very important morphological respect. Aloe produces a single stem, although there may be lateral branches, and the leaves are formed in the rosette arrangement characteristic of the majority of the Liliaceae. Asparagus aerial stems, although sometimes very well developed and woody (e.g. A. buchananii), may last a few years but are eventually replaced by further aerial stems produced by branching of the subterranean rhizome, and there are no foliage leaves. The aerial stems of *Asparagus* possess comparatively long internodes and there is no tendency to rosette formation. However, the rhizome, although possessing only brown or more or less colourless scale-leaves, does possess the short internodes necessary for the formation of a rosette.

It is suggested that the rosette habit is a primitive one from which the majority of Liliaceae (not perhaps such tribes as the Uvularieae) can be derived. It is suggested that the aerial stem of *Asparagus* cannot be readily derived from the rosette-forming type and that a different origin must be sought for it. The basal rhizomatous part of the axis may, on the other hand, have a common origin with the axes of most Liliaceae.

Bowiea and *Schizobasis* may offer an important clue to the origin of the frutescent habit in *Asparagus*. If the rosette form is a primitive one, it is likely that *Bowiea* and *Schizobasis* are derived from the *Urginea-Drimia* group rather than vice versa. This involves the rather (apparently) simple transitional stages described above. In both genera axial, rather than foliar, elements provide for photosynthesis by the presence of chlorophyll in the fertile branches of the inflorescence, but also in some cases in sterile branches formed by the abortion of flowers. There are, therefore, sterile photosynthetic organs (modified pedicels) present. These structures may well be the forerunners of the structures generally regarded as cladodes in *Asparagus*. This topic was reviewed by Jessop (1966).

The suggestion is made, therefore, that in *Asparagus*, as in *Bowiea* and *Schizobasis*, the aerial axis must be regarded as a development from the inflorescence and the photosynthetic organs as modified pedicels.

If this proposal is accepted, one must return to the question of the spurred bracts present in both groups. Does this imply a common ancestor for both groups, or is the similarity in habit a product of parallel evolution? The flowers are essentially similar. The flowers of *Asparagus asparagoides* and of *Drimia* (sensu stricto), for example, are separable mainly on the degree of fusion of the perianth segments, which is not regarded by the present author as a taxonomically reliable characteristic in this group. However, the fruit of all species of the *Urginea-Drimia* group (and also of *Bowiea* and *Schizobasis*) is a capsule, while the fruit of the great majority of *Asparagus* species is a berry. A few species of *Asparagus* (e.g. *A. exuvialis*) do have a dry fruit although lacking the dehiscence arrangement of the more specialised capsule. And the large rounded *Asparagus* seed, rich in endosperm, is quite unlike that of the other two groups, although it is possible that the differences are, despite the very different appearance, a matter of degree, and may not reflect essential differences. However, Huber (1969), in his very comprehensive survey of the seeds of the Liliiflorae, found no evidence for associating these two groups, or even for separating the Urginea-Drimia group from the other members of the Scilleae.

There is also cytological evidence in favour of a close relationship. As mentioned (page 108) the basic number of 10 (or 5) is common to the Urginea-Drimia group, Bowiea and Schizobasis, and Asparagus. It is difficult to evaluate the importance of this aspect, but it can be taken as evidence for, rather than against, relationship.

3.4 Conclusions

The aerial stems of Asparagus, Bowiea and Schizobasis were derived, by the abortion of flowers, from inflorescences.

The axial structure homologous to the vegetative axis of most Liliaceae is restricted in Bowiea and Schizobasis to the bulb axis and in Asparagus to the rhizome.

The photosynthetic organs of Asparagus (cladodes) are modified pedicels.

The spurred bracts and basic chromosome number suggest a common origin for Bowiea, Schizobasis and Asparagus from the Urginea-Drimia group. But this point cannot be regarded as more than a suggestion in the absence of further information.

If the above points are accepted, the bulb must be regarded as rather an early development in the Liliaceae.

PART 4

GENERIC CONCEPTS

4.1 Introduction

The South African bulbous Liliaceae were placed in three tribes by Hutchinson (1959). These tribes were distinguished as follows:-

A. Flowers not in heads or umbel-like heads:
  B. Flowers in unbranched racemes or spikes .. . Scilleae
  BB. Flowers in panicles .. .. Bowieae
AA. Flowers in umbel-like heads .. .. Massonieae

Within the Massonieae Hutchinson recognised only Massonia and Daubenya (both endemic to South Africa). Phillips (1951) did not deal with tribes, but did link Massonia, Polyxena, Neobakeria, Whiteheadia, Neopatersonia, Androsiphon and Amphisiphon into a single group on the basis of their "connate stamens". These additional genera were placed by Hutchinson in the Scilleae. Unfortunately, Phillips' characteristic linking these genera was faulty as Polyxena does not have connate filaments and he overlooked the fact that Eucomis, Pseudogaltonia and several species of Scilla (in the sense in which he used the name) also have connate filaments. Florally Neobakeria is indistinguishable from Massonia and most of the genera linked by Phillips (including Polyxena) do have a very similar bulb and leaf morphology and much floral similarity. In addition, Hyacinthus (the Cape species) has flowers identical to those of *Polyxena* and differing from that genus only in having a rather more corymbose inflorescence with fewer flowers, and in having a larger number of narrower leaves. It is proposed to deal with this group, that is Phillips' group and *Daubenya* and *Hyacinthus*, under the general heading "*Massonia* group" in the following discussion.

In the Bowieae, Hutchinson placed *Schizobasis*, *Bowiea* and *Eriospermum*. He separated them as follows:-

A. Seeds glabrous: flowering stem much branched:
  B. Bulb tuber-like: panicle scandent .. .. .. *Bowiea*
  BB. Bulb tunicated: panicle erect .. .. . *Schizobasis*
AA. Seeds covered with long hairs: flowering stem usually simple, with long pedicels: leaves usually solitary .. .. *Eriospermum*

It is not clear what Hutchinson meant by a "tuber-like bulb". *Bowiea* has a bulb identical in all essential features with that of *Schizobasis*, although it is larger. The rootstock of *Eriospermum*, which he does not mention, is, in fact, a tuber. In view of the presence of a tuber, *Eriospermum* will not be dealt with in this work, but it is also very doubtful if it is closely related to any member of the bulbous Liliaceae in view of the pilose seeds and the characteristic leaf.

Bowiea and *Schizobasis* are unlike any other members of the bulbous Liliaceae in having a branched aerial stem and no foliage leaves in the mature plant. They are readily separable as Bowiea is a succulent climber and Schizobasis a more or less wiry, usually erect plant. Their affinities have been discussed in the previous section.

The Scilleae contain the remainder of the South African bulbous Liliaceae (except a few species of Aloe and Chortolirion which is going to be reduced to synonymy in Haworthia by Obermeyer - personal communication). In addition to those genera removed in the present work to the Massonia group Hutchinson recognised:- Eucomis, Scilla, Brachyscypha, Ornithogalum, Drimiopsis, Albuca, Urginea, Lachenalia, Veltheimia, Dipcadi, Pseudogaltonia, Galtonia, Drimia, Urgineopsis, Rhadamanthus,and Litanthus. Brachyscypha is a group somewhat intermediate between Lachenalia and Polyxena. Baker (1896/7) placed it as a subgenus in the former, with a single species - L. pusilla. This species does have a slightly zygomorphic flower and this character is regarded by Barker (personal communication) as sufficient to place it in Lachenalia. As Barker is working on a monograph of Lachenalia the position of Brachyscypha has not been pursued. Phillips recognised all the above genera, except Brachyscypha, but separated Thuranthos from Urginea.

Table 21 indicates the characters considered by the present author to be particularly important in discussing generic concepts. In most cases only a small number of samples of each genus was examined. The term "tubular scales" refers to those bulbs where each scale is tubular at the base as opposed to "imbricate" scales in which the base of each scale does not describe a complete circle. "Peduncle axillary" is only applied to those genera for which information has been obtained on the bulb axis anatomy. Superficial observation is excluded.

The principle subdivision is believed to be the recognition of a group including Urginea, Drimia, Rhadamanthus, Litanthus, Urgineopsis, Thuranthos, Schizobasis and Bowiea. The principle characteristics identifying this group were discussed in Part 3.

The remaining genera are not as readily subdivided, but it is believed that seed surface characters may prove to be one of the most valuable, despite their great variability in the Urginea-Drimia group. The Massonia group all (except Neopatersonia) have seeds in which the epidermal cells are not identifiable or in which there is some doubt as to whether or not the patterns of the surface do reflect an underlying cellular arrangement. To this group must be added Eucomis, Lachenalia and Scilla section Ledebouria and probably Veltheimia. Neopatersonia is excluded as the cellular pattern is extremely clear and totally unlike the patterns (cellular or otherwise) in the Massonia group. It is possible that Drimiopsis might belong to this group too, but its seeds have not been examined under the scanning electron microscope. Under the light microscope they do appear to have similar surface characters. Linked with seed surface characters there are

	Schizobasis	Bowiea	Urginea	Urgineopsis	Rhadamanthus	Thuranthos	Drimia	Litanthus	Massonia	Daubenya	Androsiphon	Amphisiphon	Neobakeria	Polyxena	Hyacinthus	Whiteheadia	Eucomis	Veltheimia	Lachenalia	Scilla (Ledebouria)	Scilla (Euscilla)	Drimiopsis	Resnova	Neopatersonia	Galtonia	Pseudogaltonia	Ornithogalum	Albuca	Dipcadi
Starch in bulbs	–	–	–	–	–	–	–	–	+				+	+	+		+	+	+	+	+	+			+		+	+	+
Bulb scales tubular	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+				+	–	–	–				–	+	+	
Leaves marked	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	–	?+		+	+	–	+	+	–	–	–	–	–	–
Leaves paired	–	–	–	–	–	–	–	–	+	+	+	+	+	+	–	+		–	+	–	–	–	–	–	–	–	–	–	–
Peduncle axillary																			+	+	–	+							
Coma present	–	–	–	–	–	–	–	–	–	–	–	–	±	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Spurred bracts	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Filaments connate	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	+	+	–	–	–	+	–	–	+	–	+	–	–	–
Inflorescence a head	–	–	–	–	–	–	–	–	+	+	+	+	±	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Flowers zygomorphic	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–
Heterandrous	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Perianth tube	–	–	–	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	±	+	+	–	–	+
Perianth marscecent	+	+	+			+												–	–	–	–	–	–	–		–	–	–	–
Loose testa	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Seed surface cellular	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–		–	–	+	?–		+	+	+	+	+	+

TABLE 21
Generic characters of the bulbous
Liliaceae

several other features:-

1) *Lachenalia*, *Scilla* section *Ledebouria* and *Drimiopsis* appear to have axillary inflorescences. The rest of the genera in the group have not been determined.
2) Most of the genera have species with spotted or striped leaves.
3) The *Massonia* group itself consists of genera which are separated from each other in a fairly small number of characters - for example *Daubenya* from *Massonia* on the zygomorphic flower, *Neobakeria* from *Massonia* on the absence of large spathe-like bracts, *Polyxena* from *Neobakeria* on the insertion of the filaments and the membranous bulb scale.
4) *Lachenalia pusilla*, which has very slightly zygomorphic flowers, links *Lachenalia* (zygomorphic) with *Polyxena* (actinomorphic). Both genera and *Hyacinthus* (Cape species only) have a tubular membranous bulb scale as well as fleshy scales.
5) The *Eucomis* flower is similar to that of *Massonia*, and *Whiteheadia* forms an intermediate between these genera. The coma occurs in one species of *Neobakeria* as well as in *Eucomis*, although it is not as well developed in the *Neobakeria*. A coma does also occur in genera not included in this group - for example in *Muscari* (European and Asian).
6) *Drimiopsis* and *Scilla* section *Ledebouria* are separated only on the incurving, subcucullate perianth of the former. In all other respects these two genera are

extremely close.

The remaining genera, not placed either in the *Urginea-Drimia* group or with the *Massonia* group, form a heterogeneous assemblage, with little to link the genera. However, as the only member of this group dealt with in detail by the author is *Scilla* section *Euscilla*, this group will not be examined in detail.

For historical reasons, those genera regarded by Baker (1896/7) as synonymous with *Scilla* will be dealt with as a single unit in the following discussion, followed by the *Drimiopsis-Resnova* unit, then the *Massonia* group and finally the *Urginea-Drimia* group.

4.2 The *Scilla* group

In 1781, C. Linnaeus the younger described *Hyacinthus revolutus* from the Cape of Good Hope, basing it on a specimen collected by C.P. Thunberg. Other related species were subsequently described by Thunberg, Jacquin and others under a range of generic names including *Lachenalia* and *Drimia*. It was not until 1820 that a South African species was placed in the genus *Scilla*, a genus originally described by Linnaeus Senior for several northern hemisphere species. Then, in the second half of the nineteenth century, J.G. Baker transferred *Hyacinthus revolutus* and several species, placed in other genera, to *Scilla*. He contributed nearly seventy species, either new or by new combinations, to the list of South

African species placed in *Scilla*.

Towards the middle of the present century, F.Z. van der Merwe did much to build up the herbarium record of the genus *Scilla* in its wider sense, describing new species and working on the generic concepts. He recognised three genera within *Scilla*, as had been recognised by, for example, Baker. Most of the species he retained in his concept of *Scilla*, but he described (1943) a new genus for a small group in which the tops of the bulbs are fibrous. This he called *Schizocarphus*. He also described (1946) a new genus *Resnova* for a small group, which the present author considers to have significant similarities with *Drimiopsis* Lindl., and to differ from the other species on both floral and vegetative characters. Phillips, in his "Genera of South African Flowering Plants" (1951) preferred to include both *Resnova* and *Schizocarphus* within *Scilla*.

In 1821, Roth described *Ledebouria hyacinthina* from India. No further species have been described under this generic name and this species was transferred to *Scilla* by Baker in 1870. However, in the "Flora Capensis", Baker retained the name *Ledebouria* for the largest section of *Scilla* in South Africa.

Table 22 indicates the significant morphological features of *Scilla* (sections *Euscilla* and *Ledebouria*) and *Schizocarphus*. The species of *Resnova* sensu Van der Merwe are not included in this discussion as they are dealt with under Drimiopsis.

Euscilla	Schizocarphus	Ledebouria
Bulb scales without fibres at apex.	Bulb scales with fibres at apex.	Bulb scales without fibres at apex.
Leaves uniformly green.	Leaves uniformly green or with a pink or reddish colouring towards the base.	Leaves usually conspicuously spotted.
Inflorescence terminal.	Inflorescence terminal.	Inflorescence axillary.
Inflorescence erect and rigid.	Inflorescence erect and rigid.	Inflorescence usually flexuose and softer.
Perianth segments blue or rarely pink or white.	Perianth segments more or less white.	Perianth segments often pink, or white strongly marked with green or brown.
Filaments united towards the base.	Filaments united towards the base.	Filaments free of one another.

TABLE 22 (continued on p. 129)

Comparison of significant features of Scilla (sections Euscilla and Ledebouria) and Schizocarphus.

Ovary oblong.	Ovary oblong.	Ovary conical, expanding to a wide base below which it contracts very abruptly to the distinct pedicel.
Ovules axile, several (rarely 2) in each locule.	Ovules axile, several in each locule.	Ovules basal, paired in each locule.

TABLE 22 (concluded)

In addition to the morphological characters in table 22 there are other characters, which have been discussed in previous sections:-

1) Both Schizocarphus and most South African species of Scilla (Euscilla) have lignified bundle sheaths, while Scilla (Ledebouria) does not. But this must be qualified as S. plumbea (Euscilla) resembles the Ledebouria section in this respect.

2) Seed characters place Scilla (Ledebouria) in a group with Massonia, while they place Scilla (Euscilla) and Schizocarphus apart and with such genera as Dipcadi and Ornithogalum.

The important conclusion to be drawn from this data is that there are a comparatively large number of characters uniting Euscilla with Schizocarphus - the origin of the inflorescence, the leaf anatomy, the fusion of the basal parts of the filaments, the shape of the ovary and arrangement of the ovules and the surface characteristics of the seeds.

By all these characters *Ledebouria* must be treated as a separate genus and is, being the oldest validly published name typified by a member of this genus, therefore resurrected.

It is also concluded that *Schizocarphus* should be retained as a synonym for *Scilla*.

4.3 *Drimiopsis* and *Resnova*

The genus *Drimiopsis* was described in 1851/2 by Lindley, with a single species - *D. maculata*. Baker described a further seven species from South Africa between 1870 and 1897. In addition, he described *Scilla humifusa* and *S. lachenalioides*, which are considered by the present author to belong to this genus. A further three species have been described from South Africa this century and four species from South West Africa. The South West African species are, however, considered by the present author to belong to the genus *Ledebouria*.

In 1946, Van der Merwe described a new genus, *Resnova*, from South Africa. Two species, described by Baker under *Scilla*, and four new species were recognised. No further species have been described in *Resnova* and Phillips (1951) treated *Resnova* as a synonym for *Scilla*.

As pointed out by Van der Merwe (1946), Baker did apparently place very closely related species under different sections of Scilla - S. lachenalioides under Euscilla and S. humifusa under Ledebouria. What has not been discussed is the relationship between Scilla (sensu lato) and Drimiopsis.

Baker (1896/7) described Drimiopsis as having "Perianth -segments cucullate, connivent", and Scilla as having "Perianth-segments spreading, 1-nerved". Phillips (1951) also employed the cucullate apices of the perianth segments in his key.

In describing Resnova, Van der Merwe (1946) distinguished his new genus from the section Euscilla by its having ascending perianth segments, which are never blue or blue-purple. From the section Ledebouria he separated it by its not having spreading perianth segments, in the sessile ovary and in the colour (undefined) of the perianth.

From these published comments, it would seem that the perianth affords the principal diagnostic characters of the groups - spreading in Scilla (both sections), ascending in Resnova and cucullate and connivent in Drimiopsis.

On morphological characters, Drimiopsis, Resnova and Ledebouria appear to be very closely related. The bulbs of Resnova and Drimiopsis are made up entirely of rather loose fleshy scales, while those of Ledebouria tend to be more closely packed and the outermost are usually dry and papery. However, in *L. cooperi* bulbs very similar to those of the other two genera are frequent. The leaves of all three are similar in texture, and are frequently spotted or in other ways marked. Petiole-like structures occur more frequently in *Drimiopsis* and *Resnova* than in *Ledebouria*. The inflorescence is similar. The ovary of *Ledebouria* is of a very characteristic form - being generally markedly conical and stipitate, with two basal ovules in each locule. The ovaries of both *Drimiopsis* and *Resnova* are oblong and sessile but also have two basal ovules per locule. The perianth characters are not considered to be as significant as previous authors have suggested. Many specimens of *Ledebouria* have minutely cucullate perianth segments. The colour of the perianth segments is extremely variable in *Ledebouria*, *Drimiopsis* and *Resnova*. Leaf anatomy and seed surface characters place *Ledebouria* and *Drimiopsis* very close to one another.

The differences between *Drimiopsis* and *Resnova*, and *Scilla* (sensu stricto) are more clearly defined. *Scilla* always has some dry bulb scales, has firmer, unspotted leaves, and a more rigid peduncle. The filaments are always distinctly connate towards the base, and there is frequently more than two ovules in each locule of the ovary. Leaf anatomy and seed surface characters (especially the latter) are very different in *Scilla* and *Drimiopsis*.

It is, therefore, considered that *Drimiopsis* is very much closer to Ledebouria than to Scilla. The only characters for separating Drimiopsis from Ledebouria are the ascending perianth, usually with a pronouncedly cucullate apex to the segments, and the truncate base to the ovary of most species of Ledebouria. It is rather doubtful whether it is better to separate or unite these two genera. Because they can generally be very easily separated on floral characters, the two genera are separated in this treatment, although this may be considered to be a rather artificial division.

Although many aspects of Resnova have not been examined, because of the lack of suitable material, it is considered that there is no character on which Resnova can be separated from Drimiopsis. The species described in Resnova by Van der Merwe form an almost continuous series from R. lachenalioides at the one extreme to forms placed here in D. maxima which form a very good link with Drimiopsis (sensu Baker). It is, therefore, proposed that Drimiopsis and Resnova be combined under the older name - Drimiopsis.

4.4 The Massonia group

In 1753, Linnaeus Senior described Hyacinthus, but it was not until 1771, in his "Mantissa", that he described a South African species - H. corymbosus. Although this species was transferred by Ker-Gawler first to Massonia in 1807 and then to Scilla in 1812, and by Kunth to Periboea in 1843, most authors have until the present continued to treat it as correctly assigned to Hyacinthus.

The next genus in this group to be described was Massonia, which was described by Houttuyn in 1780, based on a name proposed by Thunberg. Its affinities were not discussed.

In the nineteenth century three further genera were described. Of these, one, Whiteheadia, has always been regarded as monotypic. Prior to Harvey's (1868) erection of a new genus for it, this species had been variously placed in Eucomis, Basilaea and Melanthium, but Harvey's opinion has not since been challenged. Daubenya was described in 1835 by Lindley for a newly discovered species and his decision, too, has never been queried. A further two species have been described. Hall (1970) has recently suggested that the genus be treated as monotypic. The third genus, Polyxena, is both larger in terms of species and more complex in its relationships. It was described by Kunth (1843) for a species previously placed by Jacquin in Polyanthes. Species have been transferred to Polyxena from Mauhlia, Agapanthus, Massonia and Hyacinthus. Baker (1896/7) recognised ten species, but since then a further four epithets have been included.

Baker (1896/7) recognised five genera in the group treated in this section - Daubenya, Hyacinthus, Massonia, Polyxena and Whiteheadia. He placed Massonia and Daubenya in the tribe Allieae on the basis of their "umbel, which is subtended by a spathe of 1-2 or more membranous bracts". This description is based on a very superficial resemblance to the inflorescence of other members of the Allieae. A better description would probably be a raceme with a very short axis and with large, often showy, sterile lower bracts. The pedicels are clearly individually subtended by the fertile bracts. The two genera were distinguished from one another on the basis of the "regular perianth limb" of *Massonia* and "irregular perianth limb" of *Daubenya*. The remaining three genera were placed in the tribe Scilleae. *Whiteheadia* was distinguished from *Polyxena* by having a short perianth tube and connate filaments - in *Polyxena* the tube is cylindrical and the filaments free. His reasons for distinguishing *Hyacinthus* from these two are not apparent to the present author.

A further three genera have been described this century.

In 1924 Schlechter published two new genera - *Androsiphon* and *Neobakeria*. The former he considered to have affinities with *Massonia*, but to be clearly distinct because of the staminal tube which he refers to as a gynostegium. Schlechter recognised a single species of *Androsiphon* and no further combinations have been made. Baker (1896/7) had recognised two subgenera in *Polyxena*. Subgenus *Astemma*, consisting of six species, was recognised by Schlechter as sufficiently distinct to justify its erection to generic status. Baker separated these subgenera because Astemma had its stamens uniserial in the throat of the perianth tube, while Eupolyxena had biserial filaments. Schlechter regarded this character as indicating a generic rather than a subgeneric distinction and added a further species to Neobakeria - as well as transferring a species to Polyxena from Lachenalia. This species (L. pusilla) is regarded by Miss W.F. Barker, on the basis of examination of fresh and dried material, as having a sufficiently zygomorphic perianth to retain it in Lachenalia (personal communication). But this species may be regarded as indicating an affinity between these two genera.

Barker (1936) described Amphisiphon - a further monotypic genus. She linked it with Androsiphon on the basis of its long staminal tube. It differs in having a long perianth tube and in lacking a disc at the end of the staminal tube. The capsule differences seem to be especially important; "that of Androsiphon being obovate, sharply angled at the top, leathery and dehiscing loculicidally, whereas in Amphisiphon the roundly angled membranous capsule is broadest at the base, and narrows gradually into the long persistent style, an unusual character within this group of genera, so far as known. In dehiscence the fruit drops from the pedicel, the three carpels then separate from the base upwards and finally each splits down the septum."

Krause (1930), Hutchinson (1959) and Phillips (1951) provide the most important reviews of the genera of the Liliaceae since Baker (1896/7).

Krause recognised six genera in the Massonia group - all that had been described at that time except Neobakeria which was treated as a synonym for Polyxena. He included them all within a single tribe - Scilloideae. The characters he used in his key for distinguishing these genera are summarised in table 23.

Hutchinson regarded Neobakeria as a synonym for Polyxena and placed Amphisiphon under Androsiphon. Massonia and Daubenya were placed in a tribe Massonieae (with only two genera) on the grounds of their having their flowers "not in heads or umbel-like heads". The remaining genera were included in the Scilleae. The characters used are summarised in table 23.

Phillips recognised all the described genera, except Amphisiphon, which he included under Androsiphon. Phillips was one of the few authors who recognised Neobakeria. For characters used in his key see table 23.

Krause (1930), Airy-Shaw (1966) and Phillips (1951) attempted to estimate the numbers of species in each genus, as indicated in table 24.

Massonia (sensu Phillips, 1951; Hutchinson, 1959 and Krause, 1930) is characterised by being bulbous, with actinomorphic flowers arranged in an umbel-like head, and with the inflorescence surrounded by more or less showy spathe-like sterile lower bracts. Polyxena and Neobakeria differ according to the former two authors in having racemose or corymbose inflorescences and, according to Krause, in having the lowest bracts fertile.

Genus	Hutchinson	Krause	Phillips
Hyacinthus	Flowers not in heads. Ovules few.	Leaves several.	Filaments free. Inflorescence not a head.
Polyxena	Flowers not in heads. Ovules numerous. Filaments free.	Bracts all fertile. Filaments free. Leaves few.	Inflorescence a corymb. Stamens in 2 rows. Filaments connate at base.
Whiteheadia	Flowers not in heads. Ovules numerous. Filaments connate at base.	Bracts all fertile. Filaments connate. Leaves paired.	Inflorescence a dense subspicate raceme. Stamens in 1 row. Filaments connate at the base. Perianth segments longer than the tube.

TABLE 23 (continued on page 139)

Generic characters in the Massonia group employed by Hutchinson (1959), Krause (1930) and Phillips (1951).

Massonia	Flowers in umbel-like heads. Perianth actinomorphic. Stamens longer than the perianth.	Lower bracts sterile. Filaments free. Leaves paired.	Filaments united at base into a cup. Flowers regular.
Daubenya	Flowers in umbel-like heads. Perianth oblique. Stamens shorter than the perianth.	Lower bracts sterile. Filaments connate in a ring. Leaves paired.	Filaments free. Outer flowers bilabiate.
Androsiphon	Flowers not in umbel-like heads. Ovules numerous. Filaments connate in a long tube.	Lower bracts sterile. Filaments connate in a tube. Leaves paired.	Filaments united into a tube. Flowers regular.

TABLE 23 (continued)

Neobakeria	Inflorescence a lax raceme or shortly peduncled raceme or sometimes the raceme head-like. Perianth segments shorter than tube. Stamens in 1 row. Filaments connate at the base.	Not recognised	Not recognised

TABLE 23 (concluded)

Genus	Krause	Airy-Shaw	Phillips
Androsiphon	1	1	2
Amphisiphon		1	
Daubenya	1	1	1
Hyacinthus		30	75 (2 S.Afr.)
Massonia	30	45	45
Neobakeria	8	9	
Polyxena	10-12	10	10
Whiteheadia	1	1	1

TABLE 24

Species numbers estimated by Krause (1930), Airy-Shaw (1966) and Phillips (1951).

The *Massonia* inflorescence is typically a contracted raceme, and a series of specimens provides a continuous gradation from this form to the type characterising *Polyxena* and *Neobakeria*. Similarly, a range of intermediates link those specimens of *Massonia*, with conspicuous spathe-like bracts, with specimens completely lacking these structures. It is, therefore, considered by the present author that neither of these characters affords suitable criteria for distinguishing these genera.

However, several other characters are of possible value. There is a pattern of leaf structures which is apparently characteristic of *Polyxena* (and also occurring in *Lachenalia* and the Cape species of *Hyacinthus* sensu Phillips). In these groups, between each cycle of vegetative leaves there is an intermediate, generally lamina-less membranous leaf forming a tubular sheath round the proximal part of the leaves, and projecting a short distance above the bulb. This structure is not always detectable on herbarium material (although it usually is), but is thought likely to be a constant feature of *Polyxena* sensu stricto, certainly is of *Hyacinthus* (Cape species only), and has never been observed in *Massonia* or *Neobakeria*. Baker (1896/7, p.419) stated "I have followed Mr Bentham in classification, but my own view would be to unite, at any rate, the subgenus *Astemma* (i.e. *Neobakeria*) with *Massonia*". Although he did not elaborate on this point, it is clear, therefore, that Baker recognised that

Neobakeria is closer to *Massonia* than to *Polyxena*.

A second feature of possible generic significance is the insertion of all the filaments at one level on the perianth in *Massonia* and *Neobakeria*, but at two distinct levels in *Polyxena* (sensu stricto) and *Hyacinthus* (Cape species).

The close correlation between the bulb and filament characters has led the present author to the decision to unite *Massonia* and *Neobakeria* (under the older name - *Massonia*), but to retain *Polyxena* as a separate genus.

The Cape species of *Hyacinthus* share the above-mentioned characters with *Polyxena*, and it is necessary to re-examine the characters by which they are separated. The following are the characteristics used in recent keys:- Krause (1930) stated that *Hyacinthus* had several leaves and *Polyxena* only 2-5. Hutchinson (1959) stated that *Hyacinthus* had few ovules and *Polyxena* numerous ovules. Phillips (1951) stated that *Hyacinthus* had free filaments and *Polyxena* connate filaments. *Polyxena* has free filaments and Phillips' use of this character need not be considered.

Polyxena and *Hyacinthus* have a similar number of ovules, usually 10-20. *Polyxena* usually has only two leaves, but occasionally more. Hyacinthus occasionally has as few as two leaves. In practice these two genera are readily separable as *Hyacinthus* has narrower leaves and fewer flowers, but these are considered by the present author to be specific rather than generic differences.

The geographic distribution of Hyacinthus is, perhaps, also relevant. The genus is almost entirely restricted to the northern hemisphere. The Cape species are, therefore, extremely isolated from the majority of the species. While this may represent an example of a similar phenomenon to that exhibited by Viola (Jessop, 1967), the degree of isolation is greater with no other species known to the present author from south of the Sahara.

It is, therefore, proposed that the Cape species of Hyacinthus be placed in Polyxena.

The remaining genera in the Massonia group are more readily definable. The characters employed by previous authors are believed to be accurately recorded and appropriate. Daubenya, Androsiphon, Amphisiphon and Whiteheadia are recognised and regarded as monotypic. Amphisiphon is separated from Androsiphon on the characters pointed out by Barker (1936) - see page 136.

4.5 The Urginea-Drimia group

The first species to be validly published in this group were two species placed in Ornithogalum and one species in Hyacinthus by Linnaeus (fil.) in 1781. The Hyacinthus species was transferred to Rhadamanthus by Salisbury in 1866 and, in view of the recent revison of this genus

(Nordenstam, 1970), Rhadamanthus is not discussed further here.

Although Thunberg (1794) retained Linnaeus' species in Ornithogalum, the three further species (now considered to belong with his Ornithogalum spp) he described were placed in Anthericum. Anthericum is now no longer considered to include bulbous species. Jacquin (1794-7) followed Thunberg in placing a further five species in Anthericum, and one in Ornithogalum, but he also described a new genus, Drimia, for four species which differed conspicuously in having reflexed perianth segments. Although these two groups (with spreading or reflexed perianth segments) have generally been kept separate from one another, there has been much debate as to the correct names to assign to them. Poiret (1804) transferred three of Jacquin's species of Anthericum to Phalangium and, later (1813), transferred all of Jacquin's Drimia spp to Hyacinthus. However, even before this date, Ker Gawler had changed one of the species, which Poiret transferred to Phalangium, to Albuca (1805). In 1807-1821 he transferred a further three species to Albuca. But one of the species in the group which Thunberg and Jacquin had called Anthericum was transferred (1808) to Drimia, so that, for the first time, the gap between the group with spreading perianth segments (Anthericum of Thunberg) and with reflexed perianth segments (Drimia of Jacquin) had been bridged.

The next major step was when Steinheil (1834) recognised the fact that a new genus was required for the group with spreading perianth segments to differentiate them from the quite distinct genera to which they had been attached - *Anthericum* and *Ornithogalum*. He gave the name *Urginea* to both European and South African species. Essentially, *Urginea* and *Drimia* have remained the most widely accepted names for the two groups up until the present.

One important contribution in the mid eighteenth century was that of Kunth (1843), who treated most species of both *Urginea* and *Drimia* as species of *Idothea*, although several of the former were included in *Ornithogalum*.

Harvey (1844) described a new genus, *Litanthus*, allied to *Urginea*, but with a well-developed oblong perianth tube. Only a single species (*L. pusillus*) has been recognised in this genus.

Hooker (1867) published Harvey's name *Bowiea*. Hooker commented that"in botanical characters (it was) allied to *Drimia* and *Scilla*". Its affinities with *Drimia* have been largely ignored since then, however. The genus has continued to be known by only one species in South Africa, although a second species was described from tropical Africa.

A further genus, attributed by the present author to this group, was described by Baker in 1873. Baker correctly identified it as related to *Bowiea*.

In the "Flora Capensis" Baker recognised 22 species of

Drimia, of which he had described thirteen himself, and 27 species of Urginea, of which he had described or made new combinations for all but three. In Schizobasis, he recognised four species.

Since Baker, only two further genera have been described in this group - Urgineopsis and Thuranthos. Compton (1930) separated Urgineopsis from Urginea due to its greater degree of perianth fusion, but Adamson (1942) disagreed and placed it under Urginea. Wright (1916) described Thuranthos for a single species (T. macranthum) which Baker had treated as a species of Drimia. Dyer (1964) described a second species in Thuranthos.

The most recent evaluation of the generic concepts of this group is that of Phillips (1951), who recognised: Drimia (26 South African species and an additional 18 from elsewhere in Africa); Urginea (105 species from Europe, Asia and Africa, with 57 in South Africa); Litanthus (endemic to South Africa, 1 species); Rhadamanthus (endemic to southern Africa, 2 or 3 species), Thuranthos (endemic to South Africa, "1, perhaps 3" species) Urgineopsis (endemic to the Cape Peninsula, 1 species), Bowiea (endemic, 1 species) and Schizobasis (9 species, 7 species in South Africa).

The characters used by Phillips (1951), Hutchinson (1959), Baker (1896/7) and Compton (1930) to distinguish the genera with simple inflorescences are: the degree of fusion of the perianth; the shape of the filaments;

whether or not the anthers are connivent, the shape of the perianth tube (if present); whether the perianth segments spread or are reflexed; the number of flowers in the inflorescence; and whether the flowers are erect or pendulous.

Rhadamanthus was regarded by Nordenstam (1970) as very close to Urginea, but separable because the anthers dehisce either by an apical pore or by a slit initiated at the apex. In all species of the other genera dehiscence is by a longitudinal slit. This view is accepted by the present author.

Litanthus is very readily recognisable by having a single, or two, flowers in the inflorescence and by the perianth tube which is very much longer than the segments and more or less cylindrical.

The position of Urginea, Urgineopsis, Drimia and Thuranthos requires re-evaluation. Table 25 indicates the principle differences.

The complex filaments in Thuranthos consist of a flattened basal part and terete distal part, with the filaments arching out round the ovary and connivent above. This character appears likely to be a significant one and has been greatly stressed by Dyer (1964). However, as Dyer pointed out, there is a considerable similarity between the two species with this type of filament and certain other species (U. indica and U. basutica) which are generally placed in Urginea. These four species form a natural group of plants, differing in size and number of flowers and in capsule shape. U. indica and U. basutica differ from other species of Urginea only in having reflexed perianth segments and pendulous flowers, which are not considered sufficient grounds for separating them from Urginea. Therefore, in order to place these four species together, it becomes necessary to reduce Thuranthos to synonymy under Urginea.

Genus	Perianth reflexed	Perianth tube	Thuranthos type of filament shape	Flowers pendulous
Urgineopsis	no	distinctly fused	simple	no
Thuranthos	yes	more or less free	complex	yes
Drimia	yes	fused	simple	yes or no
Urginea	no	yes or no	simple	rarely

TABLE 25

Principle characters employed in separating Urgineopsis, Thuranthos, Drimia and Urginea.

Urgineopsis has been dealt with by Adamson (1942). Adamson pointed out that although Urginea is generally considered to have free perianth segments, there are species with a degree of fusion comparable with that in

Urgineopsis. The species mentioned by Adamson as having markedly fused perianths are *U. pygmaea*, *U. dregei* and *U. arenosa*. The present author considers *Urgineopsis salteri* (the only species of *Urgineopsis*) as conspecific with *U. tenella*, a species in which there is a considerable range in the fusion of the perianth.

The difference between *Urginea* and *Drimia*, when *Thuranthos* and *Urgineopsis* are included in the former, become less significant. The principal differences in the literature are the degree of fusion of the perianth, the tendency of the stamens to be connivent in *Drimia* and the reflexed perianth of *Drimia*. As stated above the degree of fusion of the perianth cannot be regarded as a generic character on its own, although *Litanthus* is partly defined on these grounds. The other two characters are present in *Urginea*, too, if *Thuranthos* is included in *Urginea*. *Drimia* cannot, therefore, be separated from *Urginea*. The degree of fusion of the perianth of *Drimia* and *Urginea* sensu Baker also shows considerable overlap, and *D. anomala*, although treated as a species of *Drimia* by Baker (1896/7), has spreading perianth segments.

A conspicuous feature of most species of *Drimia* is the red bulb, but as this also occurs in a few species of *Urginea* (e.g. *U. maritima* and *U. sanguinea*) it cannot be regarded as a generic character. No other characters appear to be correlated with either a greater degree of fusion of the perianth or with the reflexed segments.

It is, therefore, necessary to reduce *Urginea* to synonymy under *Drimia*.

The possibility of applying to have the later generic name, *Urginea*, conserved against *Drimia* requires consideration. *Urginea* is a well-known northern hemisphere genus with a species well-known for its poisonous properties - *U. maritima*. However, in Africa *Drimia* is almost as wide-spread and well-known, and the advantages of conserving the name *Urginea* do not appear to be sufficient to justify taking this step.

PART 5

ORIGIN AND EVOLUTION OF THE SCILLEAE

5.1 Geographical considerations

Table 26 indicates the distribution of the genera recognised by Hutchinson (1959), modified according to the concepts discussed in part 4 of this work. In addition to the Scilleae sensu Hutchinson, the Massonieae, Schizobasis and Bowiea are included. The distribution data is after Hutchinson, and Willis (1966).

A most important feature is the total absence of any genera from Australia or South America (or, of course, Antarctica) - those continents which, together with Africa, Madagascar and India, formed Gondwanaland. There is also only a single genus (of eight species) endemic to Madagascar, and a second widespread genus - Dipcadi. Rhodocodon, the Madagascar endemic, keys out in Hutchinson next to Hyacinthus and Krause (1930) places it between Muscari and Veltheimia. There are 23 genera in Africa south of the Sahara - all of them reaching South Africa or South West Africa - only five of these reaching North Africa or Asia and only an additional four genera occurring in Europe, Asia or North Africa but not occurring south of the Sahara.

The Scilla-Ornithogalum group has the largest proportion of genera occurring both north and south of the

Genus	S. Afr.	N. Afr.	Europe	Asia	N. America	Madagascar
Scilla-Ornithogalum group						
Scilla	x	x	x	x	–	–
Ornithogalum	x	x	x	x	–	–
Dipcadi	x	x	x	x	–	x
Galtonia	x	–	–	–	–	–
Pseudogaltonia	x	–	–	–	–	–
Albuca	x	–	–	–	–	–
Camassia	–	–	–	–	x	–
Chionodoxa	–	–	–	x	–	–
Rhodocodon	–	–	–	–	–	x
Hyacinthus	–	x	x	x	–	–
Muscari	–	x	x	x	–	–
Puschkinia	–	–	–	x	–	–
Neopatersonia	x	–	–	–	–	–
Drimia group						
Drimia	x	x	x	x	–	–
Litanthus	x	–	–	–	–	–
Rhadamanthus	x	–	–	–	–	–
Schizobasis	x	–	–	–	–	–
Bowiea	x	–	–	–	–	–

TABLE 26 (continued on p.153)

Distribution of the genera of the Scilleae.

Genus	S. Afr.	N. Afr.	Europe	Asia	N. America	Madagascar
Massonia group						
Ledebouria	x	x	-	x	-	-
Drimiopsis	x	-	-	-	-	-
Lachenalia	x	-	-	-	-	-
Veltheimia	x	-	-	-	-	-
Eucomis	X	-	-	-	-	-
Massonia	x	-	-	-	-	-
Polyxena	x	-	-	-	-	-
Whiteheadia	x	-	-	-	-	-
Daubenya	x	-	-	-	-	-
Androsiphon	x	-	-	-	-	-
Amphisiphon	x	-	-	-	-	-

TABLE 26 (concluded)

Sahara - three (*Scilla*, *Dipcadi* and *Ornithogalum*) occurring both north and south. Two genera in this group occur only north of the Sahara and four occur only in the south. It is also the only group with representatives in north America and Madagascar. It is suggested, therefore, that this may be the oldest group within the Scilleae. If the three groups of the Scilleae (the *Scilla-Ornithogalum*, the *Drimia* and the *Massonia* groups) have a common origin it is likely, on phytogeographical grounds, to have been in or close to the *Scilla-Ornithogalum* group.

In view of the absence of the Scilleae from South America or Australia it is thought likely that it arose after the separation of the Gondwanaland masses at the end of the Triassic (Schuster, 1972) and probably to the north of the Tethys Sea.

The *Drimia* group has a single generic representative in Europe and India, but this genus (*Drimia*) also occurs in South Africa where the majority of its species probably also occur. The remaining four genera in the *Drimia* group are all restricted to sub-Saharan Africa. Although it is believed to be virtually certain that *Drimia*, *Schizobasis* and *Bowiea* are related, the differences in the morphology of these genera make it likely that their common origin is very old. The latter two genera are now restricted to sub-Saharan Africa and there is no reason to believe that they originated elsewhere. If *Drimia* originated in the north, it might have been expected to have migrated further. However, if it originated in tropical or southern Africa, where its oldest apparent allies exist, it would have had to have migrated a more considerable distance to have reached the Orient. It is, therefore, suggested that the *Drimia* group is most likely to have been of African origin - derived, perhaps, from an early member of the *Scilla-Ornithogalum* group. On the other hand, despite the phytogeographical evidence, it is possible that the *Drimia* group is, itself, older than the *Scilla-Ornithogalum* group. The occurrence of a petiole-like leaf structure and spurred bracts may indicate a primitive position for the *Drimia* group.

The *Massonia* group is almost restricted to southern Africa, with a single species of *Ledebouria* reaching India and none in Europe. Other species may exist in the land bridge between *Ledebouria*'s main centre, in Africa, and India, but it is doubtful if these are in fact specifically didferent from *L. hyacinthina* - the Indian species - which has also been recorded from east Africa.

The former link of India with Asia could explain the presence of *Ledebouria* in India, but it is thought more likely that this species migrated into India from an African origin.

The origin of *Asparagus*, in view of its possible affinity with the *Drimia* group, would be of interest. There are no species in either of the Americas. But the genus is successful in terms of numbers of species and numbers of individuals in Africa and a large part of

Eurasia. There is a single species in Australia - *A. racemosus* - supposedly conspecific with a species occurring through southern Asia and a large part of Africa. Again it is thought likely that it migrated along presently existing land bridges and, producing edible berries and seeds with copious endosperm, may well be transported over considerable distances. In view of its success in those areas where it occurs, it would be strange that it did not occur in America if it had existed at a time when migration was simpler into America than it now is. Like so many of the Liliaceae in South Africa *Asparagus* species limits are often blurred and it is thought possible that this may be due to, or associated with, rapid evolution of new genomes, without the accompanying time necessary for distinct speciation. If this hypothesis is correct, it may be that evolution is taking place very rapidly in these groups and that the present large number of species - probably at least 100 in *Asparagus* - is not indicative of a particularly old genus. *Asparagus* occurs in desert or semi-desert areas, macchia, grassveld and forest, showing a ready adaptation to its environment. There is more variation in South African *Asparagus* species than elsewhere. The *Myrsiphyllum* subgenus (probably the greatest deviation from the more typical forms) is South African as is the *Asparagus striatus-subulatus* group which also shows a greater deviation from what is thought of as the norm than does any group known from any other part of its range.

Other groups or species of *Asparagus*, showing particularly unusual morphological features, also predominate in South Africa, for example the *A. capensis-suaveolens* group and *A. crispus*.

Asparagus is, therefore, also considered to be likely to be originally an African genus, with a centre in southern Africa. This agrees with the theory that it may have a common origin with the *Drimia* group, which is also thought to be of southern African or tropical African origin.

5.2 Summary of evolutionary trends

5.2.1 The *Drimia* group

Within the *Drimia* group it is suggested that the following are the more important evolutionary developments:

1) Fusion of the perianth segments;
2) Stamens becoming connivent;
3) Anthers becoming apically dehiscing;
4) Leaves becoming reduced, first by loss of the petiole (i.e. from a primitive form resembling *D. anomala*) and then by total loss of aerial leaves in the mature plant;
5) Branching of the inflorescence.

The most widespread subgroup is *Urginea* sensu stricto - occurring over the whole range of the *Drimia* group. This subgroup also shows all the primitive characters. *Drimia* sensu stricto represents a block of species differing to some degree on most of the above characters, with *Rhadamanthus* forming possibly the most highly evolved form still possessing leaves.

Schizobasis and *Bowiea* have not diverged from one another to any great extent. Certain forms of *D. tenella* have an identical bulb and flower structure to plants in *Schizobasis* and the inflorescence, although simple, is very similar in texture. It is suggested that this widespread and very complex species, which is also the closest to *Litanthus*, represents the nearest approximation to a primitive species for the group. For summary see table 27.

5.2.2 The *Massonia* group

Ledebouria and *Drimiopsis* are by far the most widespread members of this group and are considered for the most part to be likely to show the largest proportion of primitive characters. In *Ledebouria*, there is the conical ovary with basal ovules, which it is thought unlikely to be primitive. *Drimiopsis* also has paired basal ovules. It is believed that the primitive ovary type is more likely to be ellipsoid with several or many axile ovules - characters found in the great majority of the Liliaceae.

Within the group it is suggested that the following are the more important evolutionary developments:

1) Fusion of perianth segments;
2) Floral parts becoming zygomorphic;

3) Incurving of perianth segments, or at least their becoming ascending;
4) Condensation of the inflorescence to become a head;
5) Development of showy sterile bracts;
6) Fusion of filaments to one another;
7) Insertion of filaments on perianth segments at different levels;
8) Development of tubular leaf bases;
9) Specialisation of a membranous leaf base;
10) Development of a coma;
11) Reduction in number of leaves to two;
12) Reduction in number of ovules and their becoming basal.

If the primitive member of this group, is considered to be very close to *Ledebouria* and *Drimiopsis*, but with an ellipsoid or ovoid ovary with several axile ovules, the remaining genera are undoubtedly very early derivatives. *Veltheimia* is, except for its tubular perianth and paired ovules, probably very close to the ancestral stock.

A form close to *Massonia angustifolia* might be regarded as the ancestor of the majority of the genera. This species also has a tubular perianth, but little condensation of the inflorescence, no tendency towards zygomorphy, a comparatively simple bulb, and free filaments. From *Massonia*, *Androsiphon*, *Amphisiphon* and *Daubenya* are readily derived. *Whiteheadia* may be nearer the common origin rather than derived from any existing group, and *Eucomis* and *Whiteheadia* probably deviated from one another comparatively recently. Polyxena, except for the membranous scale leaf and insertion of the filaments, is probably close to Massonia. Lachenalia has not diverged far from Polyxena, with L. pusilla as a possible link. Table 27 indicates relationships within the group.

5.2.3 The Scilla-Ornithogalum group

This group has not been investigated in as much detail as the other two.

Ornithogalum, a wide-spread genus, may have retained most of the primitive floral characters, close to those of Drimia and the hypothetical primitive member of the Massonia group. Albuca has retained very similar bulb and floral characters in its section Falconera, but the links are even more obvious in A. aperta which has a slender style, spreading perianth segments and six equally developed anthers. Verdoorn (1959) wrote of this species: "..... while it may be considered a border-line species, its affinities are with Albucas in general and only with a small group of Ornithogalum species". It is with the Suaveolens group of Ornithogalum that there is the strongest link.

Dipcadi, Scilla and Galtonia can be derived by fairly small stages from the Ornithogalum type, e.g. fusion of the filaments or perianth segments. The genera occurring only in Madagascar or Eurasia have not been investigated by the present author, although it is believed that Muscari and Hyacinthus are very close to Scilla. Neopatersonia may prove to be polyphyletic, but its similarities are possibly close to the origins of Scilla and Pseudogaltonia, both of which also have connate filaments.

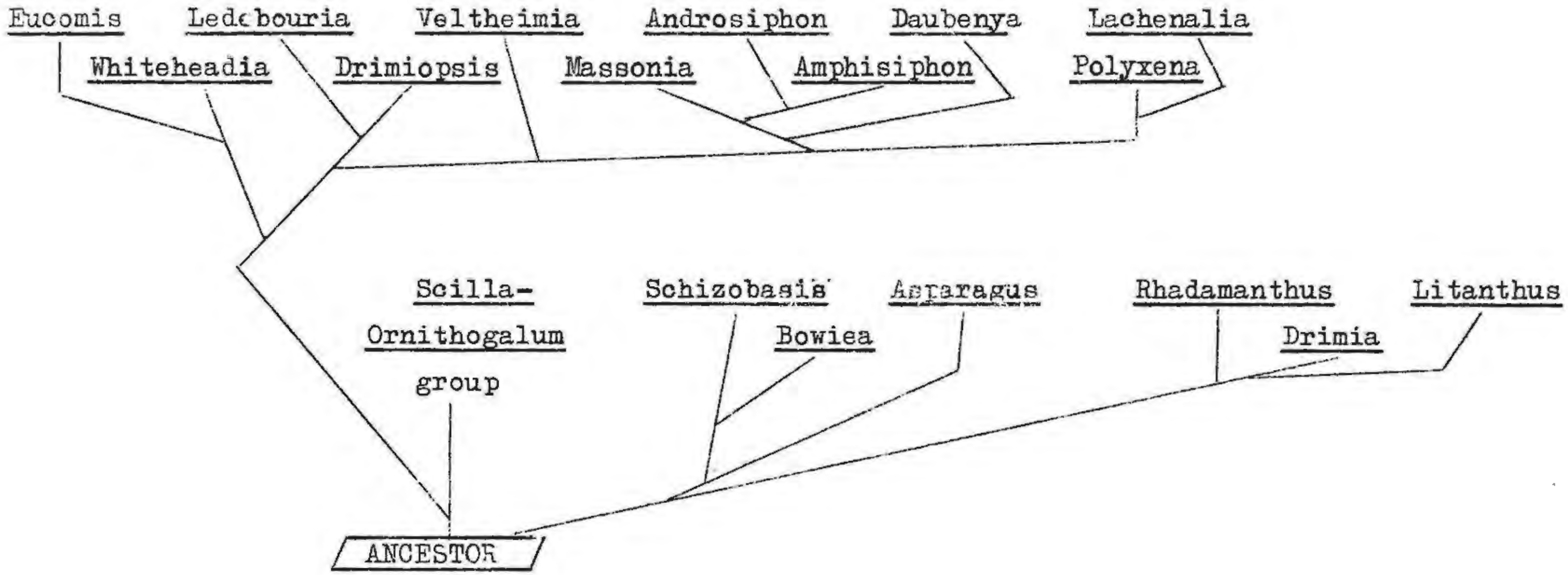


TABLE 27

Suggested relationships between the South African Scilleae (excluding the Scilla-Ornithogalum group). The names of genera have only been placed on different levels because of limitations of space.

PART 6

ARTIFICIAL KEY TO THE GENERA OF SOUTH AFRICAN BULBOUS LILIACEAE

1 Inflorescence branched; without foliage leaves.

  2 Stems wiry, erect or rarely climbing to less than 1 metre .. .. Schizobasis

  2a Stems succulent, climbing usually to more than 1 metre .. .. Bowiea

1a Inflorescence simple or, if branched (Scilla firmifolia) then with synanthous foliage leaves.

  3 Filaments connate at the base.

    4 Flowers arcuate; bulb scales with fibrous apices .. .. Pseudogaltonia

    4a Flowers straight; bulb scales rarely with fibrous apices.

      5 Inflorescence over-topped by a distinct coma .. .. Eucomis

      5a Inflorescence without a coma or, at most, with a few inconspicuous sterile bracts. ..

        6 Perianth segments free or, if fused, not forming a distinct tube.

          7 Perianth ascending, often cucullate; placentation of ovules basal Drimiopsis

          7a Perianth spreading; placentation of ovules axile .. .. Scilla

6a Perianth segments fused to form a distinct tube.

8 Leaves narrowly linear; inflorescence a lax raceme .. *Neopatersonia*

8a Leaves usually ovate or ellipsoid; inflorescence a dense raceme or head.

9 Inflorescence elongate; flowers green and succulent .. *Whiteheadia*

9a Inflorescence capitate or, if elongate, flowers not green and succulent.

10 Filaments fused to form a tube at least 10 mm long.

11 Filaments attached to perianth tube below the middle of the tube .. .. *Amphisiphon*

11a Filaments attached to perianth tube at mouth .. .. *Androsiphon*

10a Filaments fused to form a tube under 10 mm long . *Massonia*

3a Filaments free at the base.

12 Bracts, often only the lower, spurred, but sometimes early caducous.

13 Anthers dehiscing apically .. *Rhadamanthus*

13a Anthers dehiscing longitudinally.

14 Perianth tube long, cylindrical .. .. Litanthus

14a Perianth segments free or, if fused, not forming a cylindrical tube .. .. Drimia

12a Bracts not spurred.

15 Perianth tube none; stamens hypogynous or inserted at the base of the perianth segments.

16 Bulb scales tubular at least at the base; leaves more or less uniformly green; ovary with more than 2 ovules per locule .. .. Ornithogalum

16a Bulb scales imbricate; leaves usually spotted or striped; ovary with 2 ovules per locule.

17 Perianth segments more or less ascending, often cucullate; ovary ellipsoid, sessile; leaves often petiolate .. .. Drimiopsis

17a Perianth segments usually spreading or reflexed; ovary conical, stipitate; leaves rarely petiolate .. .. Ledebouria

15a Perianth tube present; stamens inserted on the perianth tube.

18 Flowers (or at least the lower) zygomorphic.
  19 Inflorescence capitate; lower flowers strongly zygomorphic; upper flowers actinomorphic . Daubenya
  19a Inflorescence racemose; all flowers similar .. .. . Lachenalia
18a Flowers actinomorphic.
  20 Perianth segments distinctly dissimilar .. .. Dipcadi
  20a Perianth segments more or less similar.
    21 Ovary with two ovules per locule .. .. Veltheimia
    21a Overy with more than two ovules per locule.
      22 Bulb with a distinct tubular membranous sheath surrounding the base of the aerial parts .. .. Polyxena
      22a Bulb scales all fleshy.
        23 Inflorescence less than 300 mm long; usually capitate .. .. . Massonia
        23a Inflorescence over 300 mm long, racemose . Galtonia

PART 7

TAXONOMY OF SELECTED GENERA

7.1 Scilla L.

Sp. Pl.: 308 (1753)

Scilla sensu Bak. in Fl. Cap. 6 : 478 (1896), partly; sensu Phill., Gen. S. Afr. Flower. Pl.: 191 (1951), partly.

Schizocarphus Van der Merwe in Flower. Pl. S. Afr. 23 : t.904 (1943). Type species: S. nervosus (Burch.) Van der Merwe.

Bulbs present, sometimes fibrous towards the top. Leaves all basal, sometimes with reddish markings towards the base, but not spotted. Inflorescence erect, originating from the apical bud of the bulb, rarely branched. Bracts single or more often paired, with a small lateral bract (?bracteole), not spurred. Perianth segments similar or almost so, usually spreading. Filaments connate towards the base. Ovary ellipsoid, usually with more than 2 ovules per locule. Ovules axile. Fruit a capsule.

Type: S. bifolia L., from Europe.

The affinities of Scilla with South African genera in the Scilla-Ornithogalum group have not been fully investigated. It is worth mentioning, however, that Pseudogaltonia, in which the bulb fibres are similar to those in S. nervosa, has floral characters identical to those of Scilla except that the perianth is zygomorphic. Neopatersonia, whose taxonomic position is uncertain, also has connate filaments.

Key to the species of Scilla in South Africa

1 Perianth a vivid blue or purplish blue.

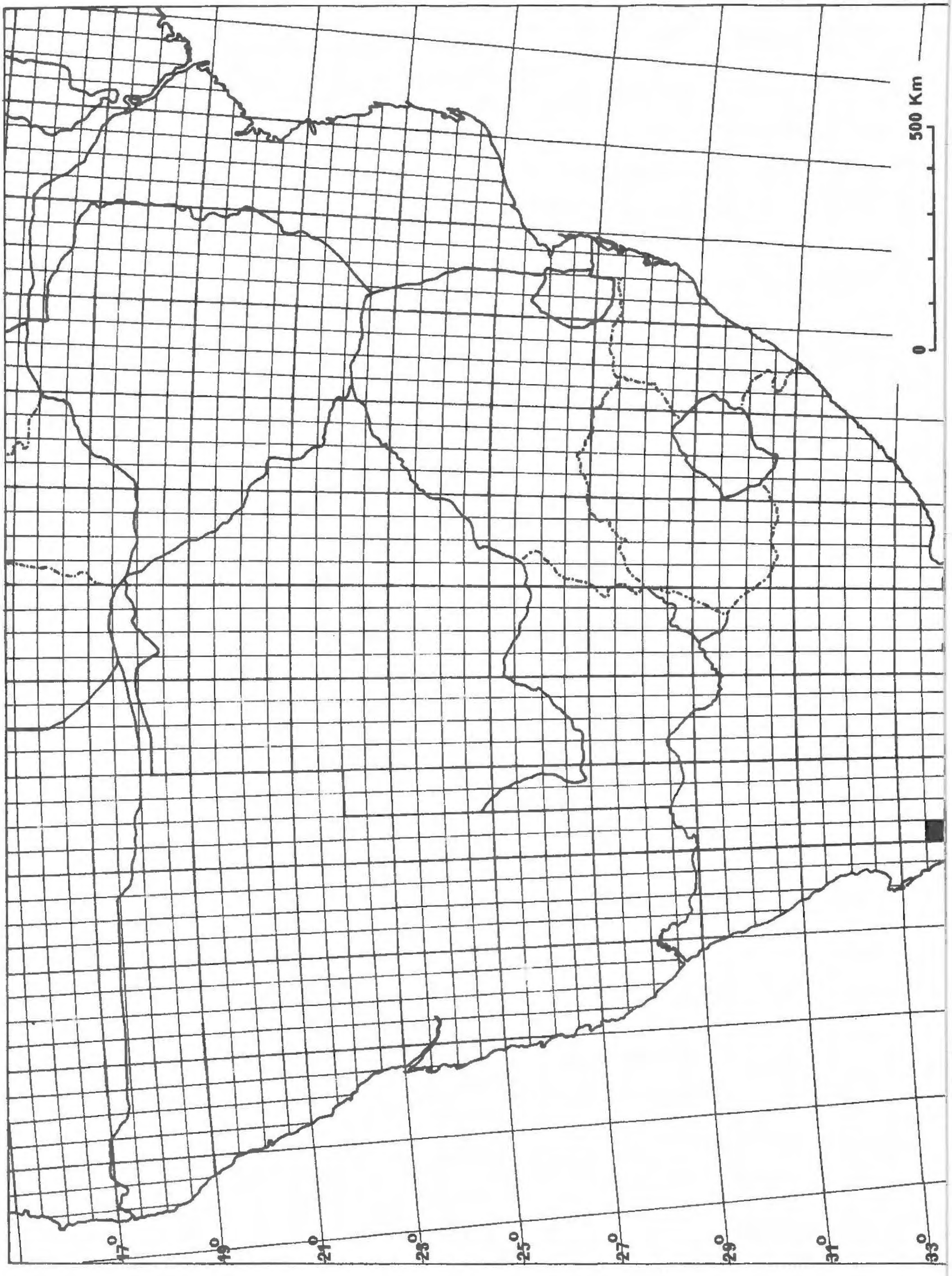
  2 Perianth segments ascending at the base, recurving from the centre; leaves linear to linear-lanceolate. Restricted to the south-western Cape .. .. 1. plumbea

  2a Perianth segments spreading; leaves lanceolate to ovate. Eastern Cape through Natal to the eastern Transvaal .. .. 2. natalensis

1a Perianth white, greenish or pale pink.

  3 Bulbs without fibrous tops; inflorescence sometimes branched; leaves usually less than 125 mm long. Restricted to the Alicedale, Bathurst, Peddie area .. .. 3. firmifolia

  3a Bulbs with fibrous tops; inflorescence always simple; leaves usually more than 125 mm long. Widespread .. .. 4. nervosa


17°
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1. Scilla plumbea Lindl. in Bot. Reg. 16 : t.1355 (1830). Type: Bot. Reg. 16 : t.1355 (1830), figured from a plant in cultivation in England.

Scilla ?natalensis sensu Bak. in Fl. Cap. 6 : 482 (1896), partly.

Bulb globose, 30-35 mm diameter, subterranean, solitary; the inner scales white, rather fleshy; the outer scales brown, membranous. Leaves hysteranthous, rosulate, 4-7, linear to linear-lanceolate, somewhat fleshy, usually 200-250 mm long, rarely exceeding 20 mm broad at the base, glabrous. Inflorescence solitary, up to 500 mm high, erect, straight. Pedicels up to 20 mm long, spreading to slightly erect-spreading. Flowers bluish mauve. Perianth segments very shortly fused towards the base, recurved from about the centre, c.10 mm long. Filaments linear, similar in colour to the perianth segments, shortly connate at base, slightly longer than the perianth segments. Ovary deeply 3-lobed, obovoid, c.3 mm long. Style slightly declinate, slightly shorter than the perianth; stigma not differentiated. Capsule distinctly 3-lobed, obovoid.

Restricted to the south-western Cape (see map 2) in the vicinity of Bains Kloof. Formerly recorded from

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Opposite- Map 2. Distribution of Scilla plumbea.

Baviaans Kloof to the south of Bains Kloof but possibly now extinct in that locality. A colony of about 100, in a permanently damp slope next to the road on the eastern side of Bains Kloof, has been examined by the author.

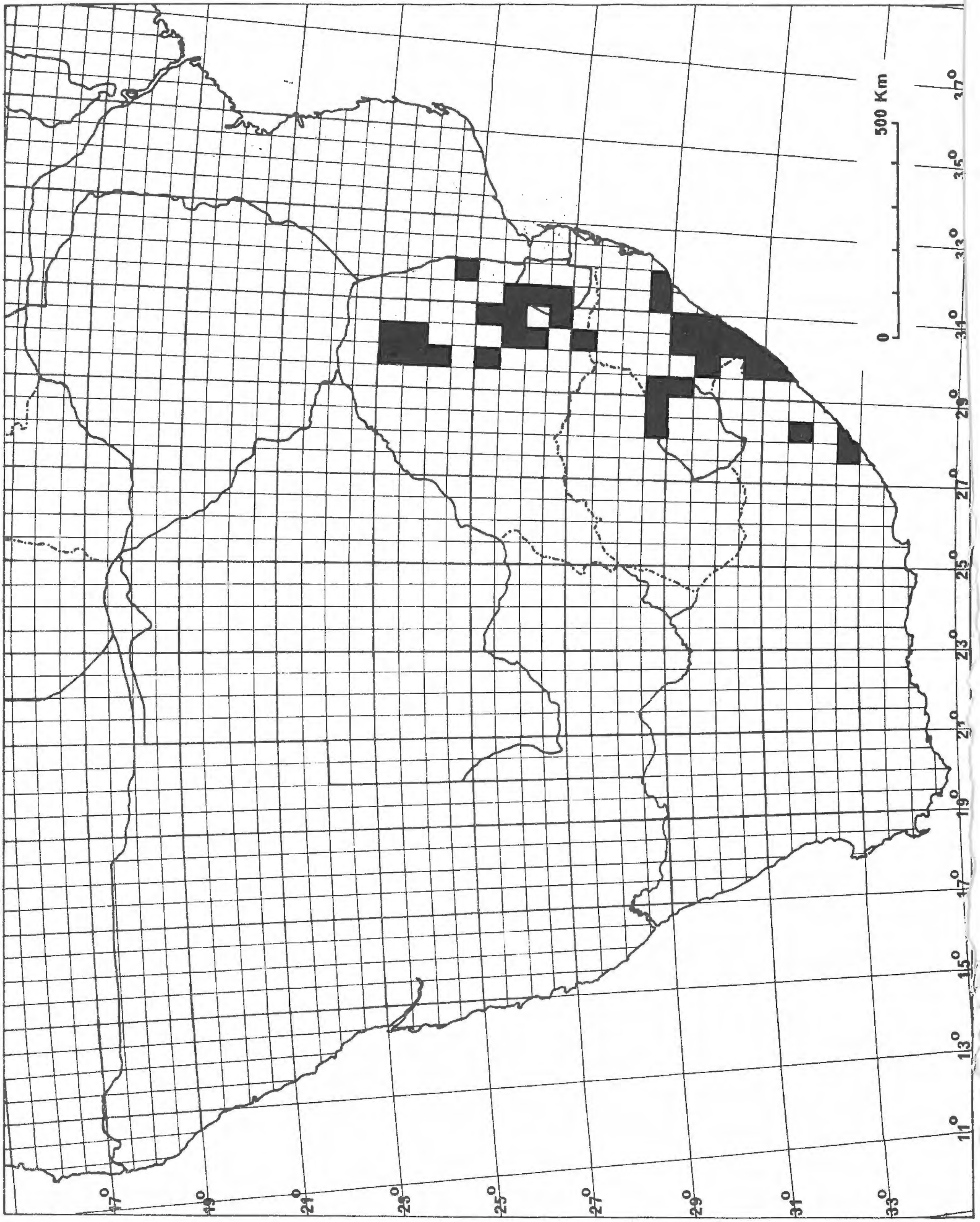
Flowers appear in December and January.

The texture of the bulb and leaves is reminiscent of a species of Ornithogalum or Lachenalia rather than of a Scilla. But the floral structure, especially the connate filaments, places it in Scilla. The absence of lignified bundle caps is also atypical for South African (but not European) species. Its geographical isolation, with the next Scilla species in the eastern Cape, suggests that if it is correctly placed in Scilla, it probably is a very early derived member.

No specimen appears to have been preserved of the plant on which Lindley based S. plumbea. It was illustrated growing in the Royal Botanic Gardens, Kew, in 1813, and there is no doubt as to the correct application of the name on the basis of the figure which has been selected as the type.

For illustration, see Lewis, G.J. in Flower. Pl. Afr. 26 : t.1006 (1947).

For list of specimens examined, see appendix, p. 1.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2. Scilla natalensis Planch. in Flore des Serres: t.1043 (1855). Type: Flore des Serres: t.1043 (1855).

Scilla kraussii Bak. in J. Linn. Soc. (Bot.) 13 : 243 (1873). Type: "Natalia", Krauss 444 (K, lecto., PRE, photo.!; TCD!), without locality, Gerrard 740.

Bulb usually ovoid, c.40-90 mm long, subterranean or epigeal, often densely colonial, the bulbs remaining attached to a woody stock; scales rather firm; the outer scales membranous to firm, yellowish brown. Leaves synanthous, but usually very small at flowering, rosulate or, less often, distichous, 4-10, ovate to linear-lanceolate, firm and often with prominent veins, (10-)15-250(-330) mm long, glabrous to densely pubescent, sometimes mauve or purple on the lower surface. Inflorescence usually solitary, (35-)100-600(-800) mm long, erect, straight. Bracts paired. Pedicels usually less than 25 mm long, more or less spreading. Flowers blue to mauve. Perianth segments free, spreading from the base, elliptic to ovate-elliptic, 4-9 mm long. Filaments elliptic to lanceolate, narrowing towards the base, connate, blue or white, shorter than the segments. Ovary 3-grooved, globose, c.2-3 mm long. Capsule 3-lobed.

Occurs in the eastern Cape as far west as Kentani, Lesotho, Natal, Swaziland, eastern O.F.S., and Transvaal

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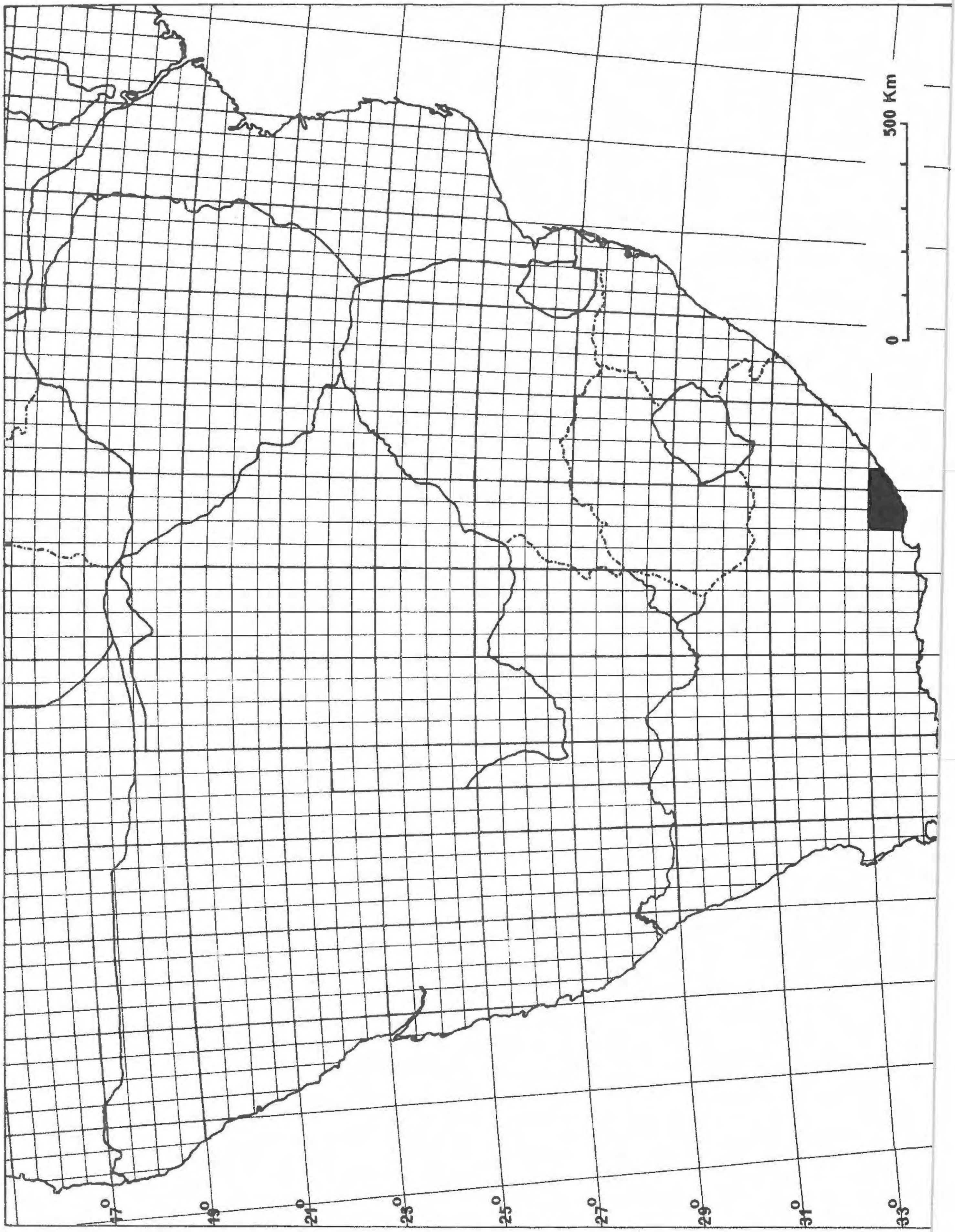
Opposite- Map 3. Distribution of Scilla natalensis.

mainly along the escarpment. It grows in both open grassland and among rocks. See map 3.

Flowers in summer.

In the south of its range, the leaves of the larger plants (peduncles more than 300 mm long) are glabrous but the leaves of small plants are pubescent. In the Transvaal, where small forms do not generally occur, they are almost always pubescent. On Rogers 12507 (BOL) is a note that in the Tzaneen area, although usually pubescent, the leaves are glabrous in plants growing in a vlei or garden.

It has been extremely difficult to decide whether or not to give the larger and smaller forms taxonomic recognition. In view of the evidence that pubescence may not be entirely a genetically determined phenomenon and in view of the range in size of the pubescent-leafed plants, only a single taxon is recognised here. A further form, with distichous leaves, appears to be a local variant of the small form. Fig. 281, showing the relationship between peduncle length, leaf length and pubescence, illustrates the practical difficuly involved in defining taxa within this concept of S. natalensis. Owing to difficulties in identification, the distichous form could not be identified on the figure. Populations examined by the present author near Kamberg and the Oliviershoek Pass (Natal) and near Tzaneen exhibited such a range in size of plant and pubescence that it did not appear likely that any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subdivision of this complex would serve any useful purpose.

S. natalensis is probably more closely related to the northern hemisphere species of Scilla than any of the other South African species are.

No specimen, with which to typify S. natalensis, has been located, but the readily identifiable illustration cited above serves as adequate type material.

For illustrations see Van der Merwe, F.Z. in Flower. Pl S. Afr. 21 : t.822 (1942) and Pole Evans, I.B. (editor), Flower. Pl. S. Afr. 10 : t.365 (1930).

For list of specimens examined, see appendix, p. 1.

3. **Scilla firmifolia** Bak. in Saund., Ref. Bot. 3, app.: 7 (1870). Type: "Cape of Good Hope", MacOwan 461 (K, lecto., PRE, photo.!; GRA!; PRE!; TCD!), "Eastern frontier", Drege 4492 (K, PRE, photo.!).

Bulb ovoid, not usually over 30 mm long, usually more or less below the ground, often densely colonial; the bulbs adhering but without a substantial woody stock; the inner scales moderately fleshy, whitish to orange; the outer few scales membranous. Leaves synanthous, rosulate, 4-7, sublinear, channelled on the face, rather firm, usually up to 200 mm long, glabrous. Inflorescence usually solitary, often with a single branch from the lowest bract,

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Opposite- Map 4. Distribution of Scilla firmifolia.

usually 200-300 (up to 450) mm long, straight, erect. Bracts paired. Pedicels 5-10 mm long, erect-spreading. Flowers white or pale pink, usually darker coloured in the median axis of the segments. Perianth segments free, spreading from the base, oblong or oblong-elliptic, 4-5 mm long. Filaments sublinear, connate towards the base, white or pale pink, shorter than the perianth segments. Ovary 3-lobed, obovoid to elliptic, c.1,5-2,0 mm long. Style sublinear; stigma capitate.

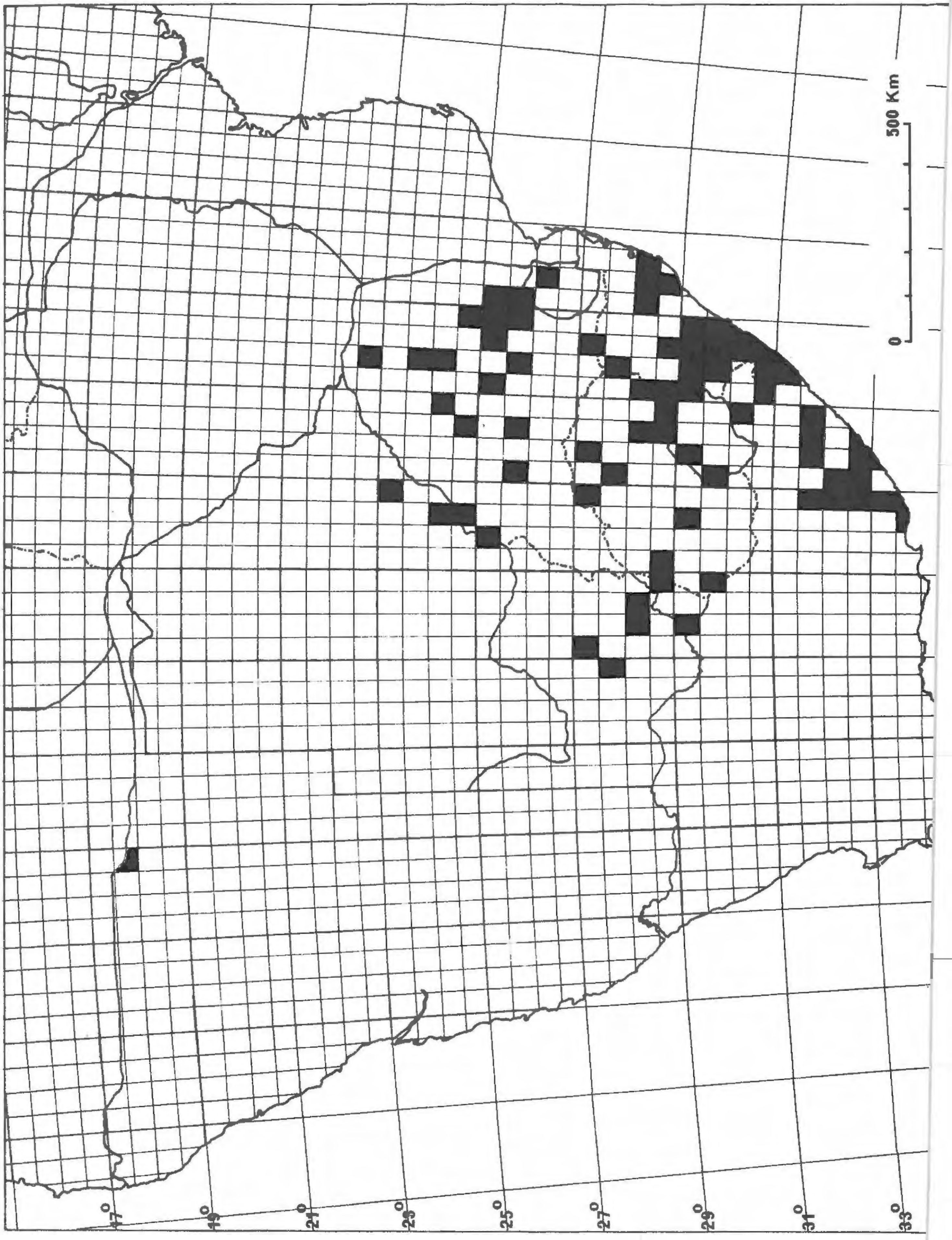
Restricted to a small part of the eastern Cape from Alexandria to Peddie and inland as far as Alicedale.

Van der Merwe's comment (Flower. Pl. Afr. 24 : t.296; 1944) that it had "been recorded over a wide area from Pondoland to the neighbourhood of Port Elizabeth" could not be substantiated, although the figure's identity with the present author's concept of S. firmifolia is without doubt. See map 4.

It occurs in rocky places and in both exposed dry areas and grassveld.

This is the only species of Scilla in South Africa in which the inflorescence is branched. Whether this is a primitive or advanced character is not known; in Drimia and Schizobasis, branching is thought to be advanced.

Its affinities are probably closest to S. nervosa, but the absence of fibres on the upper parts of the bulb and smaller size - especially in the flowers - afford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satisfactory characters for separating these species.

For illustration, see Van der Merwe, F.Z. in Flower. Pl. Afr. 24 : t.926 (1944).

For list of specimens examined, see appendix, p. 4.

4. Scilla nervosa (Burch.) Jessop, comb. nov.

Ornithogalum nervosum Burch., Trav. 1 : 537 (1822). Type: Cape, "between Griquatown and Witte Water", Burchell 1968 (K, holo., PRE, photo.!).

Schizocarphus nervosus (Burch.) Van der Merwe in Flower. Pl. S. Afr. 23 : t.904 (1943).

Scilla rigidifolia Kunth, Enum. Pl. 4 : 330 (1843). Type: Cape, Drege 4560b (K, PRE, photo.!).

Schizocarphus rigidifolius (Kunth) Van der Merwe in Flower. Pl. S. Afr. 23 : t.905 (1943).

Scilla pallidiflora Bak. in Saund., Ref. Bot. 3 : t.179 (1870). Type: Saund., Ref. Bot. 3 : t.179 (1870), no herbarium material located.

Scilla versicolor Bak. in Saund., Ref. Bot. 5 : t.305 (1873). Type: Saund., Ref. Bot. 5 : t.305 (1873), no herbarium material located.

Scilla gerrardii Bak. in J. Linn. Soc. (Bot.) 13 : 237 (1873). Type: "Natalia", Gerrard 1829 (K, lecto., PRE, photo.!), "Kaffraria", Hutton s.n., not located.

Schizocarphus gerrardii (Bak.) Van der Merwe in Flower.

Opposite- Map 5. Distribution of Scilla nervosa.

Pl. S. Afr. 23 : t.906 (1943).

Scilla pubescens Bak. in Bull. Herb. Boissier, ser. 2, 1 : 853 (1901). Type: Natal, near Howick, Schlechter 6799 (Z!).

Schizocarphus acerosus Van der Merwe in Flower. Pl. S. Afr. 23 : t.904 (1943). Type: Transvaal, Middelburg, Elandspruit, Van der Merwe 2236 (PRE!).

Bulb usually ovoid, 30-50 mm long, subterranean, solitary or forming small groups; scales moderately fleshy, white or cream-coloured, ending distally in firm fibres (persistent tissue associated with the veins of the leaves). Leaves synanthous, rosulate, firm, glabrous or pubescent, usually 3-7, linear to linear-elliptic, (20-)100-300(-400) mm long, (1-)5-30(-50) mm broad. Inflorescence usually solitary, less often paired, usually 100-200 mm high, erect, straight. Bracts paired. Pedicels erect-spreading or spreading, from less than 10 mm up to 50 mm or more long. Flowers white, usually with green in the median axis. Perianth segments free, spreading, usually 3-5 mm long, more or less elliptic. Filaments sublinear, narrowing gradually from the base, connate towards the base, shorter than the perianth segments, white; anthers yellow or blue to purple. Ovary green to blue, ovoid, 3-lobed or fairly deeply 3-grooved, often contracting very abruptly at the base to a short pedicel, usually 1,5-2,0 mm long; stigma not distinctly differentiated.

Capsule 3-lobed, subellipsoid.

Occurs throughout the eastern Cape from Alexandria eastwards through Lesotho and Natal into the northern Cape, O.F.S., Swaziland, Transvaal and Botswana as far north as Angola and Tanzania. See map 5.

Grows in open grassveld, but also among rocks.

Flowers in summer.

Attempts at subdividing the complex on the basis of leaf measurements, as used by Van der Merwe, have not been found useful. Within a single population, the variation in leaf size is considerable (see fig. 282). Variation over the whole range of this species, as defined in the present work, appears to be insufficiently interrupted to justify subdivision (see fig. 283). Van der Merwe's statement (Flower. Pl. S. Afr. 23 : t.904; 1943) that: "These (the several species he recognised in the complex treated here as a single species) resemble each other very closely, and are distinguishable mainly by the width of their leaves, the relative prominence of the veins, and the average sizes of the racemes." is not acceptable by the present author. The considerable data now available from herbarium sheets, together with field observations, does not appear to justify the use of any of these characters as specific or even subspecific diagnostic criteria.

For specimens examined see appendix, p. 5.

7.2 Ledebouria Roth

Novae plantarum species : 194 (1821).

Scilla sensu Bak. in Fl. Cap. 6 : 478 (1896), partly; sensu Phill., Gen. S. Afr. Flower. Pl. : 191 (1951), partly.

Bulbs present, never fibrous towards the top. Leaves all basal, often with reddish or green spots or markings, especially on the upper surface. Inflorescence usually cernuous, axillary in origin, always simple. Bracts poorly-developed, single or paired, not spurred. Perianth segments reflexed to ascending. Filaments free of one another. Ovary conical, expanding to a wide base below which it contracts abruptly to a short pedicel, with two ovules per locule. Ovules basal. Fruit a capsule.

Type: L. hyacinthina Roth (= S. indica Bak.), from India. (For figure, see Curtis's bot. Mag. 60 : t.3226; 1833.)

Species concepts in Ledebouria

It has been found that the members of a population do not vary greatly except in size. An example to illustrate the variation encountered in a small population has been included (fig. 285). This shows that there may be a fairly wide spread of sizes and proportions of the leaves.

In Ledebouria there are very few qualitative characters that could be used in taxonomic work. The distribution and form of spotting or marking of the leaves have been found to be extremely inconsistent in almost all populations. Similarily, whether the leaves are erect or prostrate is greatly influenced by both the time of the year and climate and the height and density of the surrounding vegetation.

Floral characters are of great value in delimiting genera, but there is little variation within Ledebouria.

It has been found that whether a broad or a narrow concept of the species limits is taken, intermediates occur between even the largest and smallest members of the genus. There are very few species of Ledebouria which are defined on really satisfactory qualitative characters. These are L. hypoxidioides, L. viscosa, L. scabrida, L. ovatifolia and perhaps L. luteola. The remainder are based on less well-defined characters and most show very considerable amounts of variation.

One possible explanation for the difficulty in defining species may be a predominance of non-sexual reproduction, particularly apomixis. Apomictic groups are notoriously difficult to describe in terms of conventional taxonomy. It would be very helpful to know to what extent, if any, apomixis occurs in Ledebouria. The possibility seems to be supported by the rarity of fruits. Even in hand-pollinated flowers, seeds are frequently not produced. The cytological evidence shows that meiotic abnormalities do occur, although they may not be sufficiently frequent to support the possibility of a high frequency of homologous chromosome incompatibility.

In eight plants examined by the present author, by the method of Alexander (1969), one showed 60% sterility of pollen, but half the plants showed less than 10% sterility. Little or no success has been had with the germination of pollen on cellophane using the method found satisfactory by Wilsenach and Papenfus (1967). The occasional presence of aborted flower buds on otherwise normal inflorescences (especially towards the base) may indicate abnormalities in floral morphogenesis, which might possibly also extend to the sexual parts of apparently normal flowers.

No conclusion as to the presence or absence of apomixis can, therefore, be reached at this point. Embryo sac studies and investigation of pollen tube development in styles (possibly by fluorescence microscopy) might ellucidate these problems.

Other than purely quantitative characters, the following appear to be the most important:-

1) bulb characters: whether or not there is a neck is probably influenced by the environment, but certain species, e.g. L. undulata, exhibit this character more frequently than do other species. The type of bulb in L. ovatifolia is usually recognisable; the outer scales are progressively shorter than the inner scales,

leading to a step-like appearance. The L. cooperi type of bulb, in which there are relatively few scales, which are more loosely packed than in other species and not usually surrounded by membranous scales, is rather characteristic.

2) leaf characters: trichomes occur in a few species and are usually diagnostic, but there are forms of L. revoluta in which there is a slight tendency towards the development of a ciliate margin or short hairs on the surface, without this developing sufficiently regularly to justify its use in separating additional taxa. Leaf shape is considered to be extremely susceptible to environmental conditions and possibly subject to frequent minor genetic variation.

3) floral characters: colour has been used as a supporting character in L. cooperi where a uniform pink is diagnostic, but other colour patterns also occur. No significant variation was found in qualitative floral characters.

In view of the lack of qualitative characters and in the presence of a very considerable morphological variation within the genus, the need was recognised for delimiting species on purely quantitative characters. To a large extent it has been found necessary to erect almost artificial criteria for subdividing continuous ranges in, for example, leaf length - as in separating L. revoluta and L. floribunda. However, in doing so, attention is given to defining taxa which will be readily recognisable and of greatest practical value. Attention is drawn in the text accompanying each species description to those species whose separation is not considered entirely satisfactory.

Key to the species of Ledebouria in South Africa

1 Bulb small, less than 25 mm long or, if longer, then less than one sixth of the length of the longest leaf at flowering, very rarely with any pink colour, often with only one membranous outer bulb scale. Leaves usually rather soft; the lamina of the outermost often greatly reduced or absent. Flowers and pedicels often uniformly pink.

  2 Bulb above ground, very rarely over 20 mm long. Leaves often with a silvery colour on the upper surface. Eastern Cape .. .. 4. socialis

  2a Bulb usually below ground. Leaves probably never with a silvery colour on the upper surface. Wide-spread.

    3 Bulb more than 40 mm long, with numerous tightly arranged scales .. .. .. 6. apertiflora

    3a Bulb 25-40 mm long, with fewer, relatively loosely arranged scales .. .. 2. cooperi

    3b Bulb less than 25 mm long, with few or many loosely or tightly arranged scales.

      4 Bulb with several dry outer scales which often form a neck. Leaves more or less erect,

not considerable narrowed to the base. Inflorescence variable. Flowers pink-striped, greenish or greyish. Mainly in dry areas .. .. 9. <u>undulata</u>

4a Bulb with several dry outer scales, never forming a neck. Leaves more or less spreading, narrowing considerably to the base. Inflorescence lax. Flowers pink-striped. Southern Cape west of Knysna .. . 1. <u>ovalifolia</u>

4b Bulb with very few (usually not more than 2 or 3) or no dry outer scales, which never form a neck. Leaves variable in shape. Inflorescence usually very compact. Flowers usually uniformly pink. Wide-spread east of Knysna .. ..2. <u>cooperi</u>

1a Bulb generally at least 30 mm long and more than one sixth of the length of the longest leaves at flowering, sometimes partly pink usually with several membranous outer bulb scales. Leaves firmer; the lamina of the outermost not appreciably smaller than the others. Flowers either greenish, greyish or with pink markings, but probably never uniformly pink.

5 Leaves distinctly scabrid on the ventral surface. Gobabis district of S.W.A. .. .. . 16. <u>scabrida</u>

5a Leaves viscid. Kransberg, Thabazimbi area of the Transvaal .. .. 15. <u>viscosa</u>

5b Leaves densely hairy. Grahamstown . 14. hypoxidioides

5c Leaves not distinctly scabrid, viscid or hairy.

6 Bulb scales of very different heights, all relatively firm, producing copious threads when broken. Leaves, at least towards the end of the flowering season, usually ovate and adpressed to the ground .. .. 13. ovatifolia

6a Bulb scales all reaching approximately the same height at the top of the bulb, the outermost forming dry tunics, not usually producing threads when broken (except in *L. luteola*). Leaves usually erect or erect-spreading and ovate to linear.

7 Bulb scales usually yellow, especially when dried, except for the few outer membranous ones, longitudinally ridged and producing thread when broken - these threads almost always showing on herbarium material.12. luteola

7a Bulb scales not as above.

8 Leaves over 150 mm long; usually much longer than the bulb at flowering.

9 Bulbs over 70 mm long. Flowers usually more than 150 per inflorescence .. .. 3. floribunda

9a Bulbs less than 70 mm long. Flowers usually fewer than 150 per inflorescence.

10 Leaves linear or narrowly linear-lanceolate, long attenuate, usually over 200 mm long, and less than 20 (-25) mm broad .. .. . 6. apertiflora

10a Leaves lanceolate to oblong-lanceolate, usually not very attenuate, and broadest near the middle, usually under 220 mm long, and more than 25 mm broad .. .. 7. revoluta

8a Leaves less than 150 mm long, often shorter than the bulb at flowering.

11 Leaves shorter than the bulb at flowering or, if longer, then lanceolate to ovate and more than 10 mm broad.

12 Leaves very glaucous, not very firm. Bulb tunics partly dark and shiny and usually with a pinkish wash .. 8. inquinata

12a Leaves not very glaucous, erect or spreading, variable in texture. Bulb tunics with or without dark shiny areas, but pink colour, when produced, generally in the form of speckling.

13 Leaves rather firm so that they retain their shape on the plant for several months after they have dried out, rather long attenuate in the distal half and usually spirally twisted .. .. 11. marginata

13a Leaves softer, wrinkling and disintegrating rapidly after their death, not as strongly attenuate or spirally twisted.

14 Bulb largely above ground. Leaves erect, usually undulate and uniformly green. Eastern Cape .. .. 5. *concolor*

14a Bulb below ground. Leaves erect-spreading to spreading, not undulate, usually spotted. Widespread .. .. 7. *revoluta*

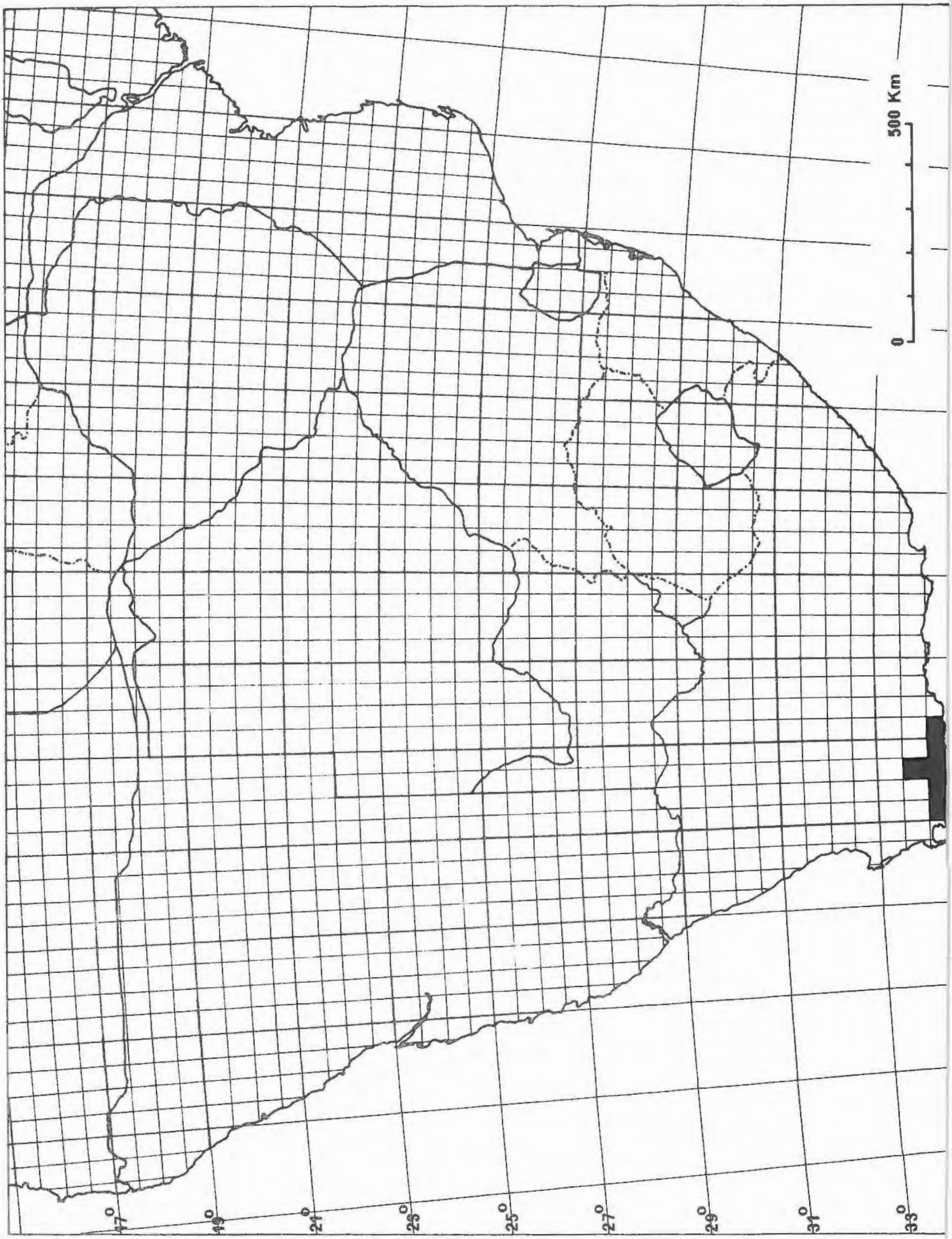
11a Leaves usually longer than the bulb at flowering, often linear to linear-lanceolate and less than 10 mm broad.

15 Leaves more than 200 mm long, linear or narrowly linear-lanceolate . 6. *apertiflora*

15a Leaves less than 150 mm long, lanceolate to linear.

16 Leaves usually 10 or more, usually twisted, less than 5 mm broad .. .. 10. *graminifolia*

16a Leaves usually fewer than 10, often 5-10 mm broad .. . 9. *undulata*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1. Ledebouria ovalifolia (Schrad.) Jessop, comb. nov.

Drimia ovalifolia Schrad., Blumenb.: 28 (1827). Type: Lodd. Bot. Cab.: 278, sub Drimia lanceaefolia, (1818).

Scilla ovalifolia (Schrad.) C.A.Sm. in Kew Bull. 1930 : 245 (1930).

Lachenalia reflexa Andr. Bot. Rep. 5 : t.299 (1803), nom illegit., non Thunb.

Drimia gawleri Schrad., Blumenb. : 30 (1827). Type: Curtis's bot. Mag. 33 : t.1380, sub Drimia lanceaefolia b, (1811).

Drimia lanceolata Schrad., Blumenb. : 28 (1827). Type: Andr. Bot. Rep. 5 : t.299, sub Lachenalia reflexa (1803).

Scilla lanceolata (Schrad.) Bak. in Saund. Ref. Bot. 3, app. : 14 (1870).

Scilla revoluta (L.f.) Bak. sensu Bak. in Fl. Cap. 6 : 485 (1896), non L.f.

Scilla genadendalensis Von Poelln. in Port. Acta biol., ser. B, 1 : 212 (1945). Type: Cape, Genadendal, Schlechter 10327 (BOL!, PRE!, Z!).

Scilla doratophylla C.A. Sm. in Kew Bull. 1930 : 245 (1930). Type: as for Drimia lanceolata Schrad.

Bulb 15-25 mm long. Leaves 3-5, 15-35 mm long, 6-11 mm broad, spreading or somewhat erect-spreading, with a distinctly petiole-like base; the sides of the leaf

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Opposite- Map 6. Distribution of Ledebouria ovalifolia.

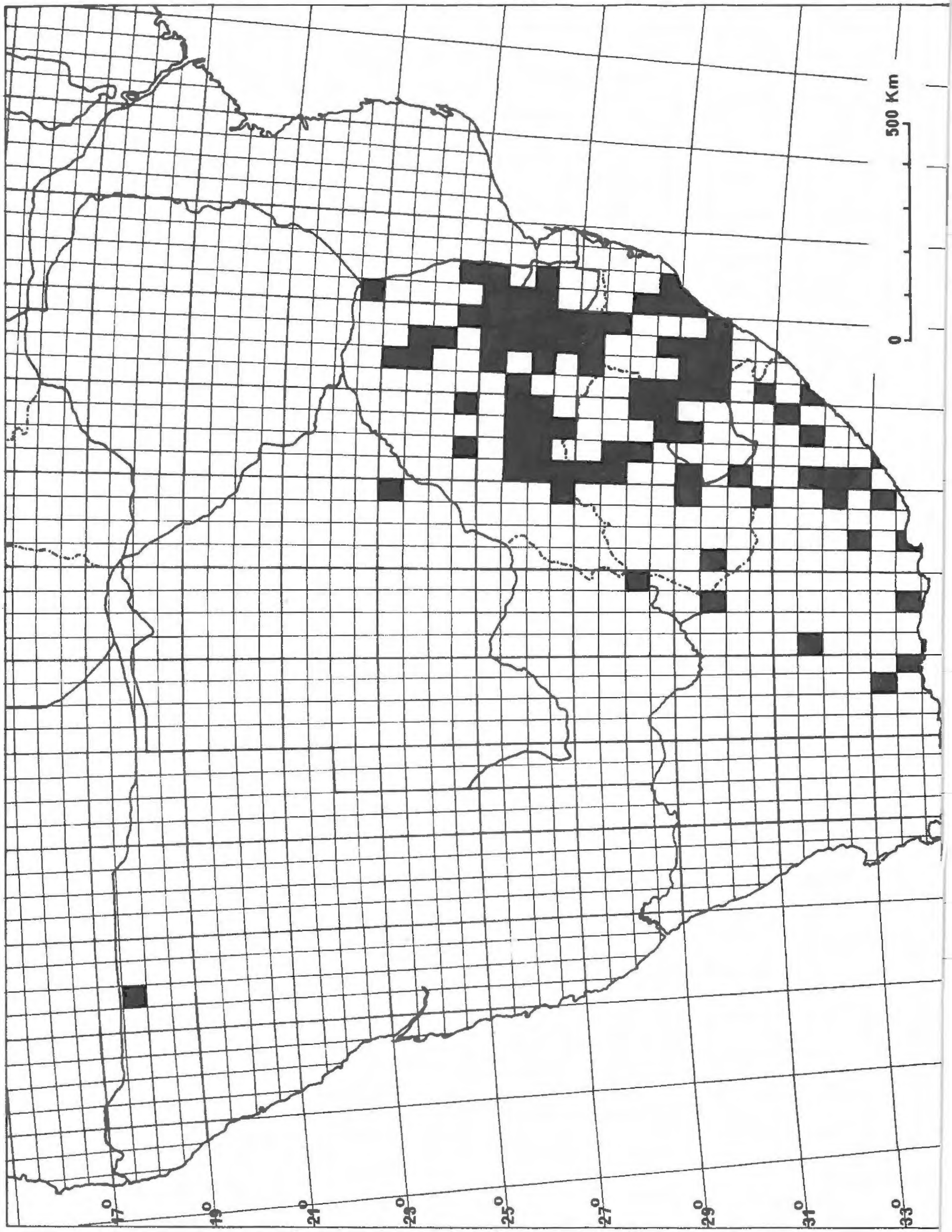
usually turned up towards the base, forming a gutter-like shape, the sides folded in in dried material. Inflorescence 60-90 mm long, with a rather lax arrangement of the spreading pedicels. Flowers usually fewer than 20, dull red.

Has been collected from Bot River, in the west, to Plettenberg Bay in the east; being restricted to the coastal belt, although occurring as far inland as Bonnievale. See map 6.

Records suggest a preference for rocky habitats.

In the east of its range this species merges with the smaller forms of *L. cooperi*. The leaf-form does not always provide adequate grounds for separation, but the laxer inflorescence in *L. ovalifolia* can generally be regarded as diagnostic. Confusion with *L. revoluta* is also possible, but the shape of the base of the leaf, the smaller bulb and the form of the inflorescence provide characters for separation.

For list of specimens examined, see appendix, p. 11.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2. *Ledebouria cooperi* (Hook.f.) Jessop, comb. nov.

Scilla cooperi Hook.f. in Curtis's bot. Mag. 92 : t.5580 (1866). Type: Cape, *Cooper* s.n. (K, holo., PRE, photo.!).

Scilla subglauca Bak. in Saund., Ref. Bot. 3 : t.186 (1870). Type: Saund., Ref. Bot. 3 : t.186, "Cape of Good Hope, *Cooper*", (1870).

Scilla sandersonii Bak. in Saund., Ref. Bot. 3, app.: 5 (1870). Type: Transvaal, *Sanderson* s.n. (K, holo., PRE, photo.!).

Scilla minima Bak. in Saund., Ref. Bot. 3, app. : 6 (1870). Type: Transvaal, Magaliesberg, *Burke* s.n. (K, holo., PRE, photo.!, BOL, drawing!).

Scilla concinna Bak. in Saund., Ref. Bot. 4 : t.235 (1870). Type: Saund., Ref. Bot. 4 : t.235, "Cape Colony" *Cooper*", (1870).

Scilla barberi Bak. in J. Linn. Soc. (Bot.) 13 : 247 (1873). Type: Cape, "ad ripas fluminosis Tsomo", *Barber* 1805 (TCD, holo.!).

Scilla exigua Bak. in J. Linn. Soc. (Bot.) 13 : 247 (1873). Type: Natal, Camperdown, Assegaai Kraal, *Sanderson* 670 (TCD, holo.!).

Scilla saturata Bak. in J. Bot., Lond. 1874 : 365 (1874). Type: Orange Free State, *Cooper* 993 (K, holo., PRE, photo.!).

Scilla macowanii Bak. in Gdnrs' Chron. 3 : 748 (1875). Type: Cape, "Somerset Division", Boschberg, *MacOwan* 1841

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opposite- Map 7. Distribution of *Ledebouria cooperi*

(BOL!; GRA!, PRE, photo.!; Z!).

Scilla pusilla Bak. in J. Bot., Lond. 1876 : 183 (1876). Type: Cape, Bazeia, *Baur* 293 (K, holo., PRE, photo.!, BOL, drawing!; SAM!).

Scilla adlamii Bak. in Gdnrs' Chron. 9 : 521 (1891). Type: Natal, *Adlam* s.n. (K, holo., PRE, photo.!, BOL, drawing!).

Scilla leptophylla Bak. in Fl. Cap. 6 : 483 (1896). Type: Transvaal, "near the Devil's Kantoor", *Bolus* 7623 (K, holo., BOL, drawing!; BOL!).

Scilla tysonii Bak. in Fl. Cap. 6 : 484 (1896). Type: Cape, "Griqualand East", *Tyson* s.n. (K, holo., BOL & GRA, drawings!).

?Scilla sphaerocephala Bak. in Fl Cap. 6 : 484 (1896). Type: Cape, Little Namaqualand, *Bolus* s.n. (Type not seen, determination from description. There appears to be no specimen at Kew or the Bolus Herbarium, but the description fits this concept of *L. cooperi* in every aspect - except that the locality has not been recorded for *L. cooperi*.)

Scilla inandensis Bak. in Fl. Cap. 6 : 483 (1896). Type: Natal, Inanda, *Wood* 630 (BOL!; NH!; SAM!); "near Tongaat", *Saunders* s.n.

Scilla globosa Bak. in Fl. Cap. 6 : 484 (1896). Type: Cape, near Kokstad, *Tyson* s.n. (?=*Tyson* 1557 in BOL!; SAM!).

Scilla baurii Bak. in Fl. Cap. 6 : 484 (1896). Type: Cape, "Tembuland, Bazeia Mountain", *Baur* 550 (K, holo., PRE, photo.!; SAM!).

Scilla rogersii Bak. in Fl. Cap. 6 : 486 (1896). Type: South Africa, *Rogers* s.n. (K, holo., PRE, photo.!).

Scilla leichtlinii Bak. in Fl. Cap. 6 : 486 (1896). Type: South Africa ex hort. Leichtlin (K. holo., PRE, photo.!, BOL, drawing!).

Scilla galpinii Bak. in Fl. Cap. 6 : 487 (1896). Type: Transvaal, "summit of Devil's Kantoor", *Galpin 672* (BOL!; GRA!; NH!, PRE, photo.!; PRE!; SAM!; Z!).

Scilla oostachys Bak. in Fl. Cap. 6 : 487 (1896). Type: Natal, "upper Umkomaas", *Wood* 4627 (K, BOL, drawing!; NH!, PRE, photo.!).

Scilla diphylla Bak. in Fl. Cap. 6 : 489 (1896). Type: Transvaal, "Saddleback range near Barberton", *Galpin* 1182 (K, holo., PRE, photo.!, BOL, drawing!; BOL!; GRA!; NH!; PRE!; SAM!; Z!).

Scilla palustris Wood & Evans in J. Bot., Lond. 1899 : 251 (1899). Type: Natal, Newcastle, *Wood* 6501 (NH, holo.!, PRE, photo.!).

Scilla rehmannii Bak. in Bull. Herb. Boissier, ser. 2, 1 : 853 (1901). Type: Natal, Inanda, *Rehmann* 8277 (Z!).

Scilla fehrii Bak. in Bull. Herb. Boissier, ser. 2, 1 : 788 (1901). Type: Transvaal, Pretoria, *Fehr* s.n. (Z!).

Scilla aggregata Bak. in Bull. Herb. Boissier, ser. 2, 4 : 1001 (1904). Type: Transvaal, Modderfontein, *Conrath* 701 (K, holo., PRE, photo.!; GRAZ, PRE, photo.!).

Scilla tristachya Bak. in Bull. Herb. Boissier, ser.2, 4 : 1001 (1904). Type: Transvaal, Modderfontein, *Conrath*

693 (GRAZ, PRE, photo.!, BOL, drawing!; Z!).

Scilla londonensis Bak. in Bull. Herb. Boissier, ser. 2, 4 : 1002 (1904). Type: Cape, East London, *Conrath* 694 (GRAZ, PRE, photo.!).

Scilla conrathii Bak. in Bull. Herb. Boissier, ser. 2, 4 : 1002 (1904). Type: Transvaal, Modderfontein, *Conrath* 132 (GRAZ, PRE, photo.!; K, PRE, photo.!).

Scilla lepida N.E. Br. in Kew Bull. 1921 : 299 (1921). Type: Transvaal, Palala River, *Breyer* s.n. in Herb. Rogers 24009 (K, holo., PRE, photo.!, BOL, drawing!; PRE!).

Scilla bella Markotter in Annale Univ. Stellenbosch, reeks A, 8, afl. 1 : 13 (1930). Type: Natal, Oliviershoekpas, *Thode* s.n. in STE 3372 (STE, holo., PRE, photo.!).

Scilla cinerascens Van der Merwe in Flower. Pl. S. Afr. 21 : t.827 (1941). Type: Transvaal, Piet Retief, Wolwekop, *Van der Merwe* 1119 (PRE, holo.!).

Scilla rupestris Van der Merwe in Flower. Pl. S. Afr. 21 : t.828 (1941). Type: Transvaal, Pilgrim's Rest near Mac Mac and Sabie, *Van der Merwe* 1586 (PRE, holo.!).

Scilla petiolata Van der Merwe in Flower. Pl. S. Afr. 21 : t.832 (1941). Type: Transvaal, near Graskop, *Strydom* s.n. (PRE, holo.!).

Scilla glaucescens Van der Merwe in Flower. Pl. S. Afr. 23 : t.912 (1943). Type: Transvaal, Carolina, Onbekend, *Van der Merwe* 2073 (PRE, holo.!).

Bulb usually lacking, or with only a few, dark membranous outer scales, usually much shorter than the leaves, generally under 40 mm long. Leaves usually 1-3, (10-)30-250(-400) mm long, 1-20(-50) mm broad, erect, soft and slightly fleshy, often narrowing appreciably to the base, oblong, ovate or linear, but rarely attenuate; the outermost leaf usually much shorter than the others, entirely clasping the bulb and hardly possessing any green colouring. Inflorescence usually more or less erect, usually with fewer than 50 flowers. Perianth segments often a very uniform pink colour, less often green or pink with a green keel.

Wide-spread in South Africa except in the drier western areas and the south-western Cape. Probably rare in South West Africa, but extending northwards into Rhodesia. The type of L. sphaerocephala has not been located but was reported to have been collected in Namaqualand. See map 7.

It frequently occurs in dampish areas in the grassveld, but also on slopes and among rocks.

Vegetative reprodcution by runners has been reported from near Belfast (Van der Merwe 1829; PRE).

There is very considerable morphological variation within this concept of L. cooperi. A number of series are indicated below. Whether or not these will prove to be worthy of taxonomic recognition has not been determined with any certainty, but it does appear that the degree of overlap between these series is such as to preclude their recognition at specific level. As the present author does not wish to accord these series taxonomic significance, it is suggested that, where it is desired to refer to them, their validly published epithets under Scilla, be used to identify them. Fig. 284 indicates the three most important leaf characters and demonstrates the difficulty which would be encountered in using any of these in distinguishing meaningful taxa.

The following series represent the more obvious morphological forms of L. cooperi. The epithets attached to them would be the correct names if the series were raised to specific rank. Because of the merging of these series with one another, it has not been attempted to indicate the series in the list of specimens cited in the appendix (p. A-12).

Cooperi series: leaves linear-lanceolate, 160-300 mm long, about 20 mm broad.

This series merges with L. apertiflora, but has a smaller bulb with fewer scales and narrower softer leaves, and often showing the characteristic longitudinal lines on the abaxial surface of the leaves and the reduced leaf lamina which is a frequent feature of specimens of L. cooperi. It also merges with L. floribunda, but the same characters may generally be used to distinguish it and, in addition, the fewer-flowered inflorescences. For illustration see Flower. Pl. S. Afr. 24 : t.943 (1944).

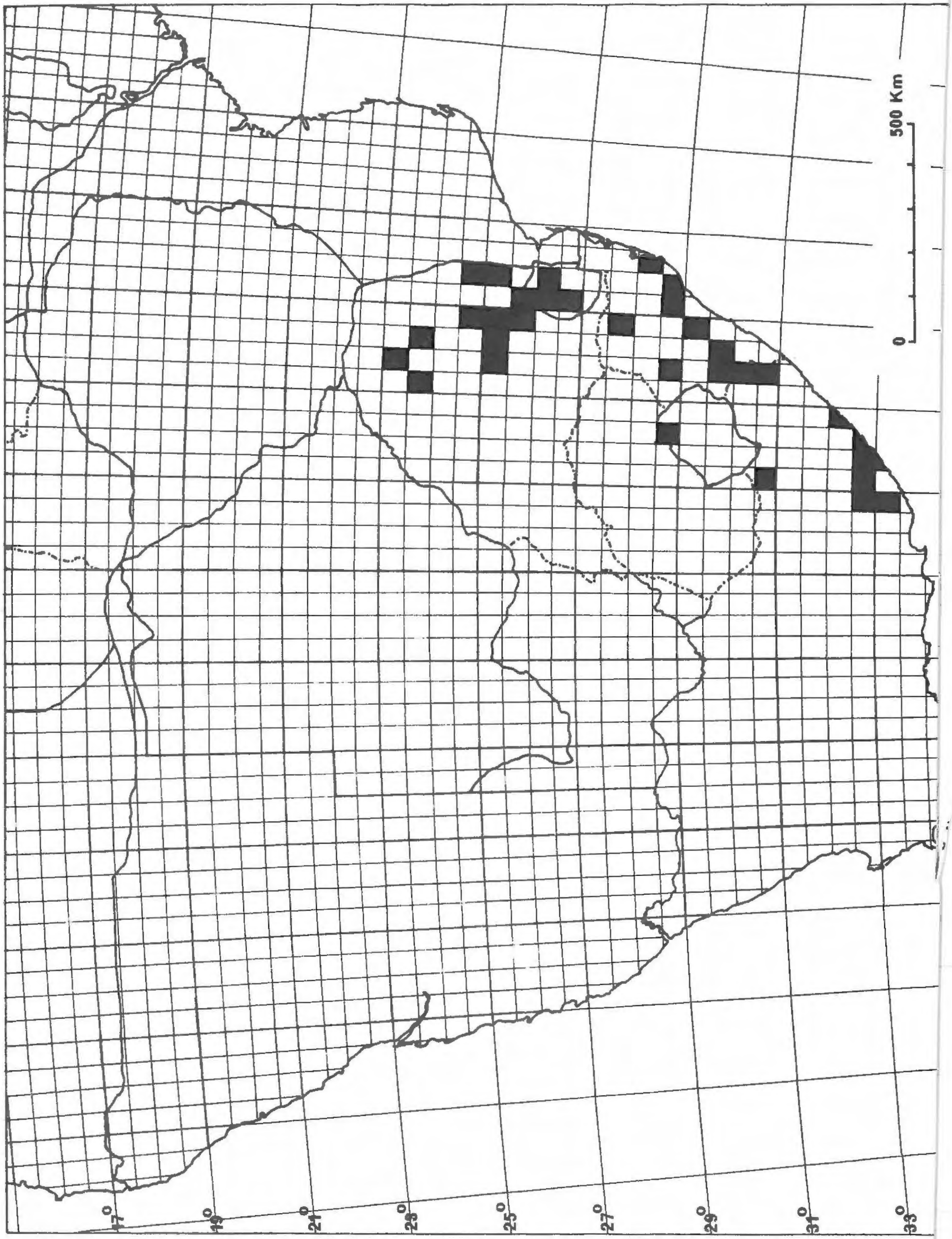
Saturata series: a smaller edition of the cooperi series.
Leaves up to 100-150 mm long, about 10 mm broad.
It is through this series that a gradation occurs between L. cooperi and L. ovalifolia of the south-western Cape. However, the inflorescence is generally more compact, and the leaves more strongly erect. For illustration see Flower. Pl. S. Afr. 17 : t.674 (1937).

Sandersonii series: similar to the saturata series, but smaller and with ovate or lanceolate to almost orbicular leaves, often distinctly petiolate.
For illustration see Flower. Pl. S. Afr. 21 : t.832 (1941).

Minima series: similar to the previous series but with narrowly linear leaves.

Galpinii series: similar to the sandersonii series but with the surface of the leaf pitted.
Probably restricted to the south-eastern Transvaal (2530 degree block). For illustration see Flower. Pl. S. Afr. 22 : t.864 (1942).

The difficulty in giving these series, other than the galpinii series, which is characterised by an apparently qualitative difference, taxonomic status is illustrated by means of a scatter diagram (fig. 284) in which the three main leaf variables are indicated. Differences in leaf size are largely genetic, but environment as well as the stage of leaf growth in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relation to flowering probably add to the difficulty of using quantitative leaf characters in defining taxa in this species complex. The *galpinii series* differs from the *sandersonii series* only in the pitting of the leaf. The fact that this is the only difference and some evidence that this is not always clear-cut motivated the decision to retain this series within *L. cooperi*. The *galpinii series* appears to be the only one which is limited to only a small part of the range of the species complex as a whole.

Specimens occur linking the *L. cooperi* complex with several other species; in particular *L. ovalifolia*, *L. graminifolia* and *L. undulata*. The smaller bulb, and frequently uniformly pink flowers are useful characters. Although several specimens, placed by the present author in the *L. cooperi* complex, do have green or striped flowers, uniformly pink flowers rarely, if ever, occur in other species or complexes in *Ledebouria*.

For list of specimens examined see appendix, p. 12.

3. **Ledebouria floribunda** (Bak.) Jessop, comb. nov.

Scilla floribunda Bak. in Saund., Ref. Bot. 3 : t.188 (1870). Type: "Cape of Good Hope", *Cooper* s.n. (K, holo., PRE, photo.!).

Scilla pendula Bak. in Saund., Ref. Bot. 3, app.: 14 (1870). Type: "Cape of Good Hope", *Burchell* s.n. (K, holo.,

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Opposite- Map 8. Distribution of *Ledebouria floribunda*.

BOL, drawing!).

Scilla princeps Bak. in Saund., Ref. Bot. 3 : t.189 (1870). Type: "Cape of Good Hope", Cooper s.n. (K, holo., PRE, photo.!).

?Scilla spathulata Bak. in Saund., Ref. Bot. 3 : t.187 (1870). Type: Saund., Ref. Bot. 3 : t.187, "Cape of Good Hope, Cooper s.n.", (1870).

Scilla zebrina Bak. in Saund., Ref. Bot. 3 : t.185 (1870). Type: Saund., Ref. Bot. 3 : t.185, "Cape of Good Hope, Cooper s.n.", (1870).

Scilla polyantha Bak. in Gdnrs' Chron. 9 : 104 (1878). Type: Natal, York, in Hort. Bull s.n. (K, holo., PRE, photo.!).

Scilla tricolor Bak. in Gdnrs' Chron. 14 : 230 (1880). Type: ?Cape, Port Elizabeth, Elwes (painting in K, PRE, photo. of painting!, BOL, copy of painting!).

Scilla subsecunda Bak. in Gdnrs' Chron. 16 : 38 (1881). Type: "Eastern districts of Cape Colony", Bowker s.n. (K, holo., PRE, photo.!, BOL, drawing!).

Scilla microscypha Bak. in Gdnrs' Chron. 16 : 102 (1881). Type: "Eastern provinces of Cape Colony", Bowker s.n. (K, holo., PRE, photo.!).

Scilla livida Bak. in Gdnrs' Chron. 20 : 166 (1883). Type: "Cape of Good Hope, imported by Messrs. F. Horsman & Co." (K, holo., PRE, photo.!, BOL, drawing!).

Scilla megaphylla Bak. in Fl. Cap. 6 : 490 (1896). Type: Transvaal, near Barberton, Galpin 1184 (GRA!; NH!; SAM!, PRE, photo.!).

Scilla moschata Schonl. in Rec. Albany Mus. 3 : 60 (1914). Type: Cape, Stutterheim, Rogers 12786 (GRA, holo.!, PRE, photo.!).
Scilla grandifolia Schonl. in Rec. Albany Mus. 3 : 61 (1914). Type: Transvaal, Tzaneen, Devil's Kloof, Rogers s.n., Dec. 1913 (GRA, holo.!, PRE, photo.!).
Scilla lauta N.E. Br. in Kew Bull. 1921 : 299 (1921). Type: Transvaal, Pietersburg Div., The Downs, Rogers 23990 (K, holo., PRE, photo.!, BOL, drawing!).

Bulb generally 70-150 mm long, usually more than a quarter of the length of the leaves. Leaves often 4 or 5, (140-)200-350(-450) mm long, 20-150 mm broad, more or less erect, fairly soft, linear-oblong to lanceolate, but not usually long-tapering; the outermost leaf not much smaller than the inner ones. Inflorescence more or less erect, often with 100 or more flowers. Perianth segments varying in colour, greyish, greenish or with pink, but not uniformly pink.

Occurs mainly in the northern and eastern Transvaal, Swaziland, Natal and the eastern Cape as far west as Grahamstown. See map 8.

Often recorded in seasonally damp places, but also occurring in drier localities, especially in shaded localities.

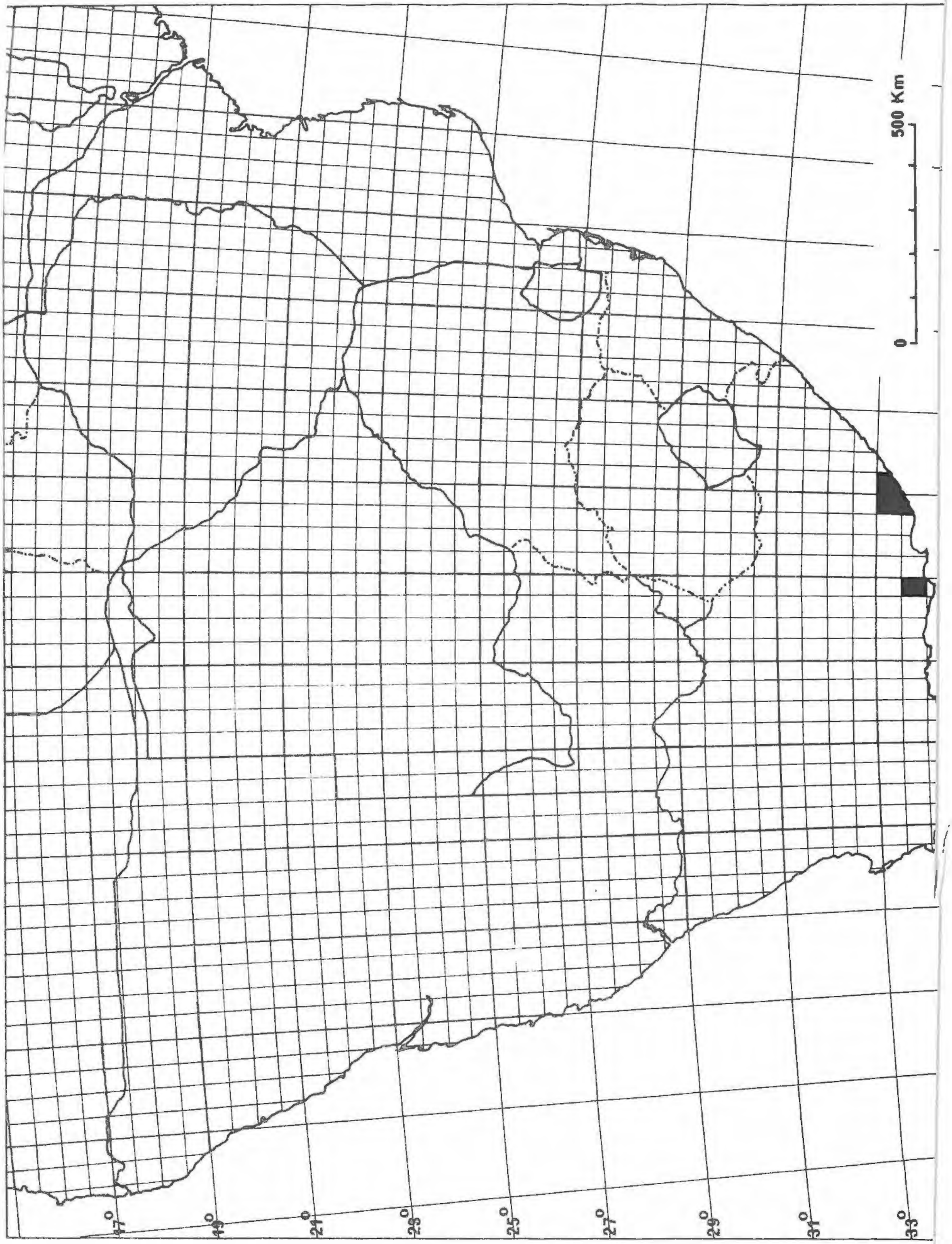
Scilla livida is placed in synonymy, but shows leaf characters reminiscent of L. concolor and bulb sharacters of L. revoluta. However, it does seem to be best placed here. S. subsecunda is also placed here with some hesitation. It shows some affinities with both L. revoluta and L. undulata.

L. floribunda is nearest to the large forms of L. cooperi, but differs in having a relatively large number of flowers, which are not uniformly pink, and in the relatively large bulb, with darker outer scales. It is also not always possible to distinguish L. floribunda from large forms of L. revoluta and L. concolor, but the large inflorescence and often relatively narrow basal region of the lamina of the leaves provide useful characters.

A number of specimens from Zululand (e.g. Ward 2822, NH, from Hluhluwe Game Reserve and Venter 602, NH, from Ngoya Mountain) appear to be best regarded as small-bulbed forms of L. floribunda.

For illustration see Flower. Pl. S. Afr. 23 : t.898 (1943).

For list of specimens examined see appendix, p. 21.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4. Ledebouria socialis (Bak.) Jessop, comb. nov.

Scilla socialis Bak. in Saund., Ref. Bot. 3 : t.180 (1870). Type: Natal, Cooper 3635 (K, holo., PRE, photo.!). Scilla paucifolia Bak. in Saund., Ref. Bot. 3 : t.181 (1870). Type: "Cape, Cooper s.n.", (1870).. Scilla violacea Hutch. in Kew Bull. 1932 : 511 (1932). Type: Cape, "Uitenhage Division", Klein River near Hankey, Hutchinson & Long s.n. (K, holo., PRE, photo.!); BOL!; PRE!).

Bulb about 15-20 mm long, developed above the ground and usually producing colonies vegetatively. Leaves 2-3(-5), 50-100 mm long, 10-15 mm broad, spreading to erect-spreading, lanceolate to oblong-lanceolate, sometimes with a petiole-like base to the lamina, somewhat fleshy, often deep pink or violet below and with a silvery sheen on the upper surface. Inflorescence usually single, more or less erect, often with fewer than 25 flowers.

Frequent in the eastern Cape between Uitenhage and East London, often on rather dry shaly slopes. Possibly extending as far east as Swaziland, but there have been no certain identifications from outside the area outlined above. See map 9.

The epigeal bulb and somewhat spreading leaves

Opposite- Map 9. Distribution of Ledebouria socialis.

distinguish this species from the smaller members of the L. cooperi complex. It also has affinities with L. concolor, which is a species of larger specimens, often with undulate leaves and usually uniformly green leaves.

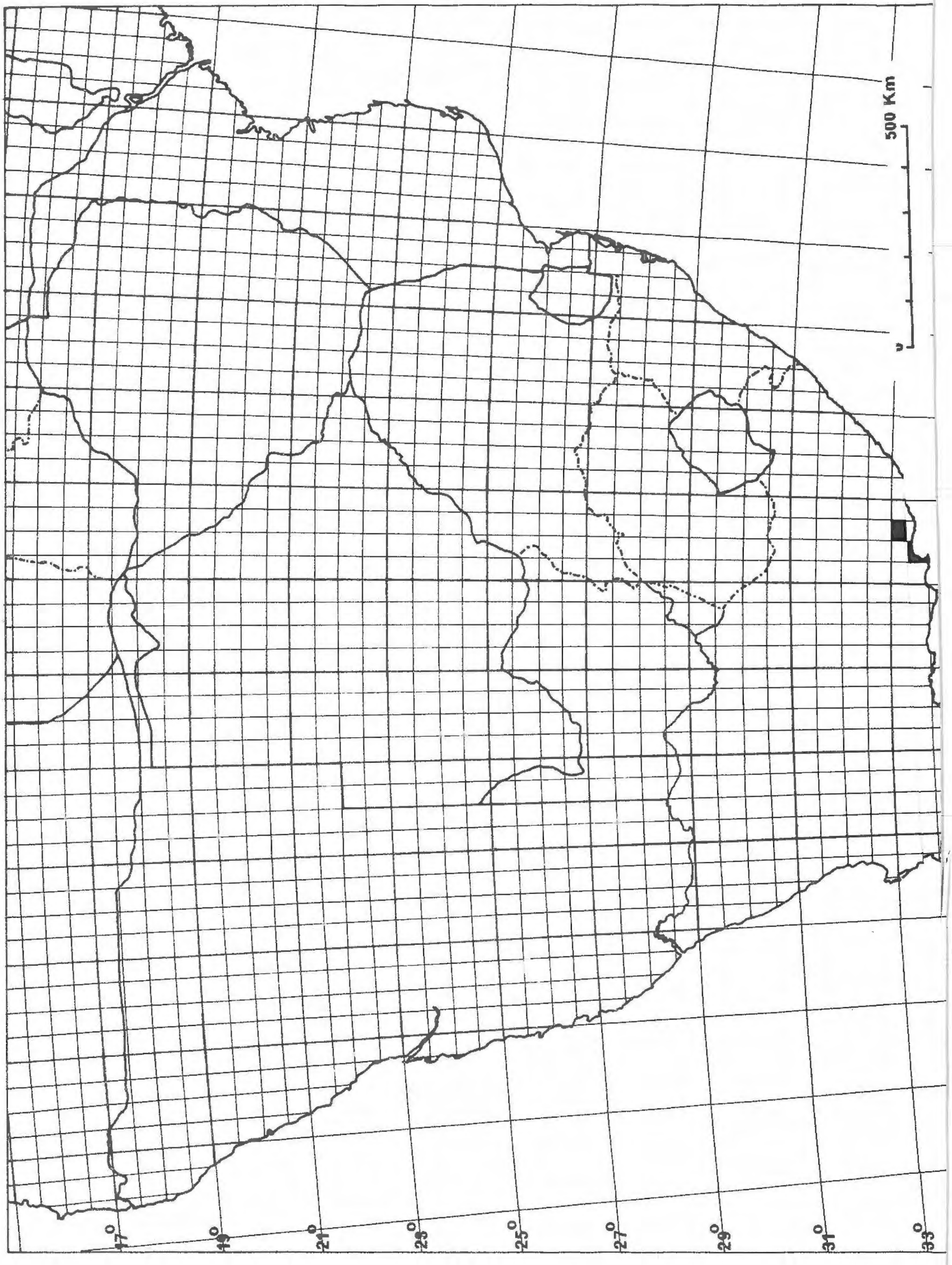
The typification of this species presents a problem. Baker cited "Cape of Good Hope, discovered by Mr. Cooper", but the locality given on the specimen, labelled "Drimia socialis, from the type plant", in the Kew Herbarium, is Natal. Whether this specimen was incorrectly labelled or whether it is a valid record from Natal, from where there are no authenticated records, cannot be determined at the present time. This specimen does conform with both Saunder's figure and with the present author's concept of L. socialis.

The specimen labelled as the type of S. paucifolia (K, PRE, photo) does not match the Saunder's figure in bulb, leaf or inflorescence characters, and is, therefore, not recognised as the type here.

This species is one of the few species of Ledebouria that regularly set seed, although often only a few capsules are produced on each inflorescence.

For illustration, se Flower. Pl. S. Afr. 21 : t.825 (1941).

For list of specimens examined, see appendix, p. 24.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5. Ledebouria concolor (Bak.) Jessop, comb. nov.

Drimia cooperi Bak. in Saund., Ref. Bot. 1 : t.18 (1868), non Scilla cooperi Hook.f., 1866. Type: "Cape of Good Hope", Cooper s.n. (K, holo., PRE, photo.!).

Scilla concolor Bak. in Saund., Ref. Bot. 3 : app.: 13 (1870). Type: as for Drimia cooperi.

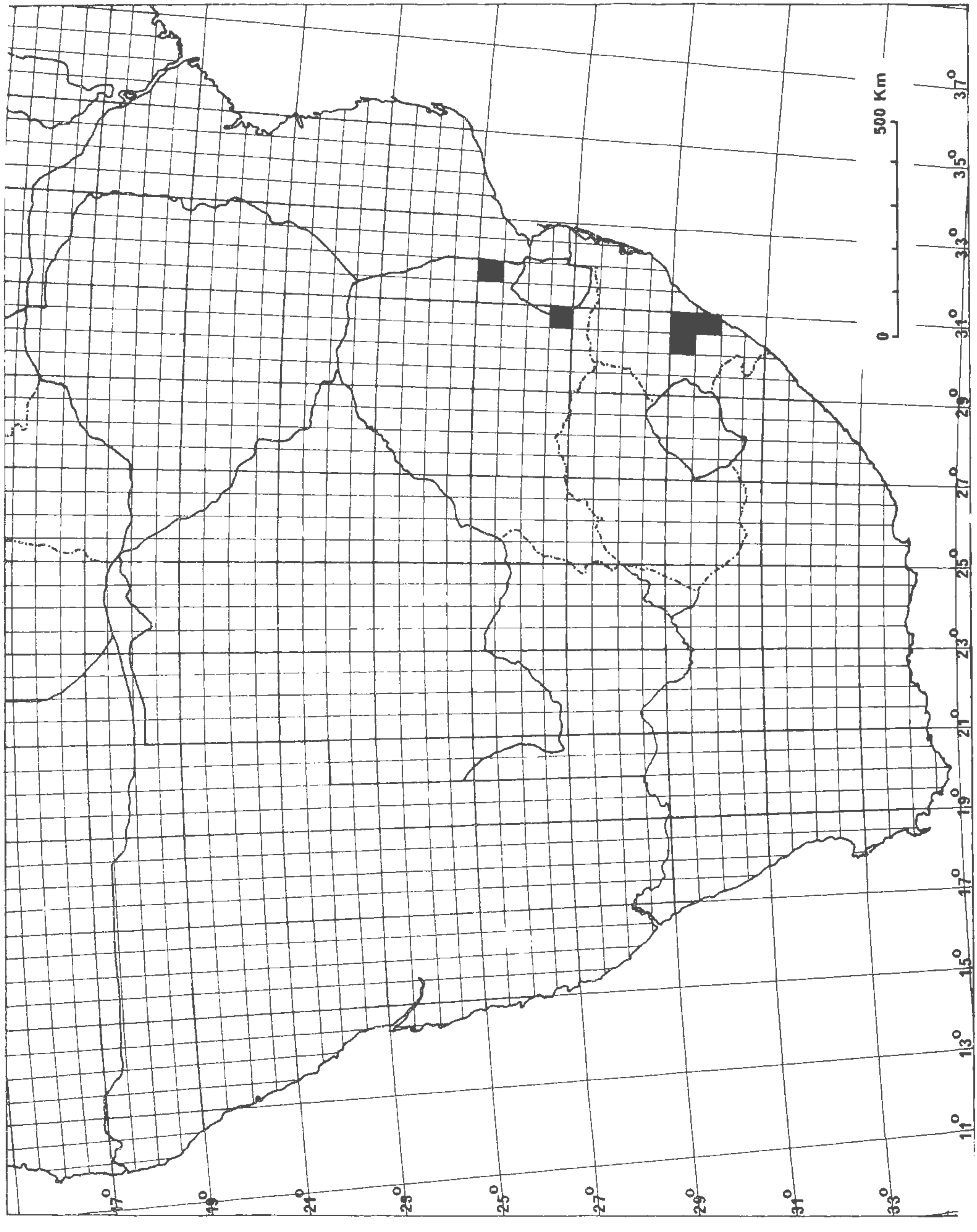
Bulb 30-50 mm long, epigeal and usually reproducing vegetatively to form colonies. Leaves 2-6, erect to erect-spreading, 50-150 mm long, 15-50 mm broad, broadly lanceolate to oblong-lanceolate, usually with undulate margins, never attenuate. Inflorescence usually single, more or less erect, not usually with more than about 100 flowers. Flowers usually (?always) green.

This species occurs only in the Port Elizabeth-Uitenhage areas of the eastern Cape. See map 10.

It usually grows in rather dry grassy or open areas.

Its habit is rather like that of a large form of L. socialis, but with undulate leaves, lacking silvery markings and probably also the pink on the lower leaf surfaces usually present in L. socialis. The leaves are probably never spotted with either pink or with different shades of green.

Opposite- Map 10. Distribution of Ledebouria concolor.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Drimia nitida Eckl. in S. Afr. Quart. J. no. 1 : 364 (1830) appears to be synonymous with L. concolor, but as no type material has been seen it has been preferred to use the later name concolor. D. nitida was reported to have been collected at Addo, eastern Cape.

For a list of specimens examined, see appendix p..25.

6. **Ledebouria apertiflora** (Bak.) Jessop, comb. nov.

Drimia apertiflora Bak. in Saund., Ref. Bot. 1 : t.19 (1868). Type: Saund., Ref. Bot. 1 : t.19, "Cape, Cooper s.n.", (1868).

Scilla lorata Bak. in Saund., Ref. Bot. 3, app.: 14 (1870), nom. superfl., type as for Drimia apertiflora.

Scilla apertiflora (Bak.) C.A. Sm. in Kew Bull. 1930 : 250 (1930).

Scilla linearifolia Bak. in Saund., Ref. Bot. 3 : t.184 (1870). Type: Saund., Ref. Bot. 3 : t.184, "Cape, Cooper s.n.", (1870).

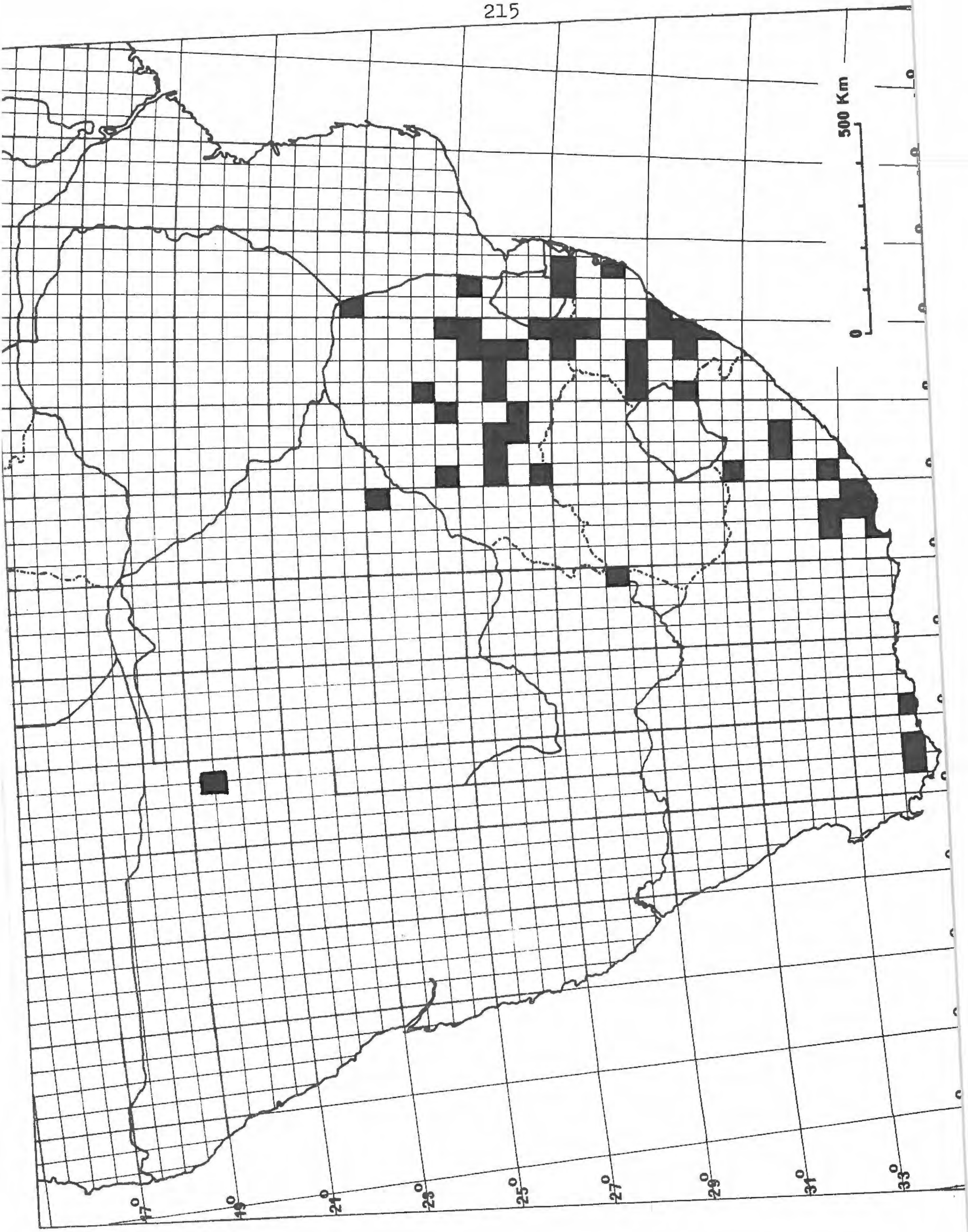
Bulb 40-60 mm long, often pink towards the top, below the ground. Leaves 4-7, erect, usually 200-350 mm long, usually less than 25 mm broad, sublinear, tapering almost from the base. Inflorescence erect or flexuose, often with 50-150 flowers.

Opposite- Map 11. Distribution of Ledebouria apertiflora.

Although both types cited above originated in the Cape, the species as defined here appears to be largely restricted to Natal and the eastern Transvaal in South African herbaria. *Strey* 4487 (NH) from "Bizaia, Bizana district", Cape, may belong here but lacks a bulb and identification is uncertain. See map 11.

Occurs in a wide range of habitats, including open grassveld and in shelter of large plants.

This species may possibly be excessively artificial and not justify recognition. The difficulty mentioned above of the type specimens occurring in the Cape, while known distribution does not include the Cape, may be a result of failure to define this species sufficiently accurately. But in taking this view, the present author is not only expressing his own opinion, but also upholding that of Van der Merwe. *Wood 1208* (NH), from Inanda, Natal, was selected by Van der Merwe as a good match of the type of *S. linearifolia* (MS in PRE). This view appears to be well-founded. Although it is felt that it is justified to place *S. linearifolia* and *S. lorata* (both sensu Baker, 1896) in a single species, the breadth of leaf mentioned in Baker's type description of *Drimia apertiflora* is exceptionally great for the species as construed here. In other ways, too, this may be shown to be an unsatisfactory grouping of the material. *L. apertiflora* shows similarities with *L. cooperi* (*cooperi series*) from which it may be separated by having a larger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bulb and more attenuate and perhaps firmer leaves. In the Transvaal it may also be confused with long-leafed forms of L. undulata. The bulb is never produced into a neck, and the leaves are longer. The low-veld forms and some plants of L. revoluta, as defined in this work, also approach this species, but have broader leaves for their length.

For a list of specimens examined see appendix, p. 25.

7. **Ledebouria revoluta** (L.f.) Jessop, comb. nov.

Hyacinthus revolutus L.f., Suppl.: 204 (1781). Type: "Cap. bonae spei", Thunberg s.n. (UPS, holo., BOL & PRE on Herb. Thunb. Microfiche no. 8508!).

Phalangium revolutum (L.f.) Pers., Syn. Pl. 1 : 367 (1805).

Drimia(?) revoluta (L.f.) Kunth, Enum. Pl. 4 : 341 (1843).

Xeodolon revolutum (L.f.) Salisb., Gen. Pl. : 18 (1866).

Scilla revoluta (L.f.) Bak. in Saund., Ref. Bot. 3, app.: 6 (1870).

Lachenalia lanceaefolia Jacq., Icones 2 : t.402 (1794). Type: Jacq., Icones 2 : t.402 (1794).

Drimia laneaefolia (Jacq.) Ker-Gawl. in Curtis's bot. Mag. 33 : t.1380 (1811).

Sugillaria lanceaefolia (Jacq.) Salisb., Gen. Pl. : 18 (1866).

Opposite- Map 12. Distribution of Ledebouria revoluta.

Scilla lanceaefolia (Jacq.) Bak. in Saund., Ref. Bot. 3 : t.182 (1870).

Lachenalia maculata Tratt., Archiv. der Gewächskunde 2 : t.168 (1814). Type: Tratt., Archiv. der Gewächskunde 2 : t.168 (1814).

Scilla maculata Shrank, Pl. Rar. Hort. Acad. 2 : fol. 100, t.100 (1820). Type: Shrank, Pl. Rar. Hort. Acad. 2 : fol. 100, t.100, "Promontorium Bonae Spei", (1820).

Drimia acuminata Lodd., Bot. Cab. : t.1041 (1825). Type: Lodd., Bot. Cab.: t.1041, "Cape of Good Hope", (1825).

Scilla asperifolia Van der Merwe in Flower. Pl. S. Afr. 24 : t.944 (1944). Type: Natal, Ladysmith, Van der Merwe 2604 (PRE, holo.!; NU!).

Scilla carnosula Van der Merwe in Flower. Pl. S. Afr. 24 : t.958 (1944). Type: Natal, Greytown, Van der Merwe 2592 (PRE, holo.!).

Scilla albomarginata Van der Merwe in Flower. Pl. S. Afr. 24 : t.947 (1944). Type: Natal, near Umzinto, Van der Merwe 2669 (PRE, holo.!).

Bulb 25-75 mm long; the outer scales often dark and glossy or with pink, often in the form of speckling, especially in the upper parts. Leaves 4-8, appressed to the ground, spreading or suberect, often not developing very far before flowering, but rarely over 150 mm long, up to 30 mm broad, ovate to, lanceolate, usually attenuate; linear to linear-lanceolate in the early stages of leaf growth. Inflorescence suberect or suberect in the distal half and spreading in the proximal half, usually with fewer than 100 flowers.

Occurs generally from Greyton (3419B; Caledon) through the belt between the karoo and the sea into Natal and the Transvaal, but rare west of Port Elizabeth. Also recorded from South West Africa and the Orange Free State. See map 12.

Occurs in a wide range of habitats - including semi-desert, grassveld and forest margins. Grows both in sandy places and among rocks.

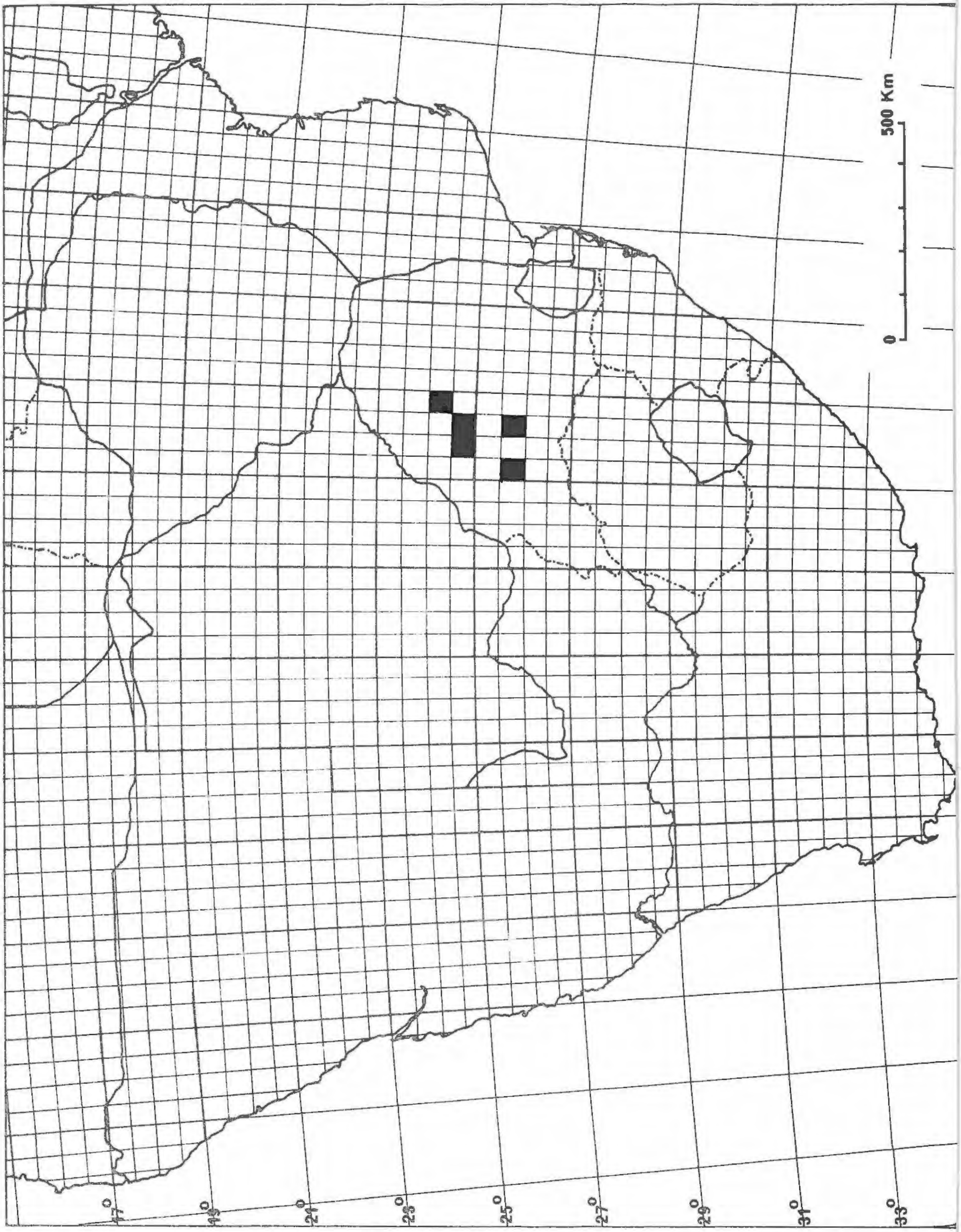
In the south-west of its range it is a relatively small plant with a more or less erect inflorescence (see Flower. Pl. S. Afr. 22 : t.913; 1943). Muir 1877 (BOL) from Riversdale is a very close match with the type of Hyacinthus revolutus. In much of the eastern Cape (e.g. Dyer 1142; GRA) the fully-developed outer leaves are firmly appressed to the ground as in most forms of L. ovatifolia, and the inflorescence is suberect. In the Transvaal highveld the leaves are erect-spreading, the bulb relatively large and the inflorescence flexuose. As the orientation of the leaves is strongly influenced by the density of the surrounding vegetation, this does not appear to offer a satisfactory character for subdividing the L. revoluta complex.

Most specimens, especially from the lowveld, for example Ward 3288 (NH) from the Hluhluwe Game Reserve in Natal, have well-developed leaves at anthesis. It has also not been found possible to separate this form taxonomically. Similarily, the gradation in the size and form of other organs makes it difficult to find any other suitable character for subdividing this complex.

The only other species with leaves appressed to the ground (as occurs frequently in eastern Cape forms) is L. ovatifolia, which has a different type,of bulb and usually broader, less attenuate leaves. Specimens linking this complex with the L. cooperi complex occur over much of its range (e.g. Van der Merwe 1554 (PRE) from near Leslie in the Bethal district). Other specimens exist which are intermediate between L. revoluta and L. floribunda (e.g. Young A365 (PRE) from Schoeman's Kloof in the Belfast district).

The leaves of the type of A. albomarginata are more like those of L. ovatifolia, but the bulb places it rather in L. revoluta.

For list of specimens examined see appendix, p. 26.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8. Ledebouria inquinata (C.A. Sm.) Jessop, comb. nov.

Scilla inquinata C.A. Sm. in Kew Bull. 1930 : 248 (1930).
Type: Transvaal, near Pretoria along the Aapies River, Burke s.n. (K, holo., PRE, photo.!; TCD!).

Bulb 25-65 mm long; the outer scales often dark and glossy or with a pink tinge especially in the upper parts. Leaves erect, ovate-lanceolate narrowing towards the base, up to 150 mm long, up to 35 mm broad, very glaucous and usually not conspicuously spotted, often poorly developed at flowering. Inflorescence flexuose to suberect, with 50-150 flowers.

Wide-spread in the Transvaal but apparently rare in, or absent from, the lowveld and not collected in the other provinces. See map 13.

Generally found in grassveld in the open.

The bulb is similar to that of L. revoluta and L. marginata but the pink colour tends to be present as a uniform wash rather than as spots, and the bulbs divide to form two cohering daughter bulbs more frequently than in the other two species. The erect very glaucous leaves, which usually lack spots are also characteristic. At flowering the attenuate apices of the leaves are often all that show of the leaf, but in the mature plant the

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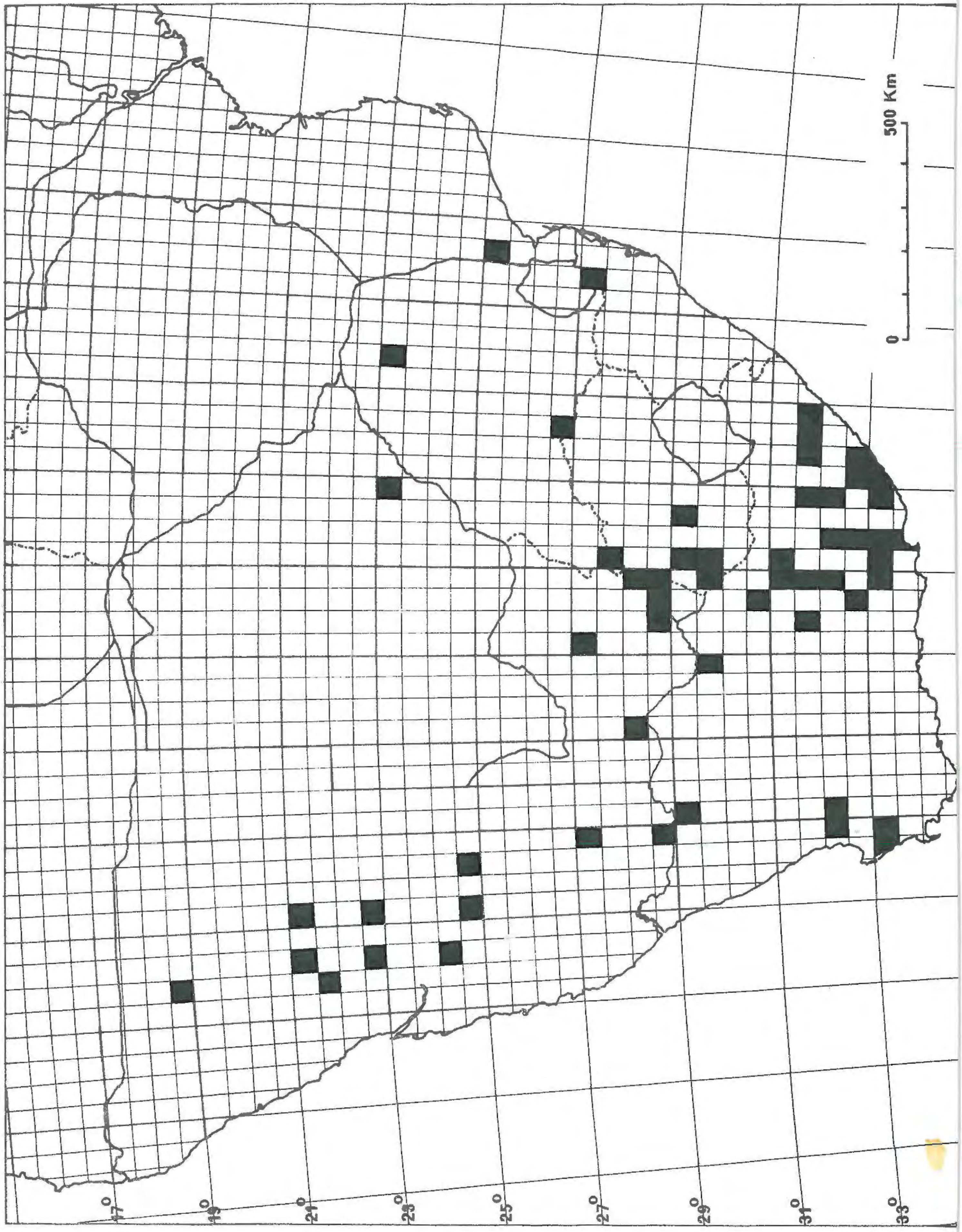
Opposite- Map 13. Distribution of Ledebouria inquinata.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narrowing of the leaf towards the base contrasts with the broader base of the other two species. Nevertheless it is not always possible to distinguish *L. inquinata* and *L. revoluta* and it is considered possible that with further data it may be decided not to uphold *L. inquinata*.

9. **Ledebouria undulata** (Jacq.) Jessop, comb. nov.

Drimia undulata Jacq., Icones 2 : t.376 (1794). Type: Jacq., Icones 2 : t.376 (1794).

Scilla undulata (Jacq.) Bak. in Saund., Ref. Bot. 3, app. : 11 (1870); nom. illegit., non *S. undulata* Desf., 1798.

Scilla undulatifolia Von Poelln. in Ber. dt. bot. Ges. 41 : 209 (1944). Type: as for *Drimia undulata* Jacq.

Drimia ensifolia Eckl. in S. Afr. Quart. J. 1 : 364 (1830). Type: Cape, Zwartkops, "Uitenhage", *Zeyher* 10 (K, holo., PRE, photo.!).

Scilla ensifolia (Eckl.) Britten in J. Bot., Lond. 46 : 201 (1908).

Scilla prasina Bak. in Saund., Ref. Bot. 3, app.: 10 (1870). Type: "Kaffirland", *Gill* s.n. (K, holo., PRE, photo.!; TCD!).

?*Scilla laxiflora* Bak. in Gdnrs' Chron. 9 : 668 (1891). Type: ?"Hort. N.E.Brown" (K, ?holo., BOL, drawing!).

Scilla ecklonii Bak. in Bot. Jb. 15, Beibl. 35 : 7 (1892). Type: Cape, *Ecklon & Zeyher* Asphod. n. 12 (B, holo.!).

Scilla nelsonii Bak. in Fl. Cap. 6 : 488 (1896). Type: South Africa, without locality, Burke s.n. (K, PRE, photo.!); Vaal River, Nelson 167 (K, PRE, photo.!; PRE! - the specimen in PRE lacks a bulb but may be nearer L. cooperi).

Scilla rautanenii Schinz in Bull. Herb. Boissier 5 : 857 (1897). Type: Kaokoveld, Rautanen 172 (Z, holo.!).

Drimiopsis engleri Krause in Bot. Jb. 51 : 445 (1914). Type: S.W.A., "Narib: am Fuss der Kalaharihügel", Engler 6534 (B, holo.!).

Bulb 20-50 mm long, often either with numerous dry outer scales and abruptly truncate at the apex or produced into a neck which may be as long as or longer than the bulb; the roots sometimes in the form of narrow, elongate fusiform tubers (see Flower. Pl. S. Afr. 21 : t.826; 1941). Leaves 2-6, narrowly linear-lanceolate to lanceolate, more or less erect to spreading, rather firm, sometimes distichous, often folding longitudinally, usually 50-150 mm long, rarely over 20 mm broad. Inflorescence usually erect.

A species-complex of the dry areas of South Africa and South West Africa, occurring from the southern Cape to the Transvaal and throughout South West Africa. See map 14.

Occurs most frequently in open sandy areas, but also under trees and in heavier soils.

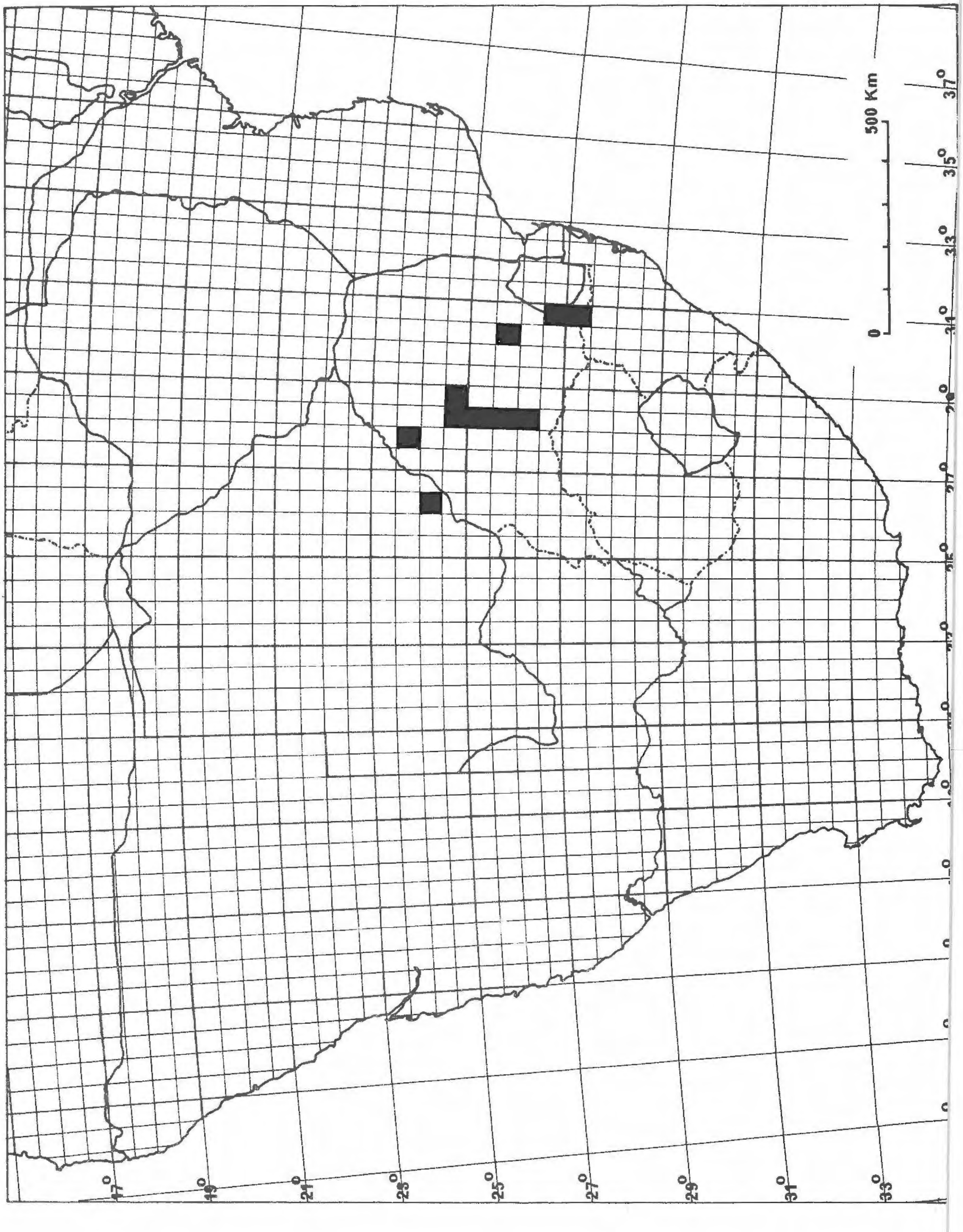
Small forms can be confused with the L. cooperi complex (e.g. Wylie s.n. sub Tvl Mus 34294 (PRE) from Greytown, Natal), but the several dry outer bulb scales, especially when these form a neck, the relatively firm leaves and bicoloured or greenish flowers assist in distinguishing them.

The type of Scilla prasina is considered by the present author to belong to this species despite having exceptionally broad leaves.

There isn't absolute certainty that the specimen cited as the type of S. laxiflora is in fact the type. But it agrees with the description and both specimen and description belong within this concept of L. undulata.

When difficulty is experienced in separating L. undulata from L. revoluta (e.g. Acocks 16315 (PRE) from Dwaal Station in the Hanover district), a pedicel length below 5 mm can be regarded as an indication of L. undulata. Other specimens, for example Strey 3475 (PRE) from Mopane in the Soutpansberg district, show affinities with L. apertiflora.

For list of specimens examined see appendix, p. 30.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10. **Ledebouria graminifolia** (Bak.) Jessop, comb. nov.

Scilla graminifolia Bak. in Bull. Herb. Boissier, ser. 2, 4 : 1001 (1904). Type: Transvaal, Modderfontein, *Conrath* 703 (K, holo., PRE, photo.!, BOL, drawing!; GRAZ!; Z!).

Scilla stenophylla Van der Merwe in Flower. Pl. S. Afr. 25 : t.959 (1944). Type: Natal, Paulpietersburg, *Van der Merwe* 2655 (PRE, holo.!).

Bulb 30-50 mm long, sometimes produced into a neck; outer scales membranous. *Leaves* 10-20, linear, 40-80 mm long, 1-4 mm broad, usually spirally twisted. *Inflorescence* suberect, rather dense, often with about 30-70 flowers.

Occurs mainly in the Transvaal, where it is widespread, and recorded from Botswana and Natal. See map 15.

Usually grows in open grassveld.

In many respects, *L. graminifolia* is intermediate between the *minima series* of *L. cooperi* and *L. undulata*. The bulbs are intermediate in size, but the length, shape and spiral twisting of the leaves are diagnostic. The twisting is, however, not always apparent, particularly at flowering when the leaves may be poorly developed. The bicoloured flowers and large number of leaves further

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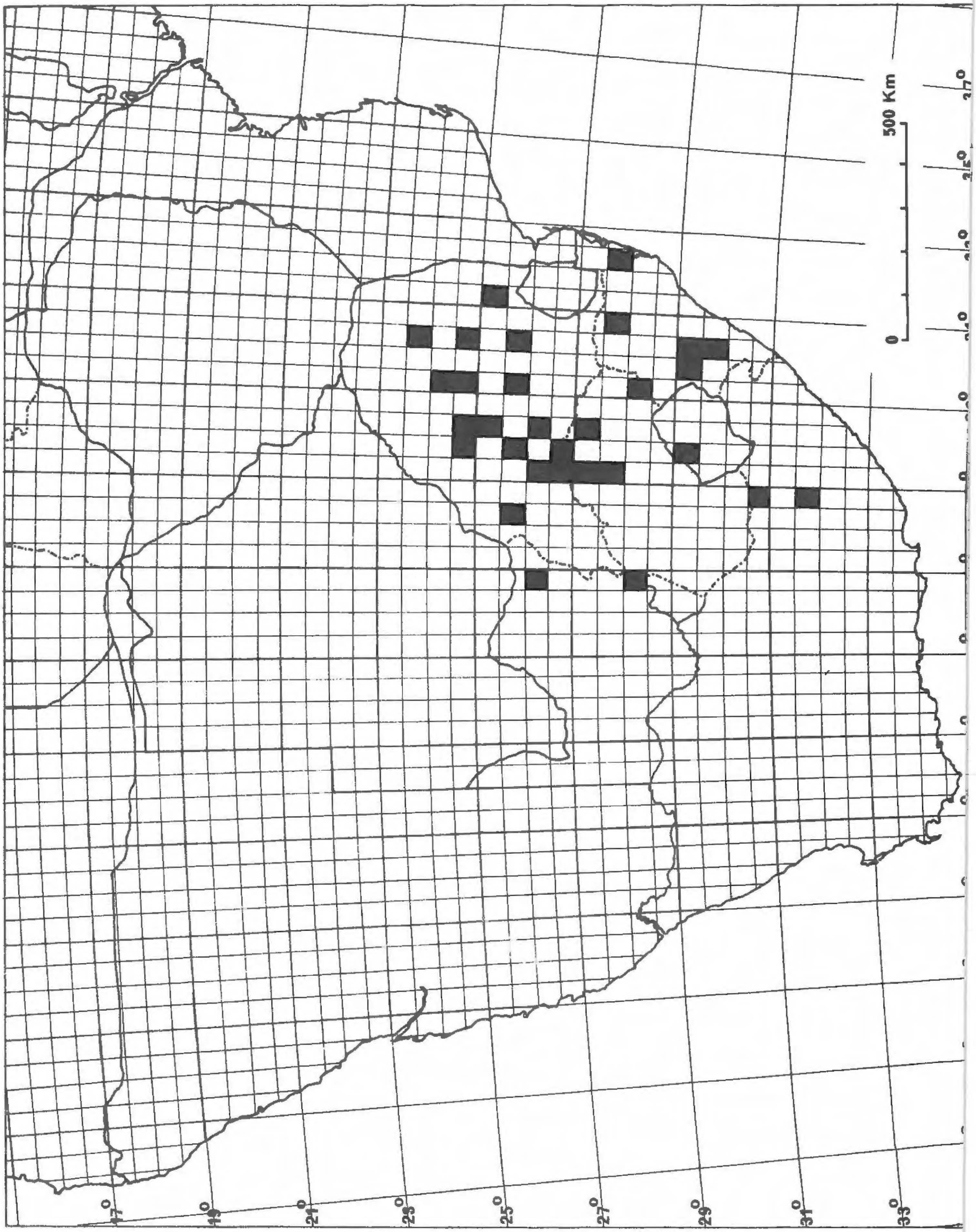
Opposite- Map 15. Distribution of *Ledebouria graminifolia.*

serve to distinguish it from *L. cooperi*. Like *L. undulata*, the bulb may be extended to form a sheath at the base of the lamina of the leaves. It may not be possible to distinguish this species from *L. marginata* before the leaves are well-formed, but the broader leaf with several raised veins characterises *L. marginata* later in growth.

In some specimens with leaves of the form characteristic of *L. graminifolia* the bulb scales may produce copious threads when torn as in *L. ovatifolia* and *L. luteola*. But such specimens are probably best placed in *L. luteola* (e.g. *Smith* 8602B (PRE) from Vaalbank in the Bloemfontein district). It does seem possible that *L. graminifolia* and *L. luteola* hybridise. Both occur at Modderfontein, near Johannesburg, and the sheet of *Conrath* 703 in Zurich shows a typical plant of *L. graminifolia* (left-hand specimen on sheet) and of a specimen intermediate between these species but probably closer to *L. luteola*.

For illustration see Flower. Pl. S. Afr. 25 : t. 959 (1944).

For list of specimens examined see appendix, p. 35.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11. Ledebouria marginata (Bak.) Jessop, comb. nov.

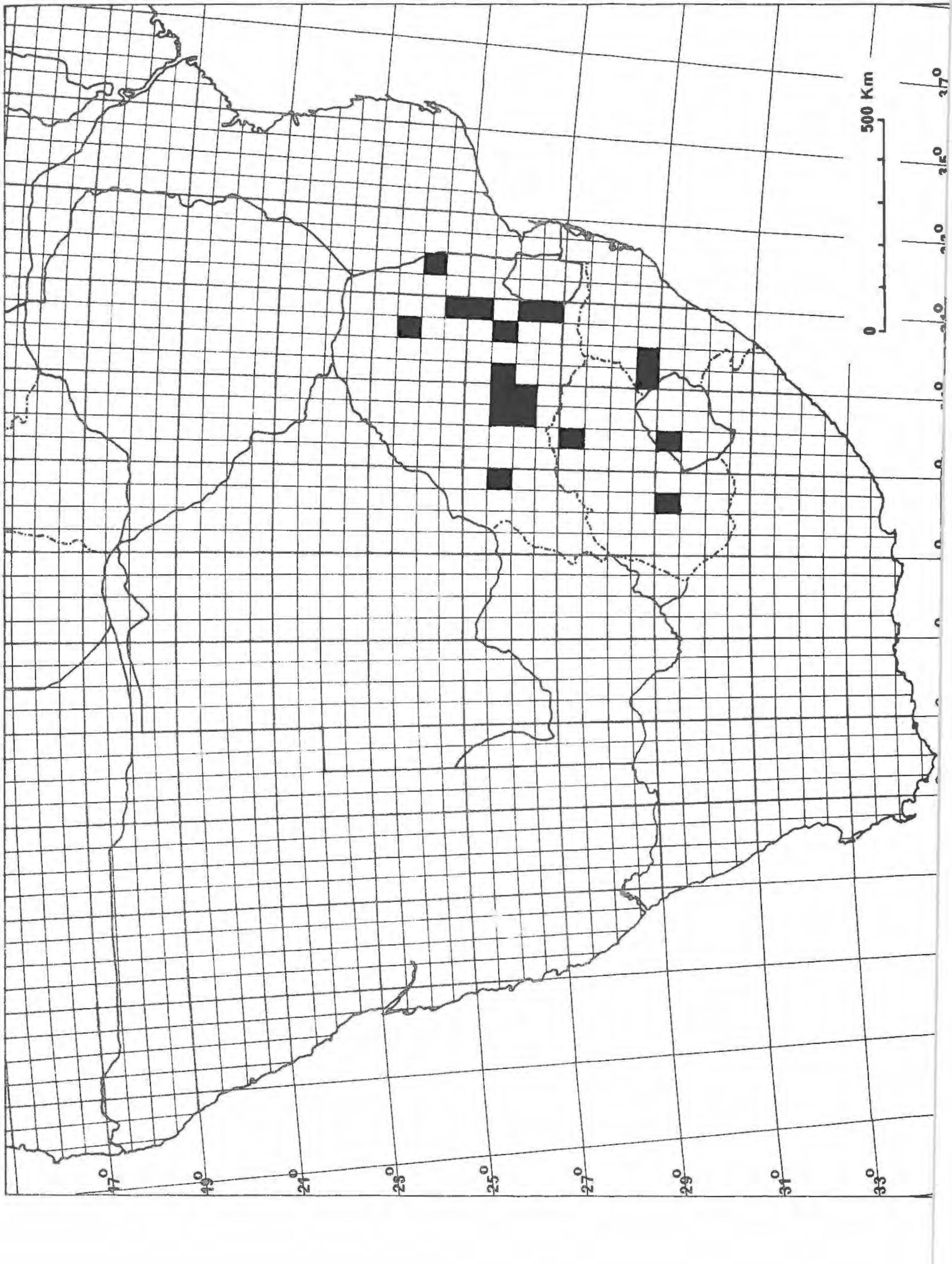
Scilla marginata Bak. in Bull. Herb. Boissier, ser. 2, 4 : 1002 (1904). Type: Transvaal, Modderfontein, Conrath 703b (GRAZ, lecto., PRE, photo.!; Z!).
Scilla neglecta Van der Merwe in Flower. Pl. S. Afr. 22 : t.865 (1942). Type: Transvaal, Pretoria, Colbyn, Van der Merwe 2441 (PRE, holo.!).

Bulb 40-80 mm long; the outer scales often dark and glossy with pink markings. Leaves 4-10(-16), erect, firm, with prominent veins, up to 160 mm or rarely more long, 10-30 mm broad. Inflorescence usually flexuose, with 50-150 flowers.

Occurs from the eastern Cape (Aliwal North and Queenstown) through the Orange Free State and Lesotho and over most of the Transvaal except, perhaps, the lowveld. The bulb is very similar to that of forms of L. revoluta from the Transvaal, but the leaves are more attenuate and much firmer - retaining their shape so that, after growth has commenced in spring, the previous season's dead leaves often persist. They are similar in texture to the leaves of Scilla nervosa, but the rigidity is given by collenchyma not sclerenchyma as in S. nervosa.

There is considerable variation in the size of the plant, even in small populations, (see, for example, fig.

Opposite- Map 16. Distribution of Ledebouria marginata.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285) this species is more uniform over a considerable geographical area than are most species of Ledebouria. The attenuate, twisted, hard leaves are remarkably characteristic in the field and readily identifiable in most herbarium material.

For illustration, see Flower. Pl. S. Afr. 22 : t. 865 (1942).

For list of specimens examined, see appendix, p. 36.

12. **Ledebouria luteola** Jessop, sp. nov., L. marginatae (Bak.) Jess. affinis, sed minor, bulbo luteolo et squamis bulbi ubi laceratis fila plurima exhibentibus.

Bulbi squamis exterioribus brunneis, sed squamis interioribus luteolis, 35-40 mm longi; squamae ubi laceratae fila plurima exhibentes. Folia 6-10, erecta, angusto-lanceolata, 45-90 mm longa, viridia, fasciis indistinctis transversis. Inflorescentiae 1 vel 2, suberectae, 80-90 mm longae, compactae. Pedicelli c. 30-50, patentes, reflectescentes. Perianthii segments suberecta, c. 4 mm longa, longitudine fasciata.

Type: Transvaal; Pretoria (2528), 6½ miles south of Hammanskraal, Codd 5625 (PRE, holo.).

Opposite- Map 17. Distribution of Ledebouria luteola.

Bulb 35-50 mm long; the scales producing copious threads when torn; the inner scales yellow. Leaves 4-10, erect or arcuate, up to 80(-130) mm long, lanceolate to linear-lanceolate, spotted or transversely marked, rather firm. Inflorescence more or less erect, with 30-60 flowers.

Occurs widely in the Transvaal, northern Orange Free State and north-western Natal. See map 17.

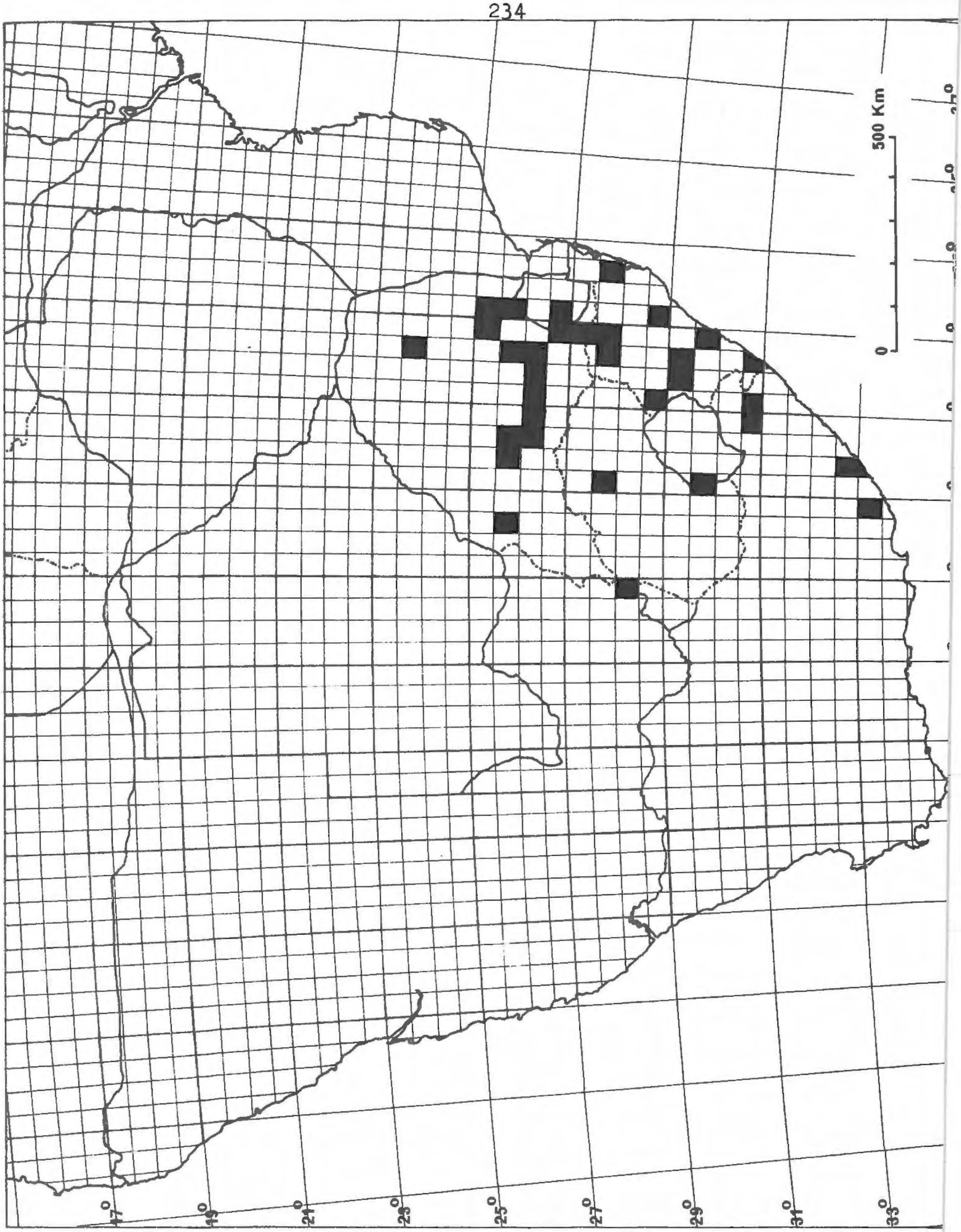
Most frequently recorded growing in dampish areas.

Small forms (e.g. Van der Merwe 1289 (PRE) from Pilgrim's Rest) are not readily distinguishable from the form of L. cooperi described by Van der Merwe as Scilla rupestris. The striped flowers and firmer leaves distinguish these species, but in small forms of L. luteola the bulb may lack membranous scales and be very similar to the L. cooperi type.

Narrow-leafed forms may be difficult to separate from L. graminifolia but the bulb colour is apparently diagnostic and the threads produced on tearing never occur in L. graminifolia. There are also specimens linking it with L. marginata (e.g. Conrath 696 (Z) from Modderfontein, near Johannesburg).

For illustration, see fig. 286.

For list of specimens examined see appendix, p. 38.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13. Ledebouria ovatifolia (Bak.) Jessop, comb. nov.

Scilla ovatifolia Bak. in Saund., Ref. Bot. 3 : t.183 (1870). Type: Natal, Cooper s.n. (K, holo., PRE, photo.!).

Scilla lanceaefolia sensu Wood, Natal Pl. 3 (4) : t.202 (1900), non Lachenalia lanceaefolia Jacq.

Scilla climacocarpha C.A. Sm. in Kew Bull. 1930 : 249 (1930). Type: Orange Free State, near Bethlehem in a damp shady ravine, Phillips 3068 (PRE!).

Scilla guttata C.A. Sm. in Kew Bull. 1930 : 243 (1930). Type: Natal, "Durban Div.", Cooper s.n. (K, holo.).

Scilla cicatricosa C.A. Sm. in Kew Bull. 1930 : 246 (1930). Type: Wood, Natal Pl. 3 (4) : t.202 (1900).

Scilla elevans Van der Merwe in Flower. Pl. S. Afr. 24 : t. 948 (1944). Type: Natal, Vryheid, Van der Merwe 2677 (PRE!).

Scilla collina Hutch., Bot. in S. Afr.: 344 (1946). Type: Transvaal, Soutpansberg, Klein Australe, Smuts & Gillett 4186 (K, holo., PRE, photo.!).

Bulb (30-)40(-150) mm long; membranous outer scales lacking or very insignificant; the scales rather truncate and verically imbricate; the outermost very short and only the innermost reaching the top of the bulb; all producing copious threads when torn. Leaves 2-5, usually firmly appressed to the ground, up to 250 mm long, ovate,

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Opposite- Map 18. Distribution of Ledebouria ovatifolia.

with a broad base. Inflorescence usually flexuose, with about 50-150 densely packed flowers.

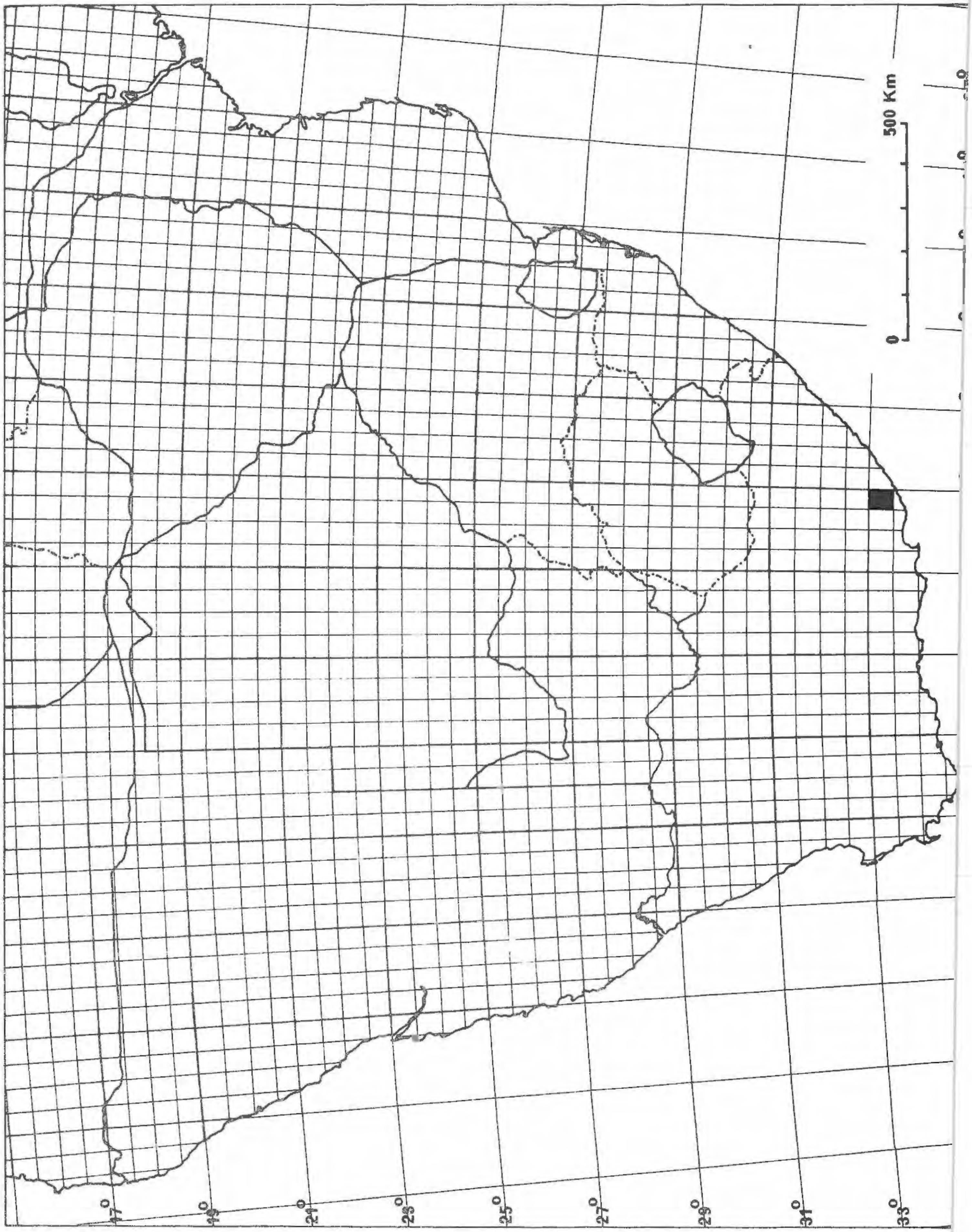
Occurs, perhaps as far west as Grahamstown in the eastern Cape, through Natal, Lesotho and into most of the Transvaal. There are a few records from the Orange Free State. See map 18.

Occurs most frequently in open grassveld, but also under trees and among rocks.

The bulb characters, described above, do not occur in any other species of Ledebouria in South Africa. Only in L. luteola are threads apparently produced in such large quantities. These threads have been described as removable spiral thickenings of the xylem conducting elements (Badenhuizen, 1954).

In his description of S. elevans, Van der Merwe stated that his new species only differed from Scilla ovatifolia in having erect leaves, "which do also sometimes occur in that species as well". This difference in leaf arrangement is almost certainly sometimes produced by genetic factors within the present concept of L. ovatifolia. But it does not, in the opinion of the present author, constitute a satisfactory character on which to subdivide the complex, particualrly as in many cases the same effect may be produced entirely by environmental factors.

In shady places, especially plantations, the leaves



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may be suberect and linear-lanceolate, making them indistinguishable from those of the larger forms of L. cooperi.

For illustration of the commonest form see Flower. Pl. S. Afr. 21 : t.830 (1941).

For list of specimens examined see appendix, p.40.

14. Ledebouria hypoxidioides (Schonl.) Jessop, comb. nov.

Scilla hypoxidioides Schonl. in Rec. Albany Mus. 1 : 48 (1903). Type: Cape, Grahamstown, behind Fort England, Daly & Sole 435 (GRA, holo.!; BOL!; SAM! & Z!).

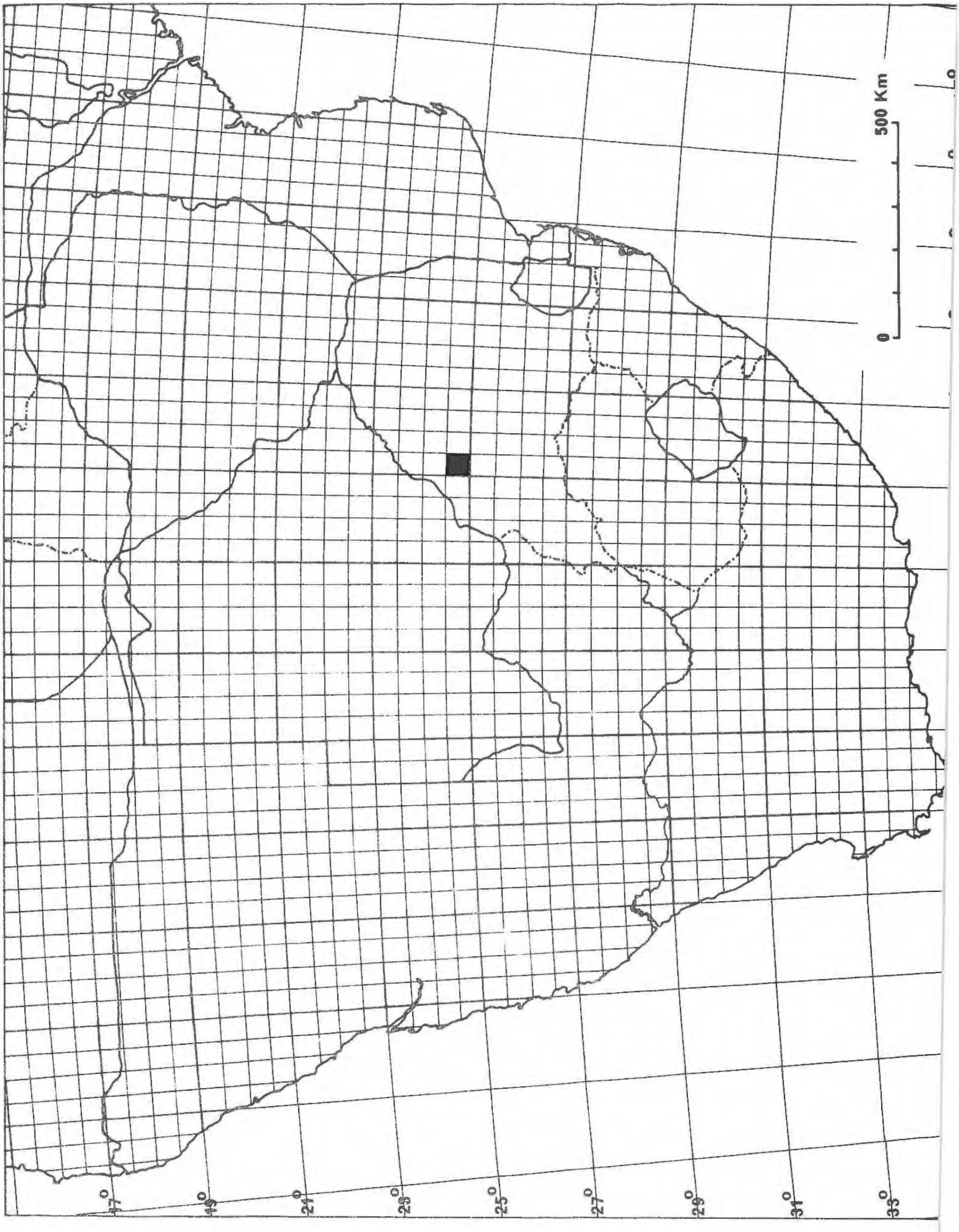
Bulb 25-40 mm long, sometimes produced into a short neck, sometimes pink towards the top. Leaves 2-4, 60-150 mm long, 15-35 mm broad, suberect, ovate-oblong to oblong-lanceolate, moderately firm, densely silky white pubescent on both surfaces. Inflorescence more or less erect, often with about 75-150 flowers.

This species has only been recorded in the immediate vicinity of Grahamstown. See map 19.

Occurs in grassveld and in bush.

The hairy leaves render it unmistakable, as there is no other known species of Ledebouria with pubescent leaves.

Opposite- Map. 19. Distribution of Ledebouria hypoxidioides.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Schonland (1903) stated: "It grows amongst grass and also in rocky situations at an altitude of about 1 700 to 2 300 feet. Its silky haired leaves resemble those of some species of Hypoxis...." Although it is likely that plants of L. hypoxidioides would be mistaken for Hypoxis, an extensive search has convinced the author that this species is on the verge of extinction.

For list of specimens examined see appendix, p.43.

15. Ledebouria viscosa Jessop, sp. nov. affinitate non manifesta. A speciebus omnibus Ledebouriae foliis viscidis differt.

Bulbi axibus basaliter elongatis, 50-55 mm longi, 12-15 mm lati. Folia ?1-3, erecta, oblanceolata-spathulata, 100-140 mm longa, 20-30 mm lata, viscida. Inflorescentiae erectae, solitariae, 150-170 mm longae. Pedicelli 20-30, patentes, c.8 mm longi. Perianthii segmenta suberecta, c.5 mm longa.

Type: Transvaal; Thabazimbi (2427), Kransberg, Meeuse 10493 (PRE, holo.).

Bulb 50-100 mm long, 12-20 mm broad, with the axis greatly extended below the succulent parts of the leaf

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Opposite- Map 20. Distribution of Ledebouria viscosa.

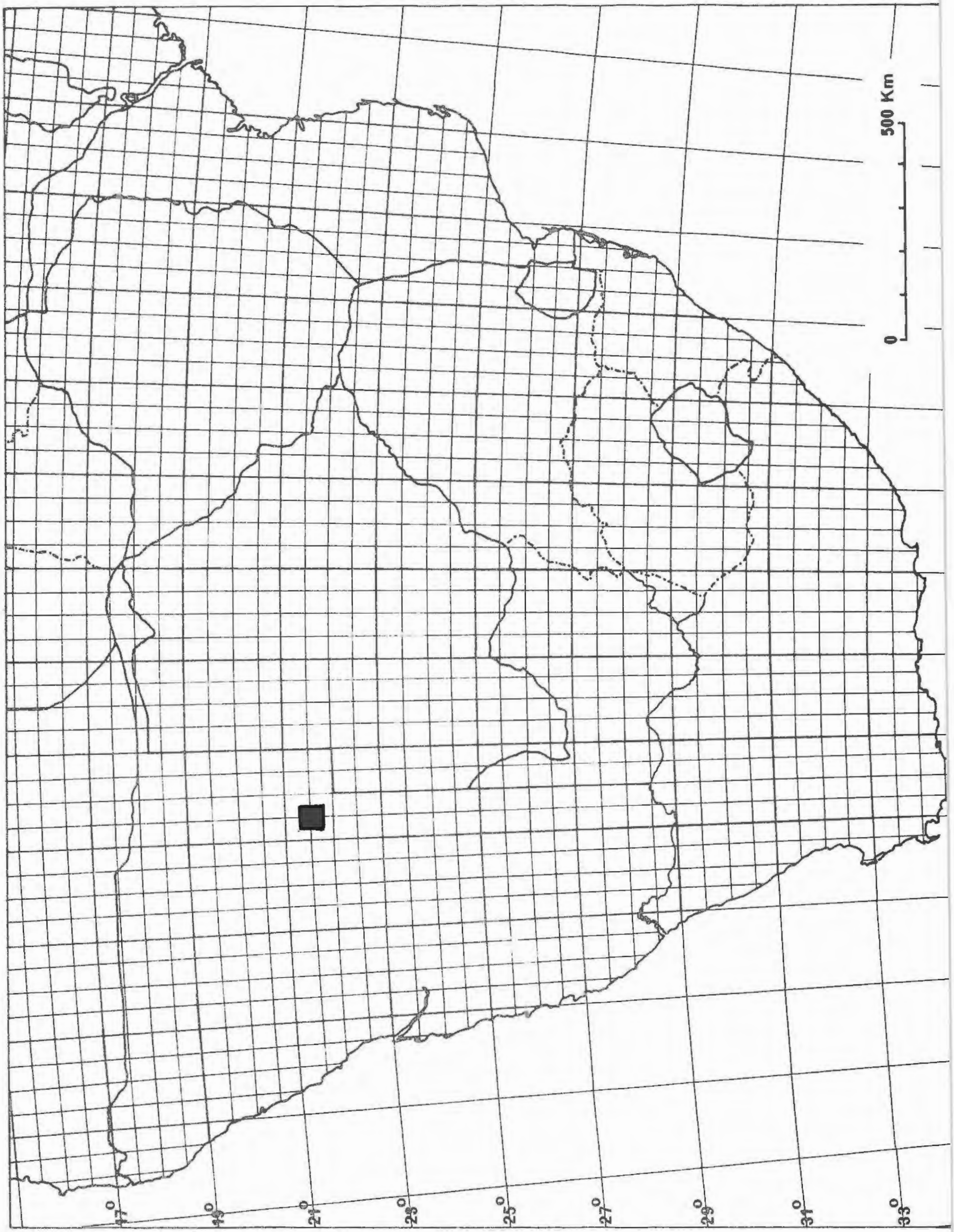
bases (see fig. 287). Leaves 1-3, erect, oblanceolate-spathulate, 90-230 mm long, 17-30 mm broad, viscid. Inflorescence erect with about 20-30 rather widely spaced flowers.

Only recorded from the type area. See map 20.

Occurs in dry loose red sand.

It differs from all other known species of Ledebouria in having viscid leaves and in the shape of the leaves and bulb. Its affinities are obscure. Although other collectors have recorded the viscid nature of the leaves and although the leaves of both herbarium specimens and specimens examined in the field by the author have large numbers of sand grains adhering, it was found that the leaves are not actually sticky to the touch. Whether the stickiness is a feature of the leaves only at certain stages of development has not been ascertained. It was also noticed that certain other plants, especially a species of grass, also had sand adhering to the leaves, introducing the possibility that it is a characteristic of the sand rather than of the Ledebouria. This is the only species of Ledebouria which, although several plants were collected, failed to survive in cultivation in the author's collection in Grahamstown.

Dyer & Ehrens 4201 (PRE) is interesting as it is in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fruit; fruit not often having been collected in Ledebouria.

For illustration see fig. 287.

For list of specimens examined, see appendix, p. 43.

16. Ledebouria scabrida Jessop, sp. nov., L. revolutae (L.f.) Jess. affinis, sed foliis scabridis et bulbo in collum sursum producto.

Bulbi 30-40 mm longi, 35-40 mm lati, in collum sursum producti, cinerei vel brunnei. Folia lanceolata, 80-170 mm longa, 20-30 mm lata, patentes vel erecto-patentes, rosulata, scabrida sursum, ubi lacerata fila plurima non exhibentes. Pedunculi solitarii, c.100 mm longi, floribus 25-30. Pedicellii 5-7 mm longi. Perianthii segments pallida, vitta dorsali roseo-brunneo, ad apicem tumidi, c.5 mm longi, sub medio reflexi. Filamenta rosea, adnata, c.4 mm longa. Antherae roseae. Ovaria viridia, 1,5 mm longa. Styli albi, 2,5 mm longi.

Type: South West Africa: Epukiro (2119), Sturmveld, Tölken s.n., December 1970 (GRA, holo.).

Opposite- Map 21. Distribution of Ledebouria scabrida.

Bulb 30-40 mm long, produced apically into a slightly fleshy neck c.25-35 mm long; outer scales membranous, grey to brown not marked with red or purple. *Leaves* 3 or 4, lanceolate, 80-170 mm long, 20-30 mm broad, rosulate, spreading to erect-spreading, marked with darker green patches or groups of dots on the upper surface; upper surface scabrid; lower surface smooth; margin ciliate. *Inflorescence* solitary, more or less erect, c.100 mm long, with 25-30 flowers. *Perianth segments* pale, with a light pinkish brown dorsal stripe.

Only reported from the Gobabis area of South West Africa. See map 21.

Occurs on the margins of calcareous depressions, with *Acacia mellifera* subsp. *detinens*. Flowers during summer.

Although there is only one other specimen known of this species, it is possible that *Drimiopsis papillosa* Dint. (Fedde. Repert. 17 : 189; 1921) is synonymous. Dinter cited his material as "H.: Etemba, in Massen in der grossen Kalkpfanne, Dtr. 3298; Eahero, Dtr". This material has not been located (perhaps formerly in Berlin). The leaves are described as being covered on the upper surface by large "glitzernden" papillae. He also remarked" "Möglicherweise handelt es sicht aber auch hier nur um eine neue *Scilla*". There is no indication in the description that the material included flowers, which would have been necessary for a generic identification.

The protuberances, giving the plant its scabrid character, are of interest as only one other species of Ledebouria possesses distinct and characteristic trichomes - namely L. hypoxidioides. However, in L. hypoxidioides, which is also known from an extremely restricted area, they take the form of distinct somewhat silky hairs (see figs 288 & 289).

For illustration see fig. 290.

For list of specimens examined see appendix p. 43.

7.3 Drimiopsis Lindl.

Paxton's Flower Garden 2 : 73 (1851-2).

Resnova Van der Merwe in Tydskr. Wetensk. Kuns N.R. 6 : 41-46 (1946). Type species: not indicated.

Bulbs present, lacking membranous outer scales. Leaves all basal, sometimes petiole-like at the base, generally with spots or patches of a different shade of green from the rest of the lamina. Inflorescence suberect, originating from an axillary bud, always unbranched. Bracts vestigial, not spurred. Perianth segments similar or almost so, ascending, sometimes with the apices incurved and cucullate, white, green pink or purple, sometimes with a purplish or brown longitudinal marking. Filaments free of one another or very shortly connate, epipetalous. Ovary oblong, sessile, with two basal ovules per locule. Ovules basal. Style simple. Fruit a loculicidal capsule.

Type: D. maculata Lindl.

Species concepts in Drimiopsis

The delimitation of species in Drimiopsis presents similar problems to those in Ledebouria. As mentioned (p. 92) meiotic abnormalities occur, and apomixis may be an important factor.

Qualitative characters are again rare. But the following are of some value:-

1) leaf characters: the shape of the base of the leaf is, with few exceptions, apparently diagnostic for some species. D. maculata has a cordate base and petiole-like structure.

2) floral characters: whether the perianth segments are erect-spreading or ascending and perhaps with a cucullate apex is important. Colour, unlike the general rule in Ledebouria, has been found to be useful and, linked with this, whether the segments have a dorsal stripe or not.

Key to the species of Drimiopsis in South Africa

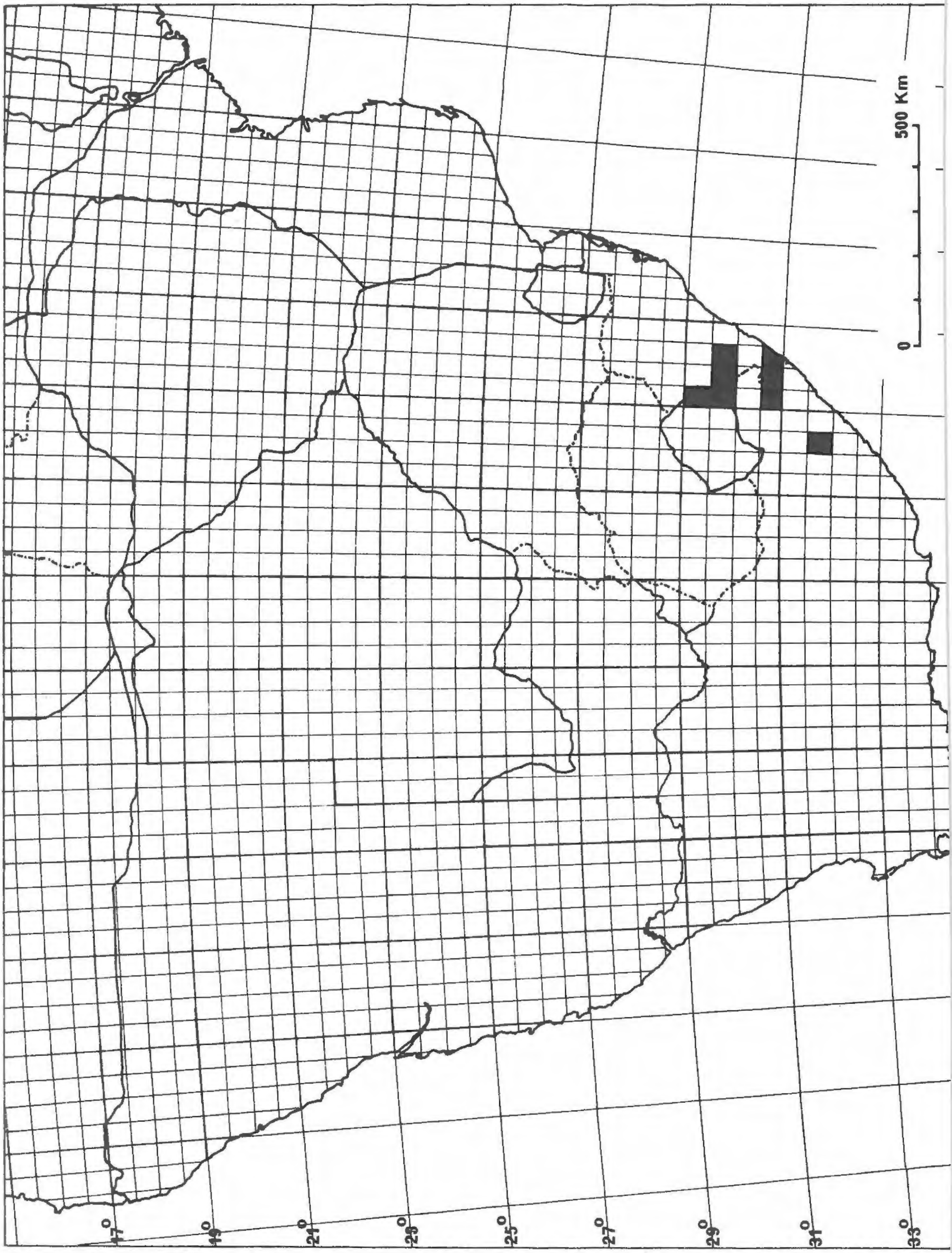
1 Apices of perianth segments erect-spreading. Flowers usually more than 5 mm long.

  2 Flowers pink to purple, not conspicuously striped, 10 mm or more long. Transkei to Underberg and Pitermaritzburg . 1. lachenalioides

  2a Flowers striped, often partly pink, 9 mm or less long. To the east and north of Durban, with a few records from the eastern Cape as far west as Bedford and East London .. 2. maxima

1a Apices of perianth segments incurved or cucullate. Flowers usually less than 5 mm long.

  3. Flowers usually 4-5 mm long, apparently always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green, often white in the bud. Leaves cordate .. .. 4. *maculata*

3a Flowers usually less than 3 mm long, often with pink or brown markings. Leaves usually cuneate, less often cordate at the base.

4 Flowers greenish, white or, if purple, then the leaves with cuneate bases .. .. 3. *burkei*

4a Flowers purple. Leaves usually cordate at the base .. .. 5. *atropurpurea*

1. **Drimiopsis lachenalioides** (Bak.) Jessop, comb. nov.

Scilla lachenalioides Bak. in Fl. Cap. 6 : 482 (1897). Type: "Transkei", *Hallack* s.n.; "Bazeia Mountain", *Baur* 549 (SAM!, PRE, photo.!); "Griqualand East", Maloine, near Clydesdale, *Tyson* 2878 (BOL!; SAM!, PRE, photo.!).

Resnova lachenalioides (Bak.) Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946).

Bulb 30-40(-80) mm long. *Leaves* 2-4, subpetiolate, glabrous to pubescent, (70-)100-200(-250) mm long, (12-)25-40 mm broad. *Inflorescence* generally a little longer than the leaves. *Pedicels* 1-3 mm long. *Flowers* pink to purple. *Perianth segments* ascending with erect-spreading, minutely cucullate apices,

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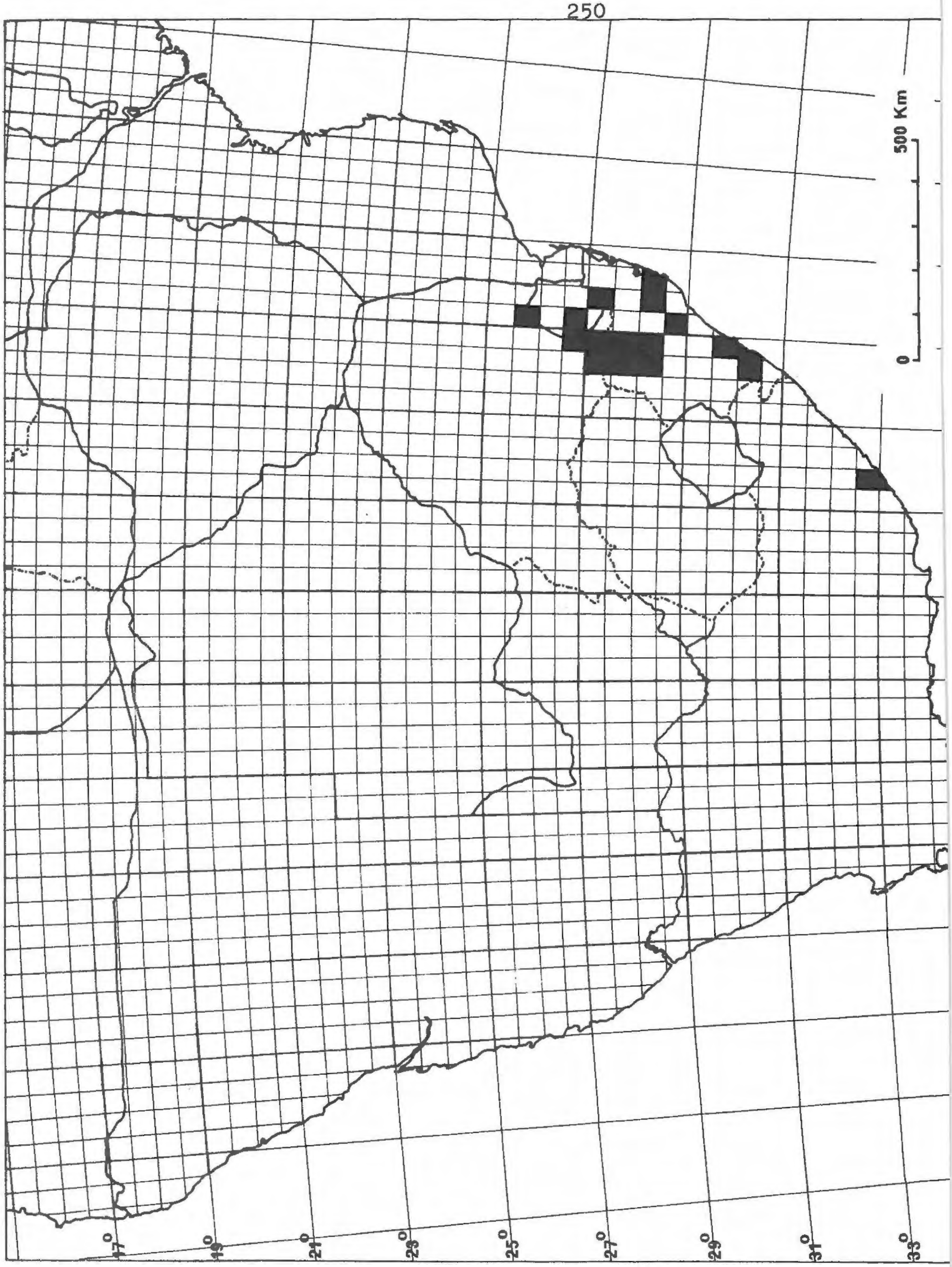
Opposite- Map 22. Distribution of *Drimiopsis lachenalioides*.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(9-)10-12(-18) mm long.

Recorded from between Umtata and Pietermaritzburg. A single record from Zululand (2728; Frankfort: Hlobane, *Johnstone* 574; NH) may be better placed under *D. maxima*. See map 22.

Occurs in grassveld and possibly forest.

Specimens linking this species with *D. maxima* do occur (e.g. 2832; Mtubatuba: Hluhluwe Game Reserve, *Ward* 3281; NH & PRE, which has been placed in *D. maxima*). Size and markings of the perianth are used, somewhat artificially, to separate these species. Distribution also provides a useful feature.

For illustration see Flower. Pl. S. Afr. 21 : t.824 (1941).

For list of specimens examined see appendix, p. 43.

2. **Drimiopsis maxima** Bak. in Fl. Cap. 6 : 474 (1897). Type: Natal, near Botha's, *Wood* 4773 (K, holo.!; NH!, PRE, photo.!).

Drimiopsis saundersiae Bak. in Fl. Cap. 6 : 474 (1897). Type: "Natal, Itafamasi", *Wood* 774 (K, lecto.!), *Wood* 938 (K, iso.!); without precise locality, *Saunders* s.n. (K!).

Opposite- Map 23. Distribution of *Drimiopsis maxima*.

Scilla humifusa Bak.in Gdnrs' Chron. 15 : 626 (1881). Type: ex cult. hort. Bull (K, holo.!).

Drimiopsis humifusa (Bak.) Bak. in Fl. Cap. 6 : 474 (1897).

Scilla schlechteri Bak. in Bull. Herb. Boissier 2 : 1002 (1904). Type: Natal, Krantzkloof, Schlechter 3174 (K, holo., BOL, drawing!; BOL!, PRE, photo.!; GRA!, PRE, photo.!; PRE!; Z!).

Resnova schlechteri (Bak.) Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946).

Resnova transvaalensis Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946). Type: Transvaal, Piet Retief district, Amsterdam, Van der Merwe s.n. sub PRE 26432 (PRE, holo.!).

Resnova pilosa Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946). Type: Natal, Vryheid, Van der Merwe 2643 (PRE, holo.!).

Resnova minor Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946). Type: Natal, Paulpietersburg, Van der Merwe 2780 (PRE, holo.!).

Resnova maxima Van der Merwe in Tydskr. Wetensk. Kuns 6 : 46 (1946). Type: "In collibus prope Magut", Van der Merwe 2710 (PRE). The specimen of the type number annotated as the type in the National Herbarium, Pretoria, is labelled "Dwarsberg (Louwsberg)". Note that this is not based on the same type as Drimiopsis maxima.

Bulb 30-50(-100) mm long. *Leaves* 2-4(-8), subpetiolate or narrowing gradually to the base, the margins sometimes undulate, glabrous to pubescent, (60-)80-150 (-300) mm long, (13-)30-50(-70) mm broad. *Inflorescence* about the same length as the leaves to several times as long. *Pedicels* 1-2(-3) mm long. *Flowers* striped, pink, white, green or brown. *Perianth segments* ascending, with erect-spreading, minutely cucullate apices, (5-)6-8(-9) mm long.

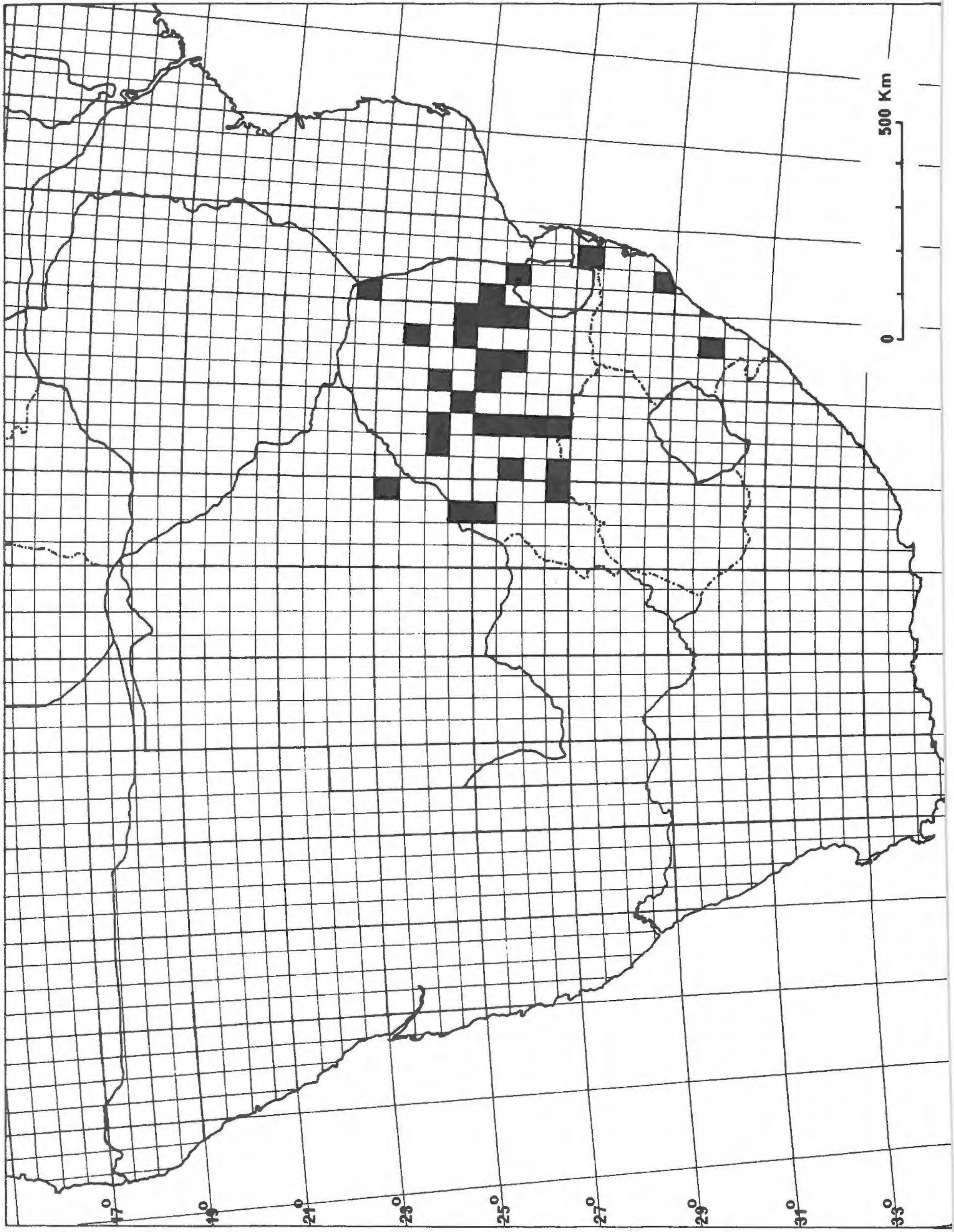
Widespread in Natal as far west as Hillcrest, Swaziland and the south-eastern Transvaal. Isolated specimens have also been collected in the eastern Cape. See map 23.

Grows in grassveld, among rocks, in shallow pans and in forest.

Specimens, intermediate between this species and *D. burkei*, have been collected. It is separated by the present author from *D. burkei* on rather artificial criteria. It is also not always readily separable from *D. lachenalioides*.

For illustration see Flower. Pl. S. Afr. 21 : t.823 (1941).

For list of specimens examined see appendix, p. 44.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3. Drimiopsis burkei Bak. in Saund., Ref. Bot. 3, app.: 17 (1870). Type: Transvaal, Aapies River, Burke s.n. (K, holo.!).

Drimiopsis woodii Bak. in Fl. Cap. 6 : 473 (1897). Type: Natal, Inanda, Wood 656 (NH!, PRE, photo.!; BOL!; SAM!); Natal, Klip River, Sutherland s.n. (K!).

Drimiopsis crenata Van der Merwe in Flower. Pl. Afr. 25 : t.975 (1946). Type: Transvaal, Rooiberg, Van der Merwe 2805 (PRE, holo.!).

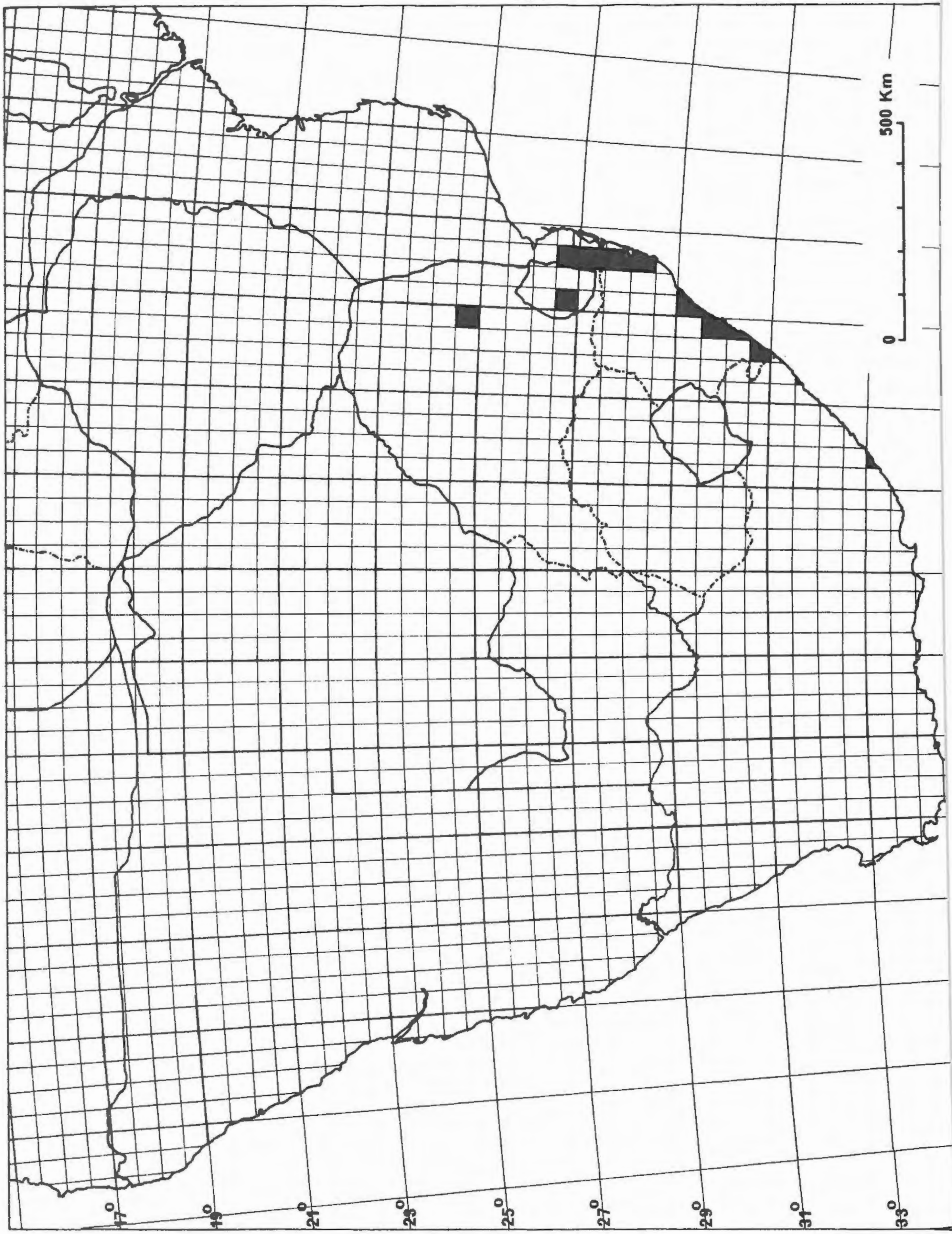
Bulb (20-)30-60(-90) mm long. Leaves usually 2-4, narrowing towards the base or sometimes subpetiolate, often with finely crenate or undulate margins, glabrous or rarely pubescent, (20-)40-100(-150) mm long, (10-) 20-40(-50) mm broad. Inflorescence about the same length as the leaves to several times as long. Pedicels 1-2 mm long. Flowers green, white or pale pink. Perianth segments ascending with incurved, cucullate apices, usually 2-3 mm long.

Widespread in the Transvaal and Natal and recorded from Botswana. See map 24.

Occurs in a wide range of habitats, but especially in the open or among rocks.

Some plants, especially those from damper areas,

Opposite- Map 24. Distribution of Drimiopsis burkei.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and the Transvaal lowveld (for example the types of D. woodii), have longer leaves than those from the highveld of the Transvaal. These plants are often close to D. maculata in leaf form, but the leaves tend to be more cuneate. Their inclusion under D. burkei is principally on the basis of their smaller flowers.

For illustration of the typical form see Flower. Pl. Afr. 25 : t.975 (1946), and for the longer leafed form see Flower. Pl. Afr. 25 : t.988 (1946).

For list of specimens examined see appendix, p. 46.

4. **Drimiopsis maculata** Lindl. in Paxt. Flow. Gard. 2 : 73, f.172 (1851-2). Type: "Cape of Good Hope, introduced by the Horticultural Society", without collector, in Herb. J. Lindley (CGE, ?holo., K, photo.!).
Drimiopsis minor Bak. in Saund., Ref. Bot. 3 : t.192 (1870). Type: Saund., Ref. Bot. 3 : t.192, "Natal, Cooper s.n.", (1870).

Bulb (15-)25-40(-50) mm long. Leaves usually 2-4, usually cordate above the distinctly petiole-like base, erect to spreading, glabrous, (50-)100-200(-300) mm long, (20-)35-70(-80) mm broad. Inflorescence usually much longer than the leaves. Pedicels 1-2 mm long. Flowers white or green. Perianth segments ascending, with

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Opposite- Map 25. Distribution of Drimiopsis maculata.

incurved, cucullate apices, usually 4-5 mm long.

Occurs in the eastern Cape, Natal, Swaziland and has occasionally been recorded from the Transvaal, especially in the east. See map 25.

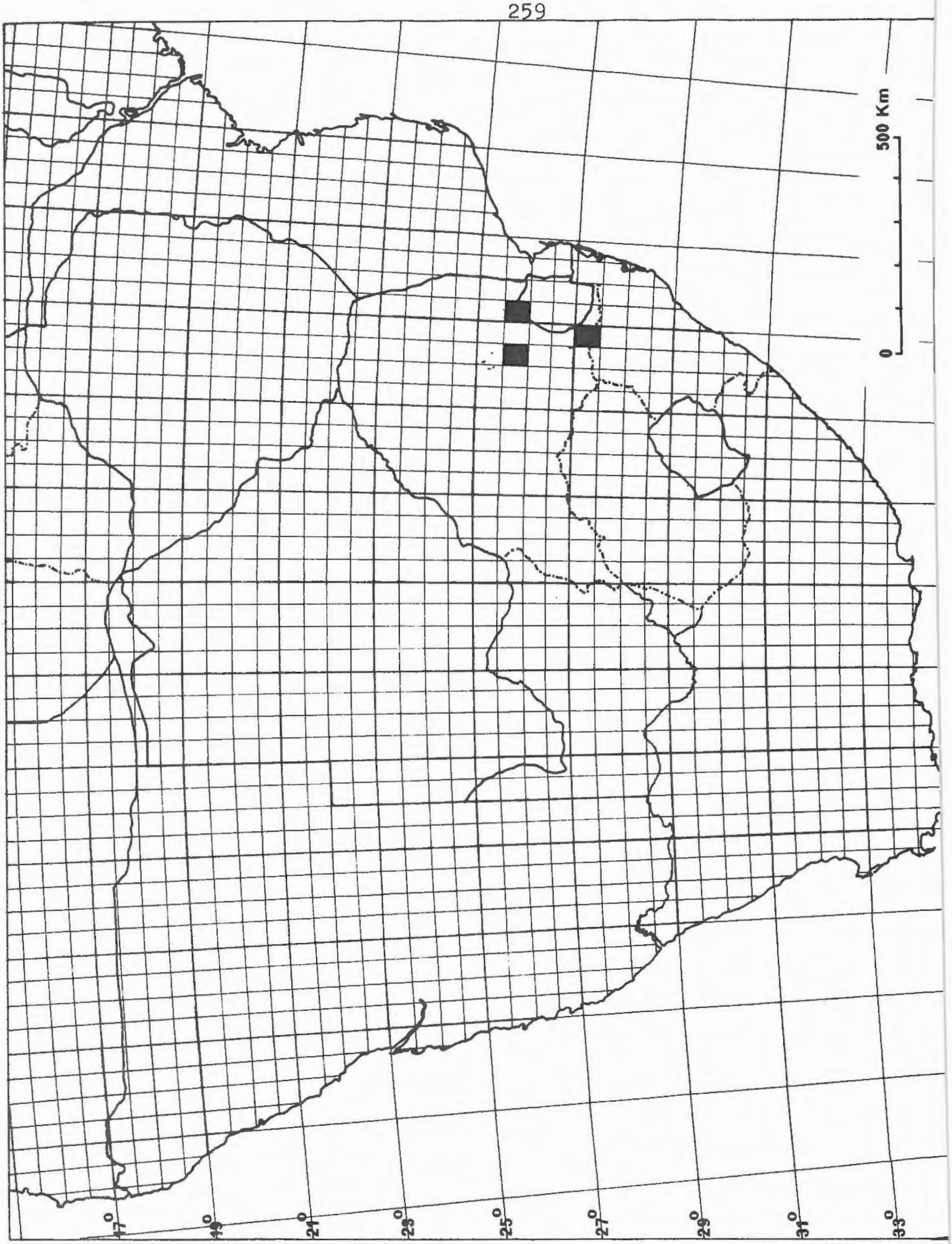
Grows mainly in shaded places in dampish areas.

The specimen cited as the type of D. maculata is a very good match of the figure in Paxton's "Flower Garden", but there is no indication on the herbarium sheet that this was made from the same material.

The type of D. woodii and other material similar to it have been collected over a wide part of the range of D. maculata as recognised by the present author. These specimens have narrower leaves, lacking the cordate base, and flowers only about 3 mm long. They are, therefore, to some extent intermediate between this and the previous species, but have been placed in D. burkei on the basis of their smaller flowers and cuneate leaves.

For illustration of D. maculata see Flower. Pl. S. Afr. 24 : t.957 (1944).

For list of specimens examined see appendix, p. 49.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5. Drimiopsis atropurpurea N.E. Br. in Kew Bull. 1921 : 299 (1921). Type: Transvaal, Barberton, Roses Creek, Thorncroft 1083 (BOL!; GRA!; PRE!).

Drimiopsis purpurea Van der Merwe in Flower. Pl. Afr. 25 : t.975 (1946). Type: Natal, Paulpietersburg district near Pivaan, Van der Merwe 2781 (PRE, holo.!).

In most respects this species is similar to D. maculata. However, it differs in the following respects: Leaves pubescent. Flowers purple, approximately 2-4 mm long.

Little is known about its distribution or habitat. It has been recorded from northern Natal and the south-eastern Transvaal. See map 26.

For list of specimens examined see appendix, p. 50.

Opposite- Map. 26. Distribution of Drimiopsis atropurpurea.

7.4 Massonia Houtt.

Natuurl. Hist., pt.2, 2 : 424 (1780).

Neobakeria Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924). Type species not designated.

Bulbs present, usually with membranous outer scales, rather small - generally less than 35 mm long; scales tubular, all fleshy. Leaves almost always paired, often spreading - often tightly adpressed to the ground - often rather broadly oblong or elliptic, less often lanceolate or narrowly oblong to orbicular, glabrous, ciliate, or with simple trichomes varying from pustules to firm bristles. Peduncles usually solitary, producing a very condensed subcapitulate raceme close to ground level. Inflorescence usually surrounded by large sterile bracts, which are usually more or less green or with a reddish colour; upper bracts very much smaller. Flowers actinomorphic, pedicillate, usually pink, white or green, less often yellow to red. Perianth fused to form a tube which usually completely surrounds the ovary and may be several times as long as the ovary, marcescent, leaving a distinct scar at the base of the young fruit, adhering to the apex of the young fruit; the free segments more or less oblong, usually with a sigmoid folding in the longitudinal axis towards the base, often minutely papillate at the apex. Stamens all usually the same length, attached at the mouth of the perianth tube; filaments free, connate at the base only, or fused for most of their length; sublinear to narrowly deltoid; anthers dorsifixed, oblong to linear, straight or slightly arcuate. *Ovary* sessile, oblong, ellipsoid or ovoid; each carpel containing several axile ovules (often c.15-25). *Style* sublinear, usually slightly longer than the stamens. *Stigma* subcapitate to undifferentiated. *Fruit* a loculicidal, winged or deeply lobed capsule, containing numerous black subglobose seeds about 1-2 mm in diameter. Flowers usually pleasantly scented and producing copious nectar.

Type: *M. depressa* Houtt.

Species concepts in *Massonia*

As in most genera of the Scilleae, most species have been defined by previous authors on the basis of quantitative characters. Within populations there is considerable variation in the measurements of the leaves and in the number of flowers and other quantitative features. This is probably often due to flowering of comparatively young plants as well as very much older plants, as well as genetic and environmental factors. Unlike *Ledebouria* and *Drimiopsis* large quantities of seeds are produced sothat there is less evidence for apomixis or other reproductive abnormalities. In selecting taxonomic characters for distinguishing species every effort has been made to employ qualitative characters where possible. The following characters are probably the more important:-

1) leaf characters: Whether the leaves are flat on the ground or more or less erect is generally constant in populations, but some variation does occur. The size and shape of leaves is not reliable except within very wide limits. This aspect is dealt with under individual species. Trichomes afford a number of characters of potential value which have been used by previous authors. They vary from coarse bristles or other types of hairs to pustules, but it has been found that within populations plants otherwise similar to one another may sometimes have trichomes and sometimes not - even plants with one hairy leaf and one glabrous leaf have been found. There is also a considerable gradation between most types of trichomes. The pustulate form, however, appears to be clearly distinguishable from other forms in almost all the plants examined and is used as the principal character for defining M. pustulata.

2) bract characters: whether or not sterile lower bracts (spathes of some authors) are formed has been used in distinguishing the genera Massonia and Neobakeria. It has generally been found possible to distinguish species on this character, but exceptions are known where plants without these bracts are placed in

species which do usually have these bracts. A coma is formed in a few plants of M. angustifolia. However, this character varies within otherwise relatively homogeneous populations.

3) floral characters: In many plants there is a very pronounced folding of the proximal part of the perianth segments so as to form a curve, referred to in the text as a sigmoid curve (fig. 291). Although this form is not linked with the straight, erect or spreading forms, it does not show a strong association with other characters. It is, therefore, not used here as a specific character. Although species, such as M. depressa sometimes have it, but not always, there are species, such as M. angustifolia, which probably never show this character.

Key to the species of Massonia

1 Largest bracts less than 10 mm long or early deciduous; inflorescence axis usually somewhat elongate.

  2 Perianth tube more than 20 mm long .. 6. comata

  2a Perianth tube less than 20 mm long. 5. angustifolia

1a Largest bracts more than 10 mm long; inflorescence axis usually capitate.

  3 Anthers more than 2 mm long; leaves usually glabrous or very rarely with a minutely ciliate

margin.

4 Perianth tube more than 5 mm long, more or less cylindrical .. .. 1. <u>depressa</u>

4a Perianth tube less than 5 mm long, more or less cup-shaped .. .. 2. <u>grandiflora</u>

3a Anthers usually less than 2 mm long or, if more, then the leaves hairy or papillate.

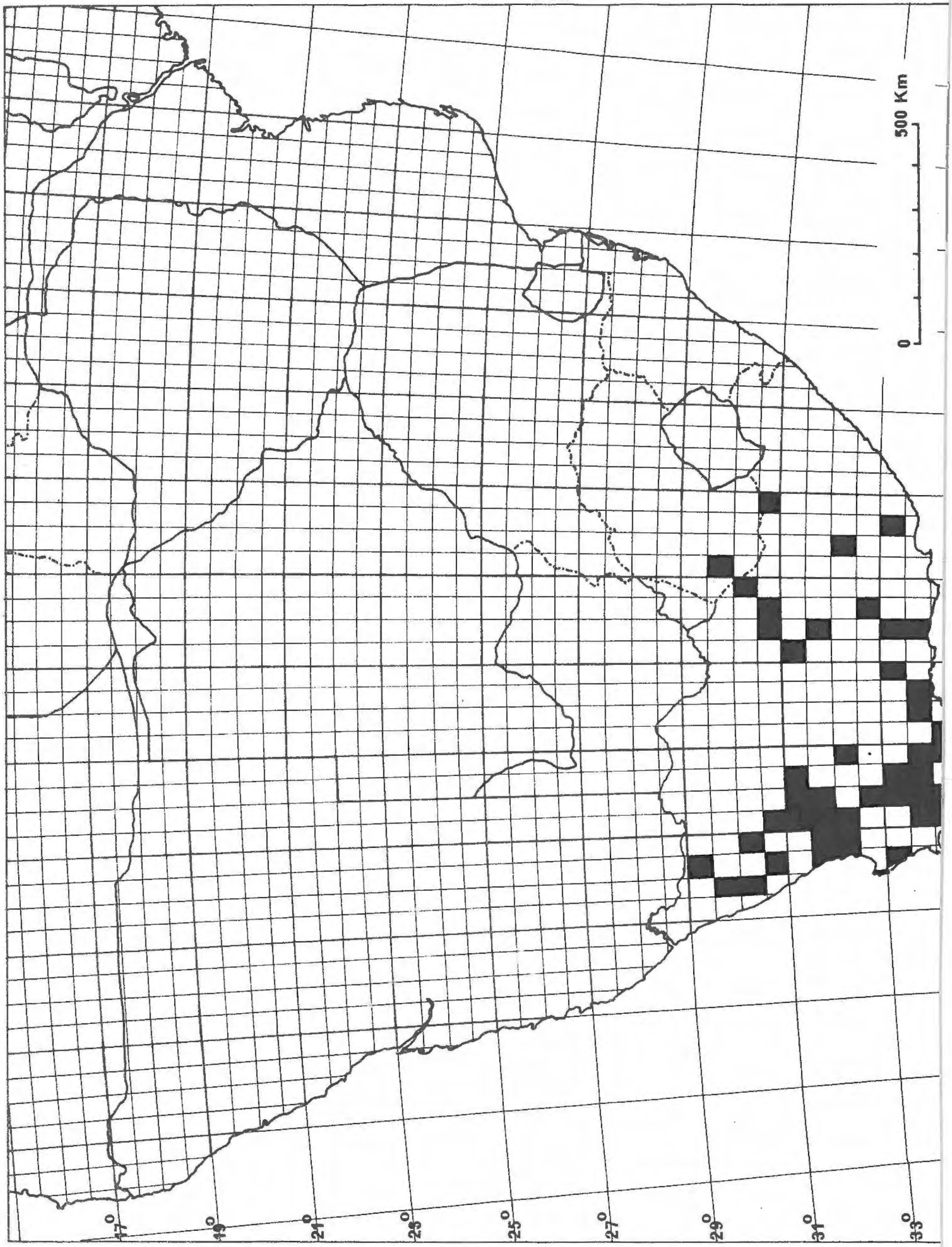
5 Filaments usually of two lengths in each flower: leaves usually pustulate and less than 30 mm long .. ..8. <u>heterandra</u>

5a Filaments usually all of the same length in each flower; leaves glabrous, hairy or pustulate and usually more than 30 mm long.

6 Leaves glabrous or rarely pustulate; filaments usually with the free part 3 mm long or less; perianth segments approximately half the length of the tube; tube less than 3 mm in diameter .. .. 7. <u>jasminiflora</u>

6a Leaves often hairy or pustulate; filaments usually free or with the free part more than 3 mm long; perianth segments usually approximately the same length as the tube; tube usually at least 3 mm in diameter.

7 Leaves with papillae or pustules on upper surface .. .. 4. <u>pustulata</u>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7a Leaves glabrous or with simple hairs,
but not papillae or pustules .. ..
.. .. 3. echinata

1. Massonia depressa Houtt., Natuurl. Hist., pt.2, 2 : 424, t.85, fig.1 (1780). Type: "De eenigste soort, mischien, daar van tot heden bekend (Massonia Thunb.)", ?Thunberg s.n., not traced; Houtt., Natuurl. Hist., pt.2, 2 : t.85, fig.1 (1780), lecto.

Massonia latifolia L.f., Suppl. 193 (1781). Type: "Cap. bonae Spei. F.Masson"; not located.

Massonia sanguinea Jacq., Hort. Schoenbr. 4 : 31, t.461 (1804). Type: South Africa without precise locality or collector, Jacq., Hort. Schoenbr. 4 : t.461 (1804), lecto.

?Massonia obovata Jacq., Hort. Schoenbr. 4 : 29, t.458 (1804). Type: Jacq., Hort. Schoenbr. 4 : 29, t.458 (1804), lecto.

Massonia brachypus Bak. in J. Bot. 1874 : 368 (1874). Type: "Caput Bonae Spei, Hort. Kew., Feb., 1874" (K, holo.!, BOL, drawing!).

Massonia namaquensis Bak. in Fl. Cap. 6 : 411 (1897). Type: "Little Namaqualand; near Kook Fontein, 3000 ft.", Bolus 6596 (BOL, lecto.!; K!); Scully 27 (K!).

Massonia triflora Compton in Trans. Roy. Soc. S. Afr. 19 : 276 (1931). Type: Whitehill Ridge, south side, Compton 3515 (BOL, holo.!).

Opposite- Map 27. Distribution of Massonia depressa.

Bulb usually ovoid, (17-)20-30(-45) mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, orbicular to oblong, acute or apiculate, flat on the ground, coriaceous to fleshy, glabrous, rarely ciliate on margins, sometimes with conspicuous longitudinal grooves, (50-)70-150(-260) mm long, 40-100(-150) mm broad, green, with or without green or purple flecks, patches ot striations. Inflorescence capitate, with often about 20-30 flowers. Lower bracts conspicuous, ovate to obovate, acute to sub-attenuate, glabrous, (15-)30-40(-50) mm long, 10-15 (-20) mm broad, green, often pale or reddish or purplish towards the base, or purplish with a green margin. Pedicels 5-20 mm long, rather thick. Perianth green, yellow, white, cream, [illegible] pink to red (especially in the tube) or brown, occasionally flecked with purple; tube (5-)10-15(-17) mm long, (2-)4-6(-8) mm broad at mouth, narrowing slightly to base; segments oblong, slightly broader at base, usually with a sigmoid curve in the longitudinal axis towards the base, (7-)8-10(-12) mm long. Filaments (8-)10-16(-18) mm long, connate portion at base up to 1-2 mm long, linear-lanceolate. often cream, yellow or green, less often purplish; often red or purple in the tube, with yellow or purple anthers which are (2-)2½-4 mm long. Style 10-14 mm long. Ovary obovoid, with up to 30 ovules per locule; septa at least sometimes hollow. Capsule obovoid

3-winged, emarginate, (10-)15-20(-30) mm long.

Widespread in the Cape Province except the eastern parts. See map 27.

Occurs in a range of habitats in shade and in the open. Frequents both sandy flats and rocky slopes. Flowers are produced in winter, with a strong peak in July and August. There appears to be correlation between geographical distribution and flowering times - climatic variation probably being significant, however.

Usually scented and producing copious nectar.

Leaf measurements are very variable, but as indicated in fig.292 there appears to be no likelihood that overall measurements could provide characters for subdivision of the species. Fig. 293 shows variation in a population.

Houttuyn's figure of the flowers of M. depressa shows the large anthers characteristic of the present concept of this species. As he made no reference to surface characters of the leaves, it seems likely that his specimen had glabrous leaves and that Houttuyn's epithet is correctly applied here. Houttuyn ascribed the generic name to Thunberg, but the binomial does not appear in the Thunberg collection in Uppsala, although it is likely that Houttuyn based this species on a Thunberg specimen. The specimen has also not been traced in the Rijksherbarium, Leiden. Two specimens, either of which could possibly be the one on which Houttuyn based his description, are known. In the Linnaean Herbarium, London, there is a specimen labelled, according to Savage (1945): "414.1 Massonia (m.L.) latifolia (m.Lf.)". If this is a correct identification of the script, then Linnaeus, the elder, may deserve the credit for commemmorating Masson's name, but there is no evidence that Masson collected the plants on which this name was based. However, in 1781, Linnaeus the younger described *M. latifolia*, based on a Masson specimen. Both Houttuyn and Linnaeus compared the plant with a *Haemanthus*, but whereas Houttuyn described the leaves as "ovaalachtig", Linnaeus called them "orbiculati". Linnaeus, but not Houttuyn, referred to the capsules, and it is probable that these two authors were referring to different specimens. The Thunberg (UPS) specimen of *M. latifolia* is in fruit and can, therefore, not be regarded as the type. The figure accompanying the type description has been selected as the lectotype. There is a specimen, collected by Masson, in Geneva (G), but this is of *M. echinata*.

Typification of *M. latifolia* is similarly complicated by the failure to trace a specimen definitely collected by Masson, other than the one mentioned above of *M. echinata*. The type description of *M. latifolia* described the plant as "Massonia foliis orbiculatis glabris", which makes it very likely that the name is correctly placed in synonymy under *M. depressa*. Baker (1896/7) placed *M. depressa* in synonymy under *M. latifolia*.

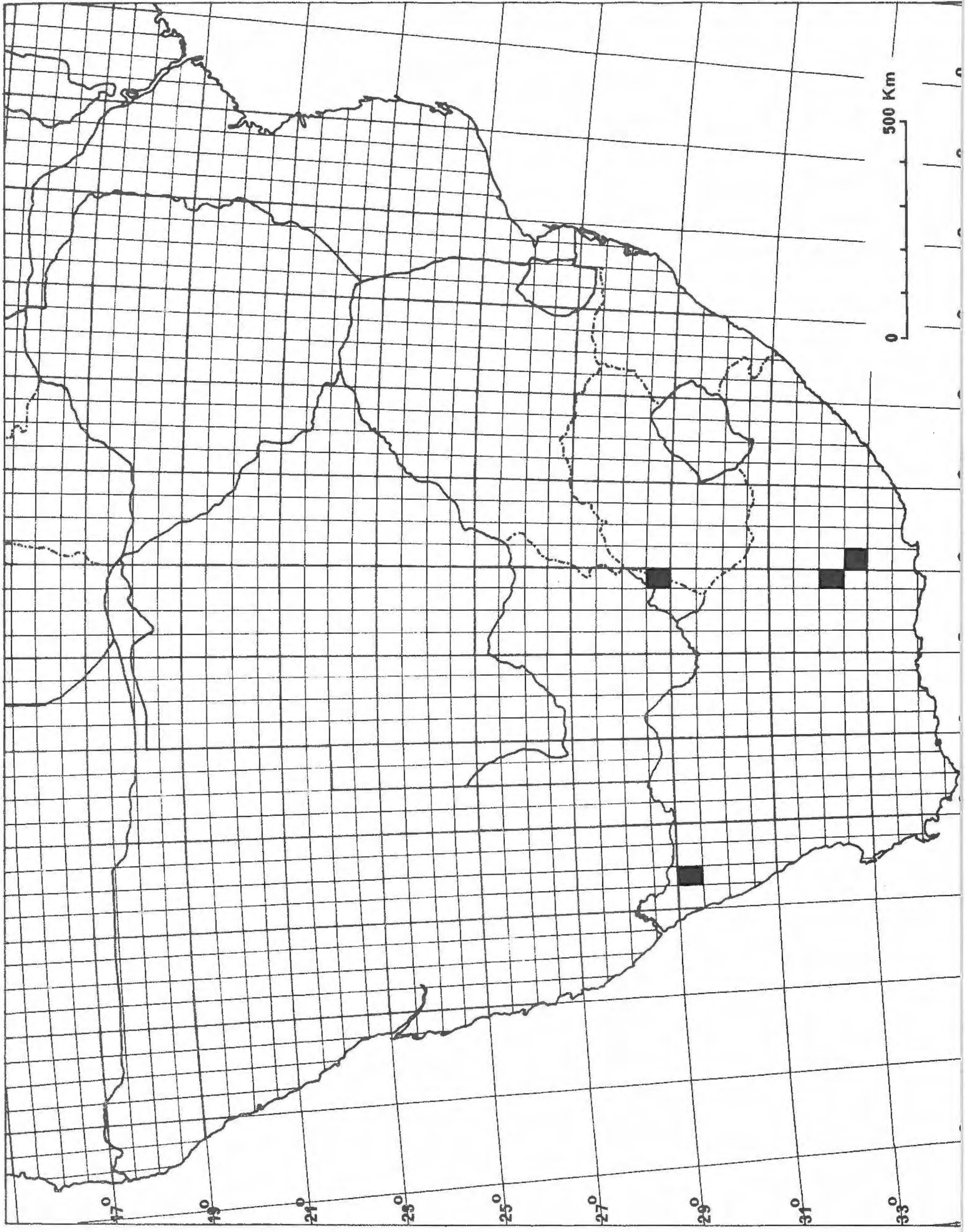
The assigning of two of Jacquin's epithets to this species, is based on the type descriptions and the illustrations which are barely adequate to be certain of their identity. The illustration of *M. sanguinea* is, however, a particularly good match for typical specimens of *M. depressa*.

M. latifolia sensu Ker-Gawl., Bot. Mag. 22 : 848 (1805), was treated by Baker (1896/7) as not synonymous with *M. latifolia* L.f., but with *M. sanguinea* Jacq. However, Gawler did cite *M. latifolia* L.f. and his figure appears to be correctly assigned to this species.

The selection of the Bolus Herbarium material as the lectotype of *M. namaquensis* Bak., is because this specimen is annotated in Baker's hand.

For illustration see Flower. Pl. S. Afr. 2 : t.46 (1922).

For list of specimens examined see appendix, p. 51.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2. Massonia grandiflora Lindl. in Bot. Reg. 12 : t.958 (1826). Type: "The interior of the Cape of Good Hope, brought by Mr Synnet, in Mr Colvill's nursery", Bot. Reg. : t.958 (1826).

Bulb ovoid, 25-35 mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, broadly oblong to ovate, flat on the ground, fleshy, glabrous, (50-)100-150 mm long, 40-110 mm broad, nerves depressed, dark grey-green suffused with purple, with some scattered oblong purple spots. Inflorescence capitate, with about 20-25 flowers. Lower bracts ovate, 20-30 mm long, green. Pedicels 8-10 mm long, fleshy. Perianth green to white; tube cup-shaped, 3-5 mm long, 4-6 mm broad; segments rather narrowly deltoid, 6-10 mm long, erect or reflexed, straight. Filaments 8-14 mm long, connate portion c.2 mm long, linear-lanceolate, greenish yellow or greenish purple. Anthers brown or purple, 2-3 mm long. Style 3-5 mm long; stigma not differentiated. Ovary broadly oblong to obovoid, with numerous ovules, c.8 mm long. Capsule obovoid, 3-winged, emarginate, c.18 mm long.

Recorded from a few localities over a large part of the drier regions of the Cape. See map 28.

Flowers have been recorded in August.

Opposite- Map 28. Distribution of Massonia grandiflora.

Obermeyer (Flower. Pl. Afr. 37 : t.1451; 1965) referred to the following features as being characteristic of M. grandiflora (this species has not been examined in the living state by the present author):-

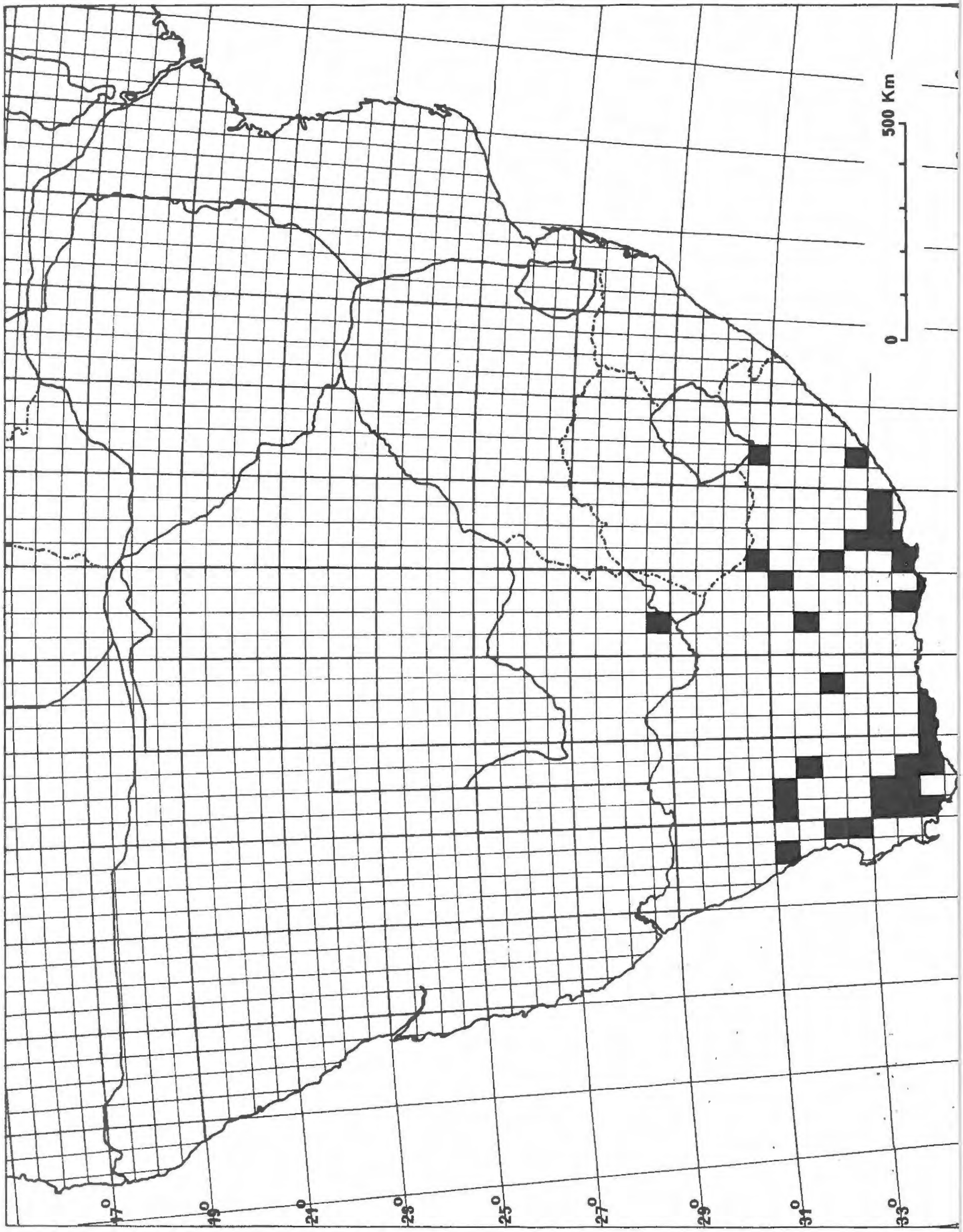
1) Fleshy, rather than delicate, perianth.
2) Short and wide tube.
3) Triangular straight segments.

The texture of the perianth cannot be determined from herbarium material, but has not been found to be consistent in living material of plants of M. depressa (which is its nearest ally). The short wide tube appears to be a more reliable character, but the shape of the segments of M. depressa is certainly not consistent. Earp s.n. from Murraysburg (BOL), for example, has straight segments, but a tube 8 mm long, which places it with M. depressa.

The isolated distant localities for this species suggest that the populations may be aberrant forms of M. depressa, but it is considered that the morphological characters suffice to separate M. grandiflora until further material clarifies its position.

For illustration see Flower. Pl. Afr. 37 : t.1451 (1965).

For list of specimens examined see appendix, p. 55.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3. Massonia echinata L.f., Suppl. 193 (1781). Type: "Cap. bonae spei, Thunberg", (UPS - 7988, holo., microfiche!).

Massonia scabra Thunb., Prodr. 188 (1800). Type: Cape, without further locality, Thunberg s.n. (UPS - 7992, holo., microfiche!).

Massonia muricata Ker-Gawl. in Curtis's Bot. Mag. 16 : t.559 (1802). Type: "our drawing was made in the garden of Ed. Woodford, Esq.", Curtis's bot. Mag. 16 : t.559 (1802).

Massonia scabra Andr., Bot. Rep. 4 : t.220 (1802). Type: "introduced to Britain, in the year 1796, by Messrs. Lee and Kennedy", Bot. Rep. 4 : t.220 (1802), nom. illegit., non Thunb.

Massonia longifolia Jacq. var candida Burch. ex Ker-Gawl. in Bot. Reg. 9 : 694 (1823). Type: "Raised at Mr Colvill's nursery from a plant that had been raised two years before from seed from Mr Burchell"; "Little Brak River, Mossel Bay Div.", Burchell 5746 (K, lecto.!).

Massonia candida Burch. ex Kunth, Enum. Pl. 4 : 297 (1843), nom. nud.

Massonia candida Burch. Ex Bak. in Fl. Cap. 6 : 415 (1897). Type: Little Brak River, Burchell 6197/5 (K, holo.!).

Massonia hirsuta Link & Otto, Icon. Pl. Rar. 1 : t.1

Opposite- Map 29. Distribution of Massonia echinata.

(1828). Type: Type description not located. Baker (1896/7) cited Masson s.n., Zeyher 4273 and Ecklon & Zeyher 130. (Ecklon & Zeyher 130, TCD!) The choice of epithet places this species with a high degree of probability.

Massonia pygmaea Schlechtdl. ex Kunth, Enum. Pl. 4 : 298 (1843). Type: "Cap. b. spei", Mund & Maire s.n. sub HAL 33834 (HAL!).

Polyxena bakeri (Schlechtdl. ex Kunth) Dur. & Schinz, Consp. Fl. Afr. 5 : 366 (1895), nom. nov. for M. pygmaea.

Massonia huttonii Bak. in J. Linn. Soc., Bot. 11 : 389 (1871). Type: "Cap. B. Spei", Masson s.n. (BM, lecto., BOL, drawing!); Drege 3509 (K, BOL, drawing!).

Massonia setulosa Bak. in J. Linn. Soc., Bot. 11 : 389 (1871). Type: "Cap. B. Spei.", Ecklon & Zeyher s.n. (TCD, holo.!).

Massonia versicolor Bak. in J. Bot., Lond. 1876 : 184 (1876). Type: "C.B.S. in argillaceis apricis fluminis Klyn Visch rivier, alt. 2500 pedes", MacOwan 2178 (K, holo.).

Massonia calvata Bak. in J. Bot., Lond. 1878 : 321 (1878). Type: "Cape Colony, eastern district", Bolus 749 (K, holo.).

Massonia orientalis Bak. in J. Bot., Lond. 1878 : 321 (1878). Type: "Cape Colony on sand-dunes at Port Elizabeth", Bolus 2239 (not located).

?*Massonia latebrosa* Masson ex Bak. in J. Bot., Lond. 1886 : 336 (1886). Type: "Bokeveld, Aug. 1792", *Masson* s.n. (BM, drawing, holo., BOL, copy!). A Masson specimen, without locality, in G matches the BM drawing.

Massonia amygdalina Bak. in Gdnrs' Chron. 1889, 6 : 715 (1889). Type: plant cultivated by Sir C.W. Strickland (K, holo., BOL, drawing!).

Massonia parvifolia Bak. in Engl. Bot. Jahrb. 15, Beih.3 : 8 (1892). Type: "C.B.Spei", *Ecklon & Zeyher* Asphod. 25 (B, holo.!).

Massonia dregei Bak. in Fl. Cap. 6 : 412 (1897). Type: "Clanwilliam Div., Lange Vallei", *Drege* 2688 (K, holo., BOL, drawing!; G!; HAL!; L!).

Massonia concinna Bak. in Fl. Cap. 6 : 414 (1897). Type: "Stockenstrom Div.; stony ground above the waterfall, Elands River", *Scully* 54 (K, holo., BOL, drawing!; SAM!).

Massonia bolusiae Barker in Flower. Pl. S. Afr. 11 : t.429 (1931). Type: "The farm Bangor near Middelburg", *Miss Pamela Bolus* s.n. sub BOL 19615 (BOL, holo.!).

Massonia modesta Fourc. in Trans. Roy. Soc. S. Afr. 21 : 79 (1932). Type: "Div. Humansdorp: Karreedouw", *Jeppe* s.n. sub Fourcade 4592 (BOL-Fourcade collection, holo.!).

Neobakeria visserae Barnes in J. Bot. 71 : 72 (1933). Type: Lamberts Bay, *Visser* s.n. sub BOL 19616 (BOL!).

Massonia inexpectata V. Poelln. in Portug. Acta Biol., ser. B, 1 : 384 (1947). Type: locality and collector unknown "in Herbar Breslau". Not located.

Massonia bokkeveldiana V. Poelln. in Portug. Acta Biol., ser. B, 1 : 384 (1947). Type: "Onder Bokkeveld", Schlechter 10935 (BOL!; G!; GRA!; PRE!).

Bulb usually ovoid, (5-)10-20(-40) mm long, with whitish scales, surrounded by few firm membranous brown scales. Leaves paired, ovate to oblong, acute or obtuse, usually flat on the ground, coriaceous to fleshy, usually hairy or at least ciliate on the margins, sometimes with conspicuous longitudinal grooves, (15-)20-80(-150) mm long, 10-60(-130) mm broad, often subpetiolate with the narrow basal part up to 25-50 mm long, green, often with darker green or purplish flecks, patches or striations. Inflorescence capitate, with (3-)5-20(-25) flowers. Lower bracts conspicuous, ovate to obovate, glabrous to hairy, 10-20(-30) mm long, 5-10 mm broad, green, sometimes marked with red or purple. Pedicels 4-8(-12) mm long. Perianth yellow, white or, especially in older flowers, pink; tube (4-)5-7(-16) mm long; segments oblong to narrowly lanceolate, with or without a sigmoid curve in the longitudinal axis towards the base, 4-8(-9) mm long. Filaments sublinear or narrowly conical, free or shortly connate, 4-8 mm long, 0,75-1,5 mm broad at the base; anthers 0,5-1,25 mm long, yellow or purple.

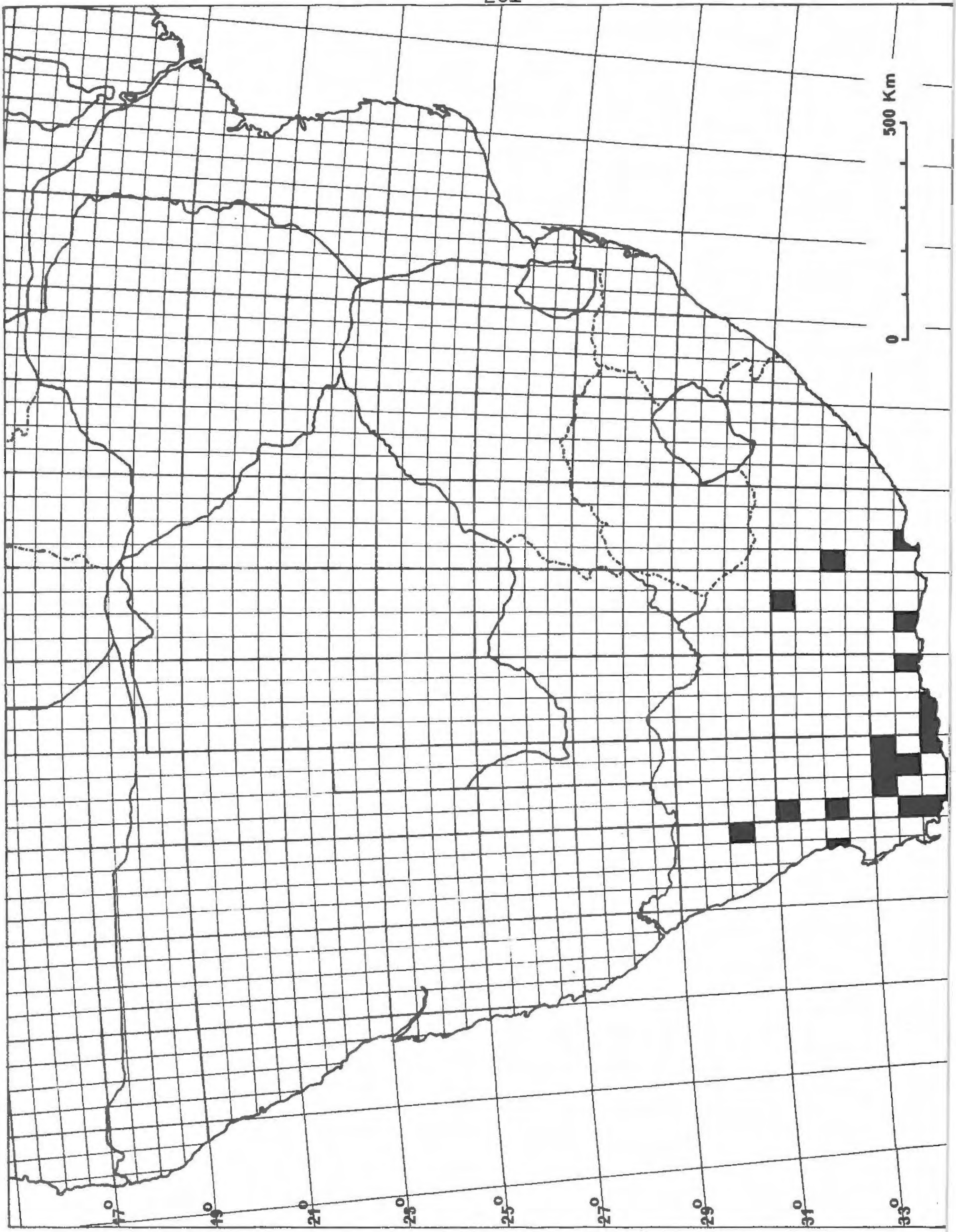
Style 5-10 mm long. Ovary obovoid. Capsule c.12-40 mm long, narrowly obovoid, emarginate, usually (?always) with 3 wings well developed.

Widespread in the Cape Province. See map 29.

Recorded from open sandy areas, clay soils and rock crevices, but rarely found in shade. Flowers are often sweetly scented.

Flowering is in winter, with a peak in May, June and July. It does, therefore, flower before M. depressa, although there is some overlap.

M. echinata, as defined in this work, includes many of Baker's species. He used mainly types of trichomes, leaf shape and length of perianth and filaments. These, approximately 25 species, were known to him by illustrations and a total of probably fewer than 20 actual specimens altogether! Fewer than two thirds of the species he recognised were known to him by specimens from recorded localities. The present author has been unable to correlate any two of these characters or any one morphological character with geographical distribution. Further, it has been found that, in practice, these characters show continuous ranges of gradation linking all the forms. As in M. depressa, there is considerable range in the dimensions of leaves of flowering plants for this species (see fig. 294).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M. pustulata is closely allied to *M. echinata* and, it might be justifiably argued, should possibly be placed in the same species. The decision to maintain two distinct species was taken because it was felt that the pustules graded into the other trichome types less than the other type graded into one another and because the plants with pustules tended, on the average, to be larger than those without.

For illustration see Flower. Pl. S. Afr. 11 : t.429 (1931).

For list of specimens examined see appendix, p. 56.

4. **Massonia pustulata** Jacq., Collect. 4 : 177-178 (1791). Type: Jacq., Hort. Schoenbr. 4 : 454 (1804). It is thought likely that this figure was made from the same material as the type description and is selected as the lectotype or, should it be shown to be derived from other material, the neotype.

?Massonia schlechtendalii (sphalm. *schlechtendahlii*) Baker, 1896/7) Bak. in J. Bot., Lond. 1874 : 5 : (1874). Type: "Caput Bonae Spei", *Schlechtendal* in Herb. DC. Although this specimen has not been traced, the type description makes it likely that it belongs in the present concept of *M. pustulata.*

Opposite- Map 30. Distribution of *Massonia pustulata*.

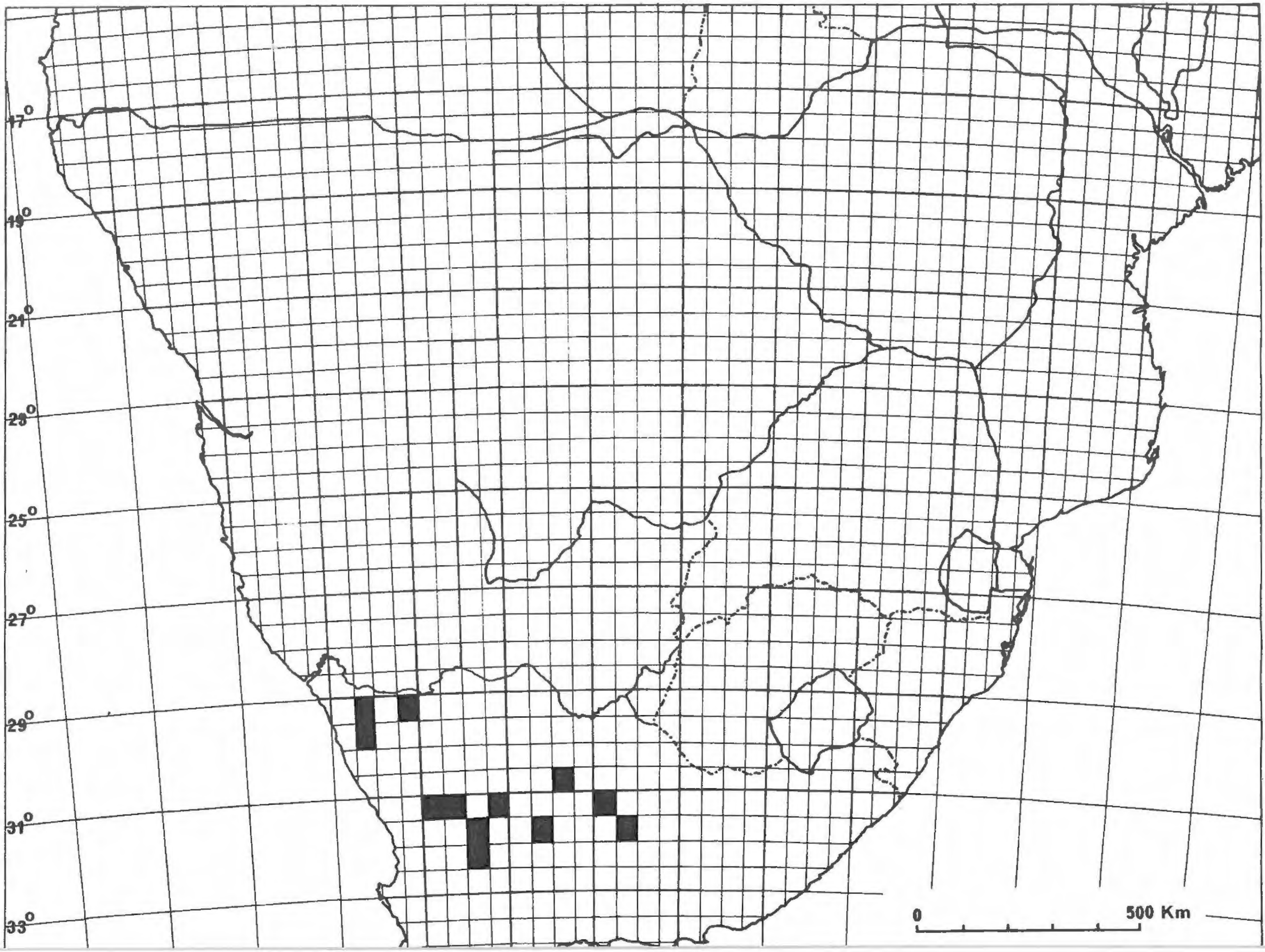
Bulb globose or ovoid, 10-25(-35) mm long, with whitish scales surrounded by a few, rarely up to 20, firm membranous brown scales. Leaves paired, ovate to oblong, acute, flat on the ground, thin to subfleshy, sometimes with conspicuously depressed veins, pustulate (pustules not always present on both leaves,) and tending to be more abundant towards the apex), often with minutely ciliate to minutely dentate margins, 30-100(-150) mm long, (15-)20-70(-130) mm broad, green with or without markings in purple, red, brown or another shade of greem, sometimes subpetiolate, with a narrow basal portion up tp 20-30 mm long. Inflorescence capitate, with often about 15-25 flowers. Lower bracts conspicuous, ovate to obovate, acute, glabrous (12-)15-30(-43) mm long, 7-16(-24) mm broad, green often with reddish areas particularly towards the margins and base. Pedicels (5-)10-12(-15) mm long. Perianth pink, white, yellow or greenish; tube 6-11(-14) mm long, 3-4(-5) mm diameter at the mouth; segments oblong, usually more or less reflexed and with a sigmoid curve in the longitudinal axis towards the base, 4,5-10(-14) mm long, 1,5-3 mm broad. Filaments 4-12(-18) mm long, free of connate portion at base up to 1 mm long; segments 1-1,5 mm broad, linear or narrowly deltoid, with yellow or reddish anthers 1-1,75 mm long. Style 10-12(-30) mm long. Ovary obovoid, 5-6(-8) mm long. Capsule obovoid, 3-winged, emarginate, c.30-35 mm long, 12-20 mm broad.

Widespread in the Cape Province. See map 30.

Occurs, generally in the open, in coastal sand with fynbos, in dry inland areas and in rich humic soils and on clay. Flowers are sweetly scented and produced in winter (June to September).

Pocock s.n. (sub Marloth 11888) (PRE), from the Cold Bokkeveld, with leaves pustulate and c.40 mm long, is intermediate between M. pustulata and M. heterandra, but the absence of heterandry places it closer to the former.

Esterhuysen 12199, from the northern Cedarberg (PRE), Esterhuysen 10349, from Orchard, Hex River Valley (BOL) and Marloth 12087, from Matjesfontein (PRE) have anthers 2,5 mm long, but the characteristic pustules on the leaves. The long anthers suggest a relationship with M. depressa. However, the pustules on the upper surface of the leaves are otherwise unknown in M. depressa and the specimens are, therefore, preferred in M. pustulata. There is, alternatively, the possibility that these plants are hybrids. Except for these two characters, M. depressa and M. pustulata are rather similar. The measurements given here for the capsule are taken from the only available specimen, but they suggest that the capsule may prove to be appreciably larger in this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species, although mesurements of almost all other morphological features of the plant are smaller.

Barker 10435, from Elands Bay (NBG), belongs to this species, but has an unusually large perianth - the tube 18 mm long and the segments 10 mm long.

For illustration (of exceptionally large specimen) see Flower. Pl. S. Afr. 23 : t.915 (1943).

For list of specimens examined see appendix, p. 59.

5. Massonia angustifolia L.f., Suppl. 193 (1791). Type: "Cap. bonae spei", Thunberg s.n. (UPS, microfiche!).
Polyxena angustifolia (L.f.) Bak. in Fl. Cap. 6 : 419 (1897).
Neobakeria angustifolia (L.f.) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).
Massonia lanceolata Thunb., Prodr. 60 (1794). Type: Cape, without precise locality, Thunberg s.n. (UPS - 7990, lecto., microfiche!).
Massonia marginata Willd. ex Kunth, Enum. Pl. 4 : 299-300 (1843). Type: "Cap. b. spei." in Willd. Herb. no. 6373 (B, holo., photo.!).
Polyxena marginata (Willd. ex Kunth) Bak. in Fl. Cap. 6 : 420 (1897). Baker cited M. undulata Willd. ex Kunth, Enum. Pl. 4 : 299 (1843) as the basionym, but there is

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Opposite- Map 31. Distribution of Massonia angustifolia.

no such name. However, M. marginata does appear on p. 299 of this work and M. undulata appears, therefore, to be an error for M. marginata.

Neobakeria marginata (Willd. ex Kunth) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).

Massonia zeyheri Kunth, Enum. Pl. 4 : 298 (1843). Type: "M. lanceolata Zeyh. in herb. reg. Berol. - Cap. b. spei" (?K!) - this specimen lacks a collector's number, but has been treated as type material at Kew. It does agree with the type description.

Massonia rugulosa Lichtenst. ex Kunth, Enum. Pl. 4 : 299 (1843). Type: "Cap. b. spei", Lichtenstein s.n. (?destroyed in B).

Polyxena rugulosa (Lichtenst. ex Kunth) Bak. in Fl. Cap. 6 : 420 (1897).

Neobakeria rugulosa (Lichtenst. ex Kunth) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).

Massonia burchellii Bak. in J. Linn. Soc., Bot. 11 : 393 (1871). Type: "Cap. B. Spei", Burchell s.n. (K!, BOL, drawing!).

Polyxena burchellii (Bak.) Bak. in Fl. Cap. 6 : 420 (1897).

Neobakeria burchellii (Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).

Polyxena haemanthoides Bak. in Hook., Ic. Pl. 17 : t.1727 (1888). Type: "Nieuweld (sic) Mountains near Fraserburg" Bolus 5493 (BOL!; G!; SAM!).

Neobakeria haemanthoides (Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).
Massonia pedunculata Bak. in Engl., Bot. Jahrb. 15, Beibl. 35 : 8 (1892). Type: "Malmesbury prope Hopefield", Bachmann 2043 (K, holo., BOL, drawing!).
Neobakeria namaquensis Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924). Type: Zabies, Namaqualand, M. Schlechter 90 (BOL!; GRA!; PRE!).
Polyxena namaquensis (Schltr.) Krause in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 15a : 350 (1930).

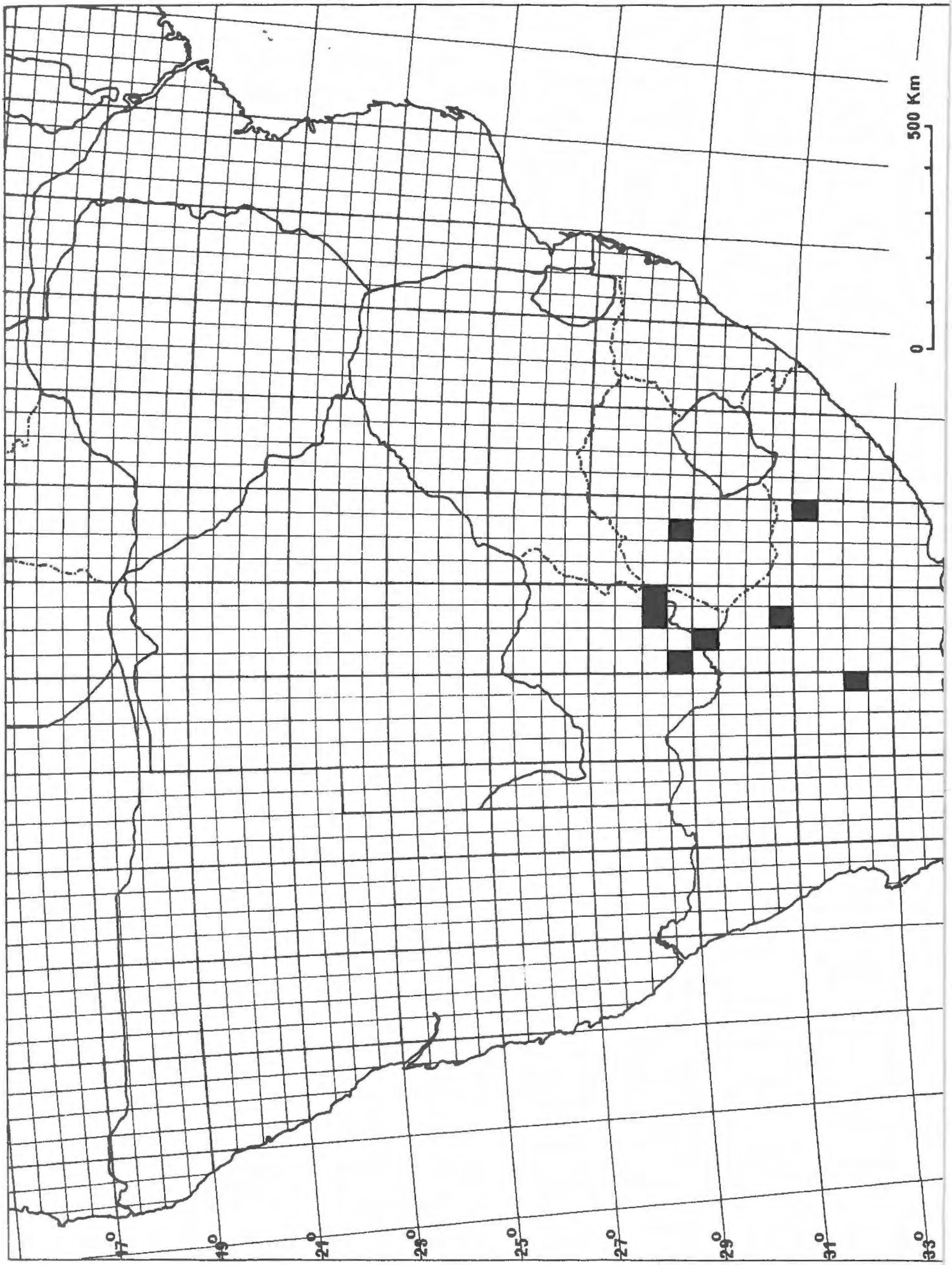
Bulb globose or ovoid, (15-)20-35 mm long, with whitish scales, surrounded by a few membranous brown scales. Leaves paired, oblong to oblong-ovate, acute, flat on the ground, spreading to erect-spreading, usually shiny, usually with several to many depressed veins, glabrous, sometimes with a minutely serrulate or crisped margin, (35-)60-140(-180) mm long, (13-)20-60(-100) mm broad. Inflorescence dense, capitate or somewhat elongate to 100 mm above the ground, rarely with up to 50 or more flowers, occasionally with a coma of sterile bracts above the fertile region. Lower bracts rather inconspicuous, ovate to obovate, (1-)3-8(-12) mm long. Pedicels very variable in length (1-)12-18(-29) mm long. Perianth white, sometimes tinged with reddish brown, or yellow to red, sometimes with the tube purple or purplish blue, often subchartaceous; tube usually longer than the segments, (4,5-)7-12(-17) mm long, 1,5-3 mm broad; segments erect, less often spreading, without a sigmoid fold towards the base, 7-11(-15) mm long, 2-4 mm broad, ovate-oblong to linear. Filaments (8-)10-16(-18) mm long, free or connate to 1,5 mm, usually linear; anthers 1,25-2,75 mm long, yellow or reddish to almost black. Style 11-22(-28) mm long. Ovary 4-8 mm long, ellipsoid. Capsule ellipsoid, with obtuse apex, 9 mm long.

Recorded from the inland dry parts of the Cape Province. See map 31.

Occurs in dry, usually stony, areas, but also on sandy soils. Flowers, apparently never scented, are produced mainly in May and June.

M. Schlechter 90, from Zabies, Namaqualand, the type of Neobakeria namaquensis, has a tube "usque supra medium 6-fido" according to Schlechter (1924). But in a specimen in the Bolus Herbarium flowers examined had very short tubes (4,5-6 mm long) and longer segments (8,5-10 mm long). In all other respects this specimen matches other material placed in this species.

The most distinct species recognised by previous authors, but reduced to synonymy here, was Polyxena haemanthoides, characterised by a coma-like development of the sterile bracts above the inflorescence. The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Bolus Herbarium sheet, however, comprises three specimens, in one of which the coma is rather well developed, while in another (as in the sheet in the South African Museum collection) there is very little or no evidence of this development.

Fig. 295 indicates variation in leaves in a population at Paternoster.

For illustration see Flower. Pl. S. Afr. 2 : t.56 (1922).

For list of specimens examined see appendix, p. 61.

6. Massonia comata Burch. ex Bak. in J. Linn. Soc., Bot. 11 : 392 (1871). Type: "Cap. B. Spei", Burchell 2751 (K!).

Polyxena comata (Burch. ex Bak.) Bak. in Fl. Cap. 6 : 419 (1897).

Neobakeria comata (Burch. ex Bak.) Schltr. in Notizbl. Bot. Gart., Berlin 9 : 150 (1924).

Bulb globose to ovoid, 15-25 mm long, with white scales, surrounded by a few membranous brown scales. Leaves usually paired, occasionally more numerous, lanceolate to ovate, acute, spreading, more or less flat on the ground, glabrous, usually with an undulate or crisped margin, sometimes with petiole-like sheath up to 70 mm long, 80-220 mm long, 15-60 mm broad. Inflorescence

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Opposite- Map 32. Distribution of Massonia comata.

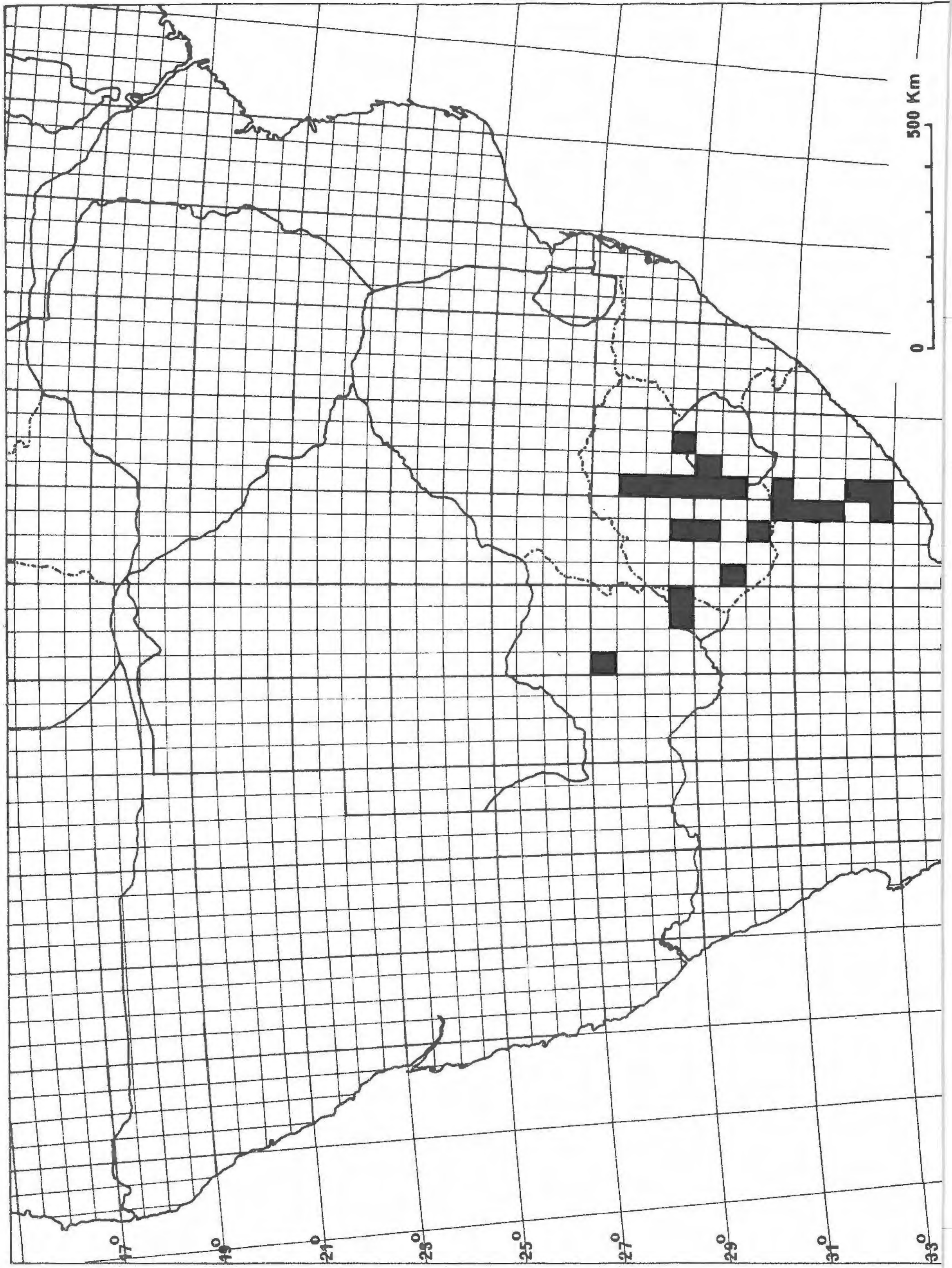
dense, capitate or somewhat elongate to 70 mm above the ground, with up to about 50 flowers. *Lower bracts* early deciduous, but probably up to 15 mm or more long. *Pedicels* 0-1 mm long. *Perianth* white, less often pink; tube cylindrical, 23-45 mm long, c.1 mm broad; segments erect, without a sigmoid fold towards the base, 5-9 mm long, 1-1,5 mm broad, linear-oblong. *Filaments* 5-9 mm long, free, attached at the same level in the mouth of the perianth tube, linear; anthers about 1 mm long. *Style* 25-50 mm long. *Ovary* ellipsoid, 3-4 mm long, with c.12 ovules per locule.

Recorded from the south-western Transvaal, Orange Free State and north-western Cape Province, although the records are rather scattered. See map 32.

Occurs in heavy soils and reported from sandy alluvium. Flowers are scented, and are produced in winter.

The nearsst affinity of this species is with *M. angustifolia*. Fig. 296 indicates the lengths of the perianth segments and of filaments in plants of these two species and indicates the justification for recognising two species.

For list of specimens examined, see appendix, p. 62.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7. *Massonia jasminiflora* Burch. ex Bak. in J. Linn. Soc., Bot. 11 : 390 (1871). Type: "Cap. B. Spei", *Burchell* B.7 (K, holo.!).

Massonia bowkeri Bak. in J. Linn. Soc., Bot. 11 : 390 (1871). Type: "Orange Free State", *Barber* s.n. (TCD, holo.!).

?*Massonia greenii* Bak. in Fl Cap. 6 : 413 (1897). Type: "Griqualand West; stony places near Kimberley", *MacOwan* 2842 (K, holo., BOL, tracing!).

Bulb ovoid to ellipsoid, 10-20 mm long, with whitish scales, surrounded by few firm membranous brown scales. *Leaves* paired, ovate to broadly oblong, acute, glabrous or rarely pustulate, occasionally with ciliate margins, flat on the ground, green, sometimes with red elongate markings, (25-)30-60 mm long, 15-50 mm broad. *Inflorescence* capitate, generally with fewer than 15 flowers, but up to 35 recorded. *Lower bracts* ovate to obovate, 8-30 mm long, 6-20 mm broad, rarely minutely ciliate on the margins. *Pedicels* 3-5 mm long. *Perianth* white or pink; tube cylindrical, 8-20 mm long, 1,5-2,5 mm broad; segments with or without a sigmoid curve in the longitudinal axis towards the base, ascending or reflexed, 4-8 mm long, 1,5-2 mm broad. *Filaments* inserted in the throat of the perianth, 2-4,5 mm long, free or connate to 2 mm, deltoid, c.15 mm broad at the

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Opposite- Map 33. Distribution of *Massonia jasminiflora*.

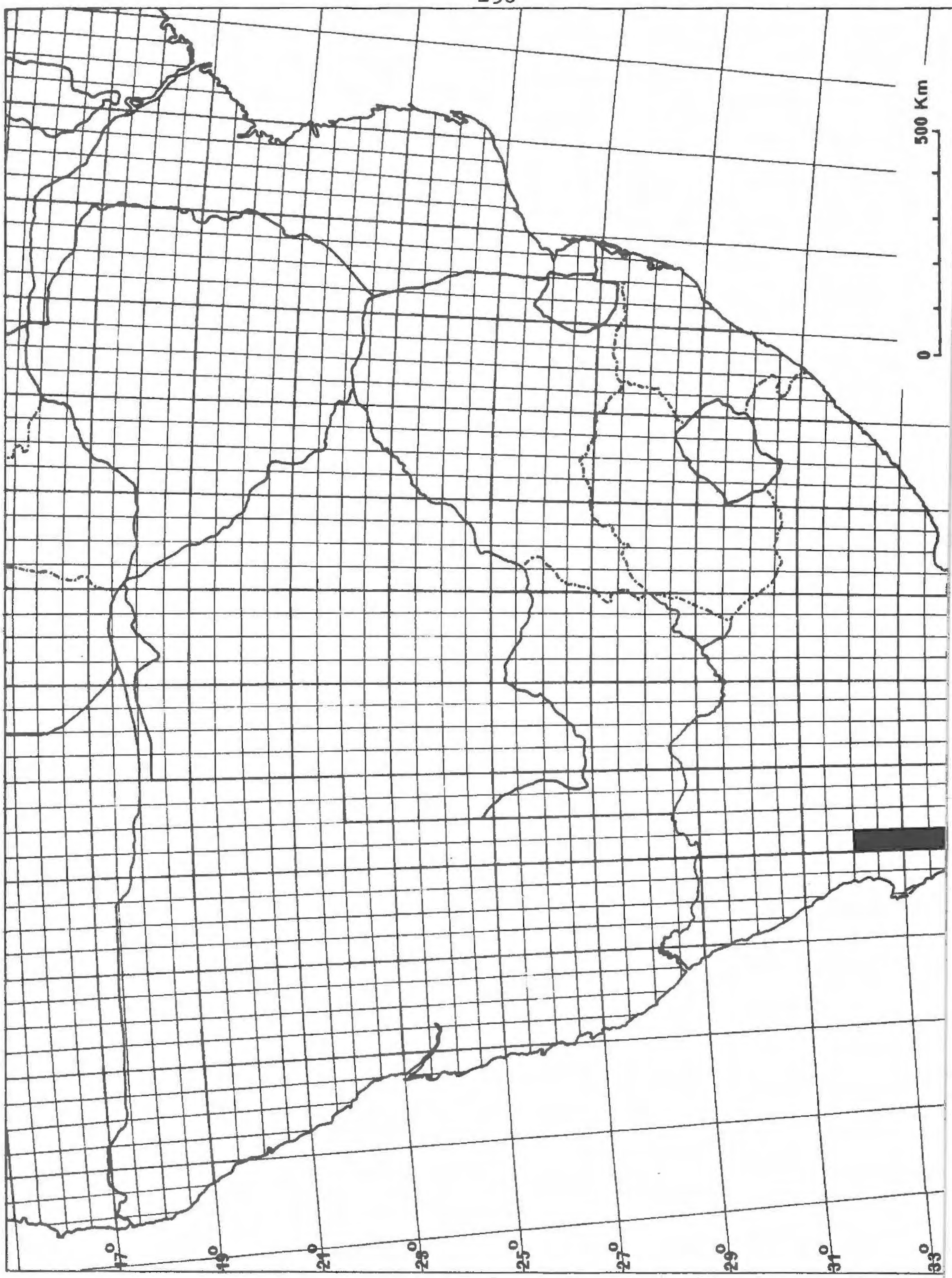
base, white or pink; anthers green to blue, dark purple or black, c.1-1,5 mm long. Style generally 5-7 mm long, sometimes minutely capitate. Ovary oblong-obovoid, shorter than the style.

Occurs in the eastern Cape, Lesotho, the Orange Free State, and northern Cape across the Orange River. See map 33.

Recorded from limestone gravel and surface calcrete tufa, but occurring generally in open grassveld. The flowers are strongly scented and produced in May and June almost exclusively.

Twelve leaves were taken from flowering plants in a small population from the central Orange Free State to determine variation. These ranged in length from 25 to 42 mm and in breadth from 22 to 44 mm (30 miles S.W. of Winburg, 2/7/72). See fig. 297.

D. Collett, in a note on Galpin 2612 (PRE), states that M. bowkeri, in which the filaments are free almost to their bases, is distinguishable from M. jasminiflora, in which they are connate below for approximately half their length. "A second distinguishing feature is that in M. bowkeri the perianth segments are erect while in M. jasminiflora they are reflexed." Fig. 298 shows the lack of correlation found by the present author for these characters, indicating why the separation of these two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species has not been upheld.

For illustration see Flower. Pl. S. Afr. 10 : t.367 (1930).

For list of specimens examined see appendix, p. 63.

8. Massonia heterandra (Isaac) Jessop, comb. nov.

Neobakeria heterandra Isaac in Flower. Pl. S. Afr. 19 : t.729 (1939). Type: Villiersdorp, Stokoe s.n. sub BOL 22309 (BOL, holo.!; PRE!; SAM sub SAM 52826!).

Bulb ovoid, (12-)15-20(-25) mm long, with whitish scales, surrounded by a few firm membranous brown scales. Leaves paired, glabrous, papillate or more often pustulate (sometimes the pustules muricate), often with ciliate margins, green with or without purple spots or streaks, erect-spreading to spreading, ovate to obovate or almost orbicular, with acute apex, 14-30 (-40) mm long, 7-18 mm broad; petiole-like base 0-30 mm long. Inflorescence capitate to shortly corymbose, with usually 2-6 flowers. Lower bracts oblanceolate to obovate, with acute apex, 12-20 mm long, (2,5-)3-5 mm broad. Pedicels 5-12 mm long. Perianth pink or white; tube 6-14(-17) mm long, 0,5-2 mm broad, linear; segments linear-oblong, 4-7 mm long, 0,5-2 mm broad,

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Opposite- Map. 34. Distribution of Massonia heterandra.

erect to spreading. Filaments inserted at mouth of perianth tube, almost free or connate to 1 mm, usually of two different lengths in one flower but not always with all members of each whorl of the same length as one another, 2,5-7(-8) mm long; anthers dark purple-black, 1-1,5 mm long. Style c.11-12 mm long, cylindrical. Ovary ellipsoid, green, 3-4 mm long. Capsule obovoid, shortly acute at the apex, c.6-7 mm long; seeds c.1-1,5 mm diameter.

Restricted to the south-western Cape. See map 34.

Inhabits high altitudes in sand and in rock crevices. Flowers mainly in April and May.

For illustration see Flower. Pl. S. Afr. 19 : t.729 (1939).

For list of specimens examined see appendix, p. 65.