A systematic study of *Leonotis* (Pers.) R. Br. (Lamiaceae) in southern Africa

by

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To Unus and Lorna Vos

Preface

The practical work incorporated in this thesis was undertaken in the Botany Department, University of Natal, Pietermaritzburg, from January 1990 to May 1994, under the guidance of Mr. T.J. Edwards.

I hereby declare that this thesis, submitted for the degree of Doctor of Philosophy, University of Natal, Pietermaritzburg, is the result of my own investigations, except where the work of others is acknowledged.

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Harare (CAH); Royal Botanic Gardens, Edinburgh (E); Genéve Herbarium (G); The National Herbarium of Botswana (GAB); Albany Museum (GRA); München Herbarium (M); Missouri Botanical Garden (MO); Compton Herbarium, National Botanic Gardens, Kirstenbosch (NBG); Natal Herbarium, Durban (NH); Natal University, Pietermaritzburg (NU); Royal Botanic Gardens, Kew (K); Museum of Natural History, Paris (P); National Herbarium of Pretoria (PRE); Swedish Museum of Natural History, Stockholm (S); South African Museum, Kirstenbosch (SAM); Natural History Museum, Wien (W); National Herbarium of Namibia (WIND) and Institute for Systematic Botany, Zürich University (Z).

Abstract

The southern African species of *Leonotis* (Pers.) R. Br. are revised. Nine taxa are recognised including a new species and two new subspecies.

A multidisciplinary approach was adopted involving: floral, vegetative, seedling and fruit morphology, karyology, palynology, pollination biology, phytogeography, phytochemistry and cladistics. Of these characters the most important in delimiting species is leaf morphology.

Phytochemistry revealed qualitative and quantitative differences in essential oils between taxa. Germacrene is the dominant essential oil in seven species, particularly in *L. dubia* E. Mey. and *L. nepetifolia* (L.) R. Br. Caryophyllene dominates in *L. randii* S. Moore. Although certain species have characteristic aromas, no inter-specific differences are apparent in the levels of α-copaene, the dominant volatile essential oil extracted with Tenax. Essential oil data is in partial agreement with the phylogeny and species concepts presented in this document.

Ornithophily accounts for most fruit set in perennial species but in the annual species (*L. nepetifolia*) autogamy prevails. Neither ornithophily nor entomophily improved nutlet vigour which was gauged from nutlet germination. *Leonotis* species are predominantly pollinated by a variety of sunbirds, although bees are also involved. Nectar is sucrose-dominant in perennial species but hexose-dominant in the annual.

The majority of species are concentrated along the eastern seaboard with the eastern Cape forming the centre of diversity. The widespread distribution and tropical affinities of *L. leonurus* (L.) R. Br., suggest an origin for the genus in tropical Africa. Migration to southern Africa and subsequent speciation are suggested. Habitat diversity and edaphic conditions probably played an important role in the evolution of narrowly distributed xerophytic species.

A cladistic analysis re-emphasised that *Leonotis* is a monophyletic group of closely related species. The lack of floral divergence in perennial species indicates the constraints imposed by ornithophily. The annual, *L. nepetifolia,* is highly derived and displays numerous autapomorphies. The morphology, distribution and tropical affinities of *L. leonurus* are interpreted as pleisiomorphic. The proposed phylogeny is reasonably compatible with phytogeographic data.

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Chapter 1

Introduction

Leonotis (Pers.) R. Br. is a member of the Lamiaceae or mint family, well known as ornamental plants, in confectionery, as cosmetics and as culinary herbs (eg. basil, mint, rosemary, sage and thyme). The Lamiaceae are also well known for their aromatic leaves which are used medicinally and *Leonotis* is no exception (Medley Wood, 1899; Moore, 1911-1912; Dyer *et al.* 1962; Watt and Breyer-Brandwijk, 1962).

Leonotis leonurus (L.) R. Br. is the type for the genus and as Linnaeus (1771) remarked in his Mantissa "is the most showy in the genus". It was one of the earliest South African plants to be cultivated in Europe, being recorded as early as 1663 in the Netherlands by Jacob Breynius, and was then claimed as one of the most beautiful exotic plants in cultivation (Dyer, 1942). In Turkey it is known as the "Minaret flower". In the Cape Province of South Africa it is known as "wild dagga" as it is supposedly used as a tobacco and smoked by the Hottentots (Medley Wood, 1899). Despite the implication, *Leonotis* is not related to true "dagga" (*Cannabis sativa* L.) (Cannabaceae), however, according to A.E. van Wyk (pers comm.) it is narcotic when smoked.

The Lamiaceae are one of the largest and most distinctive angiosperm families with about 170 genera and up to 5000 species with 37 genera and 232 indigenous or naturalised species in southern Africa (Codd, 1985). The Lamiaceae are cosmopolitan in warm and temperate areas. *Leonotis* is essentially endemic to Africa, although *L. nepetifolia* (L.) R. Br. is a pan-tropical weed (Dyer, 1975). The majority of species occur in South Africa. Three species are recorded in Kenya (Agnew, 1974). *Leonotis* was described by Persoon in 1807 and validly published by Robert Brown in 1810.

Leonotis consists predominantly of perennial herbs with woody bases, producing annual flowering stems that bear dense axillary whorls (or verticillasters) of orange flowers. *L. nepetifolia* is the only annual in the genus. The flowering plants become conspicuous in autumn and are visited by sunbirds for their copious nectar. The Lamiaceae are often referred to as the Labiatae due to the irregular bilabiate (or 2-lipped) corolla which characterises many of its members. It shares with the Verbenaceae typical quadrangular stems and decussate exstipulate leaves.

The classification of the Lamiaceae that is most widely in use (Briquet, 1895-1897) is based on the work of Bentham (1832-1836, 1876) who recognised eight tribes. Briquet's treatment differs from Bentham's in that he recognised the large subfamily Lamioideae ("Stachoideae"), to which *Leonotis* belongs, which Cantino and Sanders (1986) consider paraphyletic and probably polyphyletic.

An alternative classification of the Lamiaceae was proposed by Erdtman (1945) based on palynological evidence. The two sub-families recognised are the Lamioideae, with tricolpate pollen shed at the 2-celled stage and Nepetoideae, with hexacolpate pollen shed at the 3-celled stage. This division correlates well with a variety of embryological and phytochemical characters (Wunderlich, 1967; Cantino and Sanders, 1986). Erdtman's subfamilial classification is highly congruent with Bentham's (1876) tribal classification (Cantino, 1992). A numerical phenetic study by El-Gazzar and Watson (1970) yielded two primary groupings providing further support for Erdtman's subfamilies.

It is now widely accepted that the Lamiaceae evolved from the Verbenaceae, the latter being paraphyletic (Cantino, 1992). The two families form the core of the order Lamiales of Cronquist (1981) and have traditionally been distinguished on the basis of stylar position, terminal in the Verbenaceae and gynobasic in the Lamiaceae. However there is a continuum in the degree of lobing, with intermediates in the Lamiaceae and Verbenaceae. The taxonomic limits of the Lamiaceae are unclear and as presently circumscribed are considered polyphyletic (Cantino, 1992).

The apparent lack of floral differentiation in *Leonotis* and variable vegetative morphology within species has led to taxonomic confusion and the description of 36 species including 11 varieties. Phillips (1951) listed 12 species and Dyer (1975) "about 14" for South Africa. However, Iwarsson (1985), in the most recent revision, listed three species for southern Africa. The major revisions of *Leonotis* are summarised in Table 1.

In this study nine taxa are recognised, including a new species (*) and two subspecies:

1. *L. leonurus* (L.) R. Br.
2. *L. randii* S. Moore
3. *L. schinzii* Gürke
4. *L. nepetifolia* (L.) R. Br.
5. *L. ocymifolia* (Burm. f.) Iwarsson ssp. *ocymifolia* W. T. Vos and T.J. Edwards
6. *L. ocymifolia* (Burm. f.) Iwarsson ssp. *transvaalensis* W.T. Vos and T.J. Edwards
7. *L. dubia* E. Mey.
8. *L. pauciflora* W.T. Vos and T.J. Edwards *
9. *L. intermedia* Lindl.

The taxonomy of *Leonotis* is problematic, present circumscriptions (Iwarsson, 1985) are controversial and rather simplistic.

A multidisciplinary approach was adopted involving: floral, fruit, seedling and vegetative morphology; karyology, palynology; pollination biology; phytogeography; phytochemistry and cladistics.

The objectives of this study are 1. to assess the taxonomic value of characters in order to re-define the boundaries between southern African species of

Table 1. Major revisions of *Leonotis* excluding Tropical African species. References are cited in the bibliography.

Bentham (1834)	Meyer (1837)	Gürke (1895)	Baker (1900)	Skan (1910)	Iwarsson (1985)
L. leonurus (L.) R. Br.	*L. leonurus*	*L. bachmanii* Gürke	*L. leonurus*	*L. leonurus*	*L. leonurus*
L. nepetifolia (L.) R. Br.	*L. dubia* E. Mey.	*L. laxifolia* MacOwan	*L. nepetifolia*	*L. laxifolia*	*L. nepetifolia*
L. obovata Spreng.	*L. obovata*	*L. malacophylla* Gürke	*L. dubia*	*L. leonitis* (L.) R. Br.	*L. ocymifolia* (Burm. f.) Iwarsson
L. intermedia Lindl.	*L. dysophylla* E. Mey.	*L. latifolia* Gürke	*L. schinzii*	*L. intermedia*	
L. parvifolia Benth.	*L. molliss* E. Mey.	*L. schinzii* Gürke		*L. schinzii*	
				L. microphylla Skan.	
				L. galpinii Skan	
				L. dubia	
				L. brevipes Skan	
				L. bachmanii	
				L. latifolia	
				L. dysophylla	
				L. westae Skan	
				L. molliss	

Leonotis; 2. to investigate the breeding biology and 3. to revise the taxonomy of *Leonotis* in southern Africa.

Chapter 2

Materials and methods

Field work and plant cultivation

Field work was conducted in Zimbabwe, Kenya and throughout South Africa. Field excursions enabled wild plants to be studied, collected and cultivated at the Natal University Botanic Gardens (Pietermaritzburg). Plants were cultivated under uniform soil, light and water regimes. Herbarium specimens and cultivated plants provided the basic material for all studies undertaken. Vouchers are housed at Natal University Herbarium (NU) and cited in Chapter 15.

Leaf morphology

The terminology of Stearn (1973) was adopted for leaf indumentum. Mature leaves were studied from preserved, wild and cultivated plants. Lamina length and width, and petiole length were measured from approximately 10 leaves from 10 herbarium specimens which covered the widest known range of variation. Leaf outlines were drawn from herbarium specimens using tracing paper.

Leaves were cleared to study vascular patterns using the methodology of Kluckling (1986). Cleared leaves were placed in petri dishes on a light box and photographed with a Pentax Spotamatic equipped with bellows and a 50 mm macro-lens on Pan F (50 ASA) monochrome film. A green Kodak gelatin filter (number 58) was used to enhance contrast.

Venation terminology follows that outlined in Radford *et al.* (1974). Minor veins are all those excluding the primary, secondary, tertiary and quarternary veins. A eucamptodromus condition is where the secondary veins terminate at the sinuses of the marginal teeth and the tertiary veins terminate at the leaf apices. A craspedrodomus condition is where the secondary veins terminate in the apices of the marginal teeth.

Leaf surface ornamentation was viewed on material fixed in glutaraldehyde or FAA (83% water: 8.3% formalin: 8.3% acetic acid) and washed in 0.05 M cacodylate buffer (2x30 minutes).

Leaf micromorphology was studied with the aid of: a dissecting microscope (Wild-Heerbrugg), a compound light microscope (Olympus BH2) and a scanning electron microscope (SEM) (Hitachi: S 570). Trichomes were measured on micrographs and with the SEM.

Leaf preparation for SEM, involved the following procedures: an alcohol dehydration series (30 to 100% with 10 minutes for each 10% increase in ethanol), critical point drying and coating in gold palladium for 15 minutes using a Polaron ES 100 Sputter-coater. Collapsed glands on leaves are preparation artifacts.

Leaf and flowering stem anatomy

Anatomical studies were conducted using herbarium specimens and fresh material cultivated under uniform conditions. Sample size (2-3 per species) was limited by the time taken to prepare sections (2-3 weeks) and differences observed between species may reflect sample inadequacy. Material of *L. pauciflora* was not available at the time of this investigation.

Stems and petioles were sectioned by hand, stained with toluidine blue and studied with the aid of a compound microscope. Stem sections were also stained with phloroglucinol which stains lignified tissues dark purple to red (Radford *et al.*, 1974). Serial stem sections were taken from the first internode below the inflorescence to check for the presence of leaf traces. Serial sections were taken from the base to the apex of the petiole.

Leaf embedding procedure (1-5)

1. Fixation

3% glutaraldehyde in 0.05 M sodium cacodylate buffer for 8 hours
0.05M sodium cacodylate buffer for 2 x 30 min

2. Dehydration

Graded ethanol series 30, 50, 70, 90 and 3 x 100% for 10 min per solution
Transfer to 1,2 propylene oxide for 2 x 30 min

3. Embedding

Epon resin and araldite
25:75 Epon : 1,2-propylene oxide plus DMP for 2 hours
50:50 Epon : 1,2-propylene oxide plus DMP for 2 hours
75:25 Epon : 1,2-propylene oxide plus DMP for 2 hours
100% Epon resin overnight under vacuum

4. Polymerization

5. Fresh 100% Epon plus DMP for 24 hours in oven at 70°C

Leaf slide preparation and photography

Leaves were sectioned (± 1 μm thick) with an ultra-microtome, stained with Ladd's multiple stain, mounted in Spurr's resin on microscope slides and left

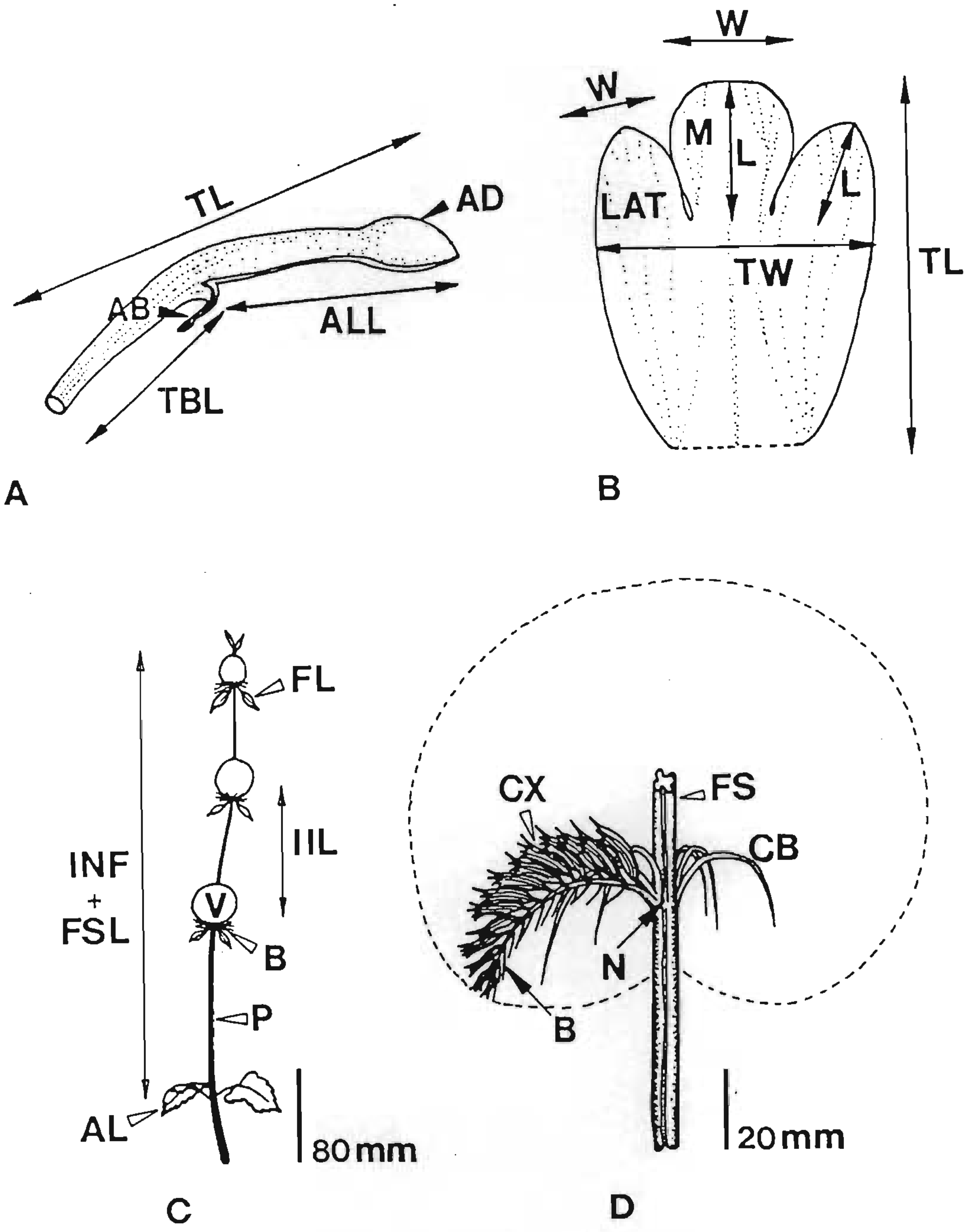


Figure 1. Definition and measurement of the corolla (A-B) and inflorescence (C-D) of *Leonotis*. (A) Lateral view of corolla, (B) flattened abaxial corolla lip, (C) flowering stem and (D) part of a verticillaster (the original outline of the verticillaster is indicated with a dashed line).
Abbreviations: (A) TL=total length, TBL=tube length, ALL=adaxial lip length, AB=abaxial lip, AD=adaxial lip. (B) TL=total length, TW=total width, M=medial lobe, LAT=lateral lobe, L=length, W=width. (C) INF=inflorescence, FSL=flowering stem length, AL=apical leaf, FL=floral leaf (or primary bract), IIL=inflorescence inter-node length, V=verticillaster, B=bract (or secondary bract), P=peduncle. (D) FS=flowering stem, CB=cyme branch, N=one of two opposing nodes, B=bract (or secondary bract), CX=calyx.

overnight to dry at room temperature. Leaf sections were photographed with PAN F (50 ASA) monochrome film and a Pentax Spotamatic 35 mm camera attached to a Olympus BH-2 light compound microscope. A light purple filter was used to enhance contrast. Stem and petiole sections were used to construct line drawings. Fresh material of *L. schinzii* was not available and leaf thickness is probably underestimated in this species as preserved material shrinks upon drying. Leaf midrib width was measured along a vertical line through the centre of the vascular bundle.

Crystals

Stem sections were tested for the presence of calcium oxalate crystals according to the method of Pobeguin (1954). Mature leaves and stems were sectioned by hand, stained with toluidine blue and safranin and mounted on microscope slides. Crystals were drawn from observations under the compound light microscope. The terminology of Metcalfe and Chalke (1979) was employed for crystal morphology.

Calyx

Tissue clearing, preparation, viewing and photography follow that outlined under Leaf morphology.

Inflorescence and floral morphology

Corollas and inflorescences were measured according to Figure 1 A-D, using a linear rule and callipers. Flower throat diameter was measured at the apex of the corolla tube on flattened herbarium specimens.

For each species two inflorescence measurements were taken from 25-35 plants and for corollas from 10-15 plants. The number of mature calyces was used as a measure of the number of flowers produced per verticillaster. Flower tagging experiments (Chapter 12) confirmed this assumption. Verticillaster diameter was measured as the distance between the outermost calyx spines.

Senescence and or twisting of the abaxial lip makes linear measurement difficult. The abaxial lip was therefore dissected, boiled in water and flattened under a microscope slide prior to measurement.

The corolla, androecium and gynoecium were studied with the aid of a dissecting microscope (Wild-Heerbrugg), a light compound microscope (Olympus BH2) and a scanning electron microscope (SEM) (Hitachi: S 570). Preparation and viewing of material for SEM follows that outlined under Leaf morphology.

Fruit morphology

Nutlets were measured under a dissecting microscope with a graticule. Nutlet preparation, viewing and photography follows that outlined under Leaf morphology. In addition to herbarium material which was often distorted or covered in fungal hyphae, fresh nutlets from cultivated plants were studied. Five nutlets were measured per plant from four populations.

Seedling morphology

Nutlets were germinated under uniform condition as outlined in Chapter 12. Measurements were taken from 30 seedlings and three populations (two in the case of *L. dubia*) per species. The seedling terminology of Vogel (1980) has been adopted.

Palynology

A minimum of four fresh and or preserved pollen samples were analysed per species. Pollen measurements were taken from micrographs and directly from the SEM screen. Pollen preparation, viewing and photography follows that outlined under Leaf morphology. The pollen terminology of Radford *et al.* (1974) was adopted.

Karyology

Mitotic preparations were made from root tips dissected from 10 mm long radicles. Root tips were obtained from plants grown from seed. Cultivated and wild plants were used for meiotic studies.

Mitotic studies were carried out on actively growing root tips which were pretreated in 8-Hydroxyquinoline (0.002M) and or colchicine and fixed in Carnoy's solution (6:3:1 absolute alcohol: chloroform: glacial acetic acid) for 24 to 48 hours. Thereafter the material was hydrolysed in 1N HCl (60°C for 6-15 mins) and stained in the dark in leucobasic fuschin for 2-3 hrs at 4°C. The dark purple-stained portion of the root where active divisions occur was dissected and squashed in 1% aceto-orcein on a microscope slide.

Flower buds for meiotic studies were removed hourly from plants between 05h00 and 11h00 hours, fixed for 24 to 48 hours in Carnoy's solution (6:3:1 absolute alcohol: chloroform: glacial acetic acid) and left in a fridge in 70% ethanol. Anthers were dissected in aceto-carmine plus iron-acetate and heated for 2-3 seconds before being squashed.

Chemosystematics

For each species EOs from at least three different plants from different localities (or populations) were analysed to avoid making erroneous conclusions based on one genotype. Material of *L. pauciflora* was not available at the time of this investigation.

Essential oil extraction

Three approaches were tested in EO extraction to find a quick, simple but efficient method:

1. Direct extraction in a diethyl-ether

Twenty-five ml bottles were filled with leaves and anhydrous diethyl-ether for extraction times varying from 15 minutes to 48 hours. Optimal extraction occurred within 10 minutes. The extract was concentrated to 10 ml under a stream of nitrogen, centrifuged for 5 minutes to remove particulate matter and further concentrated under nitrogen to 1 ml at room temperature.

The use of dichloromethane and methanol as solvents for EO extraction were not as efficient as diethyl-ether.

2. Extraction by steam distillation

Standard distillation to extract EOs requires several kilograms of plant material and takes several hours and is therefore not practical for a large number of extractions. A small steam distillation unit was therefore employed to extract EOs from approximately 350 grams of fresh leaves. Chromatograms showed that complete extraction of EOs occurred within 15 minutes at 60°C.

Following distillation diethyl-ether was added to dissolve the EOs, after which the aqueous phase was removed with a separating funnel and 10 grams of sodium sulphate added to the ether extract to remove traces of water. The extract was then concentrated to 1 ml under a stream of nitrogen at room temperature.

3. Collection of volatile EOs

The volatile oils were studied by drawing nitrogen through a gas-trap bottle filled with leaves attached to a 10 cm long glass tube (inside diameter of 5 mm) filled with Tenax and plugged with glass fibre. The Tenax tube was attached to a suction pump. Optimal extraction occurred within 15 minutes, after which 5 ml of diethyl-ether used was used to elute the EOs from the Tenax. Thereafter the sample was concentrated under a stream of nitrogen to 1 ml. Leaves were also crushed in liquid nitrogen, placed in the gas-trap bottle and warmed in a water bath whilst the volatile oils were being extracted. However, this had no significant advantage over the previous method.

Extracts were decanted into 1 ml glass vials and stored in a refrigerator at 8°C. Analyses involved thin-layer chromatography (TLC), GC and GC-MS.

Thin-layer chromatography

Thin-layer chromatography was carried out on Merck silica gel G60 plates. The solvent phase used was 10% ethyl acetate in hexane. The plates were allowed to run for approximately 55 minutes after which they were removed and the solvent front marked with pencil. The plates were heated at 100°C for four minutes then sprayed with a reagent consisting of 0.5 ml anisaldehyde in 10 ml of glacial acetic acid with 85 ml of ethanol and 5 ml of conc. sulphuric acid. An alternate spray reagent consisting of 5% vanillin in conc. sulphuric acid was used but proved unsuccessful. The developed TLC plates were immediately photographed with Agfa 100 ASA film in daylight to record colour and intensity of the bands before they faded. TLC plates were observed under visible light, UV-365 nm and fluorescing zones were marked with pencil.

Most EOs are sesquiterpenic hydrocarbons and do not exist as pure chemicals because of their instability and hence a limited number of "pure" standards were available. Essential oil standards were diluted in diethyl-ether (1:10), 0.5 ml streaked onto TLC plates and run simultaneously with *Leonotis* extracts for tentative identification of unknown EOs.

For TLC 0.5 ml of the extract was streaked onto two TLC plates. Compounds with Rf values corresponding to known standards, or those in the literature, were scraped off TLC plates, re-dissolved in 5 ml of diethyl-ether, concentrated to 1 ml under a stream of nitrogen and their identity further confirmed by GC and GC-MS analysis.

Gas chromatography

Gas chromatography was carried out with a Varian 3300 GC, fitted with a Carbowax megabore column (30 m, inside diameter of 0.53 mm). Peak integration was carried out by a Hewlett Packard 3800A integrator. The column was initially held at 100°C for 6 minutes, thereafter increased by 2°C/minute to 170°C and held for 10 minutes. The carrier gas was helium (flow rate of 10 ml/minute) with an injection temperature of 120°C and detector temperature of 290°C. One μl aliquots of EOs were injected for GC analysis.

Some EOs were tentatively identified by comparing GC retention times with those of known EO standards. Identification of EOs was confirmed with GC-MS.

In the analysis of data an EO was considered dominant if its area percentage on a chromatogram was greater than 30%.

Gas chromatography-mass spectrometry

Gas chromatography-mass spectrometry was conducted with a Finnigan ITS 40 GC-MS, fitted with a fused silica capillary column (DB 1, 12 m, inside diameter of O.25 mm). The column was initially held for 5 minutes, increased at 4°C/minute to 80°C, held for 5 minutes, thereafter increased to 170°C, held for 5 minutes, and finally increased to 220°C at 15°C/minute and held for a further 10 minutes. The carrier gas was helium (flow rate of 1 ml/ minute) with an injection temperature of 120°C and detector temperature of 290°C.

One μl aliquots of EOs were injected for GC-MS analysis. Spectra were tentatively identified by library search using the INCOS data system. Peak integration was accomplished using the computer data system of mass spectrometry.

Pollination biology

Exclusion experiments were conducted on the Behn/Chinn Estate near Table Mountain (Pietermaritzburg - 29° 30′ S 30° 28′ E) between May and June 1992 on *L. leonurus* and *L. intermedia.* The study site was in grassland on a steep northern slope (± 30°). All other experimental work was carried out on cultivated plants at the Natal University Botanic Gardens (Pietermaritzburg).

Pollinator efficacy was studied by means of graded exclusion experiments and comparison of subsequent nutlet production. Within a population five plants were chosen and each plant was subject to three inflorescence treatments: 1) birds and most insects excluded, 2) birds excluded, and 3) a control or uncaged inflorescence. An average of 800 flowers was assessed for each of these treatments.

Bird exclusion cages were constructed with 20 mm^2 squared mesh and insect exclusion cages with 2 mm^2 gauze. Exclusion cages were cylindrical (750 x 230 mm) and were mounted upon metal poles which were driven into the ground next to the flowering plants. Cages were held away from the floral axes by three metal rings to prevent pollination caused by bags contacting the flowers.

Sunbird foraging was observed and insects were collected with a swipe net for identification. Bees and the crown feathers of sunbird pollinators were prepared, viewed and photographed in the same manner as leaves outlined under Leaf morphology.

Nutlet set

Nutlet-set data was tested for statistical significance using one-way Anova and a Tukey multiple range test at the 95% confidence level. Percentage data were transformed using an Arc-Sine transformation.

Potential nutlet-set was estimated by counting calyces and multiplying fourfold (since each flower can potentially produce four nutlets). Underdeveloped flowers which occur distally on cyme branches were ignored in calculating seed- potential because these were not available for pollination. Actual nutlet-set was then expressed as a percentage of the potential nutlet-set.

For each species five plants within a population were sampled and each plant was subjected to three inflorescence treatments. The mean number of flowers analysed per treatment per species was 400 (*L. nepetifolia*), 1500 (*L. leonurus*) and 560 (*L. intermedia*). The mean number of fruits analysed per treatment per species was 1045 (*L. nepetifolia*), 930 (*L. leonurus*) and 1350 (*L. intermedia*).

Interpretation of pollination frequency from nutlet production data is slightly misleading because nutlet production is sometimes influenced by limitations in resource allocation which may cause abortion of nutlets in heavily pollinated plants. Such limitations are probably more marked in perennial species, which resume growth following flowering. Consequently where nutlet production is low it should correlate closely to pollination events and where nutlet production is high, pollination will probably be underestimated due to nutlet abortion and multiple pollinator visits to single flowers.

Nutlet vigour and viability

Following pollination and fruit set experiments germination trials were conducted. Nutlet "vigour" was inferred from germination trials. Nutlets were placed on discs of Whatman number 1 filter paper in petri dishes and irrigated with distilled water. Nutlet vigour was scored once seedlings had developed cotyledons. Most germination occurred between three and nine days, however trials were continued for a 20 day period. Nutlets which had not germinated after 20 days were subjected to the Tetrazolium test (Draper, 1985) and all proved to be non-viable. No distinction was made between abnormal (or deformed) and normal nutlets.

Apomixis

The occurrence of apomixes (or asexual production of seed) was tested by emasculating closed flowers, bagging the inflorescence, and then checking for fruit development at a later date.

Floral development and longevity

For each species 25 buds from two cultivated plants were tagged and removed at half day intervals to monitor anther dehiscence, stylar elongation and stigma receptivity. Flower longevity was recorded as the time taken from anthesis to corolla abscission.

Stylar extension was measured daily and stigma receptivity was determined using 5% hydrogen peroxide. Receptive stigmas produce bubbles due to the oxidation of esterases. Stigmas were further tested for receptivity by staining with napthylacetate in fast blue salt (Heslop-Harrison and Shivanna, 1977).

Floral morphology

Corolla measurements are outlined under Inflorescence and floral morphology.

Nectar

Nectars are categorized according to sucrose/hexose ratios (Baker and Baker, 1983) namely: <0.1 (hexose-dominant), 0.1-0.499 (hexose rich), 0.5-0.999 (sucrose rich) and >0.999 (sucrose-dominant). For each species nectar samples from five different plants were analysed. Vouchers are cited in Chapter 15.

Nectar was collected from cultivated plants on Whatman number 1 filter paper, dried and stored with silica gel at 0°C. For gas chromatography (GC) the dried nectar was dissolved in 1 ml of pyridine, heated to 40°C and evaporated under a stream of nitrogen gas. Nectar sugars were converted to their oxime forms prior to trimethysilyl derivation, thereby minimizing the obscuring effects of anomerism (Tanowitz and Smith, 1984). Extracts, awaiting analysis, were stored in ependorf tubes. Nectar analyses were carried out using a Varian model 3700 gas-chromatograph, equipped with an OV-17 capillary column. The column was held at 140°C, whereafter the temperature was increased at a rate of 3°C/minute to 260°C. The carrier gas was nitrogen, peak integration was conducted by a Hewlett Packard 3800A integrator.

Sugar concentration was measured with a temperature compensated refractometer (Atago N1, Brioc. 0-32%). Refractometers are calibrated on a mass per total mass basis (i.e. grams of solute per 100 g solution) (Bolten *et al.*, 1979). Since the caloric values and refractive indices of glucose and fructose solutions are half that of an equimolar sucrose solution, the refractive index of any mixed solution may be read in terms of sucrose equivalents (Hainsworth and Wolf, 1972). Refractometer values are expressed directly as sucrose equivalents.

Nectar volume or standing crop per flower was measured with calibrated (10 μl) capillary tubes. Nectar standing crop and concentration measurements were obtained from five plants per species and 15 flowers per plant.

Flowering periods

Flowering periods were compiled from notes on herbarium labels. Herbarium specimens are cited in Chapter 15.

Habitat, habit and phytogeography

Plant distributional records are seldom complete due to uneven collecting, however we have been comprehensive in examining available herbarium material. Herbarium records depend on the accessibility and proximity of areas to settlements and this must be considered when interpreting distribution patterns.

Unfortunately at the commencement of this study herbarium material from tropical Africa was not readily available and would have made this work more complete. Specimen citations, including a limited amount of tropical material, are included in Chapter 15. A map of each species, including the widespread annual (*L. nepetifolia*), is presented in Chapter 15. The grid reference system adopted is after that outlined in Leistner and Morris (1976).

Habit cannot be evaluated reliably from herbarium specimens as only portions of the plant are collected and one must rely on collectors' field notes and field observations. Bond and Goldblatt (1984) and Arnold and De Wet (1993) were used for species diversity and habit of Lamiaceae genera in southern Africa.

An attempt was made to correlate geology, soils, vegetation and climate with *Leonotis* distribution. The complex geology of South Africa is reflected in the mosaic of soil and vegetation types. The relevant trends are reported.

The following maps were referenced: precipitation and temperature (Jackson, 1961), frost (Poynton, 1971), altitude (Anon, 1984), geology (Visser, 1984), soil (Von Harmse, 1978), vegetation (Wild and Fernandes, 1967; Giess, 1971; Acocks, 1988), *Leonotis* distribution (Lebrun and Stork, 1977; Iwarsson, 1985). In addition, information concerning altitude, plant habitat and microclimate were gathered from collectors' notes on herbarium specimens.

Cladistic analysis

The similarity in floral and vegetative morphology for the majority of species and the reasonably high variability in vegetative morphology made character polarization difficult and necessitated the use of a limited number of characters and character states in the analyses.

Character polarity is discussed in appropriate chapters of the thesis. The numerals used for coding characters in the list of Characters and character states correspond to the numerals used in the character matrix (Chapter 14, Table 19). Autapomorphies have been excluded from the character matrix because they do not affect the branching patterns and are listed under the heading Characters and character states in Chapter 14. The character matrix consists of 12 multistate characters, 10 binary characters and nine taxa. If a character is represented by both the plesiomorphic and the apomorphic states then it was scored as plesiomorphic.

The character matrix was analysed on an IBM compatible Personal Computer using the Hennig86 program, Version 5.1 (Farris, 1988). The most parsimonious tree was calculated successively with the options m* and bb. Multistate characters (characters 2 and 27) were deactivated. The XS W command was used to reduce the imact of homoplasy on the cladograms.

A hypothetical ancestor was chosen for outgroup comparison with *Leonotis*. *Leucas* Burm. ex R. Br. and *Acrotome* Benth., two closely related genera, were not chosen for outgroup comparison because of the different evolutionary constraints (or selective pressures) which operate in these predominantly entomophilous genera.

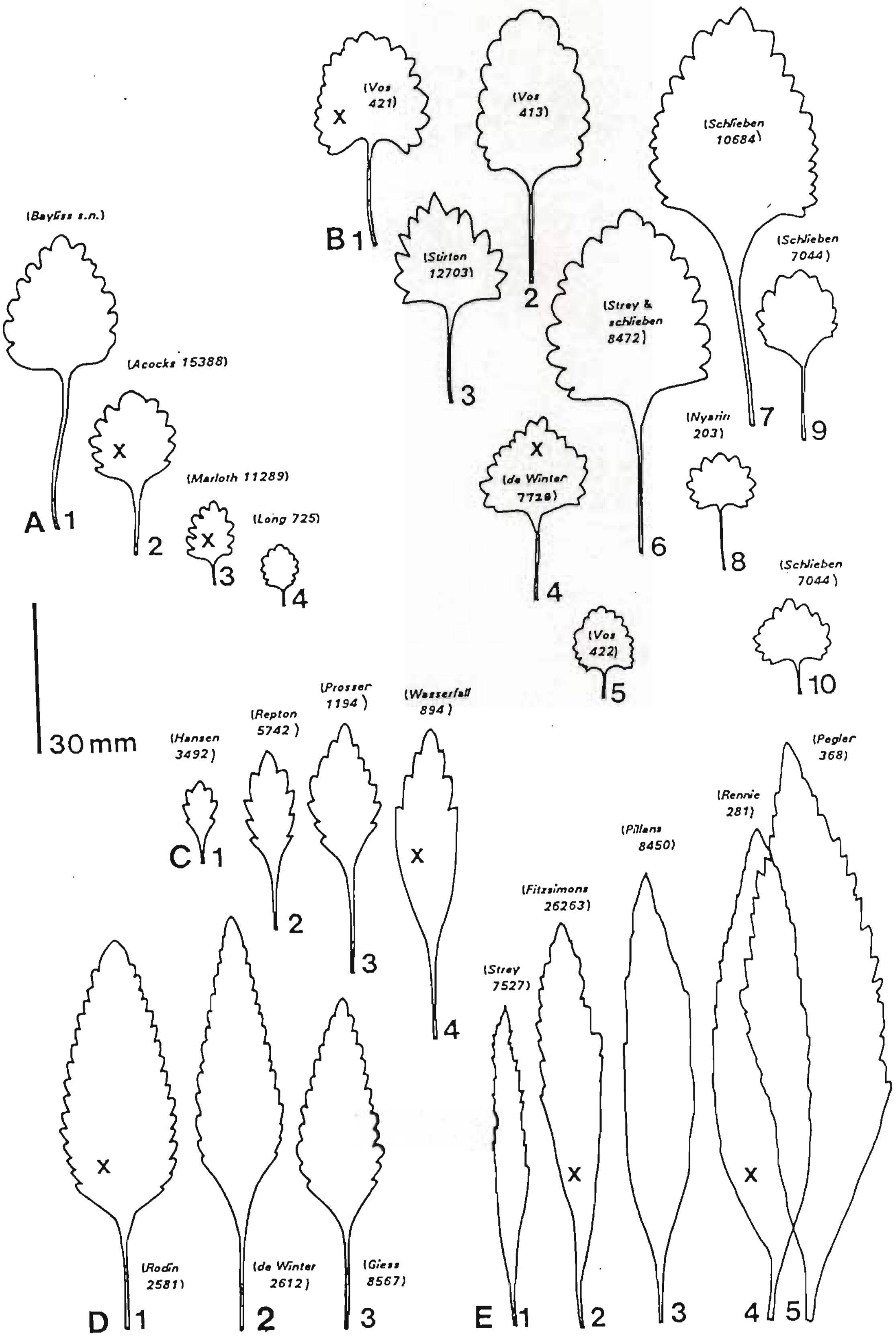


Figure 2. Leaf variation in *Leonotis*. (A) *L. ocymifolia* ssp. *ocymifolia*, (B) *L. ocymifolia* ssp. *transvaalensis*, (C) *L. randii*, (D) *L. schinzii* and (E) *L. leonurus*. Common leaf shapes are marked with a cross. Vouchers are indicated in parenthesis and cited in Chapter 15.

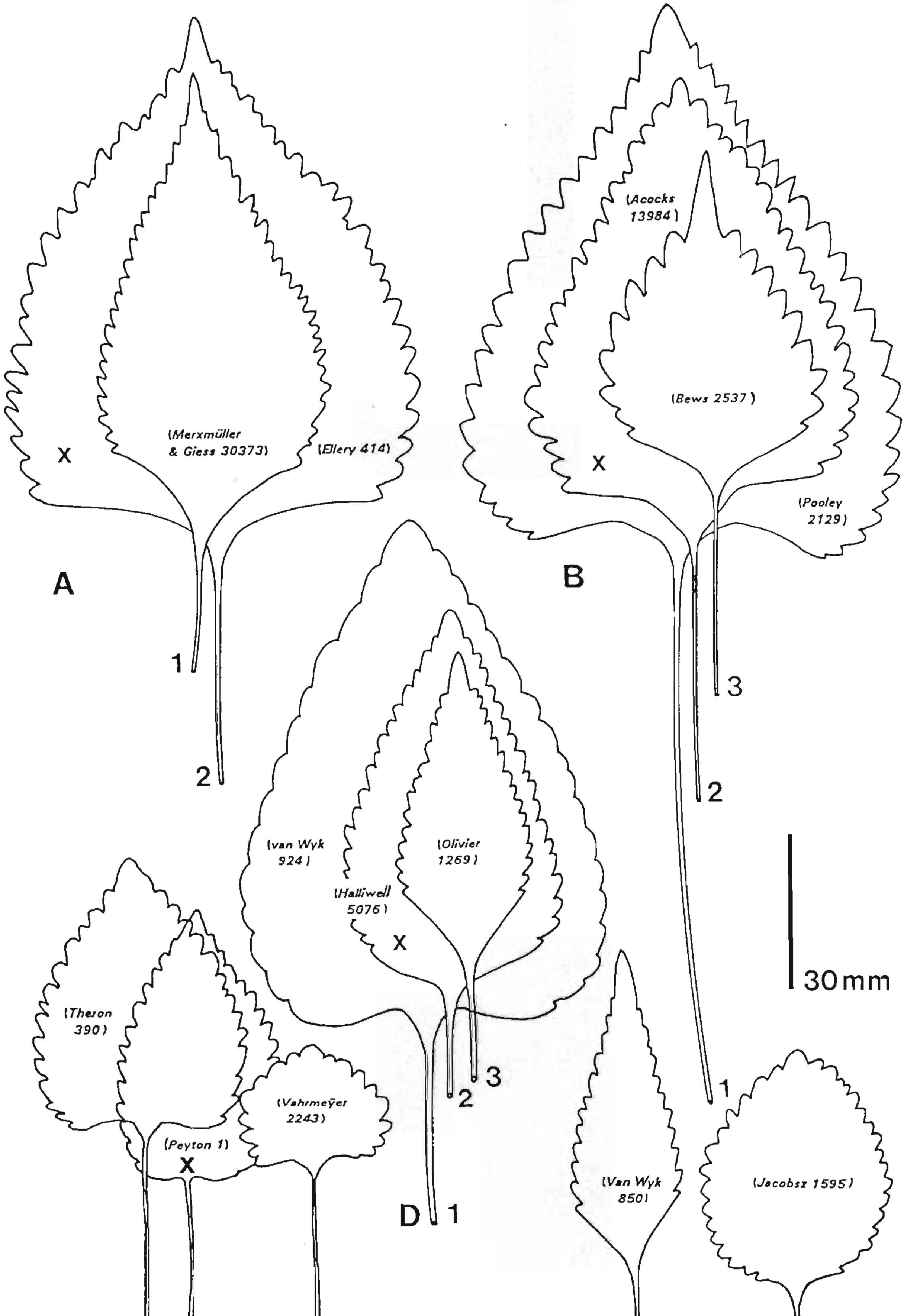


Figure 3. Leaf variation in *Leonotis.* (A) *L. nepetifolia*, (B) *L. dubia*, (C) *L. pauciflora* and (D) *L. intermedia*.
Common leaf shapes are marked with a cross. Vouchers are in parenthesis and cited in Chapter 15.

Table 2. Leaf characters of *Leonotis*.
Abbreviations: P=puberulous, G=glabrescent, S=scabrid, T=tomentose, V=velutinous, A=amphistomatic, H=hypostomatic.

Leonotis species	Leaf character					
	Shape	Base	Indumentum	Margin	No. teeth per margin	Stomata
L. dubia	broadly ovate	cordate, truncate	P, G	crenate-dentate	8-21	H
L. mollissima	broadly ovate	truncate, attenuate	S, V	crenate-dentate	8-30 (-55)	H
L. nepetifolia	broadly ovate	cordate, truncate	P, G	crenate	(6-) 15-60 (-90)	A
L. intermedia	broadly ovate	truncate, attenuate	P, G, V	crenate-dentate	(6-) 12-26	A
L. pauciflora	broadly ovate	cordate, truncate	P, G	crenate-dentate	7-18	A
L. ocymifolia ssp. *ocymifolia*	orbicular to broadly ovate	truncate, attenuate	P, G, T	crenate	5-8 (-10)	H
L. ocymifolia ssp. *transvaalensis*	orbicular to broadly ovate	cordate, truncate, attenuate	P, G	crenate-dentate	6-13	A
L. schinzii	narrowly ovate to lanceolate	attenuate	P, G, T	crenate-serrate	(4-) 6-14 (-19)	A
L. leonurus	lanceolate	acute, cuneate	P, T	crenate-serrate	(4-) 8-24	H
L. randii	oblanceolate to narrowly obovate	narrowly attenuate	S, G	crenate-serrate	3-7 (-10)	A

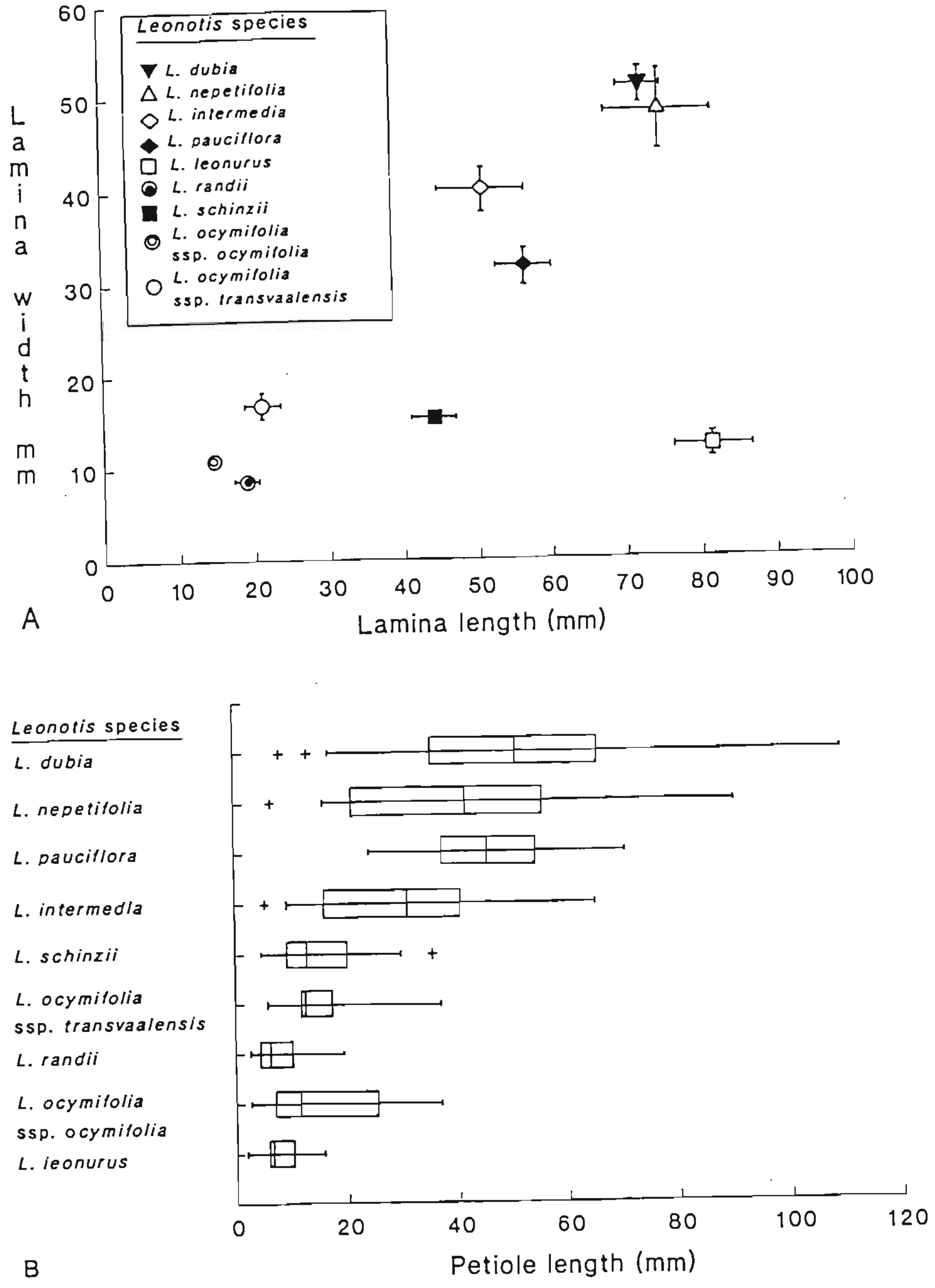


Figure 4. (A) Lamina length (y-axis) and width (x-axis) of *Leonotis* species. Symbols mark the mean value for each dimension; standard error bars are indicated. (B) Box and whisker plot of petiole length (y-axis) of *Leonotis* species. The central box covers the middle 50% of the data values, between the lower and upper quartiles. The whiskers extend to the maximum and minimum values. The central line is the median. Unusual values are plotted as separate points (i.e. those values greater than 1.5 times the inter-quartile range). For each species and all dimensions approximately 10 mature leaves were measured from 10 herbarium specimens.

Chapter 3

Leaf morphology

Introduction

In higher plants vegetative characters are often disregarded because in many cases similar vegetative features are found in distantly related plants (Stace, 1980). In addition, plant habit and leaf morphology are often notoriously "plastic".

As early as AD 60 Dioscorides in his Planta Medica used hair covering to distinguish *Origanum dictamnus* L. (Lamiaceae) from *Mentha pulegium* L. (Lamiaceae) (Morton, 1981). In a study of eleven species of *Origanum* L. (Lamiaceae), Bosabalidis and Tsekos (1982) found glandular hair morphology to be similar in all species. However, Small (in: Metcalfe and Chalk, 1950), studying the medical properties of plants, could distinguish between 20 species of Lamiaceae on indumentum alone. A scanning electron microscopic study of trichomes in conjunction with phytochemical methods (Tomás-Barberán, *et al.*, 1990) showed affinities and differences between species of *Sideritis* L. (Lamiaceae) from North Africa and southern Portugal. Moh Rejdali (1991) also found leaf micro-morphology of *Sideritis* of systematic value. Werker *et al.* (1985) found that the hair morphology of five genera of Lamiaceae coincided with their sub-familial status. Inflorescence stem and stem trichomes were used by Rivera-Núñez *et al.* (1990) to describe sub-sections of *Sideritis*. Stem and leaf indumentum are important taxonomic characters in the genera *Fuerstia* T.C.E. Fries (Paton, 1993) and *Hemizygia* (Benth.) Briq. (Codd, 1976a).

Leaf shape and margination were used to characterise *Teucrium stocksianum* Boiss. ssp. *stenophyllum* R.A. King (King, 1988). In the same study the leaf size of *Teucrium* was found to be very variable and largely dependent on the

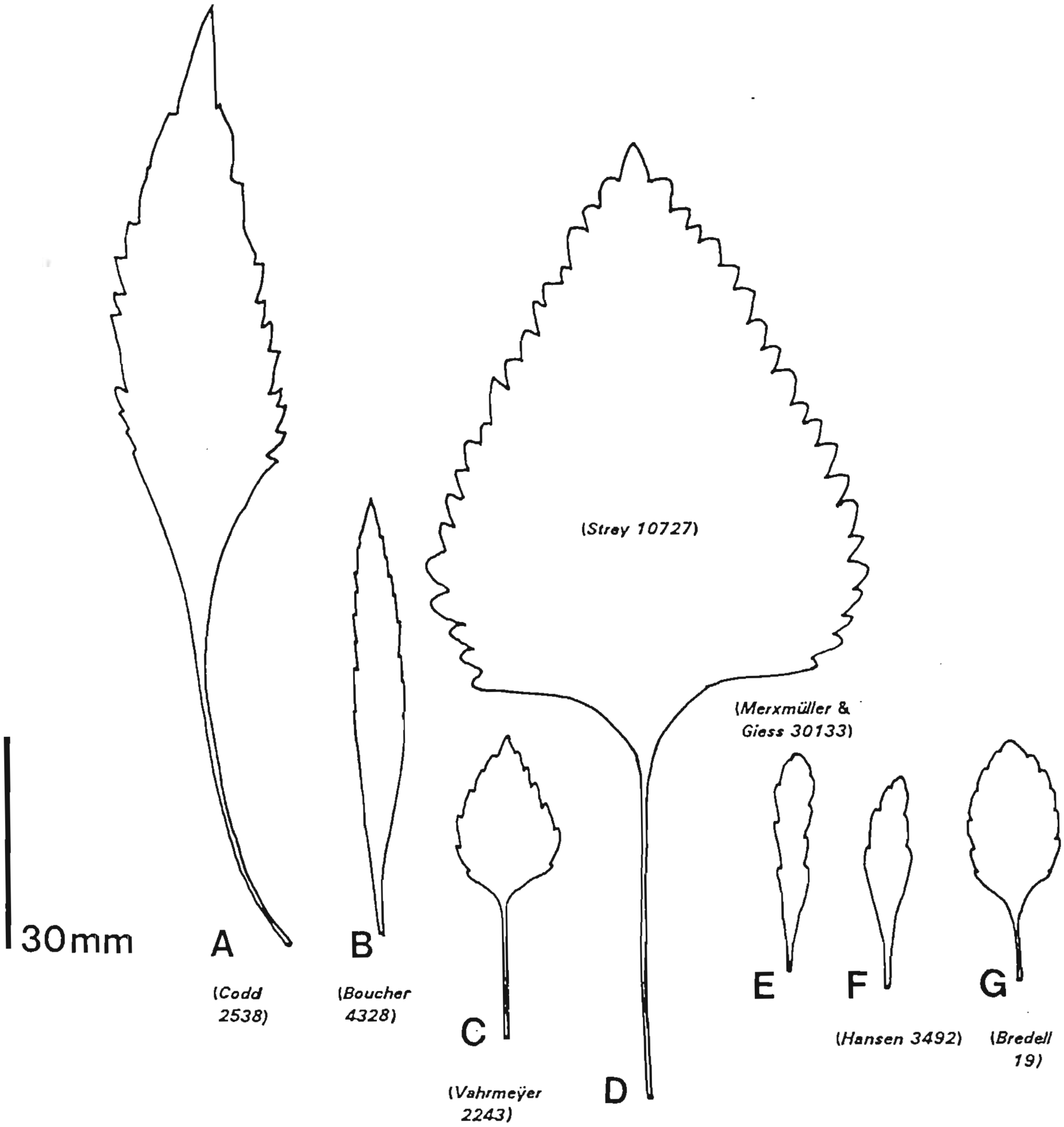


Figure 5. Floral leaves of *Leonotis*.
(A) *L. nepetifolia*,
(B) *L. leonurus*,
(C) *L. pauciflora*,
(D) *L. dubia*,
(E) *L. schinzii*,
(F) *L. randii* and
(G) *L. intermedia*.
Vouchers are given in parenthesis and cited in Chapter 15.

Figure 6. Abaxial leaf indumentum of *Leonotis*.

Leaves were photographed in the central region adjacent to the midrib.

(a) *L. ocymifolia* ssp. *ocymifolia* (*Vos 229*),

(b) *L. schinzii* (*Kolberg* and *Maggs 553*),

(c) *L. mollissima* (*Vos 363*),

(d) *L. intermedia* (*Vos 59*),

(e) *L. nepetifolia* (*Vos 174*),

(f) *L. dubia* (*Vos 77*),

(g) *L. randii* (*Vos 268*)

(h) *L. ocymifolia* ssp. *transvaalensis* (*Vos 421*) and

(i) *L. leonurus* (*Vos 538*).

The arrow in (h) indicates the ruptured cuticle of a head cell of a glandular trichome.

Abbreviations: GT=glandular trichome, GTa=large sessile glandular trichome, GTb=small stalked glandular trichome, NGT=non-glandular trichome, S=stoma. All scale bars=150 μm.

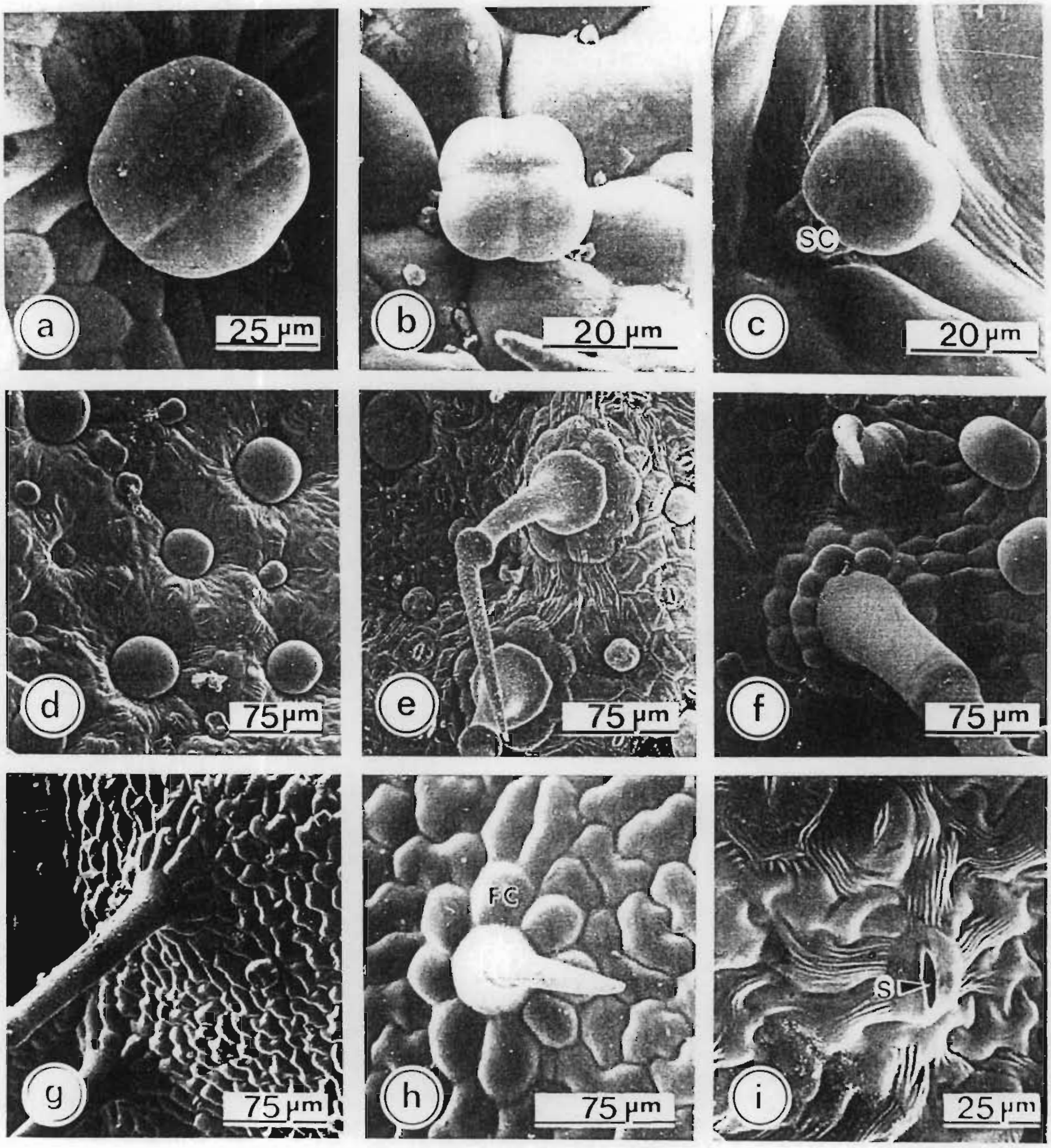

a
25 µm
b
20 µm
SC
c
20 µm
d
75 µm
e
75 µm
f
75 µm
g
75 µm
FC
h
75 µm
S
i
25 µm

Figure 7. Trichomes, stomata and surface sculpturing of *Leonotis* leaves. Leaves were photographed on the abaxial surface and unless otherwise stated micrographs represent top views.

Glandular trichomes (a-d):

(a) large sessile trichome of *L. leonurus* (*Vos 78*) with an 8-celled head,

(b) small, stalked trichome of *L. nepetifolia* (*Vos 174*) with a 4-celled head,

(c) lateral view of (b) showing the stalk cell (SC) and

(d) large sessile, indented trichomes of *L. ocymifolia* ssp. *transvaalensis* (*Vos 422*).

Non-glandular trichomes (e-h):

(e) *L. randii* (*Vos 268*),

(f) *L. intermedia* (*Vos 539*),

(g) *Leonotis* aff. *intermedia* (*Vos 336*),

(h) *L. dubia* (*Vos 77*) and

(i) stomata of *L. leonurus* (*Vos 78*).

Abbreviations: SC=stalk cell, FC=foot cell, S=stoma.

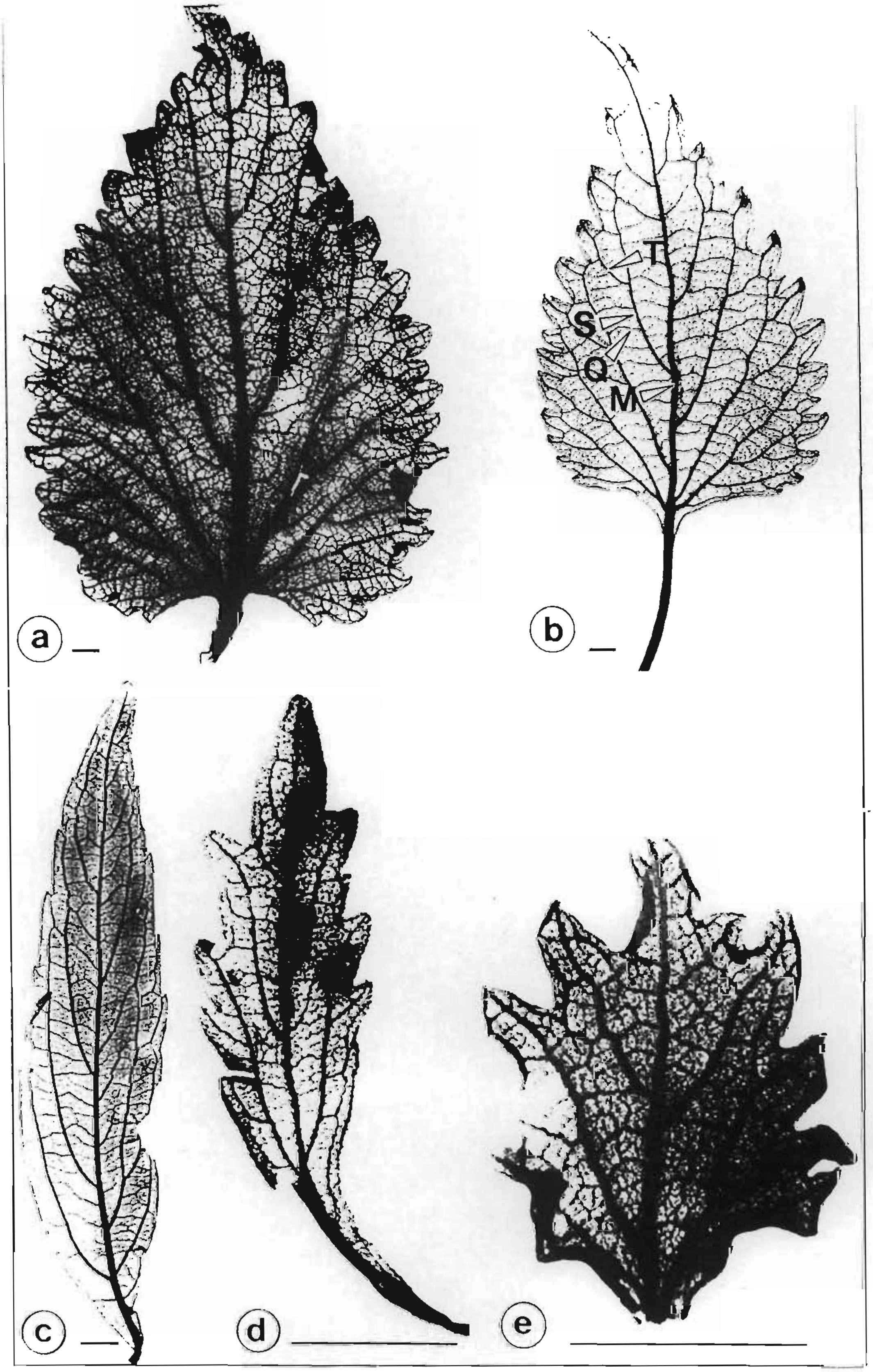

a
b
T
S
Q
M
c
d
e

Figure 8. Leaf venation of *Leonotis*.

(a) *L. pauciflora* (*Vos 98*),

(b) *L. dubia* (*Vos 77*),

(c) *L. leonurus* (*Vos 78*),

(d) *L. randii* (*Vos 268*) and

(e) *L. ocymifolia* ssp. *ocymifolia* (Bolus 8583).

Abbreviations: M=midvein (or primary vein), S=secondary vein, T=tertiary vein, Q=quaternary vein.

Scale bar=5 mm.

aridity of the immediate environment. In Codd's account (1985) of the Lamiaceae of southern Africa, leaf shape is diagnostic for many species. Leaf shape, size and indumentum were used by Skan (1910) in a key to *Leonotis* species.

Although cuticular sculpturing may serve as a diagnostic character at the specific level (Barthlott, 1981) in some plants, Stace (1965) warns that it should be used with caution. Edman (1927) found that *Thymus serpyllum* L. (Lamiaceae) has a more striate cuticle than *Thymus vulgaris* L.

The arrangement of epidermal cells is usually of minor taxonomic interest but in some families (e.g. Poaceae) it can be of systematic importance (Barthlott, 1981). In the Verbenaceae, a close relative of the Lamiaceae, three varieties of *Lantana* L. and most *Clerodendrum* L. species can be differentiated by their epidermal cell patterns (Kaushal and Tripathi, 1984).

According to Metcalfe and Chalk (1950) the stomata of the Lamiaceae are commonly diacytic, often interspersed with anomocytic stomata. However, in a large sample of Lamiaceae, El-Gazzar and Watson (1968) also found anisocytic stomata. In *Plectranthus* L' Hérit (Lamiaceae) Turner and Lersten (1983) found differences in stomatal patterns on stems and commented that stomata have taxonomic potential in the Lamiaceae.

Results

Three *Leonotis* species display diagnostic leaf shapes: *L. randii*, *L. schinzii* and *L. leonurus* (Figure 2 C-E). The remaining species have comparatively large, broadly ovate leaves (Figure 3 A-D). Leaf shape is summarised in Table 2. Leaf size and petiole length is presented (Figure 4 A and B respectively).

The majority of species display crenate to dentate leaves although *L. leonurus*, *L. randii* and occasionally *L. schinzii* display crenate to serrate leaves (Table 2). *L. randii* and *L. ocymifolia* have characteristically few marginal teeth

(Table 2) as a consequence of leaf reduction. Sub-sessile leaves are characteristic of *L. leonurus* and *L. randii* whereas *L. dubia* and *L. nepetifolia* display characteristically long petioles (Figure 4 B).

Floral leaves are small and caducous in most species but relatively large and persistent in *L. nepetifolia, L. leonurus* and *L. dubia* (Figure 5 A, B and D respectively). The floral leaves of most species are petiolate but in *L. leonurus, L. schinzii* and in *L. randii* they are sub-sessile (Figure 5 B, E and F respectively).

Leaf indumentum is variable (Table 2) and therefore of little taxonomic value. *L. schinzii* and *L. ocymifolia* ssp. *ocymifolia* are densely hairy (Figure 6 a and b respectively) in contrast to the glabrescent leaves of *L. dubia* and *L. ocymifolia* ssp. *transvaalensis* (Figure 6 f and h respectively). *Leonotis mollissima* displays characteristically discolorous leaves with filiform trichomes (Figure 6 c).

Glandular and non-glandular trichomes (Figure 7 a and e) occur on both surfaces of the leaves. Non-glandular trichomes are uni- to multiseriate (1-3 (-6) -celled), appressed, retrorse to sub-erect, 0.1-0.5 mm long and often verrucose (Figure 6 e). The two types of glandular trichomes are large globose, sub-sessile trichomes with eight head cells (Figure 7 a) and small, stalked, capitate trichomes with four head cells (Figure 7 b). Globose trichomes are usually indented and more dense on the abaxial surface of the leaf. These are particularly noticeable in *L. leonurus* (Figure 6 i) which displays a high diversity of essential oils (Chapter 11).

Epidermal cells are randomly orientated and have sinuous or straight walls (Figure 7 g and h). The cuticle of the epidermal cells surrounding the stoma is striate (Figure 7 i) or smooth. No species-specific cuticular patterns were observed. Stomata are predominantly anomocytic (Figure 7 i) and leaves are either amphistomatic or hypostomatic (Table 2).

Leaf venation is eucamptodromus in the majority of species (Figure 8 a-c) but craspedodromus in *L. randii* and *L. ocymifolia* ssp. *ocymifolia* (Figure 8 d and e respectively). Minor veins are more extensive in the leaves of *L. intermedia* and *L. pauciflora* (Figure 8 a) compared to the remaining species.

Discussion

Although leaf shape and size are variable in *Leonotis* they are nevertheless valuable for identification purposes, especially when used in conjunction with other characters such as the inflorescence (Chapter 6), habit and phytogeography (Chapter 13). A problem encountered is that different herbarium specimens do not always represent comparable portions of plants. Frequently only atypical flowering foliage is represented.

Leaf shape is intra-specifically stable in *Leonotis* (Figures 2 and 3) and the most practical, diagnostic character. *Leonotis ocymifolia* ssp. *ocymifolia* is distinguished by its small, broadly ovate to orbicular leaves with wavy, coarsely crenate margins (Figure 2 A). The narrowly ovate to lanceolate leaves of *L. leonurus* which are basally cuneate are immediately recognisable (Figure 2 E). Lamina length and width (Figure 4 A) and habit (Chapter 13) differentiate the subspecies of *L. ocymifolia* where leaf reduction is apparent. Leaf reduction has also occurred in *L. randii* but leaves are narrowly obovate to lanceolate (Figure 2 C) and often scabrid. In addition, *L. ocymifolia* and *L. randii* are allopatric.

Two tropical African species, *L. decadonta* Gürke. and *L. pole-evansii* Hutch., have similar shaped leaves to *L. leonurus*. Floral (Chapter 6) and calyx (Chapter 5) characters also reveal a close affinity between these species which suggests a tropical origin for the genus. Narrow leaves are considered synpleisiomorphic.

The leaves of *L. nepetifolia*, *L. dubia* and *L. pauciflora* are characteristically broadly ovate with a truncate or cordate base (Figure 3 A-C). *L. intermedia* also displays broadly ovate leaves but the base is usually attenuate (Figure 3 D). *L. nepetifolia* (Figure 3 A) and *L. dubia* (Figure 3 B) display longer, broader leaves than *L. pauciflora* (Figure 3 C) and *L. intermedia* (Figure 3 D).

Petiole length is variable but nevertheless a useful character for differentiating between species. Long petioles are characteristic of *L. nepetifolia, L. dubia* and *L. pauciflora* and short petioles of *L. schinzii, L. randii* and *L. ocymifolia.*

Species which occupy xeric habitats (Chapter 13) display small, short-petioled, hairy leaves often with thick cuticles (Chapter 4) whereas mesic forest dwelling species display large, long-petioled, glabrescent leaves with thin cuticles. Leaf reduction and modification to xeric or edaphic conditions (i.e. acidic and or nutrient poor soils) (Chapter 13) are considered synapomorphic characters.

The shape and persistent nature of the floral leaves of *L. nepetifolia*, *L. leonurus* and *L. dubia* (Figure 5 A, B and D respectively) are useful characters for identifying these species. Furthermore, in *L. nepetifolia* they are characteristically pendent as opposed to lying horizontal or arcing upwards around the inflorescence.

Leaf margins are crenate, dentate or serrate and seldom sub-entire (Table 2). In *L. leonurus* the distal half of the leaf is serrate and the proximal half entire (Figure 2 E).

For the majority of *Leonotis* species leaf indumentum varies intra-specifically (Table 2) and is therefore of limited value for identification purposes. Engler (1897) was one of the first to comment on the "bicoloured" leaves of *L. mollissima.* The adaxial surface of *L. mollissima* is dark green and sparsely hairy in comparison to the abaxial surface which is obscured by a dense mat of sericeous to velutinous, silvery-white trichomes (Figure 6 c). The leaves of *L. intermedia* are occasionally velutinous and discolorous (e.g. *Stewart 182)* but never as pronounced as in *L. mollissima.*

The leaf indumenta of *L. ocymifolia*, *L. schinzii* and *L. mollissima* are similar (Figure 6 a, b and c respectively), however, the leaves of the former two species are considerably smaller. In addition, these three species are allopatric. The non-glandular trichomes of *L. schinzii* are characteristically coarse (Figure 6 b) in comparison to the remaining species.

The indumentum affects leaf texture. *L. mollissima* was aptly named for its mollis or soft indumentum. The sparsely puberulous to glabrescent leaves of *L. dubia* and *L. nepetifolia* (Figure 6 e and f respectively) are soft to the touch whilst the leaves of *L. randii* (Figure 6 g) are characteristically scabrid. *L. intermedia* often has velutinous leaves.

Species occurring in semi-arid environments (*L. randii, L. schinzii* and *L. ocymifolia*) have small, hairy leaves. The strongly conduplicate and pendent nature of the leaves of *L. randii* and *L. schinzii* are useful diagnostic characters. *L. dubia* occurs in a mesic environment and has large, sparsely puberulous to glabrescent leaves.

A radial arrangement of epidermal cells at the base of non-glandular trichomes (Figure 7 g and h) is common in the Lamiaceae (Bosabalidis, 1990). This is apparent in most *Leonotis* species. In *L. leonurus* and *L. nepetifolia* two to four epidermal cells surround the base of non-glandular trichomes (Figure 7 a and b) whereas in the remaining species 8-16 epidermal cells are common (Figure 7 g and h). Occasionally two layers of epidermal cells are observed at the base of trichomes (Figure 7 f).

Craspedrodomus venation readily distinguishes *L. randii* and *L. ocymifolia* ssp. *ocymifolia* (Figure 8 d and e respectively) and is associated with leaf reduction in these species which occupy acidic or nutrient-poor soils (Chapter 13). However, this condition is not apparent in *L. schinzii* which occupies similar soil conditions and has relatively small leaves. Craspedrodomus venation is considered a derived condition.

All *Leonotis* species studied were predominantly anomocytic. In *L. intermedia* diacytic stomata were also observed interspersed with anomocytics. Similarly in *L. schinzii* tetracytic and anomocytic stomata are common. Differences in stomatal patterns between species are not consistent and therefore of little taxonomic value.

No correlations are apparent between leaf stomatal position and habitat conditions. Hypostomatic leaves are not only observed in small-leaved species occupying xeric conditions (e.g. *L. ocymifolia* ssp. *ocymifolia*) but also in forest dwelling species (e.g. *L. dubia* and *L. mollissima*).

Conclusion

Leaf shape, size, margination, venation, posture and texture are valuable for distinguishing certain *Leonotis* species. Leaf indumentum characterises *L. mollissima* but is variable and not diagnostic for any of the southern African species. Uni- and multiseriate non-glandular and two types of glandular trichomes occur on the leaves of all *Leonotis* species. Stomata are predominantly anomocytic and leaves are either amphistomatic or hypostomatic. Leaf epidermal patterns are reasonably uniform throughout the genus.

Figure 9. Transverse sections of the stem, plan diagrams of

(A) *Leonotis nepetifolia* (*Vos 174*) and

(B) *L. intermedia* (*Vos 539*).

Key:

▨ collenchyma

▤ chlorenchyma

◪ wedge of collenchyma

░ secondary phloem

■ secondary xylem

▩ primary xylem

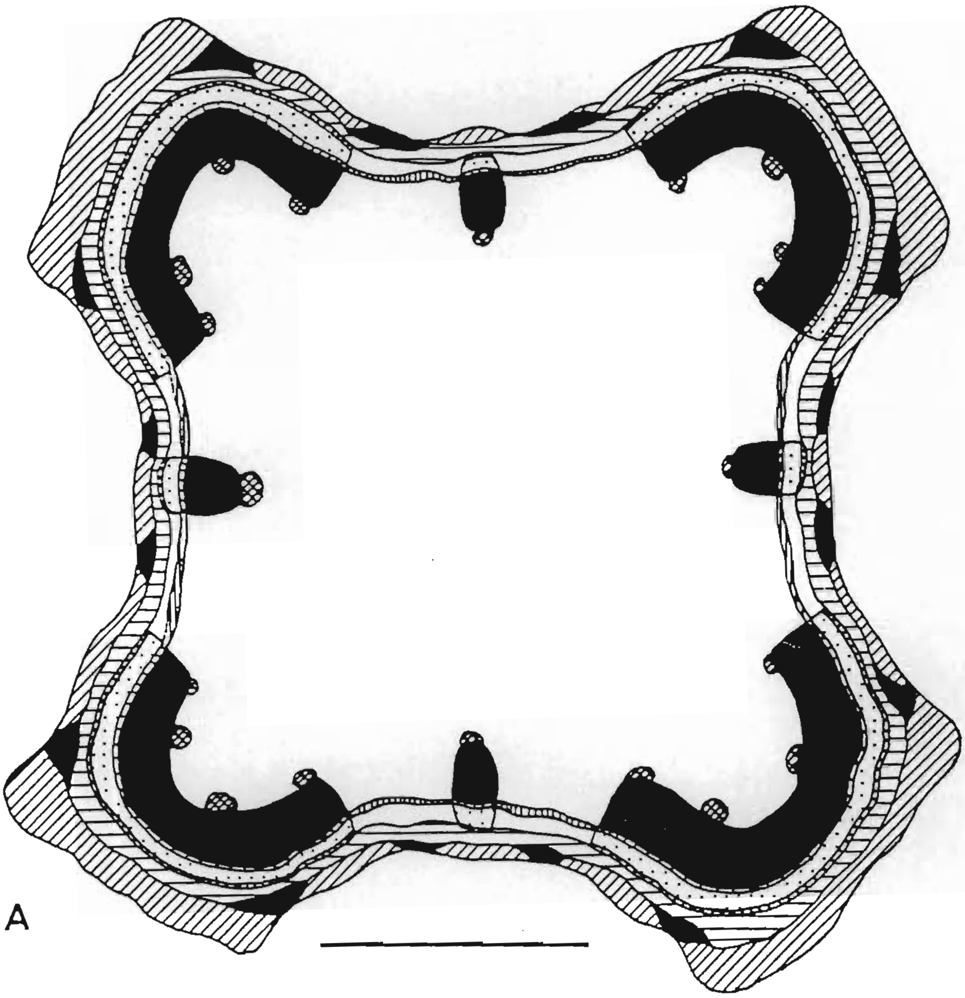
□ pith (parenchyma)

◸ pericycle (thick radiating lines)

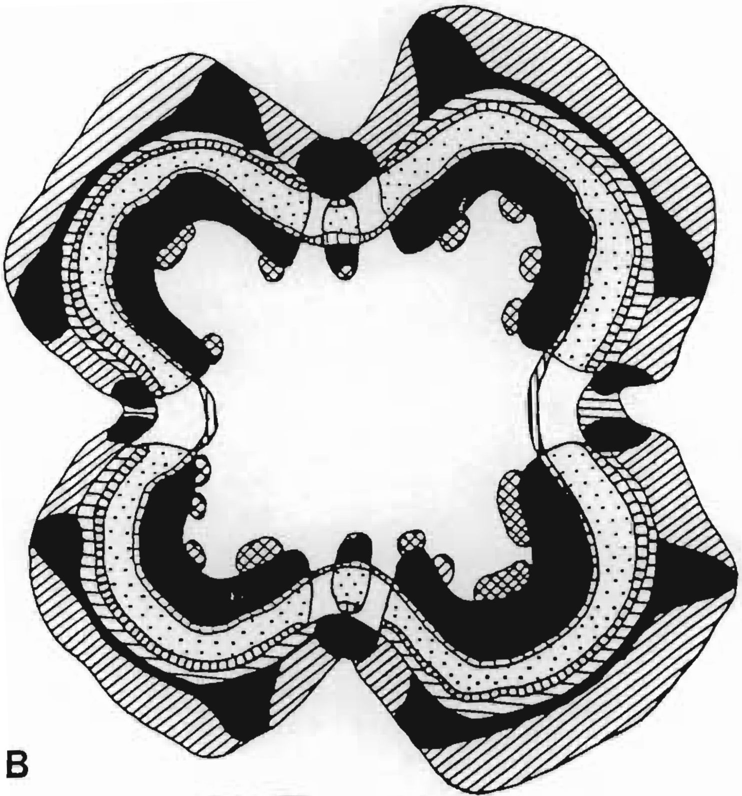
◸ fascicular cambium (thin radiating lines)

▥ inter-fascicular cambium

Scale bar=1 mm.



A



B

Table 3. Anatomical characters of the flowering stem of *Leonotis*.
L. nepetifolia represents the annual species, perennial species are listed in Table 2.

Leonotis species	Lateral grooves	Pith	Sclerotic wedges
annual	wide & shallow	large	small & disconnected
perennial	deep & narrow	small	large & connected

Table 4. Leaf dimensions from transverse sections of *Leonotis* leaves.

Leonotis species	Leaf dimensions (μm)					
	Leaf thickness	Adaxial cuticle thickness	Adaxial epidermis width	Spongy palisade mesophyll	Vascular bundle diameter	Midrib width
L. dubia	75-115	0.5-1.1	12-15	5:5	85-95	117-147
L. mollissima	90-130	1.5-2	15-23	6:4	900-1140	2200-2228
L. leonurus	175-210	2.8-5.7	9-30	6:4	800-836	1600-1631
L. nepetifolia	180-210	2.6-3	10-20	6:4	83-200	440-475
L. intermedia	180-265	3-4	15-25	6:4	200-211	522-530
L. schinzii	120-150	3-4.4	15-21	7:3	100-112	222-245
L. ocymifolia ssp. *transvaalensis*	150-220	2-6.4	12-30	7:3	112-140	275-315
L. randii	185-200	3-4.6	16-30	7:3	100-124	313-520
L. ocymifolia ssp. *ocymifolia*	125-150	6.2-11	22-50	5:5	110-119	395-402

Chapter 4

Stem and leaf anatomy

Introduction

Leaves possess many features of potential taxonomic significance. Mauseth (1988) found that petiole anatomy provides excellent taxonomic characters.

In *Eriope* Humb. *et* Bonpl. (Lamiaceae) xeromorphic anatomical and morphological characters are usually correlated (Rudall, 1980). Xeromorphic plants are those which have an anatomy and growth form that are especially adapted to dry conditions (Mauseth, 1988). A dense waxy cuticle is typical of xerophytic plants (Oppenheimer, 1960) and functions in lowering transpiration (Lyshede, 1982) by blocking excess sunlight. It also acts as a deterrent against insect feeding and egg laying (Levin 1973). A palisade of 2-5 cells thick is also characteristic of xerophytic plants. Xeromorphic leaf characters of the subtribe Hyptidinae (Lamiaceae) are taxonomically useful. The petiole and midrib vasculature in particular were often characteristic of a section, subsection or species (Rudall, 1980).

Bokhari and Hedge (1971) found the anatomy of four lamiaceous genera diagnostic. However, at the specific level, Bokhari and Hedge (*l.c.*) working on *Salvia* L. found that characters of the petiole, stem, leaf anatomy, stomata and indumentum are very uniform and they concluded that the species studied formed a close-knit alliance. Leaf anatomy in *Eriope* is considerably variable associated with a wide range in habit, from trees to woody herbs, and of limited value in elucidating relationships within the genus (Rudall, 1980).

The taxonomic value of the mesophyll may be limited. Christodoulakis and Bazos (1990) found the number of palisade layers in *Ballota acetabulosa* Benth. (Lamiaceae) are dependent upon the season. Similarly, Buch (1925)

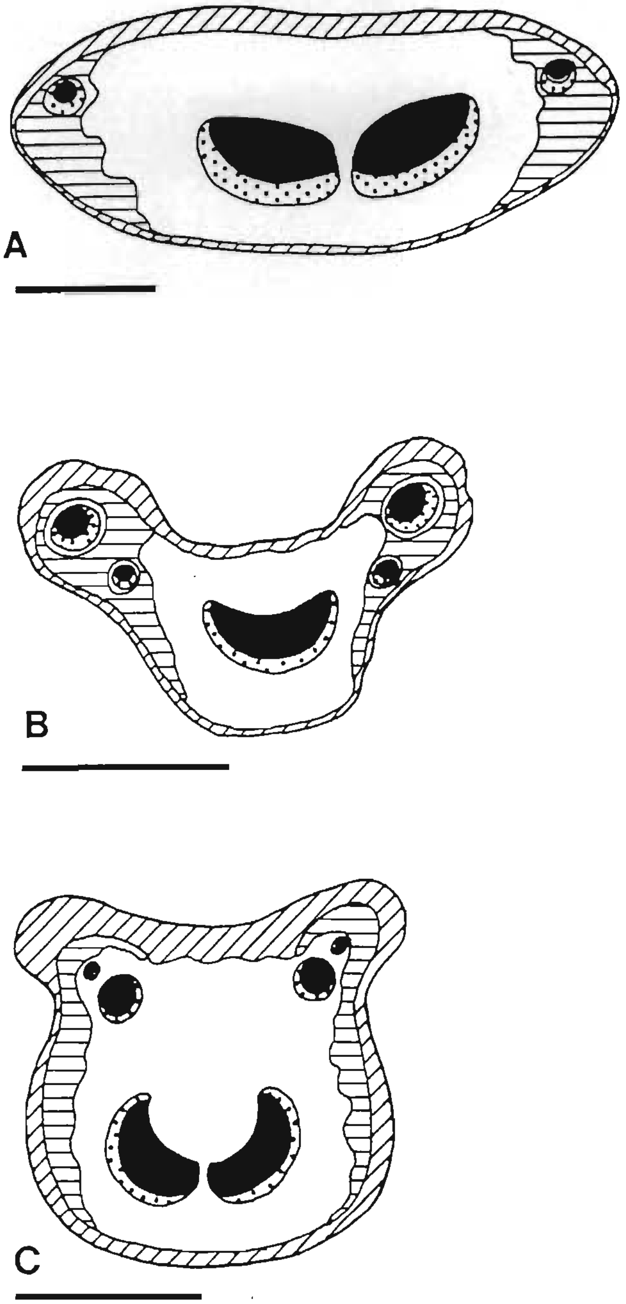

A
B
C

Figure 10. Transverse section of the petiole, plan diagrams of

(A) *Leonotis leonurus* (*Vos 78*),

(B) *L. randii* (*Vos 268*) and

(C) *L. nepetifolia* (*Vos 174*).

Key:

▨ collenchyma

▤ chlorenchyma

░ primary phloem

■ secondary xylem

□ parenchyma

Scale bar=0.5 mm.

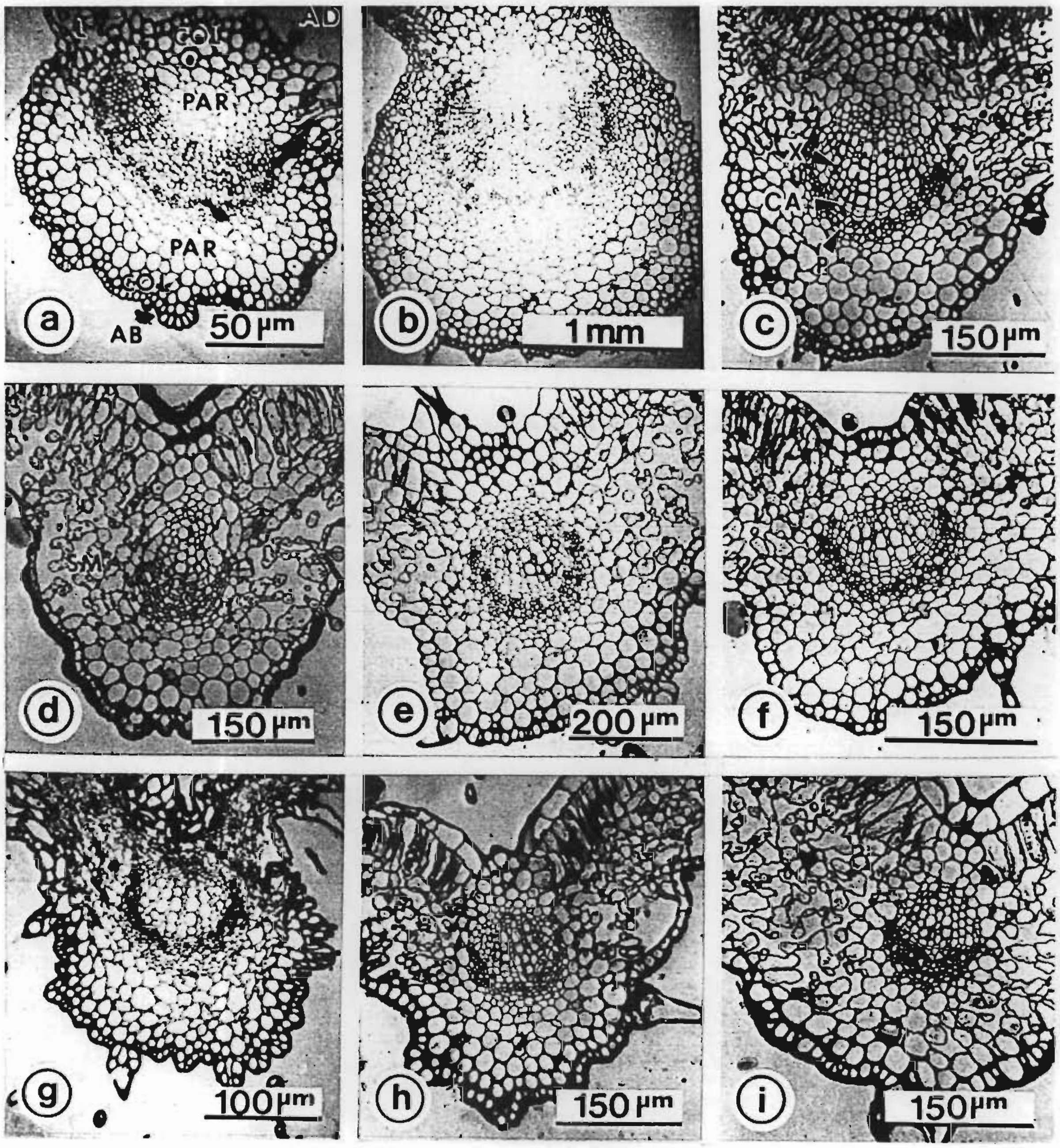

AD
COL
PAR
PAR
COL
AB
a
50 µm
b
1 mm
X
CA
P
c
150 µm
SM
d
150 µm
e
200 µm
f
150 µm
g
100 µm
h
150 µm
i
150 µm

Figure 11. Transverse sections of the midrib of *Leonotis* leaves.

(a) *L. dubia* (*Vos 77*),

(b) *L. mollissima* (*Vos 363*),

(c) *L. nepetifolia* (*Vos 174*),

(d) *L. ocymifolia* ssp. *ocymifolia* (*Vos 229*),

(e) *L. intermedia* (*Vos 59*),

(f) *L. ocymifolia* ssp. *transvaalensis* (*Vos 421*),

(g) *L. schinzii* (*Kolberg* and *Maggs 553*),

(h) *L. ocymifolia* ssp. *transvaalensis* (*Vos 422*) and

(i) *L. randii* (*Vos 268*).

Abbreviations: L=lamina, AD=adaxial, AB=abaxial, X=xylem, CA=cambium, P=phloem X+CA+P=vascular bundle, PAR=parenchyma, COL=collenchyma, SM=spongy mesophyll.

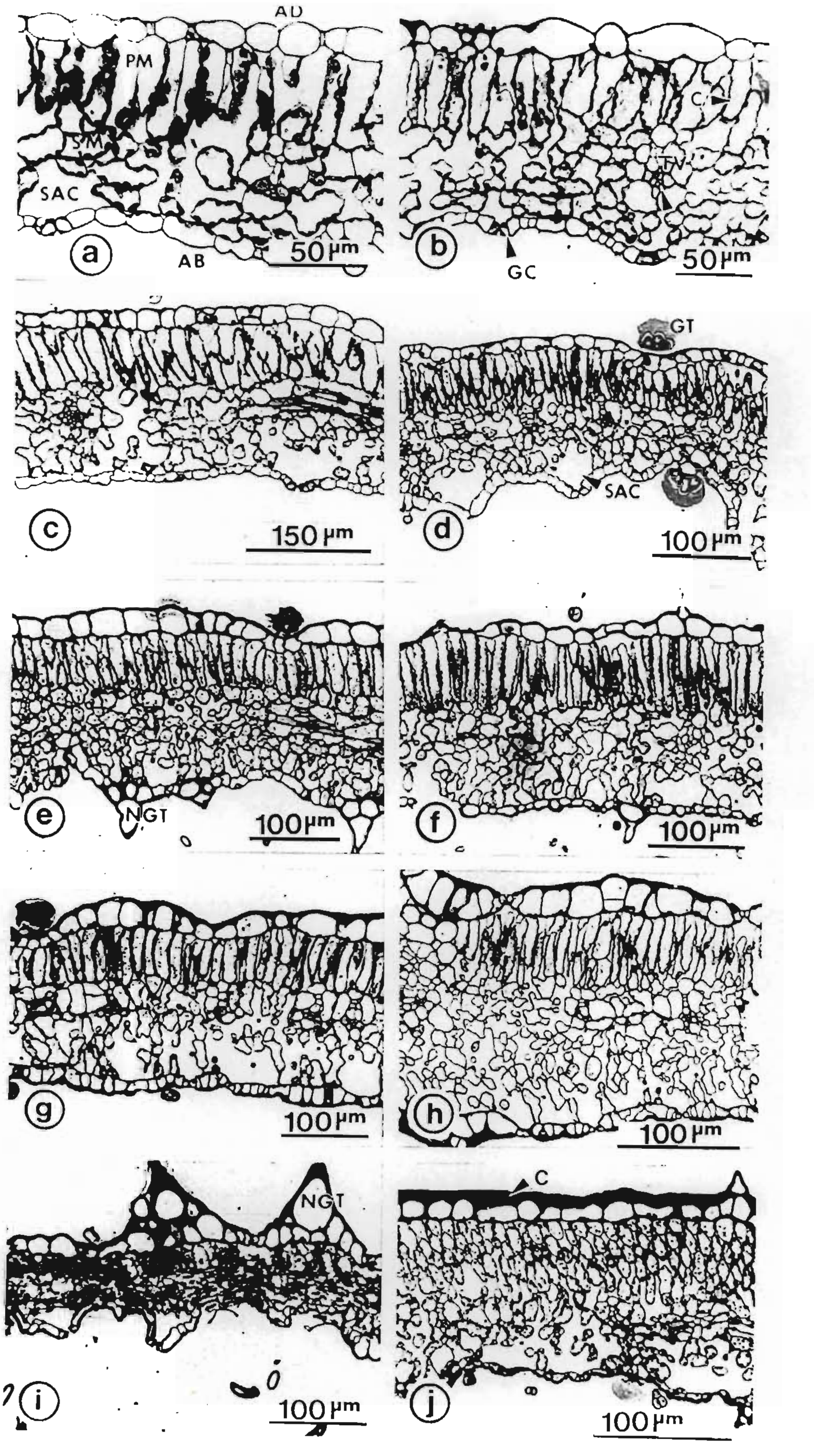

AD
PM
SM
SAC
AB
a
50µm
b
C
TV
GC
50µm
c
150µm
GT
d
SAC
100µm
e
NGT
100µm
f
100µm
g
100µm
h
100µm
NGT
i
100µm
C
j
100µm

Figure 12. Transverse sections (medial) of *Leonotis* leaves.

(a) *L. dubia* (*Vos 77*),

(b) *L. mollissima (Vos 363)*,

(c) *L. intermedia (Vos 59*),

(d) *L. ocymifolia* ssp. *transvaalensis* (*Vos 421*),

(e) *L. leonurus* (*Vos 538*),

(f) *L. nepetifolia (Vos 174*),

(g) *L. ocymifolia* ssp. *transvaalensis* (*Vos 422*),

(h) *L. randii (Vos 268*),

(i) *L. schinzii (Kolberg* and *Maggs 553)* and

(j) *L. ocymifolia* ssp. *ocymifolia* (*Vos 229*).

Abbreviations: AD=adaxial, AB=abaxial, PM=palisade mesophyll, SM=spongy mesophyll, SAC=sub-stomatal air cavity, GC=guard cell, C=acicular crystal, TV=tertiary vein, GT=glandular trichome, NGT=non-glandular trichome, C=cuticle.

reported that the mesophyll type is an unreliable taxonomic character due to environmentally induced variations.
Higher plants may contain crystals that consist mainly of calcium oxalate (Al-Rais *et al.*, 1971). Calcium oxalate crystals have been recorded in the Lamiaceae in the form of sphaerocrystals and cluster crystals (Metcalfe and Chalk, 1979).

The role that calcium oxalate crystals play in metabolism is still obscure (Metcalfe and Chalk, 1979). Some investigators believe calcium oxalate crystals are merely end products of metabolism although Harborne (1984) believes they are selectively advantageous making the plant unpalatable, thereby deterring herbivores. In addition, many crystals effectively inhibit insects chewing and laying eggs on them (Mauseth, 1988).

Genua and Hillson (1985) comment that calcium oxalate crystals are potentially useful taxonomic characters. Metcalfe and Chalk (1979) warn that one must be cautious when drawing taxonomic conclusions when not only the frequency but also the morphology of the crystals may change during the life history of the plant.

Results

Flowering stem

The anatomy of the flowering stem is similar in most *Leonotis* species although the annual species (*L. nepetifolia*) (Figure 9 A) displays less collenchyma than the perennial species (Figure 9 B). The morphology of the flowering stem is also affected by the depth and width of the four lateral grooves (Table 3).

Collateral vascular bundles are well-developed in the angles of the flowering stem where the collenchyma is interrupted by wedges of undifferentiated tissue which become sclerotic in old stems. The size of the pith and the size and

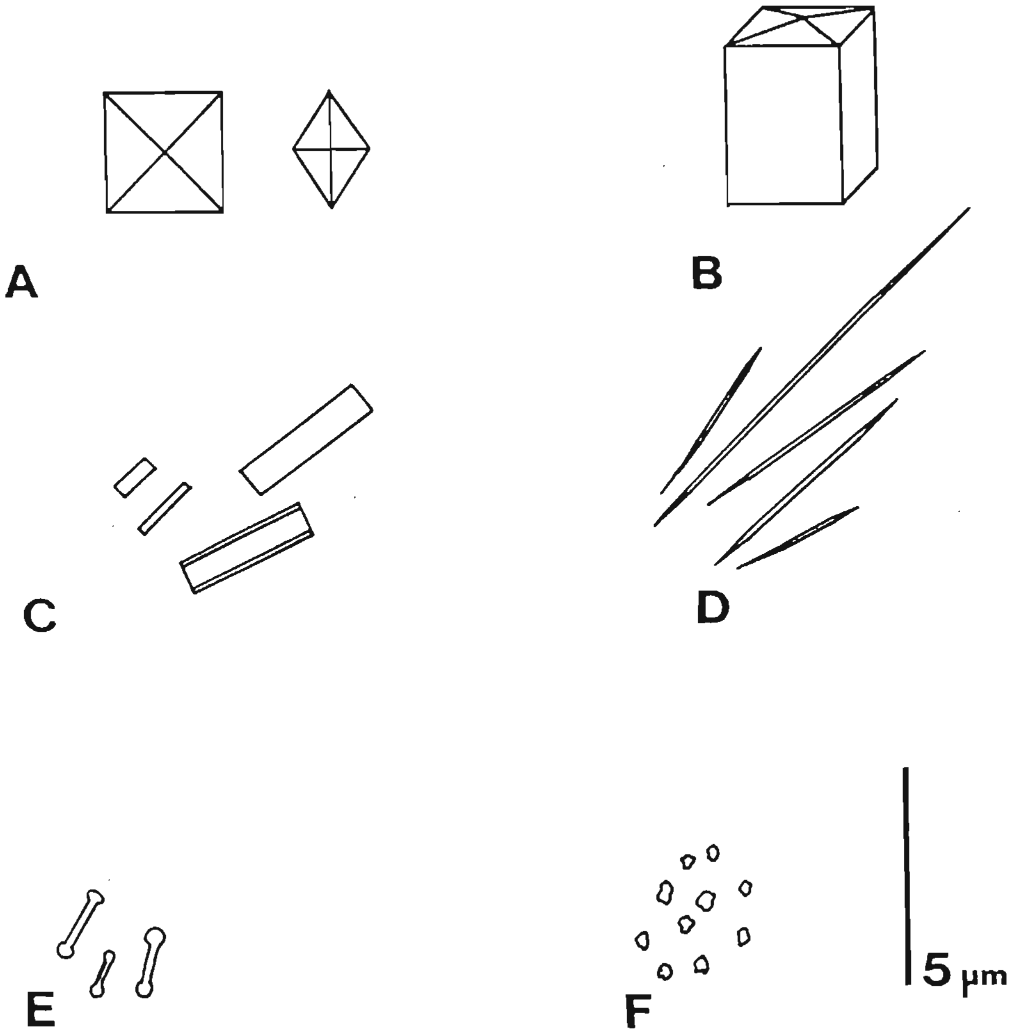


Figure 13. Crystal types found in the flowering stems and leaves of *Leonotis*.
(A) octahedral (top view on the left, side view on the right) *L. nepetifolia (Vos 174)*,
(B) prism *L. ocymifolia* ssp. *ocymifolia* (*Vos 229*),
(C and D) acicular *L. mollissima* and *L. ocymfolia* ssp. *transvaalensis* (*Vos 363 and 422*),
(E) osteoid *L. dubia* (*Vos 77*) and
(F) spherical crystals *L. ocymifolia* ssp. *ocymifolia* (*Vos 229*).

distribution of "sclerotic wedges" differs in annual and perennial *Leonotis* species (Figure 9 and Table 3).

Petiole

The petiole of *L. leonurus* is characteristically oval or flattened above and below (Figure 10 A) but oblong to crescent-shaped in the other species (Figure 10 B and C). Two vascular traces are evident in the petiole forming a crescent. In *L. randii* a single vascular trace is more common (Figure 10 B).

Leaf midrib

The vascular bundle of *L. dubia* and *L. mollissima* is crescent-shaped (Figure 11 a and b respectively) but circular in the remaining species (Figure 11 c-i).

The vascular bundle is supported above and below by a layer of collenchyma, 2-3 cells thick (Figure 11 a). The lower layer is crescent-shaped and the upper layer is oval to oblong. Collenchyma patterns are reasonably consistent amongst the species.

As expected, midrib width is proportional to vascular bundle diameter with *L. mollissima* and *L. leonurus* displaying the largest vascular bundles (Table 4).

The spongy mesophyll is confined largely to the lamina in *L. dubia* and *L. mollissima* (Figure 11 a and b respectively). In small-leaved species such as *L. ocymifolia* and *L. randii* the spongy mesophyll occurs proximal to the tissue of the midrib (Figure 11 d and i respectively).

Lamina

Leonotis leaves range from 90 to 265 μm in thickness (Figure 12 and Table 4). The adaxial epidermis is uniseriate and ranges from 9-30 (-50) μm in thickness (Table 4). In *L. ocymifolia* ssp. *transvaalensis* and *L. randii* the epidermis is irregularly thickened and corrugated (Figure 12 g and h respectively) due to the narrowing of epidermal cells near the stomata.

The palisade mesophyll is uniseriate in most species but multi-seriate (2-5 cells wide) in *L. ocymifolia* ssp. *ocymifolia* (Figure 12 j). There is a higher ratio of spongy to palisade mesophyll in most species (Table 4). Oblong palisade cells are common but characteristically oval in *L. ocymifolia* ssp. *ocymifolia.*

Calcium oxalate crystals

Six calcium oxalate crystal (Figure 12 B) forms are evident in the leaves and stems of *Leonotis* (Figure 13 A-F).

Discussion

The extensive development of collenchyma in the angles of the flowering stem give the stem a quadrangular shape which is characteristic of most Lamiaceae.

The replacement of collenchyma cells with groups of sclereid fibres is apparently common in the Lamiaceae (Metcalfe and Chalk, 1950). Leafhoppers (Membracidae) often damage the flowering stem of *Leonotis* directly below the inflorescence. and sclerification may limit such damage.

L. ocymifolia ssp. *ocymifolia* occurs in an arid environment and displays xerophytic characters such as a multi-seriate palisade and thick adaxial cuticle and epidermis. These characters are stable since plants were cultivated from seed under mesic conditions. Additional xerophytic characters (size and indumentum) are discussed in Chapter 3. *L. dubia* and *L. mollissima* occur in mesic environments and consequently large, membranous leaves which have thin cuticles (Table 4) are not surprising.

Crystals are not confined to specific tissues and different forms of crystals are not species-specific. Calcium oxalate crystals therefore have no diagnostic value in *Leonotis*. In addition to essential oils (Chapter 11), calcium oxalate crystals may play an important role in the chemical and mechanical defence of *Leonotis* against herbivores. Many insects were recorded on *Leonotis* plants (Chapter 12, Table 14) but foliage damage was negligible.

Conclusion

Although flowering stem anatomy is diagnostic for the annual and perennial *Leonotis* species it is of limited taxonomic value.

Petiole anatomy is uniform throughout the genus although in *L. leonurus* the shape of the petiole is diagnostic. Mesophytic and xerophytic leaf anatomy characterise certain species.

The types of calcium oxalate crystals and their distribution in the leaves and stems of *Leonotis* species have no diagnostic value.

Table 5. Calyx characters of *Leonotis*.
Vouchers are cited in Chapter 15.

Leonotis species	Calyx character				
	Length (mm)	Width (mm)	Adaxial lobe length (mm)	Length of remaining lobes (mm)	Tube
L. leonurus	10-16	3.5-5 (-6)	0.5-2 (-4)	0.5-2 (-4)	straight or deflexed
L. dubia	(10-) 15-22 (-24)	3-5	(1-) 3-5 (-7)	0.2-2.5	straight or deflexed
L. pauciflora	(12-) 14-23 (-26)	3-5	3-9	0.5-3	deflexed
L. schinzii	15-26	4-5.5 (-7)	(2.5-) 3-7	0.5-3.5	deflexed
L. ocymifolia ssp. *ocymifolia*	(12-) 15-22	3-6	2.5-7.5	0.5-4	deflexed
L. ocymifolia ssp. *transvaalensis*	(12-) 14-26	3-5.5	3-9	0.5-4	deflexed
L. randii	(12-) 18-27 (-30)	4-6 (-7)	4-9 (-14)	(1.5-) 2-4 (-6)	deflexed
L. intermedia	(11-) 13-22 (-26)	3.5-5.5 (-7)	1.5-6 (-9)	0.5-4.5	deflexed
L. nepetifolia	(13-) 18-25 (-32)	3-5	6-11	1-4 (-6)	deflexed

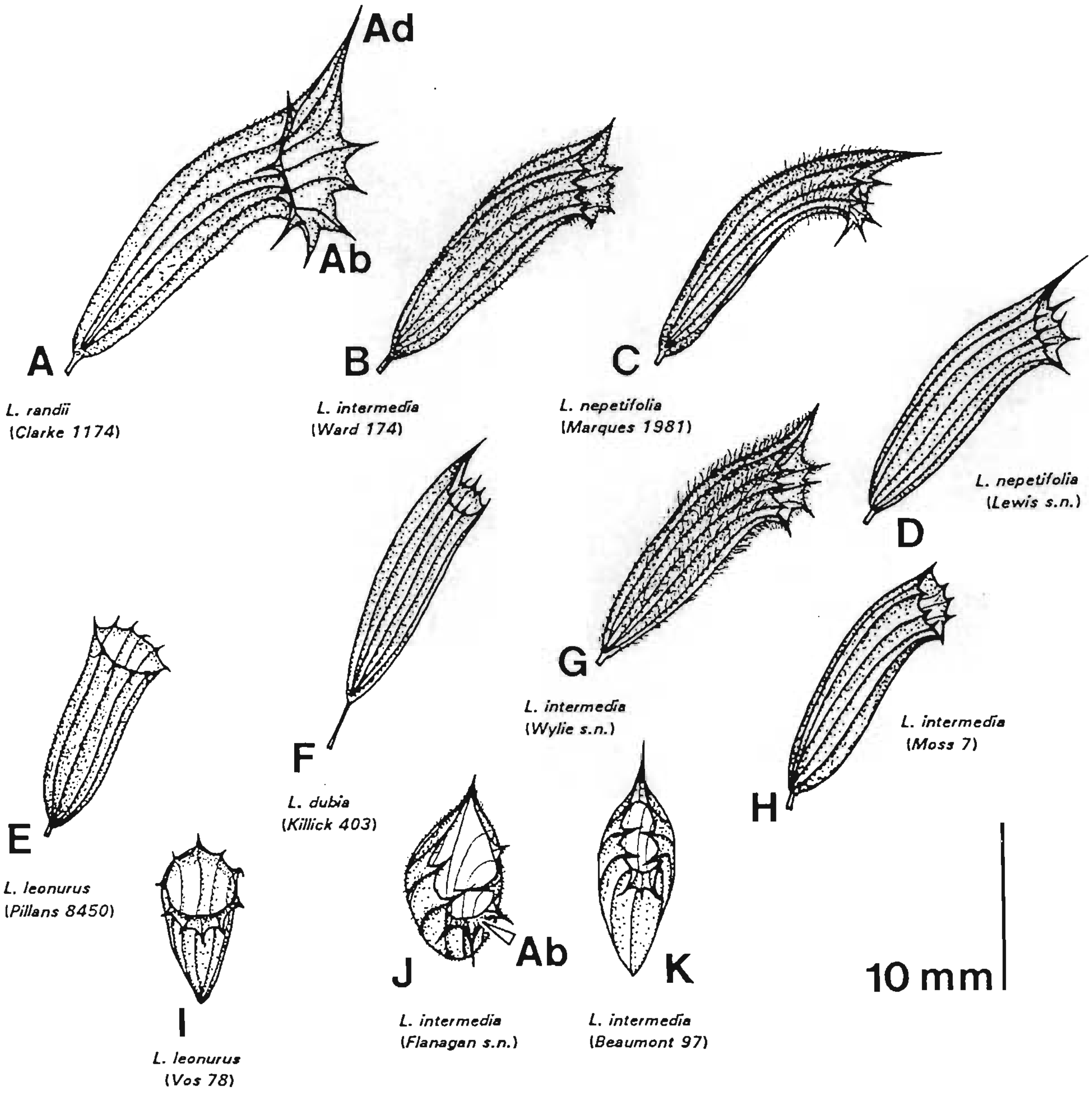


Figure 14. Lateral (A-H) and frontal views (I-K) of the calyx of *Leonotis*. Abbreviations: Ad=adaxial calyx lobe, Ab=abaxial calyx lobe. Vouchers are indicated in parenthesis and cited in Chapter 15.

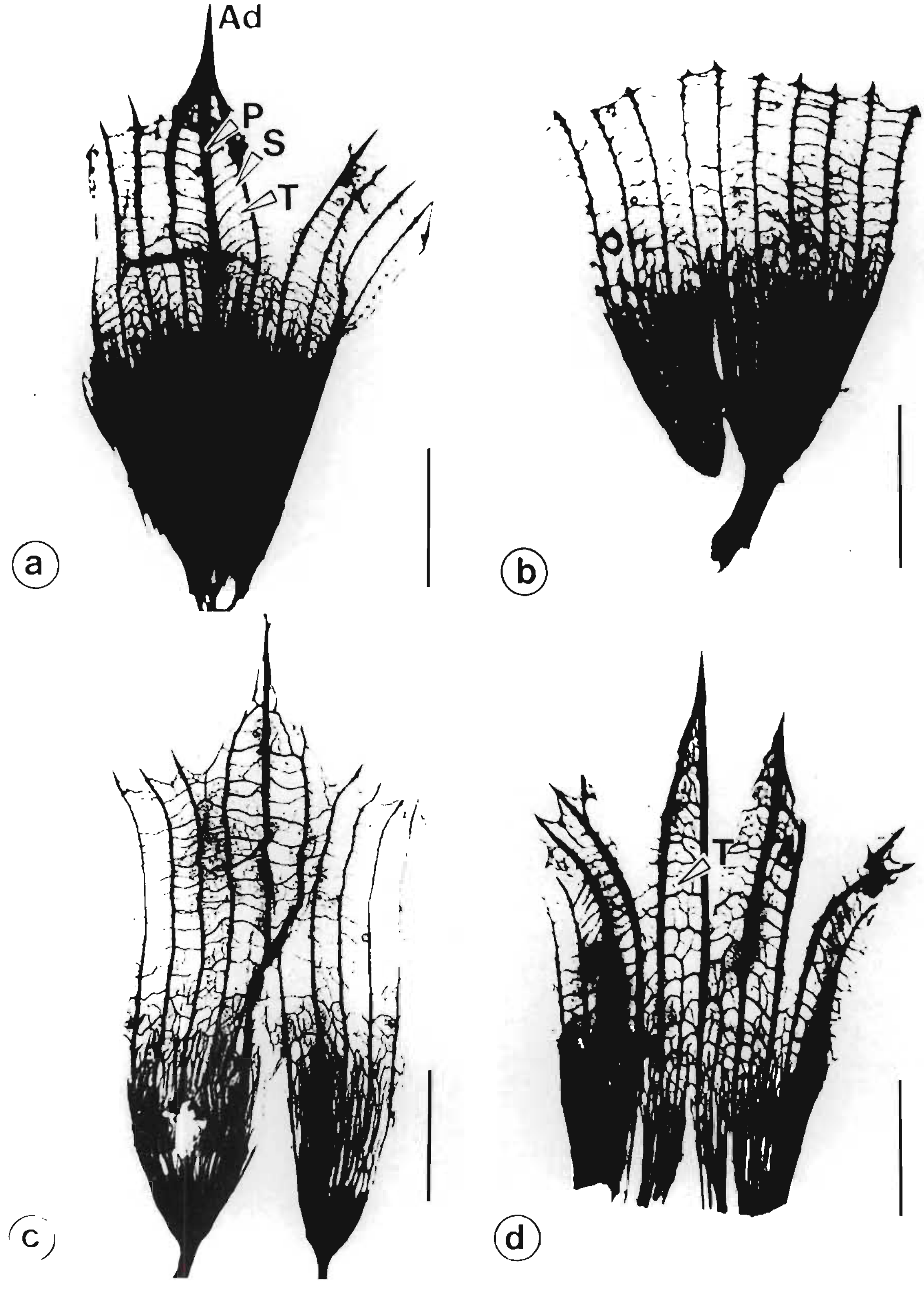

Ad
P
S
T
a
b
c
T
d

Figure 15. Calyx venation of *Leonotis* (abaxial view).

(a) *L. randii* (*Leedertz 1035*),

(b) *L. leonurus* (*Thode A982*),

(c) *L. dubia* (*Tyson 1300*) and

(d) *L. nepetifolia* (*Vos 174*).

The calyx tube has been split and flattened to ensure an even plane for photography. Abbreviations: Ad=adaxial calyx lobe, P=primary vein, S=secondary vein, T=tertiary vein. The unlabelled arrow in (d) indicates the fibrous calyx base; the labelled arrow indicates a terminal tertiary vein.

Scale bar=5 mm.

Chapter 5

Calyx morphology

Introduction

In the Lamiaceae and Verbenaceae the calyx frequently consists of five united persistent sepals with a varying number of spined lobes near the top of the calyx tube (El-Gazzar and Watson, 1970).

In many Lamiaceae the calyx protects the developing nutlets by forming a concealed chamber (Paton, 1992c). The calyx may contain calcium oxalate crystals (Figure 1b in El-Gazzar and Watson, 1970) and in 30 genera of Lamiaceae surveyed by the same authors the calyx cells were thick-walled, lignified and fibrous. The morphology of the calyx therefore affords maximum protection for the developing nutlets. In *Scutellaria* L. and *Aeollanthus* Mart. ex Spreng. the calyx plays a major role in seed dispersal (Paton, 1992c).

In Codd's (1985) revision of southern African Lamiaceae, calyx shape, vestiture and spinescence were of primary importance in keys of *Tinnea* Kotschy ex Hoof., *Stachys* L., *Salvia* and *Ocimum* L. Calyx lobe size and shape was used by Paton and Brummit (1991) to distinguish *Plectranthus seyanii* Paton from two closely related species. Similarly, lobe size and shape are important diagnostic characters for species of *Teucrium* L. (King, 1988) and *Cunila* Mill. (García-Peña, 1989).

Calyx indumentum, length and lobe shape feature strongly in a key to the African species of *Ocimum* (Paton, 1992b). Stellate trichomes distinguish the calyx of *Erythrochlamys nummularia* (S. Moore) Hedge from the calyx of *E. cufodontii* Lanza which has dendroid trichomes (Hedge and Miller, 1977).

In an extensive survey of the Lamiaceae and Verbenaceae, calyx venation was found to be of little taxonomic value (El-Gazzar and Watson, 1970). The same authors comment that the calyces of most species display an alternation of median and common lateral veins but in 11 species (out of 400) from three genera (*Leucas*, *Acrotome* and *Leonotis*), the common lateral veins expand into the five smaller calyx lobes and the median veins furnish the five larger lobes.

Calyx length (Baker, 1900), lobe shape and number (Skan, 1910) are important taxonomic characters in keys to *Leonotis*.

Results

Calyx morphology of *Leonotis* is summarised in Table 5. Calyx morphology is similar in most species (Figure 14 A-K) and therefore of limited taxonomic value. Tube shape, length and lobing are diagnostic for *L. leonurus* (Figure 14 E and I and Table 5). The venation pattern of the single annual species (*L. nepetifolia*) (Figure 15 d) differed from the remaining species (Figure 15 a-c).

Discussion

The sepals of *Leonotis* are fused into a tube with eight, or seldom 10, spinescent to blunt apical lobes. Calyx lobes vary in shape from acute to acuminate (Figure 14 A-K).

Once the corollas have fallen from the calyx the three abaxial lobes may form a small, reflexed lip whilst the lateral lobes curve inwards constricting the throat. This may allow some protection for the developing nutlets and gives the calyx a bilabiate appearance (Figure 14 J and K).

The calyx is puberulous to pubescent or velutinous and occasionally villous near the throat. The tube is normally deflexed although in *L. leonurus* and *L. dubia* it is often straight (Figure 14 E and F respectively).

A short, straight calyx tube with sub-equal, patent to reflexed lobes

distinguishes *L. leonurus* (Figure 14 E and I and Table 5). In the remaining species the calyx lobes are directed forward (except for the lowest lobes) and the adaxial lobe is straight or curved slightly upwards.
The adaxial calyx lobe is usually approximately three times longer than the remaining lobes although occasionally it is only marginally longer (Figure 14 G and H). The adaxial lobes of *L. randii, L. nepetifolia* and *L. ocymifolia* ssp. *transvaalensis* are relatively long and strongly spinescent in comparison to the short (Table 5), blunt or weakly spinescent lobes of *L. leonurus* and *L. dubia* (Figure 14 E and F). Calyx lobes are usually spinescent in *Leonotis* although blunt lobes are common.

Calyx venation is similar in most *Leonotis* species with 10, seldom eight, primary veins (Figure 15 a-d). This conforms to the familial pattern described by El-Gazzar and Watson (1970). In most species the adaxial calyx lobe is supported by three primary veins which is probably the result of lobe connation (Figure 15 a) but in *L. leonurus* a single primary vein supports each calyx lobe (Figure 15 b). The venation pattern reported for *Leonotis* (species unknown) by El-Gazzar and Watson (1970) and outlined above does not apply, at least for the southern African species. No distinction can be made in *Leonotis* between large and small lobes or common lateral and median veins. However, the 10-nerved character of the calyx is shared with two closely related genera, namely *Leucas* and *Acrotome.*

In most *Leonotis* species the secondary veins lie at right angles to the primary veins and form rectangular areoles (Figure 15 a and c). In *L. nepetifolia* adaxial lobe venation is reticulate and the areoles are irregular with tertiary veins often terminating within them (Figure 15 d).

Although the fruiting calyces of perennials also become pungent when dry this is so pronounced in the annual species (*L. nepetifolia*) that if handled carelessly the lobe apices break-off after penetrating the skin.

Spinescent calyces probably developed in *Leonotis* to deter browsing

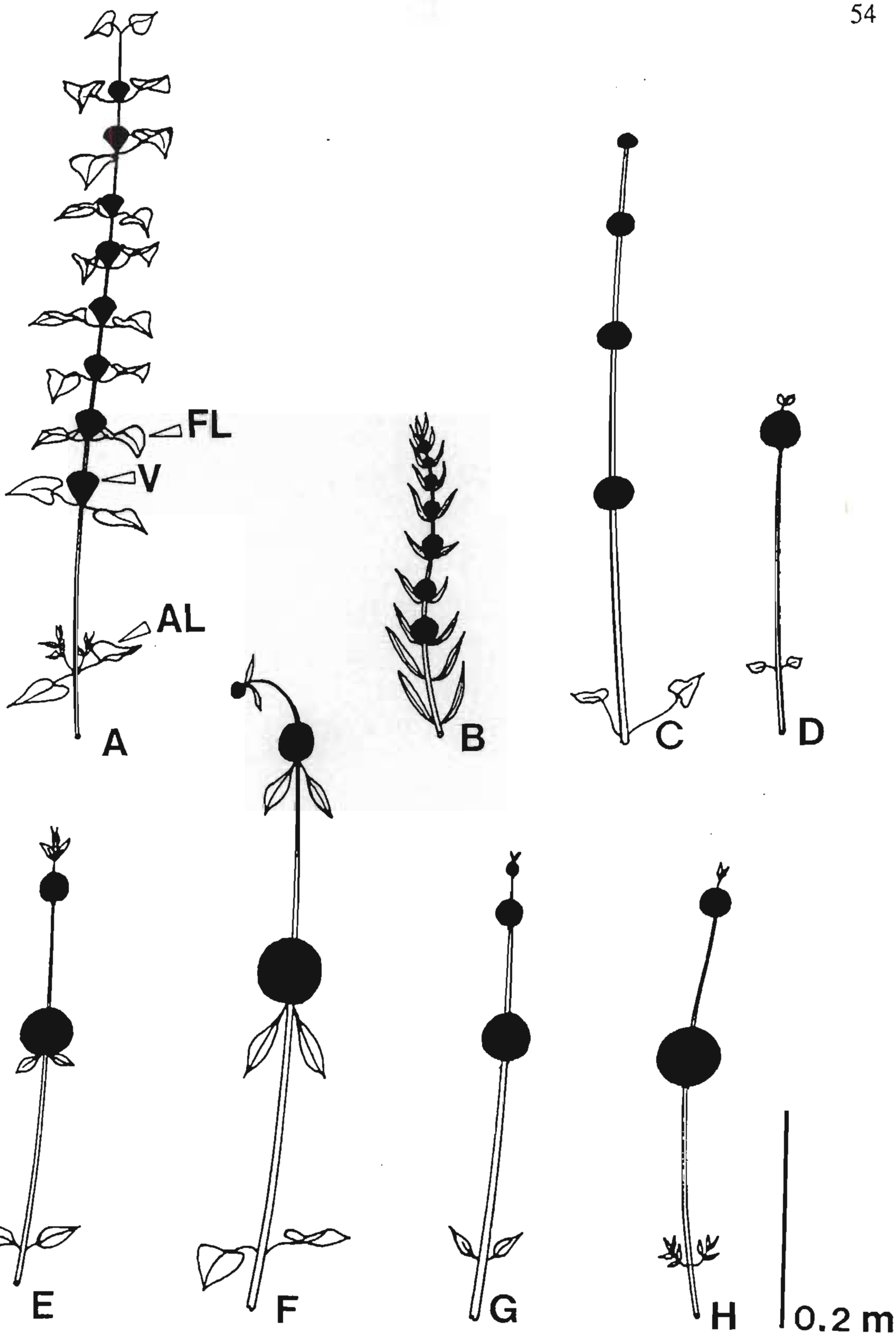


Figure 16. Schematic diagrams of *Leonotis* inflorescences.
(A) *L. dubia*, (B) *L. leonurus*, (C) *L. pauciflora*, (D) *L. ocymifolia* ssp. *ocymifolia*, (E) *L. intermedia*, (F) *L. nepetifolia*, (G) *L. schinzii* and (H) *L. randii*.
Abbreviations: FL=floral leaf, AL=apical leaf, V=verticillaster.

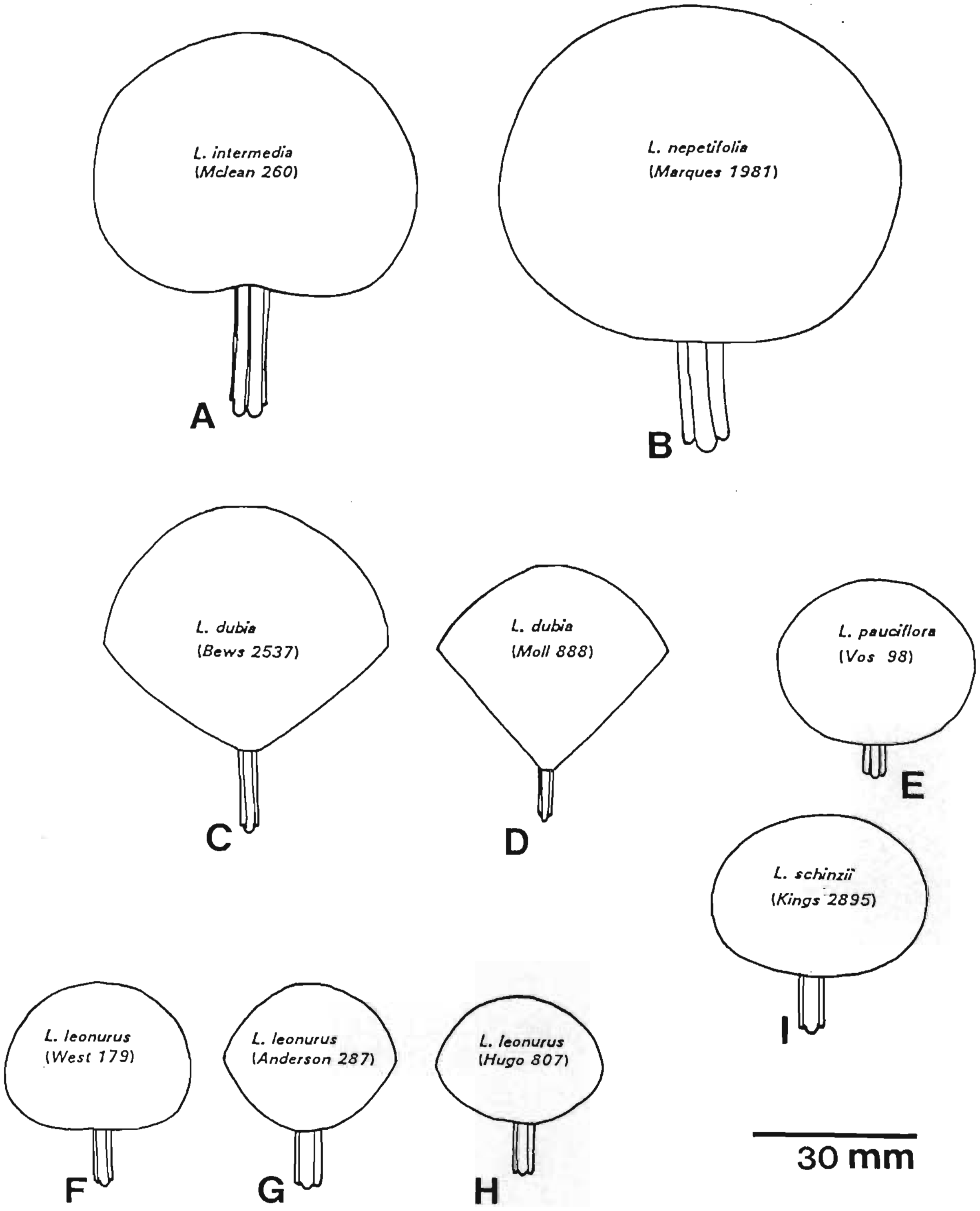


Figure 17. Outlines of *Leonotis* verticillasters.
Vouchers are indicated in parenthesis and cited in Chapter 15.

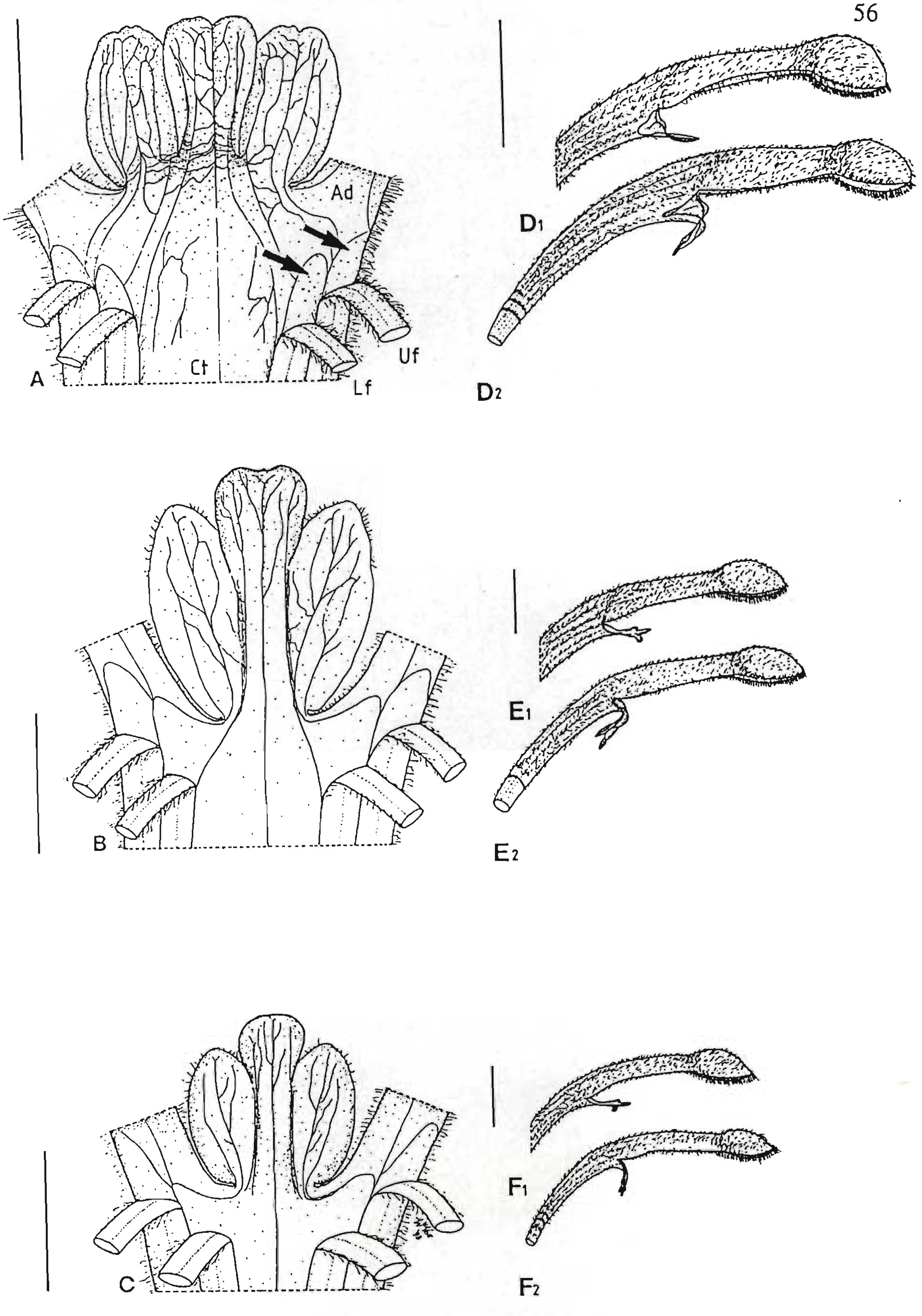


Figure 18. Corolla morphology of (A and D) *Leonotis leonurus* (*Gordon-Gray 1167*), (B and E) *L. intermedia* (*Reid 19*) and (C and F) *L. nepetifolia* (*Vos 174*). Corollas have been dissected and flattened to show the abaxial lip morphology (A-C). The filaments have been bent backwards to show the area of filament insertion in the tube (indicated with arrows). The morphology of the abaxial lip at (D_1-F_1) and after (D_2-F_2) anthesis is represented in (D-F). Abbreviations: Uf=upper filament, Lf=lower filament, Ad=base of adaxial lip, Ct=corolla tube. Scale bars A-C=4 mm and D-F=10 mm.

Table 6. Inflorescence characters of Leonotis.
A dash (-) indicates the absence of a character.
Abbreviation: verticill. =verticillaster

Leonotis species	Number of flowers per verticillaster	Number of cyme branches per verticill.	Number of flowers per cyme branch	Cyme branch length (mm)	Pedicel length (mm)	Verticill.
L. leonurus	(12-) 35-55 (-89)	-	-	-	(1.5) 2-4 (-5)	compact or loose
L. pauciflora	(15-) 28-45 (-60)	-	-	-	0.5-3.5	compact or loose
L. dubia	(9-) 18-47 (-58)	-	-	-	(4-) 5-8 (-11)	compact or loose
L. schinzii	(15-) 38-68	6-9 (-12)	up to 9	6-13	0.5-3 (-6)	compact
L. ocymifolia ssp. *transvaalensis*	20-110 (-150)	6-10	9-15	8-13 (-20)	1-2.5 (3.5)	compact
L. ocymifolia ssp. *ocymifolia*	(11-) 18-55 (-175)	6-12	7-16	2-12 (19)	1-2.5 (-4)	compact
L. randii	31-85 (-144)	13-15	6-12	5-27	(0.5) 1-3 (-6)	compact
L. intermedia	(22-) 40-125 (-185)	8-19	5-18	6-28	1-3 (-7)	compact
L. nepetifolia	(18-) 25-167 (-210)	9-18	8-21 (-28)	2-16	0.5-2	compact

Table 7. Inflorescence characters of *Leonotis*.
Abbreviation: verticill. =verticillaster

Leonotis species	Flowering stem length (mm)	Flowering stem internode length (mm)	Number of verticills. per flowering stem	Verticill. shape	Verticillaster diameter (mm)
L. leonurus	55-250 (-380)	(10-) 30-80 (-95)	5-8 (-11)	sub-spherical	20-37 (-40)
L. pauciflora	(105-) 230-530	(14-) 30-172	(1-) 2-5	sub-spherical	(29-) 31-45 (-52)
L. dubia	(160-) 210-1250 (-1900)	(25-) 30-70 (-200)	(1-) 3-9	turbinate	(25-) 30-50 (-54)
L. schinzii	(130-) 210-630 (-700)	(35-) 60-190 (-270)	1-3 (-5)	spherical	30-45 (-58)
L. ocymifolia ssp. *transvaalensis*	(32-) 45-170 (-380)	(27-) 74-140 (-255)	1-2 (-3)	spherical	(19-) 32-44 (-58)
L. ocymifolia ssp. *ocymifolia*	(30-) 70-240 (-460)	40-160 (-220)	1-2	spherical	(26-) 30-45 (-56)
L. randii	100-350 (-600)	65-220 (-250)	1-2 (-5)	spherical	(30-) 40-60 (-75)
L. intermedia	180-600	60-190 (-260)	1-3 (-5)	spherical	(25-) 30-50 (-63)
L. nepetifolia	(90-) 220-650 (-1500)	20-270	1-3 (-5)	spherical	(30-) 40-60 (-65)

herbivores. A strongly spinescent calyx is regarded as a synapomorphic condition in the genus. Further protection for developing nutlets is afforded by the compact nature of the inflorescence and the fibrous calyx base (Figure 15 d). In addition the coriaceous calyx tube probably deters robbers from piercing the perianth base for nectar.

The venation pattern described by El-Gazzar and Watson (1970) for *Leucas*, *Acrotome* and *Leonotis* indicates a synapomorphic character with the former two genera representing sister groups.

Three vicariant tropical African species, *L. pole-evansii* , *L. decadonta* and *L. goetzei* Gürke, have a similar calyx to *L. leonurus* but differ in that the calyx is densely hairy with comparatively long, soft, straight lobes. *L. decadonta* is closely allied to *L. leonurus* with its 10 subequal calyx lobes and ovate-lanceolate leaves. A tropical origin is hypothesised for *Leonotis.*

Conclusion

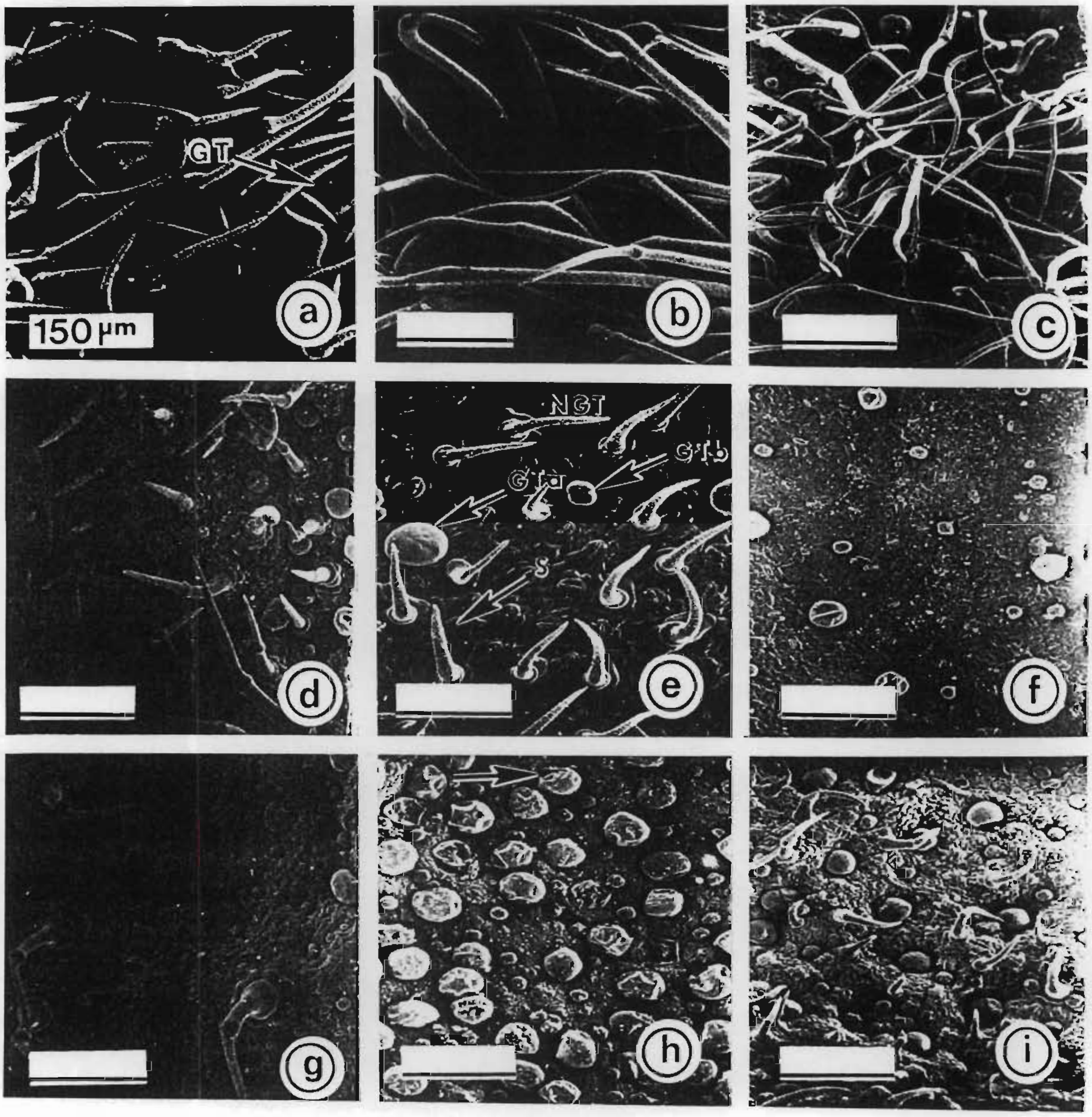
Calyx morphology is diagnostic for *L. leonurus* but of little taxonomic value for identifying the remaining southern African species. The similarity in calyx morphology between *L. leonurus* and certain tropical African species suggests a tropical origin for the genus.

Table 8. Corolla characters of *Leonotis*.
Abbreviations: O-R=orange to reddish, W=creamy white, P=peach, S=scarlet.

Leonotis species	Corolla character				
	Number of proximal trichome rings	Colour	Total length (mm)	Tube length (mm)	Throat diameter (mm)
L. leonurus	1-3 (diffuse)	O-R,W	(35-) 40-53 (-60)	(20-) 24-33 (-40)	(3.5-) 4-6
L. pauciflora	1 (distinct)	O-R,W	(26-) 32-42	(12-) 17-26	3-5
L. dubia	1 (distinct)	O-R	(16-) 26-32 (-39)	13-16 (-20)	2.5-4
L. schinzii	1 (distinct)	O-R,P	(24-) 32-39	(11-) 15-20	3-5
L. ocymifolia ssp. *ocymifolia*	1 (distinct)	O-R,W	(28-) 32-45 (-47)	(13-) 17-26	3-5
L. ocymifolia ssp. *transvaalensis*	1 (distinct)	O-R	25-36	(11-) 14-18(-20)	3-5
L. randii	1 (distinct)	O-R	34-44	14-26	3-5
L. intermedia	1 (distinct)	O-R,P,W	(25-) 32-44	(13-) 15-23	3-5
L. nepetifolia	2-3 (distinct)	O-R,S	19-32	9-18	(1.5-) 2-3.5 (-4)

Table 9. Corolla characters of *Leonotis*.

Leonotis species	Abaxial corolla lip				Adaxial corolla lip length (mm)
	Lobes	Lateral lobe (length x width) (mm)	Medial lobe (length x width) (mm)	Total length x width (mm)	
L. leonurus	separate	3-4.5 x 3-4	3.5-5 x 2.5-3.5	5-7.5 x 6.6-8.5	18-22
L. pauciflora	fused	1.5-2.5 x 3-3.8	2.5-3 x 2-4	6-9 x 6-8	12-22
L. dubia	fused	(1.3-) 2-2.5 x 2-3.5	2-3.5 x 2-4	8-10 x 5-7.5	15-21
L. schinzii	fused	1.5-3.5 x 2-3	2.5-4.5 x 2-3.5	6-9 x 6-7	12-18
L. ocymifolia ssp. *ocymifolia*	fused	1.5-3 x 2-3 (-4)	3-3.5 x 2.5-3.5	7-9 x 6-8	16-23
L. ocymifolia ssp. *transvaalensis*	fused	1.5-3 x 2-3	2-4 x 2.5-3.5	7-9.5 x 5-7	14-20
L. randii	fused	1.5-3.5 x 1.5-4	2.5-4 x 2-3	6-8.7 x 4-7 (-10.5)	14-24
L. intermedia	fused	1.5-2.5 x 2.5-3.5	(2-) 3-4 x 2.5-3.5	5.5-9 (-11) x 5-8.5	12-23
L. nepetifolia	fused	1.5-2 x 1.5-3	(1.5-) 2-3 x 1.5-2	3.5-6 x 3.5-6	11-18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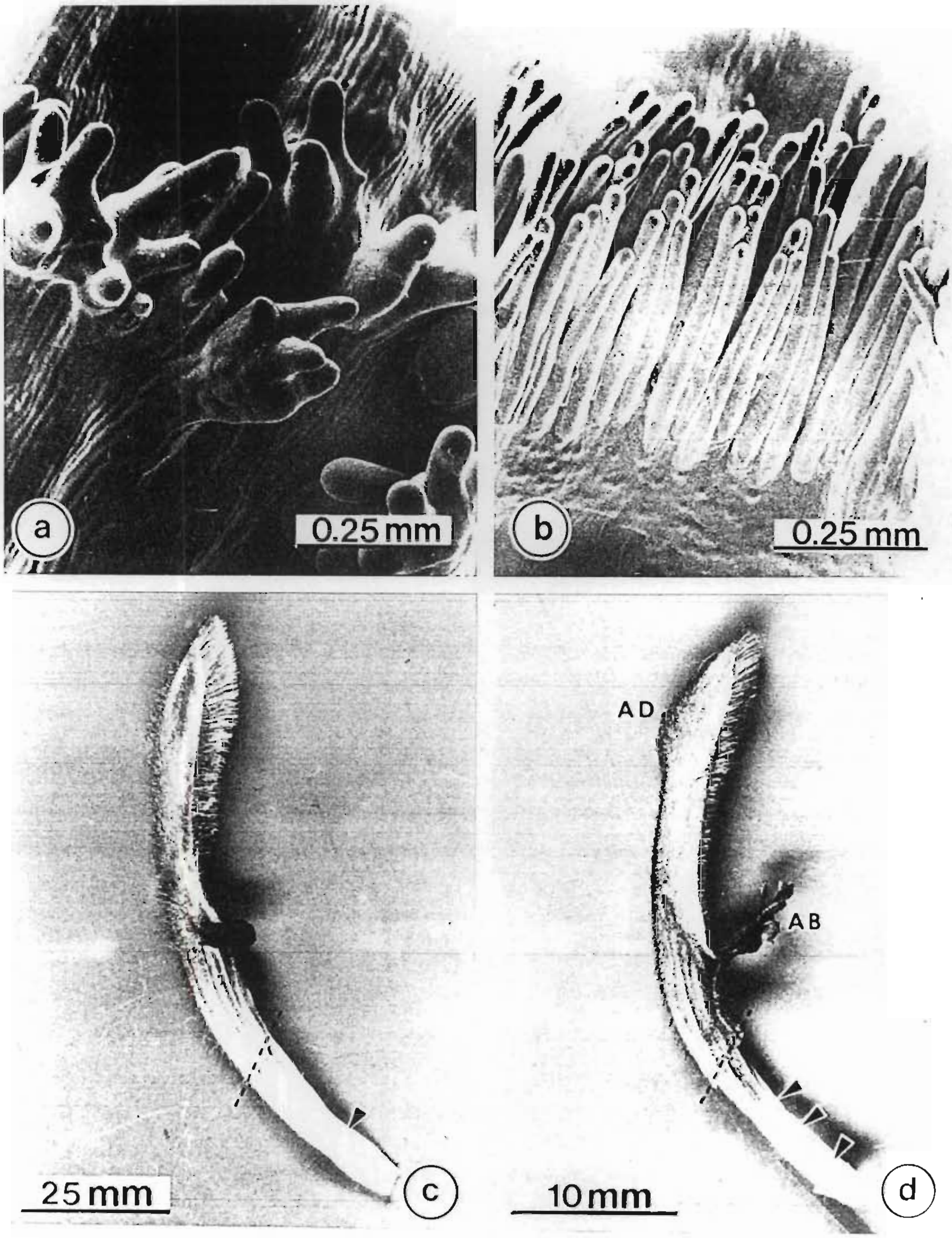

a
0.25 mm
b
0.25 mm
AD
AB
25 mm
c
10 mm
d

Figure 19. Non-glandular trichomes (a and b) from the inner, proximal part of the corolla tube of

(a) *Leonotis leonurus (Vos 292)* and

(b) *L. nepetifolia* (*Vos 174*).

The position of the trichome ring/s is indicated with arrows near the base of the corolla tube of

(c) *L. intermedia* (*Vos 539*) and

(d) *L. nepetifolia* (*Vos 174*).

The dashed line indicates where part of the corolla tube has been removed to reveal the trichome ring/s.

Abbreviations: AD=adaxial corolla lip. AB=abaxial corolla lip.

Chapter 6

Inflorescence and floral morphology

Introduction

Flowers provide a multitude of characters useful in the identification and classification of plants. These characters are fairly stable across environmental gradients and in most genera vary inter-specifically. The flora account of the Lamiaceae in southern Africa compiled by Codd (1985) is no exception in its emphasis of floral characters.

In the Scrophulariaceae and Lamiaceae the corolla and stamens are often the most diagnostic characters for taxonomic purposes (Stace, 1980). Long corollas distinguish *Scutellaria polyadena* Briq. (Paton, 1992a) and *Fuerstia adpressa* Paton (Paton, 1993). Tube length distinguishes certain species of *Syncolostemon* E. Mey. ex Benth. (Codd, 1976b). Long inflorescences distinguish *Thymus millefloris* Flores and Laencina (Rivera-Núñez *et al.*, 1987).

Corolla colour was emphasized by Baker (1900) in a key to *Leonotis* and Iwarsson (1985) used the number of proximal corolla partitions, fusion and posture of the abaxial corolla lobes in a key to *Leonotis* species.

Results

Inflorescence (Figures 16 and 17) and corolla morphology (Figure 18) are consistent for most *Leonotis* species.

Cyme branch reduction is evident in *L. dubia* and *L. leonurus* (Table 6). The flowering stems in both of the above species are condensed (Figure 16 A and B respectively) due to short internodes and unlike most species, display more than three verticillasters per stem (Table 7). Pedicels are exceptionally long in *L. dubia* (Table 6) and verticillasters are characteristically turbinate (Figure 17 C and D) and loose.

The number of proximal corolla partitions, corolla length, tube length, throat diameter (Table 8) and abaxial lip size (Table 9) are useful characters distinguishing the annual (*L. nepetifolia*) from the perennial species.

Amongst the perennial species, *L. leonurus* is readily distinguished by a long corolla and corolla tube (Table 8), the site of filament attachment (Figure 18 A) and separate abaxial lip lobes which have a characteristic posture at anthesis (Figure 18 D). Finger-like trichomes near the base of the corolla also distinguish *L. leonurus* (Figure 19 a). Except for the site of filament attachment in *L. leonurus*, no inter-specific differences are evident in the androecium or gynoecium.

Discussion

Inflorescence

The inflorescence of *Leonotis* is a verticillaster or dichasial cyme. Cyme branches radiate from opposite nodes in grooves of the flowering stem (Chapter 2, Figure 1 D). Flowers alternate along the cyme branch, the youngest flowers developing distally.

The cyme branches of *L. leonurus* and *L. dubia* are reduced (or obscure) (Table 6) and the flowers are clustered around the nodes. Except for *L. dubia*, cyme branch reduction is associated with a decrease in the diameter of the verticillaster (e.g. *L. leonurus*) (Table 7). Unlike most species which have short pedicels and compact verticillasters, *L. dubia* has exceptionally long pedicels and therefore characteristically loose verticillasters.

L. dubia has long flowering stems in contrast to *L. leonurus* where flowering stem length is reduced (Figure 16 A and B respectively and Table 7). Tall plants (*L. leonurus* and *L. ocymifolia* ssp. *transvaalensis*) display short flowering stems (up to 350 mm) and short plants (*L. intermedia, L. schinzii, L. randii, L. pauciflora*) display long flowering stems (up to 500 mm). This relates to pollination, the elevation of inflorescences in short plants, which frequent dense scrub or grassland (Chapter 13), may be an adaptation to increase pollinator attraction and therefore fruit set.

Most *Leonotis* species bear 1-3 verticillasters per flowering stem but *L. leonurus* and *L. dubia* display 3-8 (Table 7). Spherical verticillasters are common in the genus although in *L. dubia* turbinate verticillasters have developed (Figure 10 c and d).

Flowering stem internodes of *L. leonurus* and *L. dubia* are comparatively short (Table 7) and therefore the flowering stems of these two species appear condensed (Figure 16 A and B). The distal portion of the flowering stem of *L. nepetifolia* is often pendent (Figure 16 E). The inflorescence and flowering stem morphology of *L. leonurus* and *L. dubia* are considered symplesiomorphic.

Corolla

The corolla of *Leonotis* is zygomorphic, tubular, decurved and bilabiate. The adaxial corolla lip is formed by the fusion of two upper lobes whilst the abaxial lip is formed by the fusion of the remaining three lobes (Figure 18 A and B). The hooded upper lip protects the sexual organs from ultra-violet radiation, dew, rainfall and to some extent insect predation. The corolla tube which is decurved reduces evaporation of nectar and prevents dilution of nectar by precipitation.

The Lamiaceae have a common ancestral arrangement based on a pentamerous floral plan. Variations in this condition are based on the degree of fusion, enlargement, loss or reduction of perianth and androecial members. The corolla is the primary cue to pollinators. Most *Leonotis* species are pollinated by the same vector (Vos *et al.*, 1994) and therefore evolutionary pressures have caused conformity in perianth structure (i.e. shape, size and colour) rather than diversification. Corolla morphology is therefore of limited use in taxonomy. However *L. leonurus* and *L. nepetifolia*, display diagnostic floral morphologies.

The following characters distinguish the corolla of *L. leonurus*: total length and tube length (Table 8), a strongly dilated throat and separate abaxial lip lobes of equal length (Figure 18 A), a cucullate medial abaxial lobe and 1-3 proximal, diffuse rings of short, non-glandular "finger-like" trichomes (Figure 19 a). Trichome rings in the remaining species are more distinct and filiform (Figure 19 b). In addition, the corollas emerge from the verticillaster sub-vertically and randomly in *L. leonurus* but sub-horizontally and usually simultaneously in a ring in the remaining species.

Three vicariant tropical African species, *L. pole-evansii* Hutch., *L. decadonta* Gürke and *L. goetzei*, have similar corollas to *L. leonurus* with long tubes, dilated throats and similar abaxial lobe posture.

The presence of 2-3 distinct proximal trichome rings (Figure 19 d) and corolla reduction involving: length, tube length, abaxial lip and throat diameter (Table 8), distinguish the annual species (*L. nepetifolia*). Corolla reduction is also apparent in the perennial, *L. dubia*. Corolla morphology is related to pollination biology, the annual species are facultatively autogamous whilst the perennial species are facultatively xenogamous (Chapter 12).

The shape of the abaxial corolla lobes is reasonably consistent (Figure 19). Venation is slightly more extensive in the lower lip of *L. leonurus* (Figure 18 A) although this is variable.

Corolla senescence in *Leonotis* is observed as a change in colour and posture of the abaxial lip. In *L. leonurus* the abaxial lip withers and changes from cream to dull brown whereas in the remaining species it changes from tan to dark brown or black. The lateral corolla lobes of *L. leonurus* reflex at anthesis

(Figure 18 D_1) whilst the medial lobe is scalloped and remains extended for a short period before drooping (Figure 18 D_2). In the remaining species the lateral and medial lobes are flat to pendent at anthesis and soon wither, twist and often reflex immediately after anthesis (Figure 18 E and F). The prolonged extension of the medial lobe of *L. leonurus* is reminiscent of the abaxial corolla of many entomophilous taxa which provides a landing platform for pollinators.

At anthesis the medial abaxial corolla lobe of *L. leonurus* is scalloped (or cucullate) whereas in the remaining species it is flat or pendent.

Flower colour in *Leonotis* is not due to epidermal pigments as in most angiosperms but due to pigments in the carotene membranes of the trichomes which form a dense covering on the corolla tube (Vogel, 1954) which is a dull white colour. Corolla colour is reasonably uniform in *Leonotis* (Table 8) varying from peach, shades of orange, rusty orange to red or scarlet. "Red" flowers are typical of ornithophilous flowers (Jones and Little, 1983). Light yellow or cream to white corollas are rare, but observed in most species.

Gynoecium

The gynoecium of *Leonotis* is similar to that of most Lamiaceae and no intra-specific differences are evident.

The ovary is dimerous, but as the two carpels are divided by a false wall, four ovary lobes are formed, each containing a single ovule (Briquet, 1895-1897). The ovary is glabrous, ovoid and displays a truncate base. The nectariferous disc at the base of the ovary is abaxially enlarged.

The style is typically gynobasic. The four ovary lobes develop into four nutlets or fewer by abortion. The style is subulate, filiform, terete in transverse section and usually glabrous or occasionally bears the odd long non-glandular trichome. The proximal style branch is shorter.

Androecium

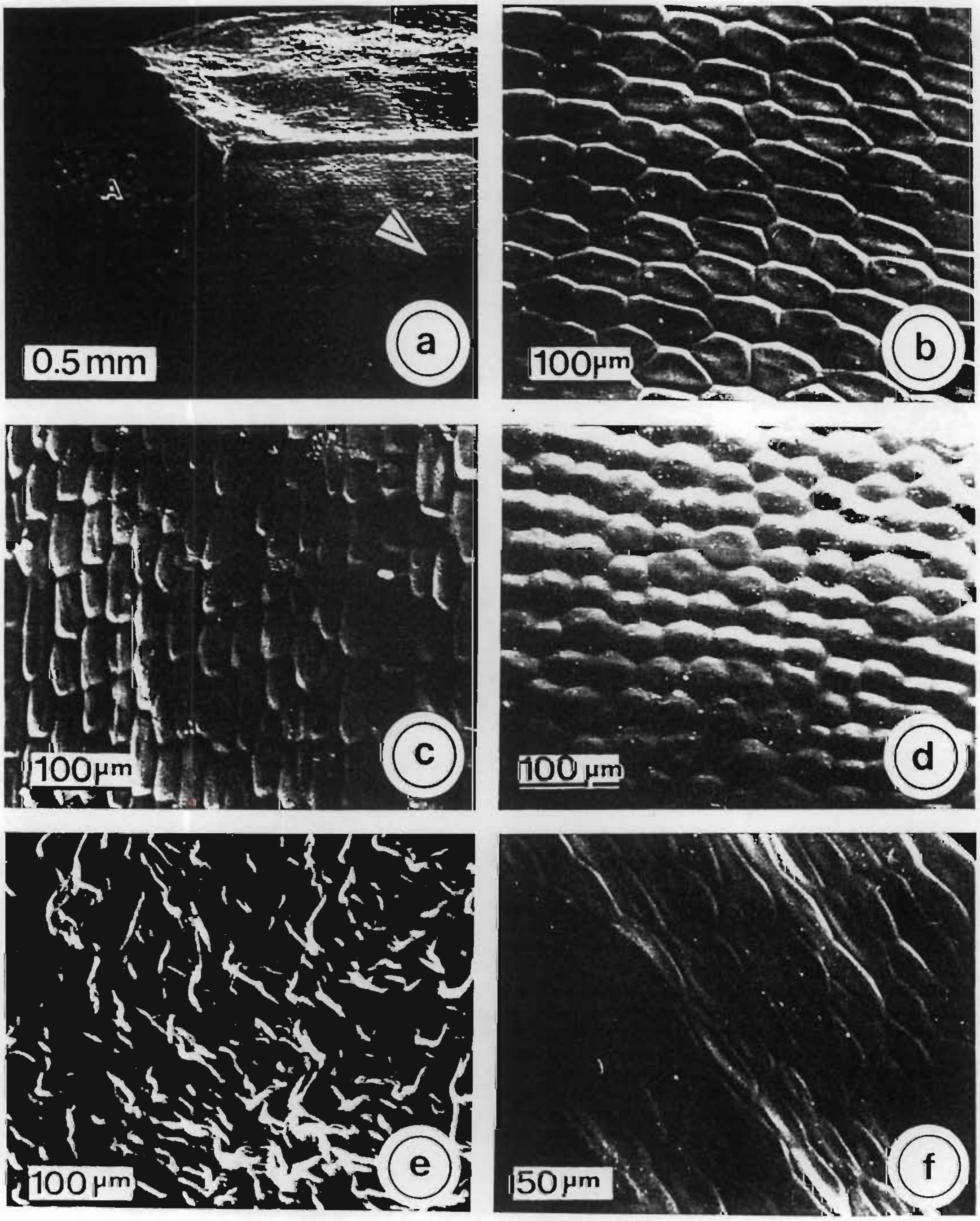
The stamens are didynamous and in most species inserted at the throat of the corolla tube, however the corolla of *L. leonurus* is distinguished by filament attachment below the corolla throat (Figure 18 A).

The stamens are included within the adaxial corolla lip, the abaxial pair being marginally longer. The filaments are glabrous or proximally connected by matted non-glandular trichomes. The 2-thecous anthers are 2-lobed, sub-confluent and divaricate and display sessile glands near the filament junction. No inter-specific differences were evident in androecial morphology.

Conclusion

Inflorescence, corolla, androecial and gynoecial morphology is conservative in *Leonotis* and consequently of limited use in classification.

However, the corollas of *L. leonurus* and *L. nepetifolia* are diagnostic. Floral reduction in the annual, *L. nepetifolia*, is considered a synapomorphic condition associated with a switch to autogamy. The flowering stem morphology of *L. leonurus* and *L. dubia* is diagnostic.


A
0.5 mm
a
100µm
b
100µm
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100 µm
e
50µm
f

Figure 20. Pericarp cell patterns of *Leonotis*.

(a) Distal half of a nutlet of *L. dubia* (*Galpin 5734*) showing the proximal lateral surfaces and glandular apex (A). The arrow indicates the positions where micrographs (b)-(f) were taken.

(b) *L. dubia* (*Vos 416)*,

(c) *L. mollissima* (*Chase 4667*),

(d) *L. nepetifolia* (*Thrash s.n.*),

(e) *L. schinzii* (*Schoenfeldon 498*) and

(f) *L. schinzii* (*Kolberg* and *Maggs 553*).

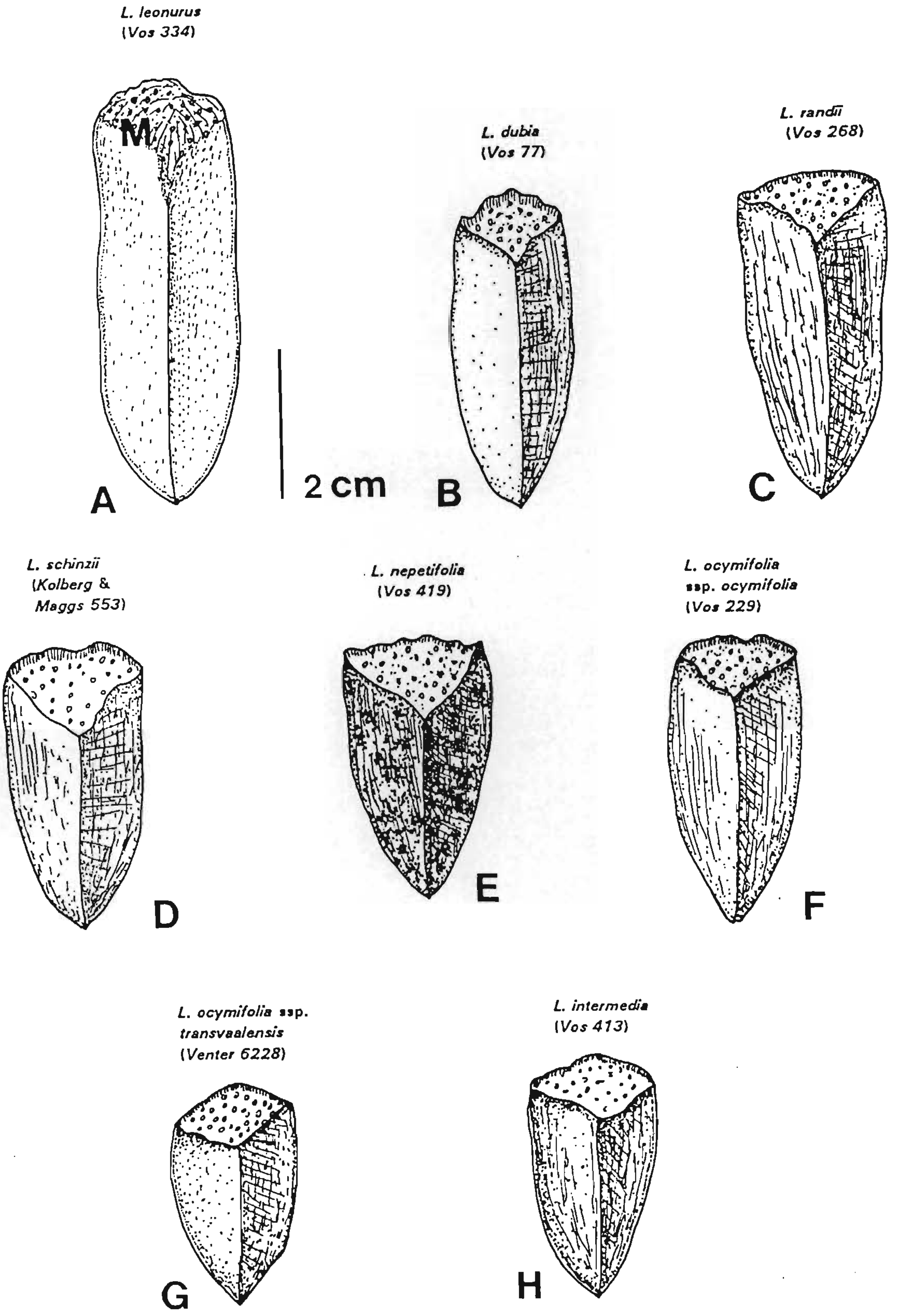

Figure 21. Morphology of *Leonotis* nutlets (inner facets). The letter M marks the inner margin of the glandular apex. Vouchers are indicated in parenthesis and cited in Chapter 15.

Table 10. Nutlet characters of *Leonotis*.
Dimensions represent the range, mean and standard deviation.
Abbreviation: s.d.=standard deviation.

Leonotis species	Nutlet dimensions (mm) and characters				
	Length (mean ± s.d.)	Width (mean ± s.d.)	Colour and texture	Shape	Exocarp cell pattern
L. leonurus	4.0-6.3 (5.2 ± 0.75)	1-2.3 (1.8 ± 0.28)	brown to blackish, glossy	oblong	flat, oblong-polygonal
L. randii	3.5-4.2 (3.7 ± 0.31)	1.4-1.8 (1.8 ± 0.37)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. ocymifolia ssp. *transvaalensis*	3-4 (3.6 ± 0.3)	1.5-2 (1.8 ± 0.20)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. dubia	3.2-4.1 (3.7 ± 0.32)	1.3-1.8 (1.4 ± 0.19)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. schinzii	2.9-3.2 (3.1 ± 0.61)	1.4-1.7 (1.5 ± 0.14)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. nepetifolia	3.1-3.8 (3.4 ± 0.23)	1-2 (1.4 ± 0.31)	brown, marmorate grey-cream, matt	obovate	domed, oblong-polygonal
L. ocymifolia ssp. *ocymifolia*	2.6-4.5 (3.2 ± 0.69)	1.3-2 (1.6 ± 0.19)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. pauciflora	2-4 (3 ± 0.42)	1.5-2 (1.3 ± 0.20)	brown to blackish, glossy	obovate	flat, oblong-polygonal
L. intermedia	2.8-3.8 (3.2 ± 0.38)	1.2-2.2 (1.7 ± 0.30)	brown to blackish, glossy	obovate	flat, oblong-polygonal

Chapter 7

Fruit morphology

Introduction

Since the advent of scanning electron microscopy many micromorphological characters which provide valuable taxonomic information have been revealed (Stace, 1980).

In a scanning electron microscope survey of epidermal and seed surface characters of approximately 5000 species Barthlott (1981) found the cell boundaries were of taxonomic significance and often distinguished species. Wojciechowska (1966) constructed a key to *Salvia* (Lamiaceae) based on fruit and seed characters and Hedge (1970) comments that the most morphologically distinct species of *Salvia* have the most distinctive pericarp patterns. Chuang and Heckard (1972) found that seed micromorphology is diagnostic for different species of *Cordylanthus* (Scrophulariaceae) and therefore useful in formulating taxonomic and phylogenetic lines. On the contrary, Canne (1979) found that although many *Agalinis* (Scrophulariaceae) species have characteristic seed patterns, infraspecific taxa cannot be differentiated on the basis of seed features alone.

Other seed characters which have proven taxonomically useful at the generic and species level include colour (Pennell, 1935), shape (Seavey *et al.*, 1977) and size.

Seed characteristics are of great potential taxonomic value as they tend to be relatively stable in external morphology in plants growing in different environments (Davis and Heywood, 1963). Surprisingly few systematic treatments emphasize seed structure (Stebbins, 1974) and the Lamiaceae are no exception.

Results

Surface cell patterns of *Leonotis* are presented (Figure 20). Nutlet morphology is summarised in Figure 21 and Table 10.

Discussion

Iwarsson (1985) described the nutlets of *Leonotis* as oblong, 3-angled in transverse section and distally truncate. In most *Leonotis* species nutlets are obovate (Figure 21 A-H) but in *L. leonurus* they are oblong (Figure 21 A).

The distal nutlet surface is covered in globose, glandular trichomes (Figure 20 a) and is truncate or irregularly rounded (Figure 21 A-H). In *L. leonurus* the two inner nutlet margins of the glandular apex are not well defined and merge with the inner surfaces (Figure 21 A).

Nutlet size and colour is similar in most species (Table 10). *L. leonurus* has relatively long nutlets. Although marmorate nutlets are typical of *L. nepetifolia* they are an unreliable character as nutlets may be uniformly brown. Marmorate nutlets were observed in other species. The lighter grey-cream patches on the nutlet surface are caused by air trapped under the pericarp.

Pericarp cell patterns are not consistent within species and, vary from oblong (Figure 20 c and f) to polygonal patterns (Figure 20 b and d). Polygonal patterns are either hexagonal or pentagonal. Occasionally the pericarp of *L. schinzii* is pitted and finely striate (Figure 20 e) although an oblong-polygonal pattern was common. In most species the outer cell walls are flat (Figure 20 b) but in *L. nepetifolia* they are diagnostically domed (Figure 20 d). The pericarp is usually ridged (Figure 20 f) and bumpy although occasionally it is smooth and cell patterns are obscure.

Conclusion

Nutlet colour is unreliable for distinguishing *Leonotis* species. Nutlet size, shape and apex morphology are similar in most species except for *L. leonurus* which has large, oblong nutlets with faint inner distal margins.

Except for *L. nepetifolia* which has a characteristic pericarp cell pattern, cellular patterns vary intra-specifically and are of limited taxonomic value.

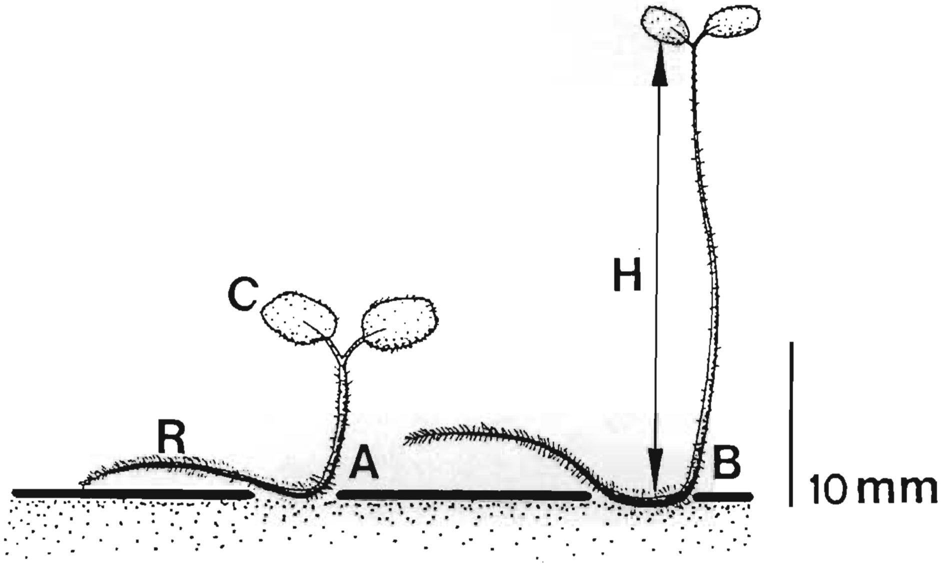

Figure 22. Seedling morphology of (A) the perennial *L. leonurus* (*Vos 78*) and (B) the annual *L. nepetifolia* (*Vos 174*).
Abbreviations: H=hypocotyl, R=radicle, C=cotyledon.

Table 11. Mean hypocotyl length (± standard deviation) and cotyledon shape of *Leonotis* seedlings.

Leonotis species	Hypocotyl length (mm)	Cotyledon shape
L. leonurus	8 ± 2.6	oblong to orbicular
L. intermedia	12 ± 3.6	oblong to orbicular
L. dubia	12.5 ± 4.3	oblong to orbicular
L. ocymifolia ssp. *transvaalensis*	13.7 ± 2.2	oblong to orbicular
L. nepetifolia	29.57 ± 5.0	oblong to orbicular

Chapter 8

Seedling morphology

Introduction

The "macaranga type" seedling is most common in herbaceous dicotyledons and almost exclusive to the more advanced orders of the Asterales, Campanulales and Lamiales (Vogel, 1980).

Seedling morphology may be diagnostic from the family to species level (Vogel, 1980). Seventeen species of *Dracocephalum* Labill. (Lamiaceae) differed at an early stage of their development in one or several characters (Alekseeva, 1990). However, Vogel (1980) concluded that the importance of seedling morphology for taxonomic purposes is variable, depending on the group under consideration.

Cotyledon shape, along with many other characters, supports Erdtman's (1945) division of the Lamiaceae into two sub-families. In the Lamioideae, seedlings display cotyledons which are longer than wide or at most equally wide as long; in the Nepetoideae cotyledons are wider than long (Cantino and Sanders, 1986).

Results

Seedling morphology is reasonably consistent in *Leonotis*. The annual species (*L. nepetifolia*) displays a significantly longer hypocotyl than the perennial species (Figure 22 and Table 11).

Discussion

Seedlings are of the "macaranga type" and germination, which is epigeal, occurs between three and nine days. By day 10 the hypocotyl has attained a length of approximately 10 mm in perennial and 30 mm in the annual species (Table 11). Moisture softens the testa and the radicle emerges from the base of the nutlet, densely vested in silky white non-glandular trichomes. The hypocotyl is initially looped and the testa persists until the cotyledons have matured and expanded.

Cotyledons are oblong to orbicular, sparsely pubescent, entire and usually apically notched (Figure 22). Cotyledon shape is consistent with that reported for other seedlings in the sub-family Lamioideae to which *Leonotis* belongs and venation is inconspicuous. Glandular trichomes develop on both surfaces of the cotyledon approximately six days after germination. The homogenous nature of *Leonotis* seedlings supports the idea that this genus is a natural grouping of monophyletic origin.

L. nepetifolia grows in disturbed sites where conditions are harsh and resources often limited. Fast growth or rapid hypocotyl elongation would be competitively advantageous in such an environment enabling better seedling establishment and therefore survival. The rapid seedling growth and long hypocotyls of *L. nepetifolia* are a derived condition and support the idea that this species is a typical "r-strategist" (Pianka, 1970).

Conclusion

Apart from the hypocotyl length, which distinguishes the annual from the perennial species, seedling morphology is uniform and of no taxonomic value.

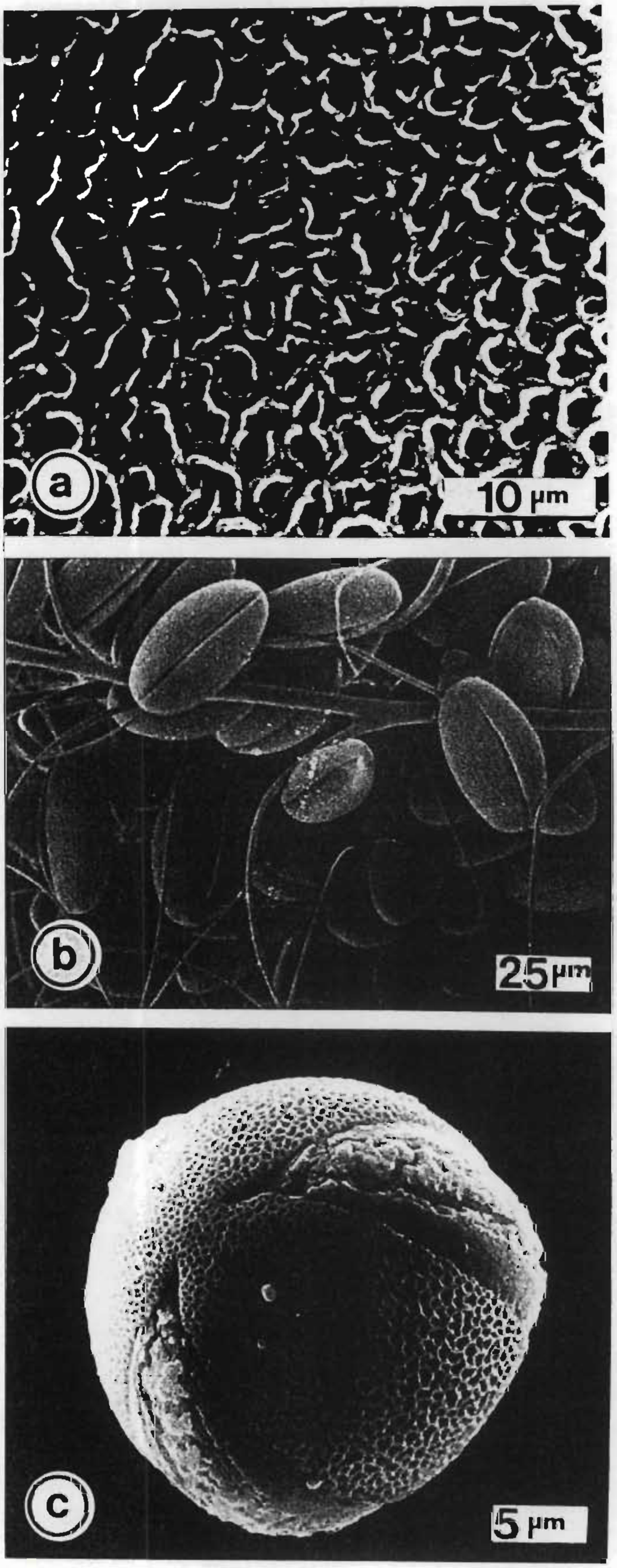
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Figure 23. *Leonotis* pollen.

(a) A detailed view of the exine of *L. dubia* (*Vos 58*),

(b) pollen of *L. intermedia* amongst the setae of a hymenopteran pollinator (*Vos 59)* and

(c) semi-polar view of *L. dubia* (*Vos 418*).

Chapter 9

Palynogy

Introduction

Pollen data is valuable at all taxonomic levels (Erdtman, 1969) although pollen grains do not usually differ within genera (Jones and Luchsinger, 1986) e.g. *Salvia* (Henderson *et al.*, 1968). Except for pollen size, the pollen of five *Mentha* L. species studied by Polić (1989) was found to be similar. However, Bokhari and Hedge (1971) found differences in the pollen of four lamiaceous genera. Suárez-Cervera and Seoane-Camba (1986) found that the sporoderm of *Lavandula dentata* L. differed from two other *Lavandula* L. species studied.

The Lamiaceae are stenopalynous and palynology indicates a close alliance to the Verbenaceae (El-Gazzar and Watson, 1970). Bentham's (1876) classification of the Lamiaceae which excluded pollen data is highly congruent with Erdtman's (1945) sub-familial system based on pollen data. According to Erdtman (1945) the Lamiaceae comprises two natural sub-families which differ in pollen morphology. The Lamioideae, to which *Leonotis* belongs, has tri-colpate pollen that is shed at the 2-nucleate stage whilst the Nepetoideae have hexa-colpate pollen that is shed at the 3-nucleate stage. This relationship holds true for 95% of the genera in the Lamiaceae (Cantino and Sanders, 1986) and throws doubt on the widely used classification of Briquet (1895-1897).

Tri-colpate pollen is common in the Lamiaceae and characteristic of advanced dicotyledons (Jones and Luchsinger, 1986) and exine sculpturing is diverse (Figures 1-6 in: Cantino and Sanders, 1986).

The cladistic analysis of Cantino and Sanders (1986) and the phenetic-numerical analysis of El-Gazzar and Watson (1970) support Erdtman's sub-families as the primary phenetic sub-groups of the Lamiaceae but question the idea of a monophyletic origin. The Lamiaceae are thought to have arisen from the Verbenaceae (Cantino and Sanders, 1986). The best evidence for monophyly is the occurrence of synapomorphies (i.e. shared derived characters), the clearest of which is the hexa-colpate pollen of the sub-family Nepetoideae (Lamiaceae).

Results

Pollen is reticulate (Figure 23 a), elliptic in equatorial view, radiosymmetrical, isopolar and tricolpate (Figure 23 b). Pollen grains are medium-sized (± 40 x 20 μm), orange or yellow and colpi are elliptic and verrucose (Figure 23 c). No inter-specific differences in pollen are evident.

Discussion and conclusion

Many species of Lamiaceae and Verbenaceae display tricolpate pollen with a reticulate exine, including the closely allied genus *Leucas*, with the result that pollen data is seldom of any taxonomic or phylogenetic value at the species level. Cantino and Sanders (1986) report bi-nucleate and tri-colpate pollen for *Leonotis* and *Leucas* which supports their position within the sub-family Lamioideae.

Pollen is predominantly elliptic, spherical grains are occasionally observed. According to the pollen size classes of Erdtman (1945), *Leonotis* pollen is medium-sized. *Leonotis* pollen is stenopalynous and therefore of no taxonomic value.

Chapter 10

Karyology

Introduction

Chromosome studies are valuable guides to taxonomic and evolutionary relationships (Radford *et al.*, 1974) for determining the possible origin of groups and for resolving problems of hybridization and lineages in phylogenetic studies (Radford, 1986).

Chromosome numbers have proved of particular value in various genera of the Lamiaceae, for example *Mentha* (Harley and Brighton, 1977) and *Sideritis* sect. *Empedoclea* (Rafin.) Benth. (Marseille, 1978). However, in a study of 63 of the 103 known lamiaceous taxa from West Africa, Morton (1962) commented that karyological data is of little taxonomic value, except in providing support for existing classifications. Similarly, in an extensive taxonomic study of the Lamiaceae and related genera, El-Gazzar and Watson (1970) commented that chromosome counts were not always in agreement with the accepted classifications.

Polyploidy is common in the Lamiaceae (Morton, 1962). Base numbers are commonly in multiples of seven, eight and 10 (El-Gazzar and Watson, 1970). There are 20 lamiaceous genera in which chromosome counts are consistent for at least two species and 21 genera in which they are inconsistent (El-Gazzar and Watson, 1970). The following diploid chromosome numbers have been recorded: 2n=28 for *L. nepetifolia* (Morton, 1962) and 2n=24 for *L. africana* Briq. (Miége, 1962). Three species of *Leucas*, a genus which closely resembles *Leonotis*, also display a diploid chromosome number of 2n=28 (Morton, 1962) further supporting the close relationship between these genera.

Results and discussion

The cymose, densely flowered verticillasters of *Leonotis* are well suited to meiotic chromosome studies as there is always sufficient pollen available at different developmental stages. However, chromosome preparations were unsuccessful for the three species studied (*L. leonurus, L. intermedia* and *L. nepetifolia*).

At the infra-generic level, chromosome numbers confirm the distinction between the annual species (*L. nepetifolia*) with a base number of seven and the perennial species (*L. africana* Briq.) with a base number of six Morton (1962) recorded a similar difference between annual and perennial *Ocimum.* (Lamiaceae) species.

Hybridization may explain the close resemblance of certain taxa, especially when one considers **the lack** of plant-pollinator specificity (Chapter 12) and the vagile nature of the sunbird pollinators. Karyological data has been used to confirm hybrids within the Lamiaceae (Morton, 1962; Harley and Brighton, 1977). This field of research warrants further investigation.

Chapter 11

Chemosystematics of essential oils

Introduction

The Lamiaceae are well known for their aromatic properties and many members are of great commercial value in the culinary and pharmaceutical industries. These aromatic properties are due to volatile essential oils or terpenoids released from glandular trichomes (Werker *et al.*, 1985).

Essential oil (EO) consists primarily of terpenes (± 90%) and phenylpropane derivatives (Wagner *et al.*, 1984). By the first century AD, Dioscorides had consolidated the aromatic mints as a single taxon (Jones and Luchsinger, 1986). Scientists during the "classical period" of taxonomy used plant odours to distinguish between closely related plants rich in scent (or volatiles) such as members of the Lamiaceae (Harborne and Turner, 1984).

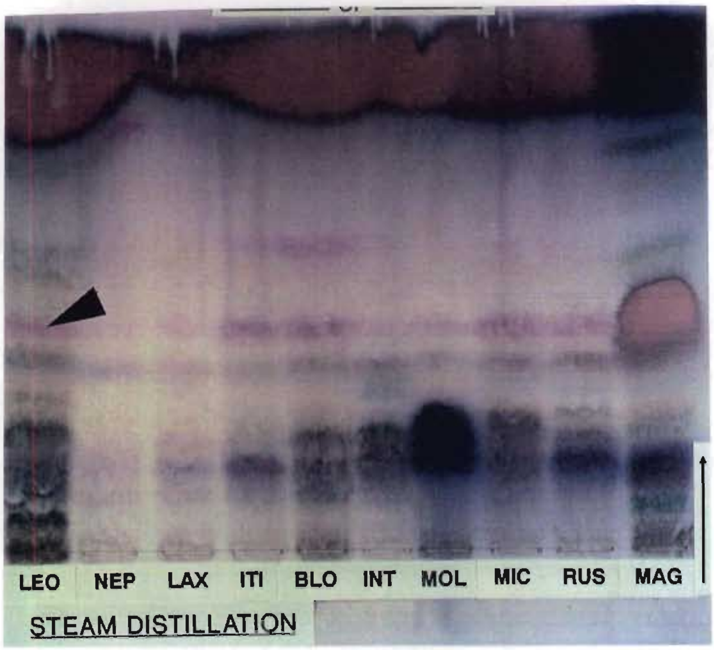
Plant chemosystematics is the application of chemical data to systematic problems and is concerned with using chemical constituents as additional characters for explaining relationships between plants and inferring phylogeny (Jones and Luchsinger, 1986). Often the distribution of plant compounds and their biosynthetic pathways correspond well with existing taxonomic arrangements based on morphological features. In other instances, chemical data contradicts existing evidence, necessitating a re-evaluation of the classification, or provides decisive information where other forms of data were inconclusive.

Scora (1967) points out that the value of terpenes lies in their consistent occurrence, their ease of processing and their yield of qualitative as well as quantitative information. Terpenoids have been used extensively in the chemosystematics of the Lamiaceae, Apiaceae, Myrtaceae, Rutaceae, Poaceae and gymnosperms. Harborne and Turner (1984) report that gas-chromatographic examination of most extracted plant parts, even relatively non-aromatic foliage such as that of *Baptisia* Ventenat (Leguminosae), yields an array of volatile compounds which are highly species-specific.

Mirov's (1965) use of volatile oils in the classification of *Pinus* (Pinaceae) included approximately 100 species which, in many instances, had diagnostic terpene profiles. Mirov's (*l.c.*) knowledge of EOs added immeasurably to the understanding of the geography and evolution of the genus. Weyerstahl (1983) found inter-specific differences in the volatile EOs of *Plectranthus*. Harley and Bell (1967) studied species of *Mentha* (Lamiaceae) using gas-chromatography (GC) and likened a chromatographic trace to a fingerprint. Many genera belonging to the Lamiaceae have been analysed for EOs using GC, namely: *Mentha*, *Salvia*, *Monarda* L., *Thymus*, *Plectranthus*, *Tetradenia* C.G.D. Nees and *Syncolostemon* (Emboden and Lewis, 1967; Harley and Bell, 1967; Scora, 1967; Granger and Passet, 1973; Harborne and Turner, 1984; Davies-Coleman and Rivett, 1987; Davies-Coleman *et al.* 1987 respectively). In most of the above genera quantitative and or qualitative EO data is diagnostic at the specific level. GC retention times are merely a tentative form of identification (Fehr, 1982). A combination of gas chromatography and mass spectrometry (GC-MS) is the only definitive analytical technique for positive identification (Harborne and Turner, 1984).

Harley and Bell (*l.c.*) were able to obtain a weak EO profile from a leaf of *Mentha* taken from a Linnaeus collection made in 1810. Thus, the technique provides a powerful and convenient tool in classification. The technique is particularly valuable where typification is involved and where material cannot be identified by more orthodox means.

Many studies are now available to suggest that most chemical constituents, including their qualitative and quantitative expression, are under rigorous genetic control (Hanover, 1966; Payne *et al.*, 1972; Flake and Turner, 1973). Murray (in: Smith, 1976) recorded the genetic basis for variations in the EO of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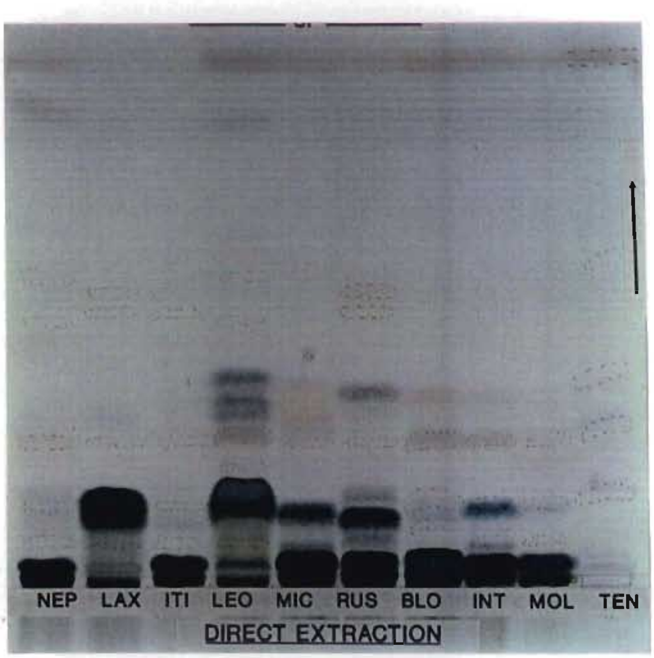
STEAM DISTILLATION

a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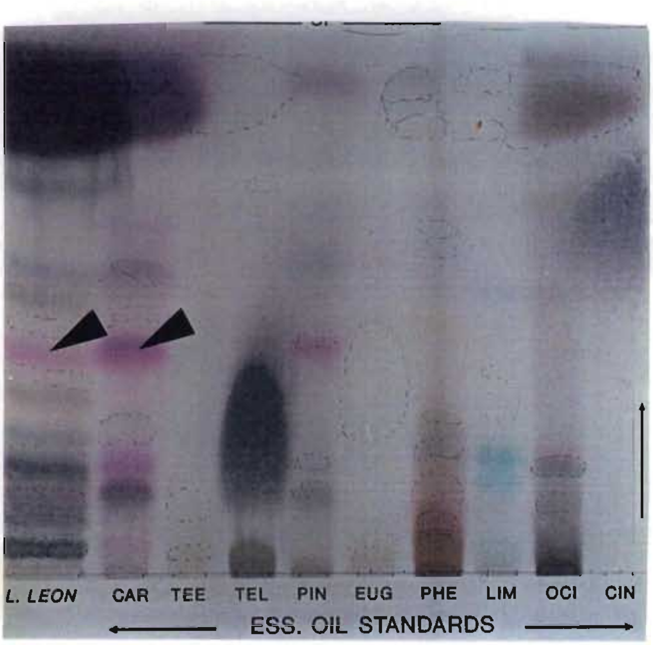
b


L. LEON
CAR
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OCI
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ESS. OIL STANDARDS

c

Figure 24. Thin-layer chromatography plates of essential oils in *Leonotis* comparing
(a) steam distillation with
(b) direct extraction methods.
(c) Essential oil standards and *L. leonurus* (left side).
Vertical arrows indicate the direction of the compound movement and arrow heads indicate the position of caryophyllene. The solvent front is marked at the top of the photographs with a horizontal line.
Abbreviations: LEO and LEON=*L. leonurus*, INT=*L. intermedia*, MIC=*L. randii*, MOL=*L. schinzii*, BLO and RUS=*L. ocymifolia* ssp. *transvaalensis*, ITI=*L. ocymifolia* ssp. *ocymifolia*, NEP=*L. nepetifolia*, LAX=*L. dubia*, TEN=volatile oil extract from *L. leonurus*.
Abbreviations for essential oil standards: CAR=caryophyllene, TEE=α-terpinene, TEL=terpineol, PIN=pinene, EUG=eugenol, PHE=α-phellandrene, LIM=limonene, OCI=ocimene, CIN=1,8 cineole.

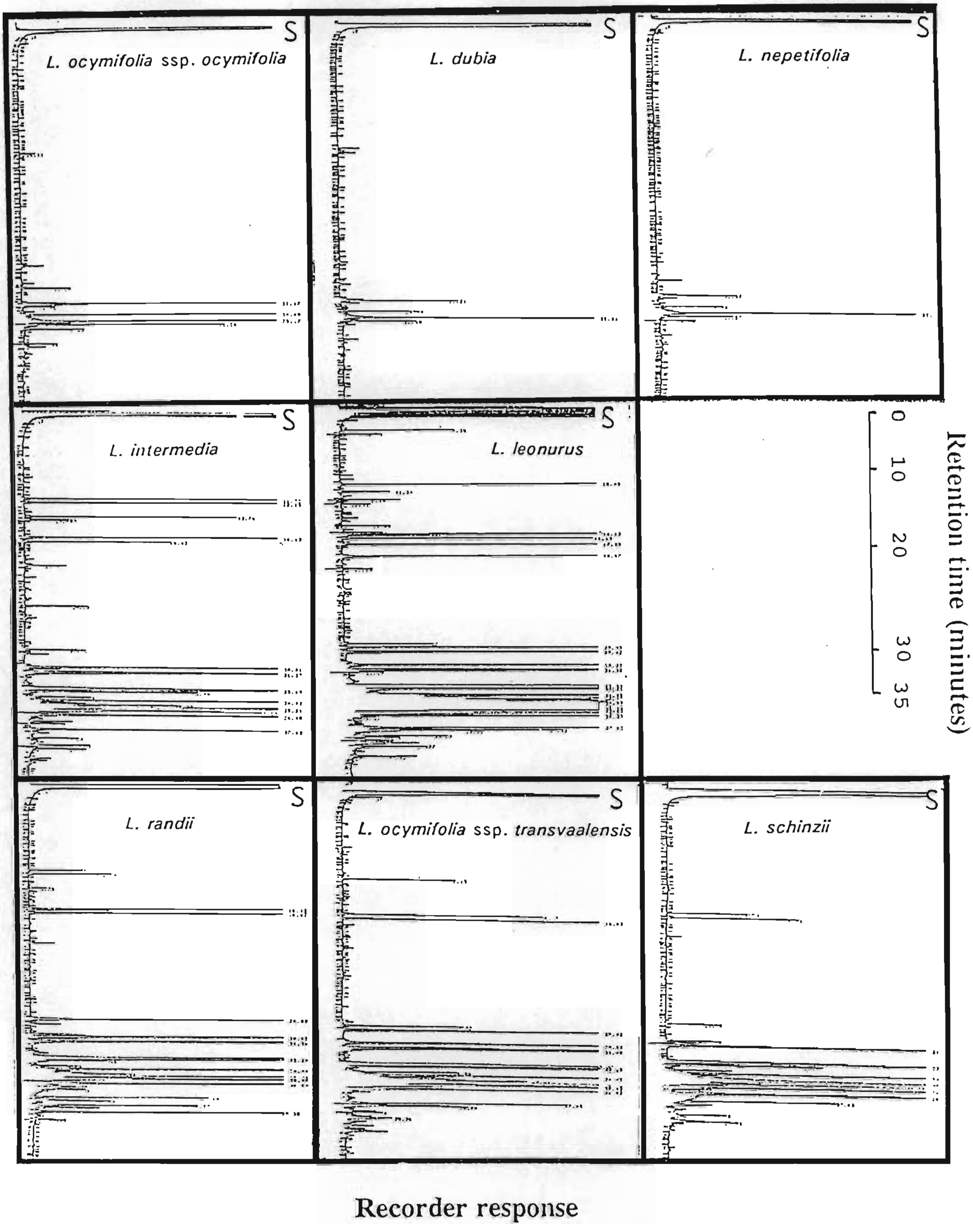


Figure 25. Gas chromatograms of essential oils in *Leonotis*. Abbreviations: S=solvent front.

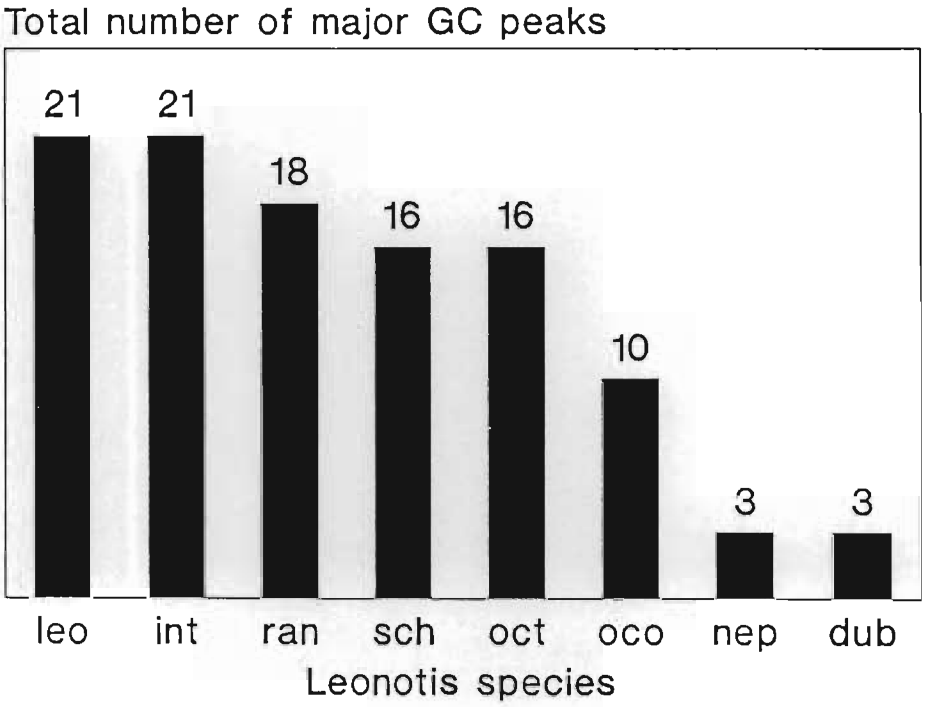


Figure 26. Total number of main GC peaks in different species of *Leonotis*. Abbreviations: leo=*L. leonurus*, int=*L. intermedia*, ran=*L. randii*, sch=*L. schinzii*, oct=*L. ocymifolia* ssp. *transvaalensis*, oco=*L. ocymifolia* ssp. *ocymifolia*, nep=*L. nepetifolia*, dub=*L. dubia*.

Mentha (Lamiaceae). Emboden and Lewis (1967) studied *Salvia* (Lamiaceae) and could identify hybrids by their "intermediate" terpenoid profiles. Van der Walt and Demarne (1988) were able to identify hybrids of *Pelargonium* L' Hérit. (Geraniaceae) by their "intermediate" EO composition. Hanover and Wilkinson (1969) created an interspecific hybrid between two species of *Picea* Dietrich (Pinaceae) by artificial pollination and found the morphology of the hybrid and its monoterpene composition to be "intermediate" between the parents. Zavarin *et al.* (1969) report that terpenoid composition in natural populations will be helpful in evaluating the evolutionary consequences of hybridization between species.

Granger and Passet (1973) record 26 chemotypes for *Thymus vulgaris* (Lamiaceae) and four for *Mentha arvensis* L. (Lamiaceae). Distinct chemical taxa within species are almost universal and may account for the wide geographical variations that have been reported. Granger and Passet (1973) comment that genetic and ecological factors, especially climate, determine the frequency of chemotypes among populations. Other factors involved in causing variations in EO are the stage of growth and position of leaf on the plant (Emboden and Lewis, 1967; Charlwood and Banthorpe, 1978); plant provenance (Bannister *et al.*, 1962; Hanover, 1966; Rhyu, 1979; Pitarevic *et al.*, 1984) and inter- and intra-populational variation (Emboden and Lewis, 1967; Harborne and Turner, 1984; Pitarevic *et al.*, 1984; Senalik and Simon, 1987).

Many studies have used EO data to support phylogenic relationships including the following: *Picea* (Pinaceae), *Monarda* (Lamiaceae), *Khaya* A.H.L. Jussieu (Meliaceae) and *Abies* P. Miller (Pinaceae) (Von Rudloff, 1966; Scora, 1967; Adesida *et al.*, 1971; Zavarin *et al.* 1977 respectively). However, morphological and chemical attributes may show different paths of evolution (Scora, 1967). Similar chemical compounds may be synthesized via different metabolic pathways (Harborne and Turner, 1984) and do not represent phylogenic similarity.

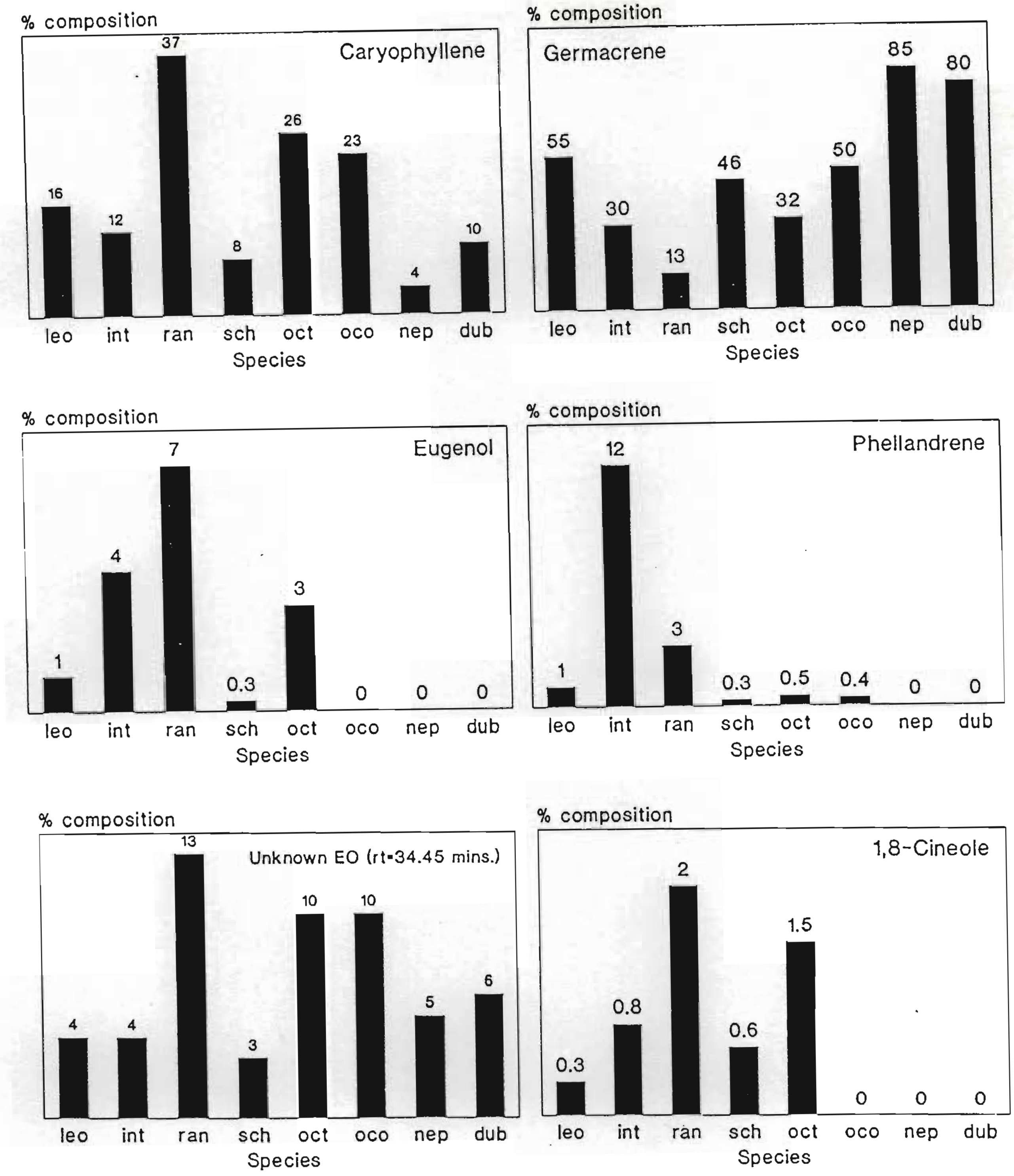


Figure 27. Percentage composition of selected essential oils in different species of *Leonotis*.
Abbreviations: leo=*L. leonurus*, int=*L. intermedia*, ran=*L. randii*, sch=*L. schinzii*, oct=*L. ocymifolia* ssp. *transvaalensis*, oco=*L. ocymifolia* ssp. *ocymifolia*, nep=*L. nepetifolia*, dub=*L. dubia*, EO=essential oil, rt=retention time.

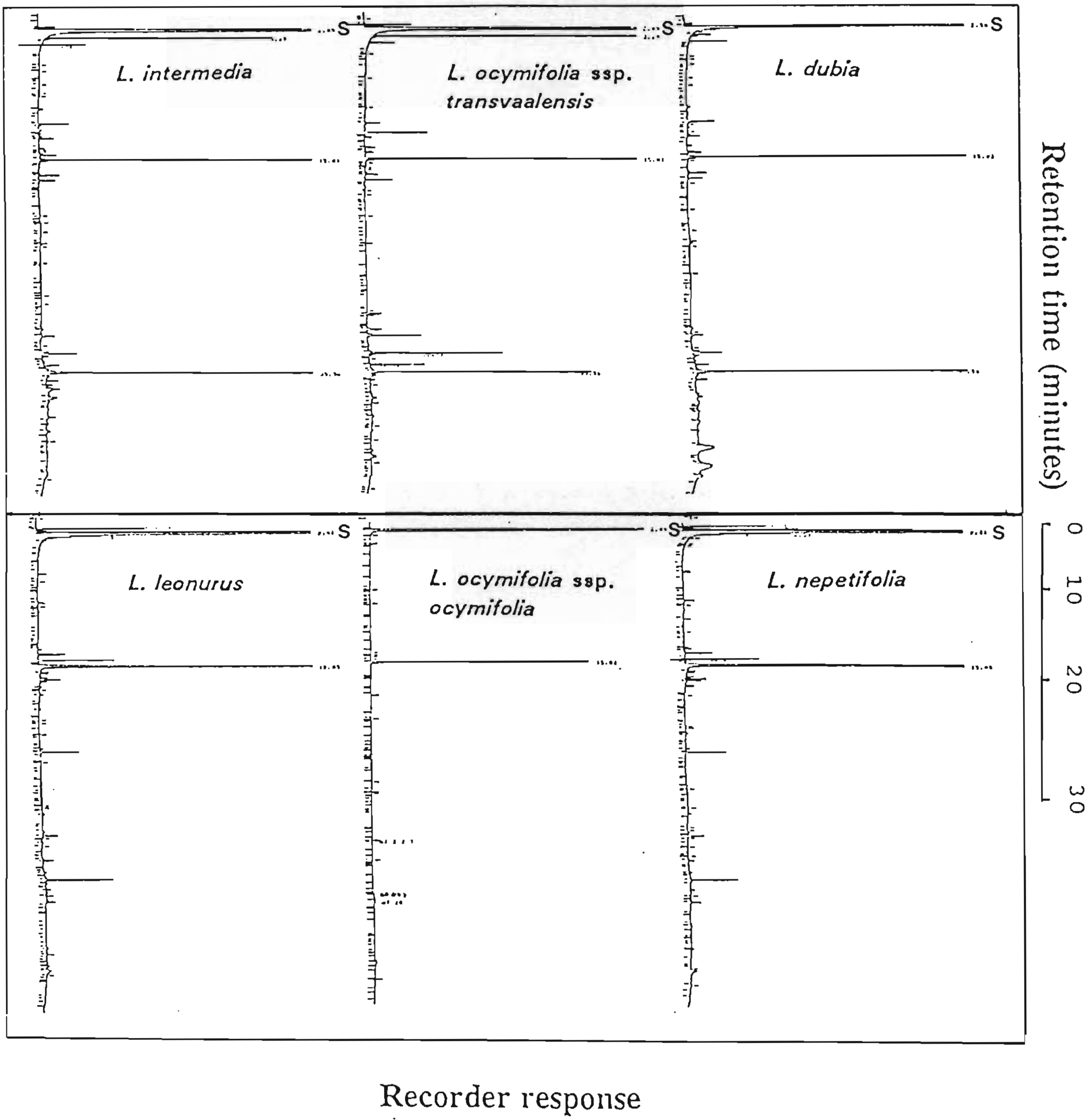


Figure 28. Gas chromatograms of volatile essential oils in *Leonotis* trapped with Tenax.
Abbreviations: S=solvent front.

Table 12. Data matrix showing the percentage area occupied by peaks of the various retention times in minutes of essential oils in fresh (1991) and preserved (1915-1971) specimens of *Leonotis leonurus*.
A dash (-) indicates the absence of a peak on the chromatogram.

Retention Peak	Area percentage			
	Voucher and year of collection			
	Vos, 300 1991	*Rennie, 4* 1971	*Moll, 2274* 1965	*Paterson, 3304* 1915
2.15	0.23	-	-	-
2.89	1.39	2.80	0.80	0.32
3.45	2.45	3.89	1.49	3.41
4.63	4.56	7.20	12.00	8.04
5.03	2.95	1.30	6.40	-
6.60	5.90	5.30	13.30	21.18
8.07	0.56	-	-	-
9.02	1.55	0.42	1.03	0.54
10.48	61.99	64.80	38.36	55.23
12.53	2.13	7.80	5.20	4.60
15.42	0.48	0.30	-	-
17.91	0.39	-	-	-
20.14	1.09	1.50	-	-
21.07	0.67	0.02	-	-
24.82	1.07	0.80	-	-
27.82	1.24	3.20	4.55	-
32.39	0.35	-	-	-
35.91	1.45	3.20	2.30	-
37.40	2.30	3.54	4.20	2.10
42.15	3.57	2.40	8.96	4.60

From a taxonomic perspective, EO studies have potential in defining species, detecting hybridization in natural populations, confirming the presence of geographical races or chemotypes and in inferring phylogeny. Before EO data can be used as a reliable taxonomic tool, one must assess intra-specific variation within and between populations, geographically, ontogenetically, seasonally, between cultivated and wild plants, and between stored and fresh extracts. Secondly, EO constituents must be identified.

The primary aim of studying the EOs of *Leonotis* is to assess their use in defining species boundaries. If EO data proves valuable it may be used to elucidate phylogenetic relationships.

Results

Essential oil extraction

Steam distillation (Figure 24 a) proved more successful than direct solvent extraction (Figure 24 b) as the latter led to erratic banding patterns on TLC plates, probably due to the simultaneous extraction of leaf phenolics and chlorophylls. Oven-dried versus wet (or fresh) leaf extraction in diethyl-ether had no effect on composition of EOs.

Thin-layer chromatography

Thin-layer chromatography revealed some of the diversity in EOs of *Leonotis*. Bands of the same colour and position on the TLC plate (eg. caryophyllene highlighted with an arrow head in Figure 24 a and c) indicate compounds that are shared between species. Qualitative differences are also apparent upon the TLC plate, however, GC and GC-MS were the preferred methods for revealing qualitative differences in EOs between species.

Gas chromatography

Essential oil composition shows limited variation within and between populations of the same species, in fresh and stored (up to one year) extracts, between flowering and non-flowering foliage, between field and cultivated

Table 13. A comparison of selected essential oils of *Leonotis leonurus* in two independent studies.
References are cited in the bibliography.

Essential oil	Rivett, 1992 % composition	This study, 1993 % composition
germacrene	45.00	55.00
caryophyllene	20.00	16.00
pinene	4.00	0.05
1,8-cineole	0.70	0.30
terpinene	0.06	0.09
phellandrene	1.34	0.11

plants, between mature and immature foliage and between plants from different localities.

Qualitative and quantitative differences in EOs between species are also evident (Figures 25 and 26 respectively). *L. leonurus* and *L. intermedia* display the greatest diversity in EOs whereas *L. nepetifolia* and *L. dubia* display low diversity (Figure 26).
A comparison of GC retention times of known EO standards and unknown compounds indicates that 1,8-cineole, citroneol, α-terpinene, α- and beta-pinene, eugenol, linalool, ocimene, terpineol, borneol, caryophyllene, germacrene and α-phellandrene are present. GC-MS confirmed the presence of these compounds.

Gas chromatography and mass-spectrometry

Germacrene was the dominant EO in seven species, whereas caryophyllene dominates in *L. randii* (Figure 27). *L. nepetifolia* and *L. dubia* are distinguished by high levels of germacrene, but lack eugenol and phellandrene (Figure 27). The two subspecies of *L. ocymifolia* display similar levels of caryophyllene, germacrene and phellandrene (Figure 27).

Tenax trapping of volatile EOs

In contrast to the results obtained using GC and GC-MS when Tenax was used to extract EOs α-copaene (retention time - 15.02 minutes) was the dominant EO in six species (Figure 28), comprising 90-97%. Minor volatile oils identified by GC-MS included trans- and cis-ocimene, α-cubebene, aromadendrene and α-terpinene.

The use of herbarium specimens in EO analysis

Chromatographic traces from herbarium specimens of different ages of *L. leonurus* were irregular, when compared with chromatograms produced using fresh material. The proportions of specific compounds (or area percentages of peaks) were lower in herbarium specimens but the major constituents were usually present (Table 12).

Discussion

It is difficult to assess the reliability and value of EO data in defining specific limits in *Leonotis* and inferring phylogenetic trends without data on the biosynthetic pathways associated with the formation of EO constituents in different species.

Smith (1895) comments that "*L. obovata* has a characteristic smell, unlike that of the other species". The fact that novel terpenoid compounds have been described from four species of *Leonotis* (Kaplan and Rivett, 1968; Kaplan *et al.*, 1970; Eagle *et al.*,1978; Eagle and Rivett, 1973) and that the leaves of certain species have different aromas (*l.c.*), clearly indicates that terpene composition differs inter-specifically.

Thin-layer chromatography

The similarity of patterns attained through TLC confirms results obtained from GC analysis, indicating that *Leonotis* is a natural assemblage of closely related species which share similar EO components.

Gas chromatography and mass spectrometry

Three EO samples of *L. intermedia*, from distant localities (Pietermaritzburg, Tugela Ferry and Weenen), and four EO samples of *L. leonurus* (two per population) also from distant localities in Natal (Bulwer, Mike's Pass and Table Mountain), yielded similar chromatograms. Although a limited number of EO samples have been analysed, inter- and intra-populational variation within species is limited. The stability of EO composition intra-specifically is advantageous with respect to interpretation and confirms that EOs are reliable and useful taxonomic characters for studying species limits.

Vegetative (Chapters 3 and 4) and distributional data (Chapter 13) support the recognition of two subspecies for *L. ocymifolia.* The levels of germacrene, caryophyllene, phellandrene and an unknown compound (retention time 34.45 minutes) are very similar in *L. ocymifolia* ssp. *transvaalensis* and *L. ocymifolia* ssp. *ocymifolia* (Figure 27) which supports the recognition of these proposed subspecies.

The two most common and widely distributed species in southern Africa (*L. leonurus* and *L. intermedia*) display the greatest diversity of EOs.

The GC-MS analysis of EOs in *L. leonurus* compares favourably with that carried out by Rivett (pers comm.) on the same species (Table 13) further, revealing the consistency of compounds within species.

Tenax trapping of volatile EOs

It is difficult to explain the different results obtained when EOs were extracted in ether as opposed to Tenax. This requires further investigation.

Alpha copaene is a sesquiterpene previously recorded in the Leguminosae, Podocarpaceae, Cyperaceae (Windholtz, 1983) and Lamiaceae (Weyerstahl, 1983) and the dominant volatile EO in *Leonotis.* Although the leaves of different *Leonotis* species have characteristic aromas (*l.c.*), no inter-specific differences were evident in the levels of copaene. Presumably the remaining minor volatiles (i.e. trans- and cis-ocimene, α-cubebene, aromadendrene and α-terpinene) are responsible for species-specific aromas. This warrants further investigation.

The use of herbarium specimens in EO analysis

The inconsistencies observed in chromatograms of EO extracts prepared from herbarium specimens may be due to the various chemical treatments that different herbaria employ to preserve specimens. Before terpene data from herbarium specimens can be used for identification purposes with confidence, the rate and nature of the changes that occur should be determined under various storage conditions (Emboden and Lewis, 1967).

The functional significance of EOs

Leaves of all *Leonotis* species bear glandular and non-glandular trichomes (Chapter 3, Figure 7). It is reasonable to assume that the glandular trichomes are responsible for EO production in *Leonotis*.

The function and significance of glandular trichomes and terpenoids produced by *Leonotis* is very difficult to assess without observations and experimentation with plant-animal interactions, which are beyond the scope of this investigation. A brightly coloured stinkbug (*Antestia* sp.) is commonly found upon the inflorescences and foliage of *Leonotis*. When handled *Antestia* emits an unpleasant odour which is known to deter insect-eating animals (Skaife, 1979). Bitter-tasting terpenoids have been recorded by Smith (1976) and it is possible that *Antestia* is sequestering the terpenoids of *Leonotis* for defence against predators. The leaves of *Leonotis* (or "wild dagga") when smoked are known to be narcotic and have a hallucinogenic effect (Van Wyk, pers comm.).

Although bovines were observed feeding adjacent to *Leonotis* patches in grasslands, they were never seen feeding upon the plants. However, *L. mollissima* Gürke is suspected of poisoning cattle (Linley and Baker, 1972). A variety of insects (Chapter 12, Table 14) feed on *Leonotis* and the bitter, odoriferous terpenoids may deter herbivores (Harborne and Turner, 1984). This may explain the paucity of EOs in the leaves of *L. dubia* which frequents forests where large mammalian herbivores are scarce. Similarly, *L. nepetifolia* displays few EOs and may be subject to limited browsing due to its annual growth habit and senescence during phenology, when alternative grazing is sparse.

Conclusion

A chemosystematic study involving EOs of *Leonotis* was carried out to clarify species concepts and phylogenetic relationships.

Table 14. Insects collected on *Leonotis* during 1992 and 1993.
All insects were adult unless otherwise stated .
Abbreviations: N=nymph, L=larvae, infl=inflorescence.

Order	Insect family	Genera	Insect activity	Plant part
Hemiptera	Pentatomidae	?	rest	all
	Scutelleridae	?	rest	infl
	Cynidae	?	rest	infl
	Lygaeidae N	?	hunt	infl
	Membracidae	?	feed	stem
	Rhopalidae N	*Leptocoris*	rest	infl
	Pyrrhocoridae	*Dysdercus*	rest	all
Coleoptera	Curculoinidae	?	rest	leaf
	Coccinellidae	?	feed	calyx
	Scarabaeidae	?	rest	infl
	Biphyllidae N	?	feed	infl
	Apionidae L	?	rest feed	infl infl
Hymenoptera	Formicidae	?	feed	flower
	Apidae	*Apis*	feed	anther
	Halictidae	*Lasioglossum*	feed	flower
	Anthophoridae	*Xylocopa*, *Amegilla*	feed	flower
Lepidoptera	Pieridae	*Catopsilia*	feed	flower
Thysanoptera	Thripidae	?	feed	flower

Table 15. Records of sunbird (Nectarinidae) visits to *Leonotis* species.
Abbreviation: ILL=illegitimate pollinator.
References are cited in the bibliography.

Leonotis species	Bird visitor
L. nepetifolia (Gill and Wolf, 1977, 1978 and 1979; Gill and Conway, 1979)	*Nectarinia kilimensis arturi* (P.L. Sclater), *N. reichenowi* (Fischer), *N. famosa* (Linnaeus), *N. venusta fakkensteini* (Fischer and Reichenow) (ILL), *N. senegalensis* (Linnaeus)
L. mollissima Gürke (Gill and Conway, 1979)	*N. reichenowi*
L. leonurus (Skead, 1967; Frost and Frost, 1980; Daniels, 1987; Getliffe-Norris, 1989)	*N. afra* (Linnaeus), *N. famosa*, *N. chalybea* (Linnaeus), *N. olivacea* (A. Smith), *N. veroxi* (A. Smith), *N. amethystina* (Shaw), *N. talatala* (Smith), *N. violaceae* (Linnaeus), *N. senegalensis*, *Promerops gurneyi* (Verreaux), *Zosterops pallidus* (Swainson) (ILL)
L. intermedia	*Anthreptes collaris* (Vieillot) (ILL), *N. senegalensis*, *N. talatala*
L. dubia	*N. talatala*, *N. senegalensis*

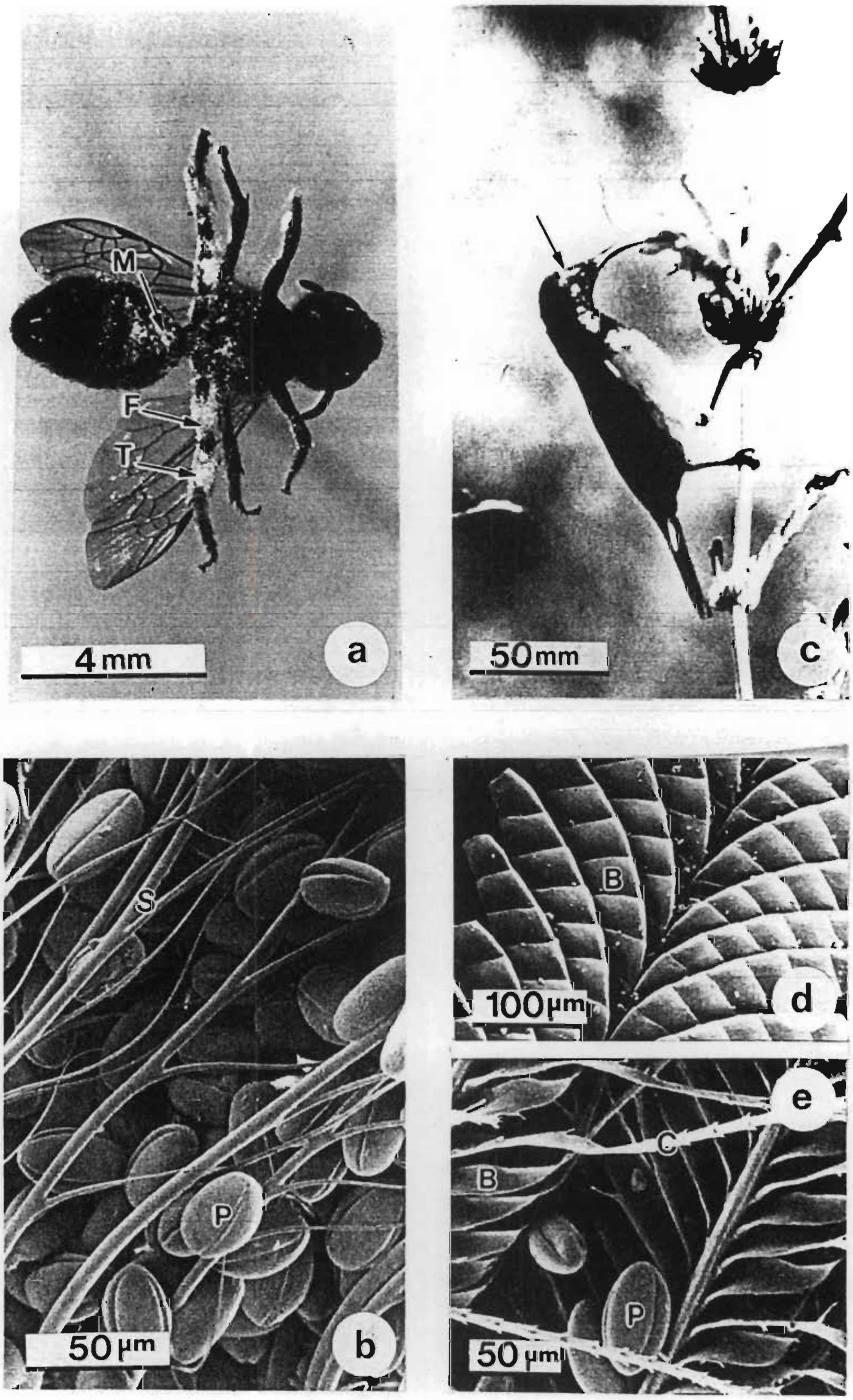

M
F
T
4 mm
a
50mm
c
S
P
50 µm
b
B
100µm
d
e
C
B
P
50 µm

Figure 29. *Leonotis* pollinators and pollen deposition sites (arrows).

(a) Ventral view of *Lasioglossum* (Halictidae),

(b) plumose setae (S) of the distal ventral hindlimb of *Lasioglossum* and *Leonotis* pollen (P),

(c) *Nectarinia afra* (Linnaeus) foraging for nectar on *Leonotis leonurus*,

(d) distal part of the crown feather of *Nectarinia famosa* (Linnaeus) showing flattened barbules and

(e) proximal or downy part of the crown feather of *Nectarinia famosa* with *Leonotis* pollen (P).

Abbreviations: M=metasoma, F=femur, T=tibia, B=barbule, C=barbicels, P=*Leonotis* pollen, S=plumose setae.

Photograph of *Nectarinia afra* by F. Getliffe-Norris.

Thin-layer chromatography, GC and GC-MS indicate quantitative and qualitative differences in EOs between species. Carophyllene and germacrene are the dominant EOs in *Leonotis* leaves, particularly in *L. nepetifolia* and *L. dubia*.

Leaves of different *Leonotis* species have characteristic aromas, the main volatile EO being α-copaene, however inter-specific differences were not evident.

EO data is in partial agreement with the proposed phylogeny and species concepts in this document (based on morphological and other evidence) but does not support the present classification of *Leonotis*.

Chapter 12

Pollination biology

Introduction

Leonotis is a suffrutescent genus concentrated in southern Africa, comprising mainly perennial species. *L. nepetifolia* is pan-tropical and the only annual species of the genus. The perennial and annual species are distinguished by differences in their floral morphology which are significant in view of the consistency of floral design amongst perennial species of the genus. Consequently this investigation was initiated to assess differences in the breeding systems between the annual and perennial species.

Pollination biology of ornithophilous plants in southern Africa has received little attention (Vogel, 1954; Skead, 1967; Frost and Frost, 1980 and 1981; Collins, 1983; Rebelo *et al.*, 1985; Siegfried and Rebelo, 1985 and 1986; Daniels, 1987; Rebelo, 1987; Getliffe-Norris, 1989). Although *L. leonurus* is pollinated by sunbirds (Nectarinidae), the role of insects in pollination is obscure (Getliffe-Norris, 1989). The effect of foraging sunbirds and insects on fruit set and subsequent germination in *Leonotis* is assessed.

Since nectar composition (Baker and Baker, 1983), concentration and rate of synthesis may influence pollinator foraging and therefore plant reproductive success, the nectar of annual and perennial *Leonotis* species was analysed.

Flowering times are influenced by competition for pollinators between species, selection against inter-specific gene flow, pollinator availability and the nature of floral rewards (Bawa and Webb, 1983). Many closely related plants which are sympatric show sequential flowering which may reduce competition for pollinators (Stiles, 1975; Feinsinger, 1976). However, this may not be the case as Waser (1983) points out there are many evolutionary constraints operating

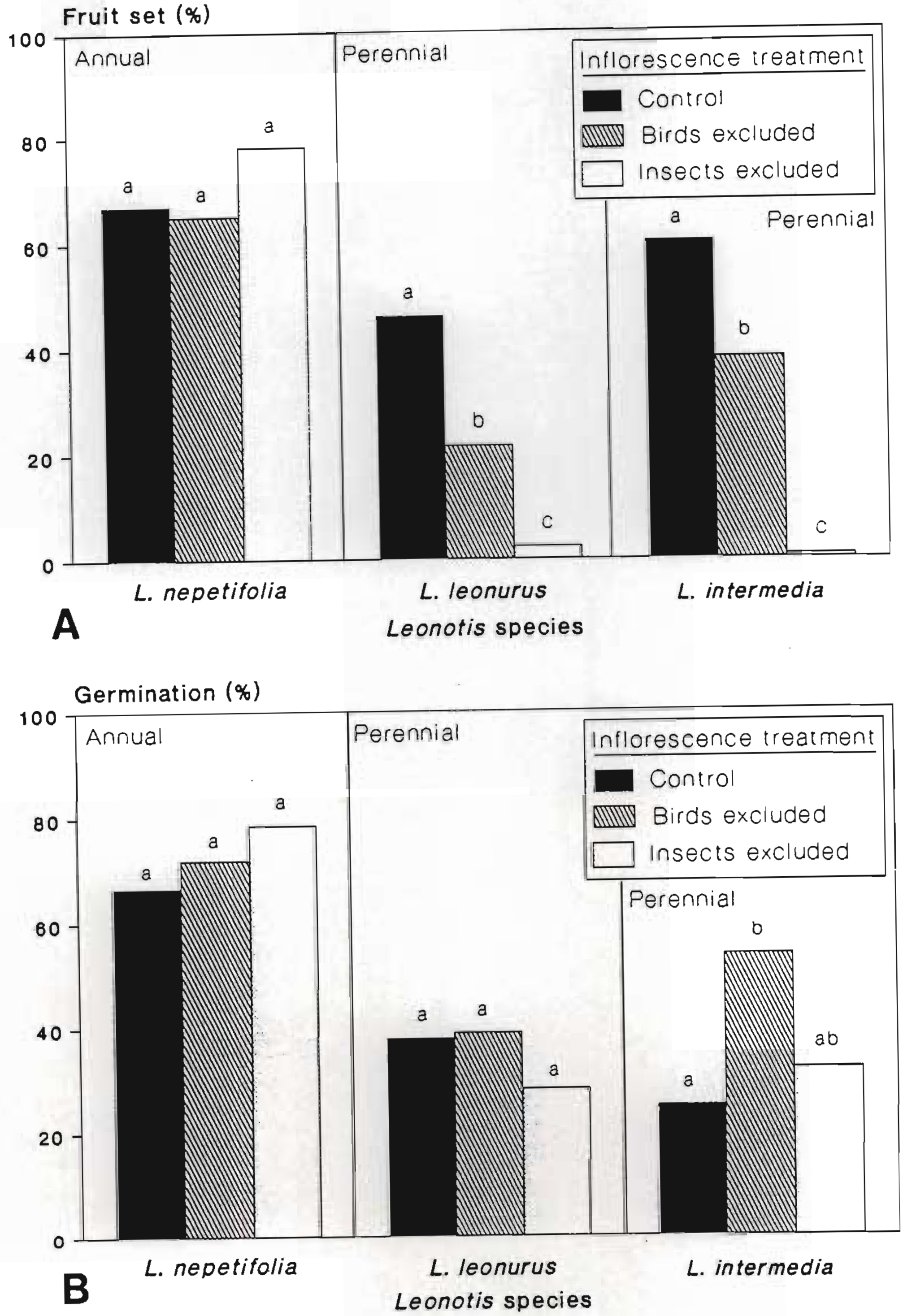


Figure 30. (A) Mean fruit set and (B) vigour (germination) in annual and perennial *Leonotis* species after selective exclusion of pollinators.
The control treatment represents an uncaged inflorescence. Within each species, bars sharing the same letter indicate no significant difference between treatments when $P<0.05$.

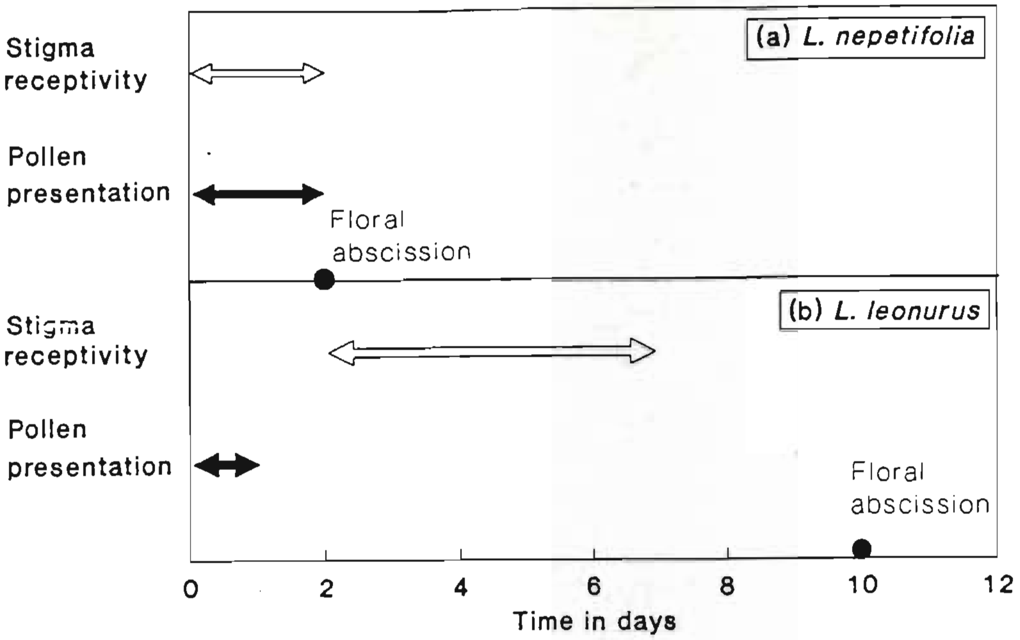


Figure 31. Schematic diagram of floral development and anther dehiscence (shaded arrows) of (a) annual and (b) perennial *Leonotis* species. Anthesis occurs on day one.

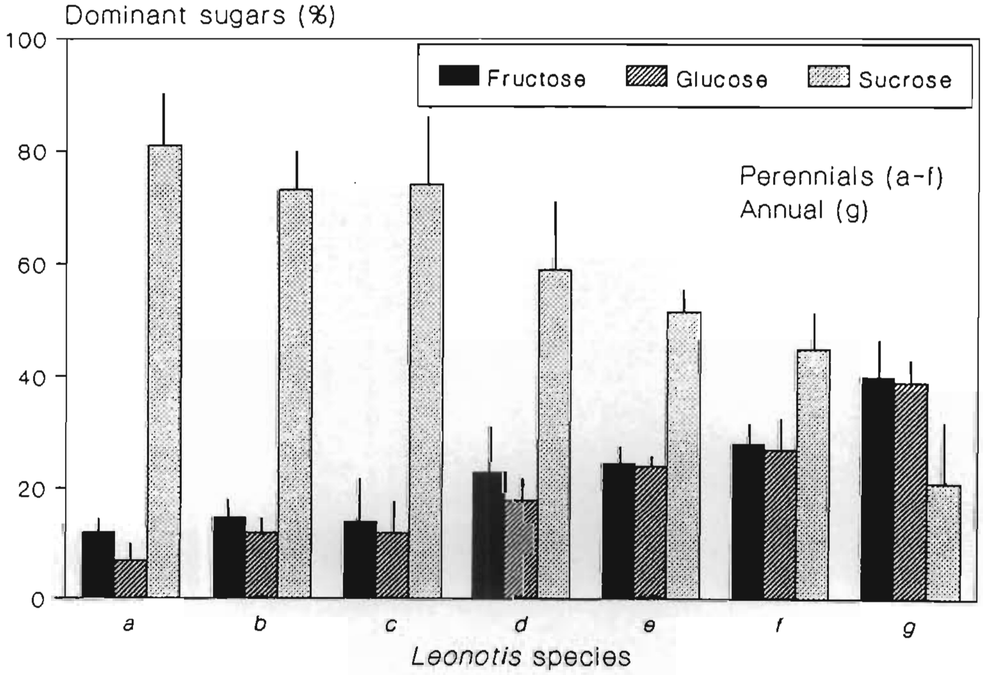


Figure 32. Dominant floral nectar sugars of *Leonotis* species.
Key: a=*L. ocymifolia* ssp. *transvaalensis*, b=*L. randii*, c=*L. intermedia*, d=*L. ocymifolia* ssp. *ocymifolia*, e=*L. leonurus*, f=*L. mollissima*, g=*L. dubia*, h=*L. nepetifolia*.
Values represent means and vertical lines represent twice the standard error.

Table 16. Floral and nectar characteristics of perennial and annual *Leonotis* species. Values represent the mean (± standard deviation).

Floral character	*L. leonurus* (perennial)	*L. intermedia* (perennial)	*L. nepetifolia* (annual)
Total length (mm)	44.78 ± 5.47	42.00 ± 4.21	24.47 ± 4.08
Tube length (mm)	27.17 ± 3.55	24.36 ± 2.73	12.88 ± 2.14
Throat diameter (mm)	5.33 ± 0.67	5.00 ± 0.43	2.56 ± 0.58
Longevity (days)	7-12	7-12	1-3
Nectar standing crop (μl/flower)	9.55 ± 1.13	11.26 ± 3.87	5.34 ± 2.02
Nectar conc. (%)	26.30 ± 2.17	28.00 ± 1.09	19.05 ± 2.47

in concert.

This chapter attempts to provide insight into how pollination systems affect evolution and speciation in *Leonotis* and may also clarify some of the debates regarding the co-evolution of pollinators and plants.

The investigation aims to: 1. make observations of pollinator behaviour, 2. assess differences in the breeding systems between the annual and perennial species, 3. assess the effects of pollinators on fruit set and germination, 4. analyse floral rewards in relation to pollinator type and 5. analyse flowering periods with regard to pollination.

Results and discussion

Most insect visitors do not affect pollination and are either phytophagous, breed or live on or within the plants (Table 14). Perennial *Leonotis* species are pollinated by at least 12 of the 18 southern African sunbirds (Table 15) and by bees (Figure 29 a). There are no specific plant-pollinator associations, any one *Leonotis* species may be visited by a variety of sunbirds which accumulate pollen on their foreheads (Figure 29 c). Bees (*Lasioglossum* Curtis) store pollen grains in scopae of the hindlegs and metasomal segments (Figure 29 a and b), whilst pollen collects on the crown feathers of sunbirds (Figure 29 d and e).

The effect of bird and insect pollinators on fruit set and nutlet germination in perennial and an annual species of *Leonotis* is summarised in Figure 30 A and B respectively.

The breeding system involves herchogamy and dichogamy (Figure 31). Buds which were emasculated and caged produced no nutlets. Floral and nectar characteristics of *Leonotis* species are presented in Figure 32 and Table 16.

In the Neotropical realm ornithophilous plants are common where there is a continuous supply of nectar. Ornithophilous plant and pollinator or hummingbird (Trochilidae) diversity is high in these regions (Snow and Snow, 1972; Stiles, 1975; Feinsinger, 1976; Wolf *et al.*, 1976; Feinsinger and Colwell, 1978) where specialization has occurred (Stiles, 1981). By comparison, their palaeotropical counterparts, the Nectarinidae (sunbirds) and Promeropidae (sugarbirds), are structurally less diverse.

The co-evolution of entomophilous angiosperms and their pollinators has led to high diversity and interdependency in these groups. In contrast ornithophilous angiosperms and their pollinators are structurally less diverse. Species of Nectarinidae (sunbirds) are similar in their bill morphology and thus exclusive co-evolutionary relationships are understandably rare (Wolf and Wolf, 1976; Gill and Conway, 1979). Most "sunbird flowers" are exploited by several species (Skead, 1967; Gill and Wolf, 1979) and *Leonotis* is no exception.

Inflorescences of perennial species from which insects and birds were excluded display the lowest nutlet production (Figure 30). Thus hymenophily augments ornithophily in *Leonotis* but it is difficult to assess its importance when both vectors are present. Getliffe-Norris (1989) and Gill and Conway (1979) observed *Apis mellifera* L. foraging for pollen at *L. leonurus* and *L. nepetifolia* respectively. A small eusocial bee, *Lasioglossum* (Figure 29 a), was the most common insect visitor to *Leonotis* during this study and *Apis mellifera scutellata* Lepeletier was occasionally observed.

Lasioglossum forages by combing the anthers for pollen while hanging upside down from the upper corolla lip. Pollination is effected when pollen-laden bees contact the stigma of the flower being visited. Pollen is stored in the predominantly plumose scopae of the bee's legs and abdomen (Figure 29 a).

In sunbirds pollen collects on the crown during foraging (Figure 29 c). The barbules of the distal portion of the crown feathers are flattened (Figure 29 d) which increases light reflectance and gives male sunbirds their iridescent appearance. The proximal portion of the crown feather is downy with barbule

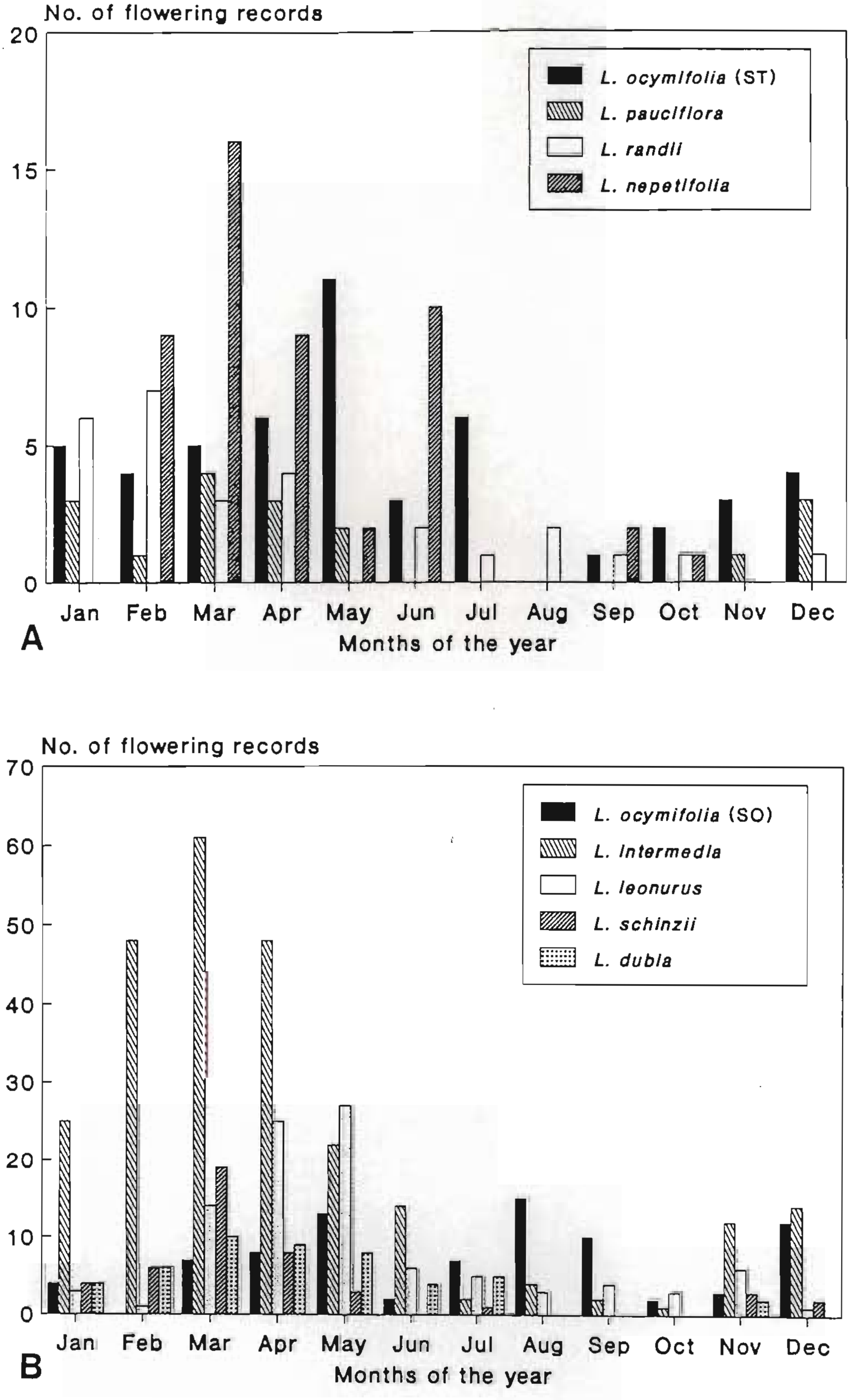


Figure 33 (A and B). Flowering records of *Leonotis* species compiled from herbarium specimens.
Vouchers are cited in Chapter 15.
Abbreviations: SO=subspecies *ocymifolia*, ST=subspecies *transvaalensis*.

elongations and is more effective in trapping pollen (Figure 29 e).

Leonotis pollen adheres in small clumps following anther dehiscence although scanning electron micrographs (Figure 29 b and e) do not reveal adhesive pollenkitt. Adherence is probably due to electrostatic forces (Figure 29 d).

Thrips (Thripidae) are known to feed on pollen (Lawrence and Britton, 1991) and were observed in flowers within caged inflorescences of *Leonotis*. They may play some role in pollination but appear to have little effect on the trends.

Nutlet vigour

A high level of fruit production would be reproductively advantageous in terms of fecundity if nutlet vigour or germination were equally high. Young (1982) demonstrated that Sunbird pollination of *Lobelia* Plum. ex Linn. (Lobeliaceae) increased the proportion of seeds that germinated. Neither ornithophily nor entomophily improved nutlet vigour in perennial or annual *Leonotis* species (Figure 30). Perennial species are largely self-incompatible with long distance pollen movement by sunbirds, outbreeding and associated heterozygosity.

Floral adaptations of perennial and annual *Leonotis* species

In *Leonotis* the lower lip recurves soon after anthesis deterring insect visitors and allowing easy access to birds. The tubular, decurved corollas force sunbirds to orientate their bills in a particular way when probing for nectar. This facilitates localized pollen deposition on the crown and increases the efficiency of pollen transfer (Stiles, 1981).

Perennial species are protandrous and herchogamous (Figure 31); the style extends up to 5 mm from the corolla mouth, elevating it above the dehisced anthers. In contrast *L. nepetifolia* has corolla tubes which are 47-52% the length of those found in perennial species, and flowers are short-lived with low nectar production (Table 16). Herchogamy and dichogamy are not expressed (Figure 31).

The basal ring of trichomes within the corolla of *L. leonurus* probably acts as a brush which maintains nectar at the base of the tube and restricts exploitation by potential pollinators. This pollinator selection increases the efficiency of pollination by decreasing mixed pollen loads (Stiles, 1981).

Floral nectar

Floral nectar composition has been related to pollinator type (Baker and Baker, 1983) and may influence pollinator foraging and therefore plant reproductive success. Nectar also reflects lineage with related plants sharing similar genetic constraints which govern nectar production.

Frost and Frost (1980) and Gill and Conway (1979) studied the nectar of *L. nepetifolia* and *L. leonurus* and suggested the presence of sucrose, glucose, and fructose which was confirmed for eight species of *Leonotis* (Figure 32). Contrary to the findings of Baker and Baker (1983) and Percival (1961), fructose was proportionately greater than glucose in the nectar of all *Leonotis* species studied. Baker and Baker (1983) found that sunbird flower nectar is hexose-dominant. The floral nectar of *Leonotis* proved to be predominantly sucrose-dominant with the nectar of the annual species (*L. nepetifolia*) being hexose-dominant (Figure 32). Within the Lamiaceae hymenophily and sucrose-dominant nectar are thought to be ancestral (Baker and Baker 1983; Percival 1961). The development of hexose-dominant nectar in *L. nepetifolia* is thus a derived condition.

Mean nectar availability in flowers of *L. leonurus* was 9.55 μl compared to 5.34 μl in *L. nepetifolia* (Table 16). Nectar concentration ranged from 19-28% sucrose equivalents (Table 16). This data compares favourably with previous records for the genus (Gill and Wolf, 1975; Gill and Conway 1979; Frost and Frost, 1980).

Nectar standing crops and concentrations were significantly lower and flower size was significantly smaller in the annual species compared to the perennial species (Table 16). This was anticipated due to differences in their respective breeding systems. Nutlet production of bagged inflorescences suggests that *Leonotis* species are self-incompatible. Two breeding systems are apparent (Figure 30). In perennial species the importance of sunbirds in pollination is clear from the 53% increase in nutlets produced on unbagged inflorescences. Only 2% of potential nutlets were produced on inflorescences from which both insects and birds were excluded. Thus these species are facultatively xenogamous. In contrast birds and insects have little effect on nutlet production in *L. nepetifolia* (Figure 30). Pollination is therefore promoted in perennial *Leonotis* species whilst the annual (*L. nepetifolia*) produces large numbers of nutlets through autogamy.

Flowering periods

Sequential flowering is not evident for different species of *Leonotis* which flower between December and June. Sunbirds are not dependent on nectar for all their food requirements (Skead, 1967; Rebelo, 1987) and the flowering periods of *Leonotis* (Figure 33) do not correspond with the breeding periods (October-January) (Maclean, 1985) of these pollinators.

In general few angiosperms flower in winter when conditions are unfavourable for insect pollinators, however *Leonotis* is not dependent on ectothermic pollination. Flowering in autumn may be a means of limiting stigma clogging, since bees which visit *Leonotis* in autumn should be carrying less foreign pollen.

Conclusion

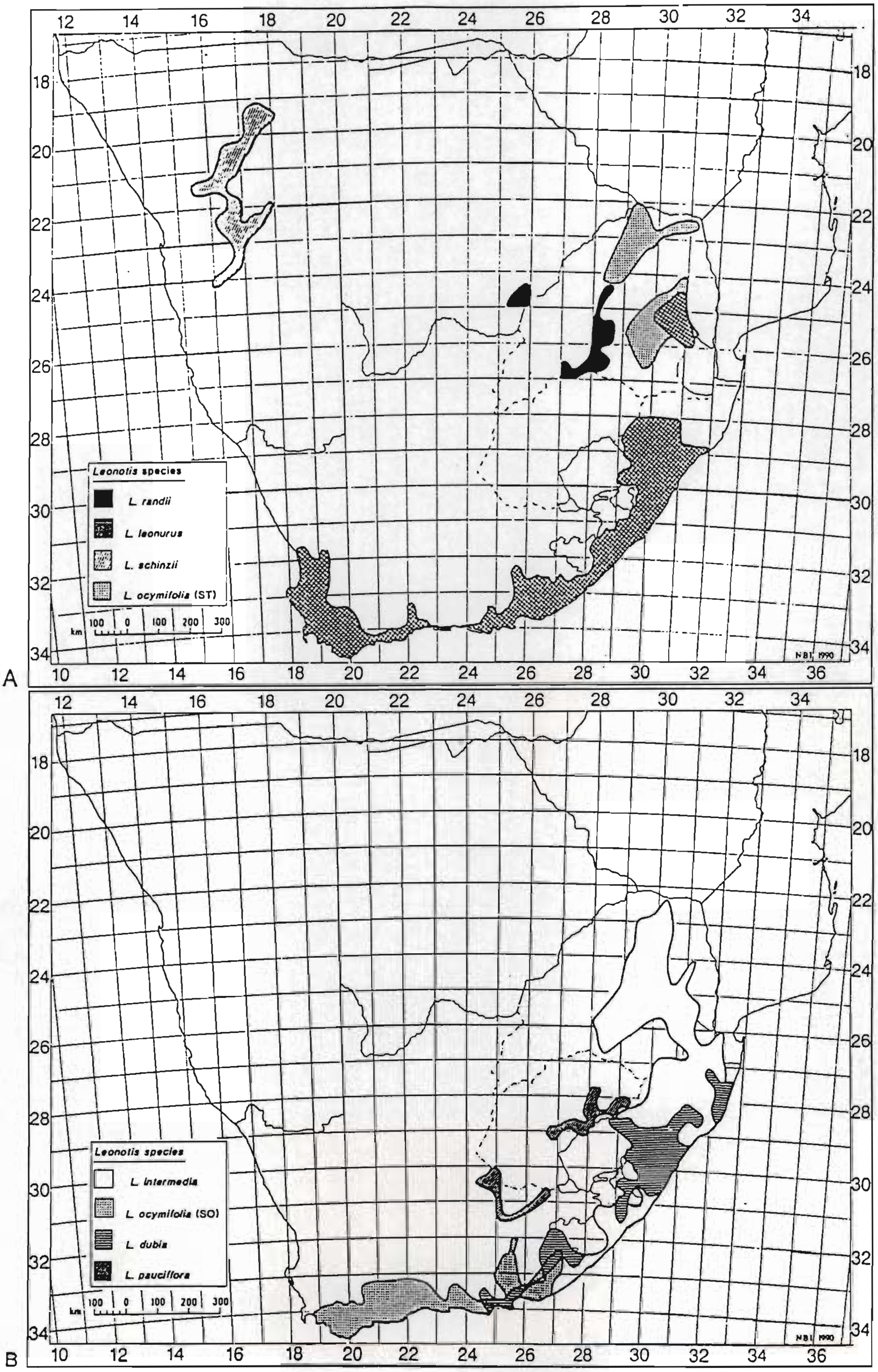


Figure 34 (A and B). Recorded distribution of perennial *Leonotis* species in southern Africa. ST=subspecies *transvaalensis*. SO=subspecies *ocymifolia*. Vouchers are cited in Chapter 15.

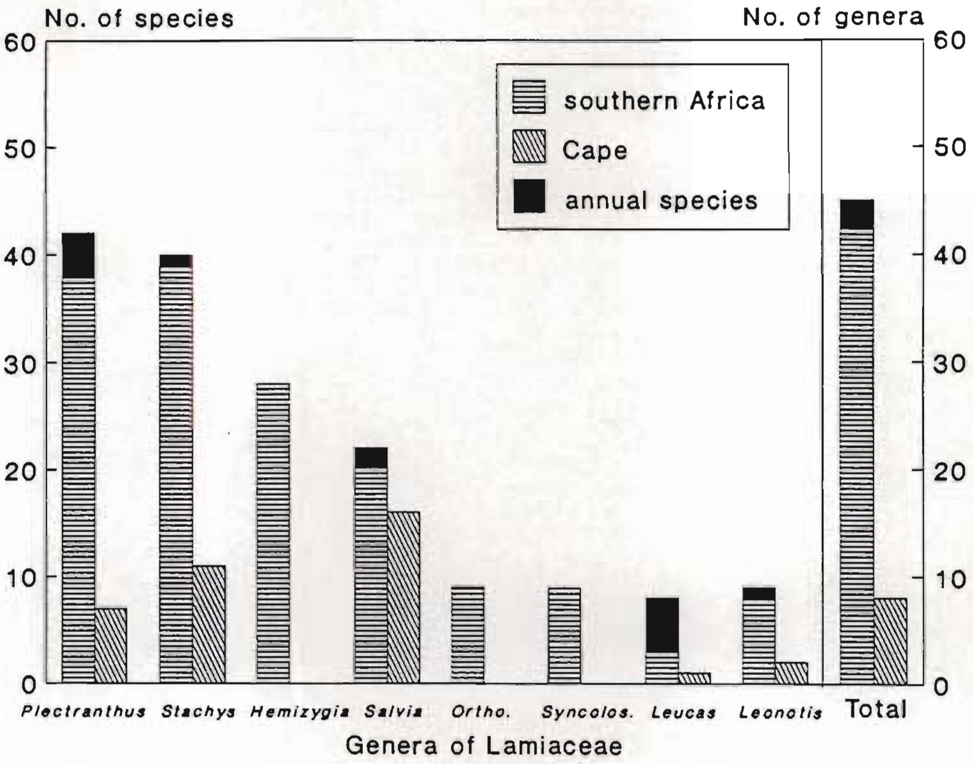


Figure 35. A comparison of species diversity between the Cape and southern Africa for the largest genera of Lamiaceae.

The proportion of annual species within genera is indicated, the remaining species are perennial.

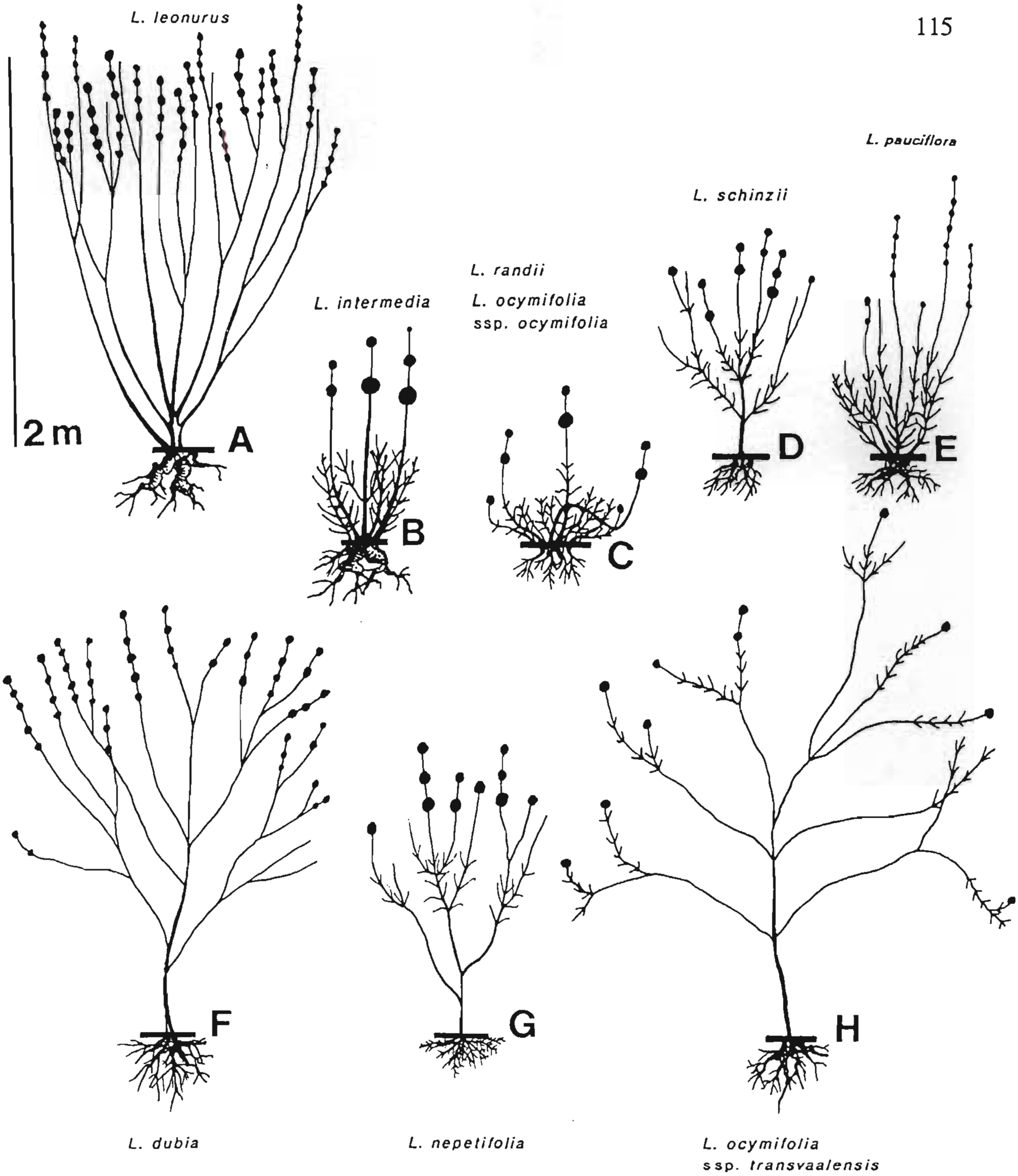


Figure 36. Schematic diagrams of the flowering habit of *Leonotis*. The horizontal bar at the base of the plant represents the soil surface and the black spheres represent inflorescences.

Table 17. Plant height, altitude and climatic conditions of *Leonotis*. Abbreviations: L=light, M=moderate, S=severe.

Leonotis species	Altitude (m)	July daily temperature range (°C)	Frost	Annual range in precipitation (mm)	Plant height (m)
L. leonurus	0-2000	10-18	L-S	400-1000	1-3 (-5)
L. dubia	0-2000	10-18	L	400-1000	1-3 (-6)
L. ocymifolia ssp. *transvaalensis*	1-2000	10-14	L-M	400-1000	1-3 (-5)
L. intermedia	0-2500	10-18	L-S	400-1000	0.5-1.5 (-2)
L. schinzii	1-2000	10-16	L-M	100-400	0.5-1 (-2)
L. randii	1-2000	8-12	M-S	400-600	0.5-1 (-2)
L. pauciflora	1-2500	6-10	S	400-600	1-1.8
L. nepetifolia	0-2000	10-18	L-M	400-1000	1-3
L. mollissima	1-2000	10-14	L-M	600-1200	1.5-8
L. ocymifolia ssp. *ocymifolia*	0-1500	10-12	L-M	400-1000	0.5-1.5

Table 18. Soil and habitat conditions of *Leonotis*.

Leonotis species	Soil category	Soil/rock type	Habitat
L. leonurus	Ferrallitic soils Lithosols Weakly developed shallow soils of arid regions Montmorrillomitic (M) clays Solonetzic & planosolic (S & P) soils Others	Red & yellow sands & loams Argillaceous & arenaceous sediments Calcareous sands & loams overlying calcrete, lime Black & red (M) clays (S & P) soils with sandy loam-horizons Others	Grassland, savanna, forest margin, scrub, rocky slopes
L. dubia	As for *L. leonurus* Alluvial & other weakly developed soils of low lying areas	As for *L. leonurus* Alluviam enriched with organic material	Forest, forest margin, scrub
L. ocymifolia ssp. *transvaalensis*	Lithosols Fersiallitic soils	Arenaceous sediments & acid igneous rocks Red & yellow sands & loams	Grassland, mountainous areas, rocky outcrops & slopes, montane forest margin, disturbed sites
L. intermedia	As for *L. leonurus*	As for *L. leonurus*	Grassland, savanna, forest margin, scrub, rocky slopes, disturbed sites, streambank
L. schinzii	Lithosols Weakly developed shallow soils of arid regions	Soils of metamorphic & acid igneous rocks Calcareous soils	Highland or mountain savanna to grassland, dry riverbed, scrub, rocky outcrops & slopes, disturbed sites
L. randii	Lithosols Fersiallitic soils Black & red Montmorrillomotic (M) clays	Soils of metamorphic & acid igneous rocks Red sands, loams & clays Black & red (M) clays	Bankenveld, Sourveld, Mixed Bushveld, rocky outcrops & slopes
L. pauciflora	Lithosols Fersiallitic soils Solonetzic & planosolic (S & P) soils	Arenaceous sediments Sands & loams (S & P) soils with sandy loam-horizons	Highland grassland (*Cymbopogon-Themeda*), scrub, mountain slopes, sandstone outcrops
L. nepetifolia	Variable	Variable	Variable, often disturbed sites
L. ocymifolia ssp. *ocymifolia*	Lithosols Weakly developed shallow soils of arid regions Arenosols	Argillaceous & arenaceous sediments Calcareous soils, lime, calcrete Arenosols, littoral sands	Grassland, scrub, Karroid & dune vegetation, fynbos, forest margin, rocky slopes & outcrops, streambank

The pollination syndromes of *Leonotis* are discussed. Ornithophily accounts for most of the nutlets set in perennial *Leonotis* species but in the annual species (*L. nepetifolia*) autogamy prevails. Ornithophily and entomophily do not affect nutlet vigour in *Leonotis*. *Leonotis* species are predominantly pollinated by sunbirds, although bees are also involved. Nectar is sucrose-dominant in perennial species and hexose-dominant in *L. nepetifolia*. The flowering periods of *Leonotis* species are not staggered and do not correspond with the breeding periods of sunbird pollinators.

Chapter 13

Habitat, habit and phytogeography

Introduction

The Lamiaceae occur in most habitats and across a wide range of altitudes (Heywood, 1978) although they are scarce in arid to semi-arid zones. They are mainly suffrutices of warm, temperate regions but also occur in the tropics usually on forest margins (Hedge, 1992).

Charles Lyell (1830) remarked "the present is the key to the past" although frequently "the past is a key to the present" in biogeography. In Africa aridification began in the mid-Tertiary (Paton, 1990) and continued into the Pleistocene (± 1.5-2 million years ago). Climatic changes that occurred over the last 2 million years in the Quaternary period have had a very strong influence on vegetation in southern Africa (Meadows, 1985). Vicariance and dispersal can be seen to have accompanied the contraction and expansion of plant ranges as they followed the cyclic changes in Quaternary climate (Poynton, 1983). Presently the increasing aridity westwards across the large interior plateau of southern Africa is reflected in the vegetation (Meadows, 1985). Moisture availability is an important limiting factor for plant distributions (Walter, 1979), although historical factors are also important.

Although there is no fossil evidence marking the origin of the angiosperms, Takhtajan (1970) estimates their origin between the Triassic and Jurassic. The Lamiaceae are diverse and highly evolved and therefore probably diverged early in angiosperm history (Goosens, 1930). The Lamiaceae date back approximately 100 million years but as we have no fossil record, our hypotheses concerning evolutionary trends, inter-relationships and biogeography, are largely inferred (Hedge, 1992).

There are no links between tropical America and tropical African Lamiaceae. The few species that are pan-tropical are weeds such as *Hyptis suaveolens* (L.) Poit. and *L. nepetifolia.* Although there are many high latitude South American links with Australasia in mainly woody tropical plants, these connections are few or absent in the Lamiaceae (Hedge, 1992).

The palaeo-botanical record from India and the Mascarene Plateau infers an extension of sub-tropical rainforest into South Africa before the spread of the dry climate. Fossil evidence also supports the idea that rainforest probably extended from coast to coast in tropical Africa (Axelrod and Raven, 1978).

Many Cape genera are thought to have originated in the north leaving scattered records of their journey southwards, and finally undergoing intensive speciation in the south-west (Levyns, 1964; Oliver *et al.*, 1983). The northward movement of Africa as a result of continental drift would result in changes of the type needed to explain the southward movement of floras (Levyns, 1964). For the Lamiaceae, patterns of radiation from a central core in south west Central Asia are apparent, such as those to the Mediterranean, western America and southern Africa (Hedge, 1992).

The Cape fynbos is considered an ancient vegetation type (Axelrod, 1975) and in the Pleistocene the Cape coast had perhaps been the most sensitive to climatic change (Oliver *et al.*, 1983; Deacon and Lancaster, 1988) being displaced from its present habitat by extension of the temperate forest (Axelrod and Raven, 1978).

In a Mediterranean-type climate, regeneration via sprouting from lignotubers appears to be a significant adaptation where fires are frequent (James, 1984). Nutrient-poor, acidic soils play an important role in the dynamics of fynbos (Meadows, 1985) and are involved in the development of many endemic taxa (Wild, 1964; Dahlgren, 1968; Acocks, 1988; Van Wyk, 1990). Many narrow endemics in the Cape are restricted to infertile acid soils of the mountains and the alkaline calcareous soils of the coast (Cowling, 1983). Such edaphic conditions are conducive to what Wild (1964) referred to as *in situ* evolution by isolated fragments of a formerly continuous flora (i.e. vicariant evolution).

During the Palaeogene the high East African mountains were sufficiently cool to allow certain tropical rainforest taxa to radiate upward into a temperate montane zone and presumably for northern and southern temperate plants to extend their ranges towards or past the equator (Axelrod and Raven, 1978). Similar vegetation shifts are thought to have taken place in the eastern highlands of Zimbabwe (Van Zinderen Bakker, 1978) although Clayton (1983) comments that extinction may be a better explanation than speciation for the occurrence of endemics on mountains. The high endemism recorded for the East African mountains (Lind and Morrison, 1974) suggests a long period of isolation (Meadows, 1985).

Present day ecosystems are the product of biological evolution, speciation, dispersal and extinction (Deacon and Lancaster, 1988). Phytogeographical data lends support to taxonomic decisions and is valuable for studying phylogeny. By referring to present and past climatic conditions and geomorphology this chapter attempts to explain the distribution and adaptive radiation of *Leonotis* in southern Africa.

Results

Leonotis predominates in the summer rainfall region (Figures 34 and 35). Species diversity of Lamiaceae is low in the winter rainfall region of southern Africa (Figure 35). Plant habit is illustrated (Figure 36) and climate (Table 17), soils and habitats are summarised (Table 18).

Discussion

Phytogeography

Although *Leonotis* is essentially an African genus, *L. nepetifolia* is a pan-

tropical weed (Hooker, 1839; Hedge, 1992) widespread in southern Africa. *L. ocymifolia* occurs in Asia and *L. leonurus* has been introduced to western Australia (Prain, 1911) and many other countries for ornamental purposes (Batten and Bokelmann, 1966).
L. nepetifolia and a closely allied genus, *Leucas*, are widespread weeds in Madagascar (Phillipson *et al.*, 1992). There are numerous plant and animal links between East Africa and Madagascar (Wild, 1975; Axelrod and Raven, 1978; Poynton, 1983), however perennial *Leonotis* species occurring in Kenya and Tanzania are absent from Madagascar.

The confinement of *Leonotis* primarily to Africa supports Hedge's (1992) observation that African Lamiaceae are isolated with few close Lamiaceae allies on other continents. Such confinement is understandable where genera evolved after the break-up of Gondwanaland in the mid- to late-Cretaceous (Axelrod and Raven, 1978; Kerfoot, 1975). The herbaceous nature of the Lamiaceae may explain their absence from the fossil record.

In a global perspective of the Lamiaceae, Hedge (1992) comments that the predominance of perennial species is a sign of generic antiquity. The development of ornithophily or bird pollination (Chapter 12) in a predominantly entomophilous or insect-pollinated family, indicates advancement and a more recent origin for the genus within the Lamiaceae. Annual species of Lamiaceae are uncommon in southern Africa (Figure 35). The presence of an autogamous annual (*L. nepetifolia*) (Chapter 12) which is pan-tropical, indicates further evolutionary advancement and is considered a synapomorphic condition for the genus.

The majority of species occur along the eastern seaboard (Figure 34) although *L. schinzii* is Namibian (Figure 34 A). *L. ocymifolia* ssp. *transvaalensis* occurs in the Transvaal, Zimbabwe, Zambia and Tanzania. *L. intermedia* and *L. leonurus* are widespread in South Africa and Central East Africa, the latter species also occurs in Angola. In southern Africa five of the eight perennial species occur in the eastern Cape which forms the centre of diversity.

The widespread distribution (Figure 34 A), distinctive habit (Figure 36 A), floral and inflorescence morphology (Chapter 6) of *L. leonurus*, suggests a synplesiomorphic condition. The occurrence of vicariant tropical African species (*L. pole-evansii*, *L. decadonta* and *L. goetzei*) suggest a tropical origin for the genus.

Ball (1975) hypothesises that ancestral populations remain at, or near their points of origin, and derived forms migrate. We propose that *Leonotis* arose in Tropical Africa and migrated to southern Africa where isolation and speciation took place. The low species diversity of Lamiaceae in the winter rainfall region of southern Africa (Figure 35) and the high diversity in the tropics (Hedge, 1992) supports this hypothesis. Migration probably took place along one or two routes, one down the east coast to southern Africa and the other to Namibia. Van Zinderen Bakker (1978) reports that a corridor was available during colder times for the exchange of semi-arid elements between Namibia in a north-easterly direction to Kenya.

Alternatively, the present distribution patterns may be explained by vicariance of a formerly more widespread genus. The upheavals of the Quaternary and associated climatic changes (King, 1978) would explain the disappearance of *Leonotis* from large parts of the interior plateau and Karoo regions between Namibia and eastern South Africa (Figure 34 A).

L. mollissima may be an ancestral relict as it is widespread on the mountains of Central East Africa (Linley and Baker, 1972; Lebrun and Stork, 1977), Malawi, Mozambique (Gorongosa massif), Sudan, Ethiopia and Zimbabwe. It occurs in lowland montane forest at altitudes of 1-2000 m and is extensively branched and tall, bearing leaves (Chapter 4) and inflorescences (Chapter 6) reminiscent of most southern African species. *L. mollissima* fits the ancestral condition, however, leaves are also specialised (Chapter 4) which contradicts this hypothesis. The vegetational shifts that took place associated with the climatic changes of the Pleistocene (Axelrod and Raven, 1978; Van Zinderen Bakker, 1978; White, 1981; Clayton, 1983) would explain the occurrence of *L.*

mollissima on mountain refugia of Central East Africa and Zimbabwe.

L. pauciflora occurs around the western part of the Lesotho Highlands (Figure 34 B) in the Orange Free State and in the vicinity of Aliwal North and Philipstown in the Cape. Its closest relative, *L. intermedia*, occurs in Natal. In the closing stages of the Pliocene, major tectonic upheavals raised the interior plateau of southern Africa and steepened the marginal monoclines (King, 1978). The climatic changes following such an event would have provided the necessary selective pressures for allopatric speciation to take place.

Habit and habitat

Although plant habit is "plastic" it is reasonably characteristic of most *Leonotis* species and therefore useful for identification. The tall, erect and sparsely branched habit of *L. leonurus* (Figure 36 A) is immediately recognizable as is the shrubby, often mat-forming, habit of *L. randii* and *L. ocymifolia* ssp. *ocymifolia* (Figure 36 C).

Tall plants (*L. leonurus* and *L. ocymifolia* ssp. *transvaalensis*) display short flowering stems (up to 350 mm) and short plants (*L. intermedia, L. schinzii, L. randii, L. pauciflora*) display long flowering stems (up to 500 mm). This relates to pollination, the elevation of inflorescences in short plants which frequent dense scrub or grassland, may be an adaptation to increase pollinator attraction and therefore fruit set.

The majority of *Leonotis* species occur within the summer rainfall region of South Africa but *L. ocymifolia* ssp. *ocymifolia* and *L. leonurus* occur within the winter rainfall region. The distribution of *L. leonurus* is unusual (Figure 34 A) in that many taxa of the summer rainfall region are depauperate in the winter rainfall region or Cape fynbos.

Two of the largest genera of Lamiaceae in southern Africa (*Plectranthus* and

Table 19. *Leonotis* data matrix employed in cladogram computation.

Taxon	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
	Character states																									
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. leonurus	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
L. dubia	0	2	2	0	2	3	0	0	0	0	0	0	0	0	0	0	2	2	1	1	1	1	1	1	1	0
L. randii	2	1	0	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	2
L. schinzii	2	1	0	1	0	1	1	1	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
L. ocymifolia ssp. *ocymifolia*	2	2	2	2	0	1	1	0	1	0	2	1	1	1	2	1	1	1	1	1	2	2	1	1	1	2
L. ocymifolia ssp. *transvaalensis*	0	2	2	2	0	1	1	1	0	1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	2
L. intermedia	1	2	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
L. pauciflora	1	2	2	1	1	2	0	1	0	0	1	1	1	0	1	1	1	1	1	1	2	2	1	1	1	1
L. nepetifolia	1	2	2	0	2	2	0	1	0	1	1	1	1	1	2	1	2	2	1	1	2	2	1	1	1	2

Stachys) display similar distributions (refer to Codd, 1985) to *L. leonurus* (Figure 34 A) and inhabit mesic forest and forest margins where frost is absent. Hedge (1992) hypothesises that the Lamiaceae probably spread from open, montane habitats into savanna woodlands which expanded at the expense of forest. The majority of species occur in grassland or savanna (Table 18) and are relatively short and shrubby, whilst *L. dubia* and *L. ocymifolia* ssp. *transvaalensis* frequent afro-montane or coastal forest or forest margins, and are extensively branched and tall (Figure 36 F and H respectively).

The majority of perennial species are suffrutescent, producing annual stems from woody subterranean lignotubers. Two of the most widespread species, *L. leonurus* and *L. intermedia*, inhabit grasslands where fire is frequent and have developed prominent lignotubers (Figure 36 A and B respectively). This is considered a synapomorphic condition associated with the invasion of grassland and savanna. The forest dweller, *L. dubia*, displays poorly developed lignotubers (Figure 36 F) and appears weakly perennial.

The lack of prominent lignotubers in *L. ocymifolia* ssp. *ocymifolia* (Figure 36 C) is understandable since fires are infrequent in the Cape fynbos where fuel loads are low. In the Bankenveld, *L. randii* avoids fire by growing on rocky outcrops and has a poorly developed lignotuber. Rocky, shallow soils have probably also affected root development in *L. randii* (Figure 36 C). The annual species, *L. nepetifolia*, channels its resources into fruit production (Chapter 12), and as expected, has a shallow, fibrous root system (Figure 36 G).

The distribution of *L. ocymifolia* ssp. *ocymifolia* coincides with the Cape Fold mountains or Cape Supergroup sequence where fynbos prevails. *L. randii* occurs in Bankenveld of the Transvaal highveld in the vicinity of the Witwatersrand sequence and *L. schinzii* occurs in highland savannas of Namibia. Precipitation and temperature are low in these areas (Table 17) and soils are coarse, nutrient-poor and acidic (Table 18). Climatic and particularly edaphic conditions, probably played an important role in the evolution of these species which are confined to what Van Wyk (1990) termed "edaphic islands".

Competition may also be playing a role in these communities. *L. randii* also occurs in southern Botswana and Zimbabwe coinciding with lithosols and fersiallitic soils.

L. randii, *L. ocymifolia* ssp. *ocymifolia* and *L. schinzii* display xerophytic characters which are maintained under cultivation in mesic conditions. These characters include a low growth (Figure 36 C and D and Table 17) and small, hairy leaves (Chapter 3). Leaf anatomy is discussed in Chapter 4. Although most species produce deciduous stems, *L. ocymifolia* ssp. *ocymifolia* and *L. randii* are weak perennial shrubs. Shrubs are common in fynbos where nutrients are limited. The ability to adapt to xeric conditions and nutrient poor soils is regarded as a synapomorphic condition.

Altitude influences environmental conditions. Four species occur at altitudes of 1-2500 m where temperatures and precipitation are low (Table 17). The distribution of *L. schinzii* correlates closely to high lying areas around Windhoek (Khomas Hochland and Bergland) and *L. ocymifolia* ssp. *transvaalensis* with mountainous areas of the north- and south-eastern Transvaal (Figure 34 A). The discontinuous range of *L. ocymifolia* ssp. *transvaalensis* is due to an extension of Lowveld from the east. The tropical African species, *L. mollissima*, also displays altitudinal isolation but precipitation is considerably higher here due to orographic rainfall.

The western part of Namibia where *L. schinzii* occurs, and particularly the Namib Desert, has experienced very little climatic change and is well known for its ancient endemic plants (Giess, 1971; Van Zinderen Bakker, 1978; Deacon and Lancaster, 1988). Altitude, climatic and edaphic factors have played an important role in the evolution of this narrowly distributed species.

L. pauciflora occurs in Highland Sourveld to *Cymbopogon-Themeda* grassland in the Orange Free State and in False Karoo vegetation of the north-eastern Cape where the altitude is lower. Palaeontological data from Aliwal North indicates that during inter-glacial times Karoo vegetation invaded the plateau and geomorphological evidence suggests that windblown sand dunes covered large areas on the western part of the plateau (Van Zinderen Bakker, 1978). These events may explain the discontinuous distribution of *L. pauciflora* and its absence from the western parts of the plateau. Under-collection may also explain this discontinuous distribution.

The Biggarsberg and other high lying areas appear to have acted as a barrier preventing the extension of *L. leonurus* from northern Natal to the south-eastern Transvaal.

L. dubia shows disjunction between the Natal midlands, Zululand and the eastern Cape. Habitats differ in these areas from Mistbelt Forest (Natal midlands) and sub-tropical coastal forest with alluvial soils (Zululand) to Alexandria Forest, Valley Bushveld and False Macchia in the eastern Cape. The Transkei discontinuity, known as the "Kaffraria interval" (Weimarck, 1941), is a common phenomenon for grassland species but not for forest taxa. *L. dubia* displays mesophytic characters such as a tall growth habit, extensive branching (Figure 36 F) and broad, long-petiolate leaves (Chapter 3). Anatomical characters are discussed in Chapter 4.

Conclusion

The confinement of *Leonotis* to Africa suggests an origin of the genus after the Cretaceous split of Gondwanaland. The development of an annual species and ornithophily imply advancement and a recent origin within the Lamiaceae.

The majority of *Leonotis* species are concentrated along the eastern seaboard in the summer rainfall region with the eastern Cape forming the centre of diversity. The distinctive morphology, widespread distribution and tropical affinities of *L. leonurus*, suggest an origin for the genus in tropical Africa. Migration to southern Africa and subsequent speciation are hypothesised. The low species diversity of Lamiaceae in the winter rainfall region also supports a tropical origin for *Leonotis*.

Altitude, climate and particularly edaphic conditions, play an important role in the evolution of narrowly distributed species which are considered synapomorphic.

Leonotis was probably more widespread in Africa and diversified at a time when forests receded with the drying climate of the mid-Tertiary. The development of lignotubers is a derived condition which has enabled many species to occupy fire-prone environments such as grassland whilst ancestral relics occupy forest or forest margins.

Chapter 14

Cladistic analysis

Introduction

The confirmation of phylogeny inevitably requires fossil evidence but it is possible by comparing characters and grouping together those organisms that share synapomorphic characters to generate putative trees. In this way, monophyletic, specialized groups are often correctly delimited (Bremer and Wanntorp, 1978).

Modern cladistics reveals hypothetical evolutionary patterns and expresses them in a way that makes them refutable. Cladistics attempts to reconstruct lineages and establish classifications which reflect phylogeny (Janvier, 1984).

Cladistic studies have been undertaken in the Lamiaceae and associated taxa (Stenzel *et al.*, 1988; Cantino, 1982, An-Ming, 1990; Cantino, 1992; Rimpler and Winterhalter, 1992). Some of these studies revealed that the Verbenaceae and Lamiaceae as traditionally circumscribed, are probably polyphyletic and require major revision. Cantino (1992) divided the Lamiaceae into eight subfamilies, based on cladistic analyses. This chapter provides an analysis of *Leonotis* for southern Africa using the computer program Hennig86 (Farris, 1988). The characters and their polarization are listed below. The data matrix used for computation of the cladogram is also presented (Table 19).

Characters and character states:

Habit

1. Plant height (m): up to 5 (0); 1 plus (1); 0.5-1 (2).

Leaves

2. Shape: lanceolate (0); narrowly ovate to narrowly obovate (1); broadly ovate to orbicular (2).
3. Base: narrowly attenuate (0); broadly attenuate (1); truncate to cordate (2).

4. Length (mm): > 70 (0); 50-60 (1); 15-25 (2).

5. Width (mm): 5-18 (0); 30-42 (1); 45-55 (2).

6. Petiole: < 5 (0); 5 (1); 30 (2); > 40 (3).

7. Teeth per margin: up to 14 (0); > 14 (1).

8. Stomatal position: hypostomatous (0); amphistomatous (1).

9. Venation: eucamptodromus (0); craspedodromus (1).

Inflorescence

10. Flowers per verticillaster: < 90 (0); > 90 (1).

11. Maximum number of verticillasters per flowering stem: 9 (0); 5 (1); 2 (2).

12. Flowering stem internodes (mm): consistent (0); irregular (1).

13. Verticillaster shape: sub-spherical (0); spherical (1).

14. Verticillaster density: loose or compact (0); compact (1).

15. Pedicel length (mm): 5-8 (0); 2.5-4 (1); 0.5-2.5 (2).

16. Floral and vegetative leaves: similar (0); distinct (1).

Corolla

17. Length (mm): 44-53 (0); 32-44 (1); 19-32 (2).

18. Minimum throat diameter (mm): 4 (0); 3 (1); 2.5 (2).

19. Abaxial lip lobes: separate (0); fused (1).

20. Site of filament attachment: at the throat (0); below the throat (1).

Calyx

21. Lobes: blunt (0); blunt or spinescent (1); spinescent (2).

22. Tube: straight (0); seldom straight (1); deflexed (2).

Nutlet

23. Shape: oblong (0); obovate (1).

24. Length (mm): > 4.5 (0); < 4.5 (1).

25. Proximal apical margins: faint (0); distinct (0).

Habitat

26. Forest or forest margin (0); grassland (1); scrub or rocky outcrop (2).

Autapomorphies

Habit

27. Perennial (remaining species) (0); annual (*L. nepetifolia*) (1).

Leaf

28. Thickness (μm): 75-115 (*L. dubia*) (0), 120-265 (1).

29. Vestiture: glabrescent to puberulous (0); slightly scabrid (*L. randii*) (1).

30. Palisade mesophyll: uni-seriate (0); multi-seriate (*L. ocymifolia* ssp. *ocymifolia*) (1).

31. Cuticle thickness (μm): 0.5-1.1 (*L. dubia*) (0); 2-11 (1).

Corolla

32. Basal ring/s of non-glandular trichomes: 1 (0); 2-3 (*L. nepetifolia*) (1).

33. Nectar: sucrose-rich (0); hexose-rich (*L. nepetifolia*) (1).

Nutlet

34. Colour and surface: uniform brown, glossy (0); marmorated, dull (1).

35. Length (mm): > 4 (0); < 4 (1).

Breeding system

36. Facultatively: xenogamous (0); autogamous (1).

Results & Discussion

A single cladogram was generated for *Leonotis* in southern Africa using the data matrix outlined above. To improve the consitancy index characters were weighted using the command XS W this however did not alter the topology of the cladogram and thus homoplasy was not altering the initial trees generated. The resulting tree (figure 37) had a length of 256 steps, a consistency index of 81 and a retention index of 255.

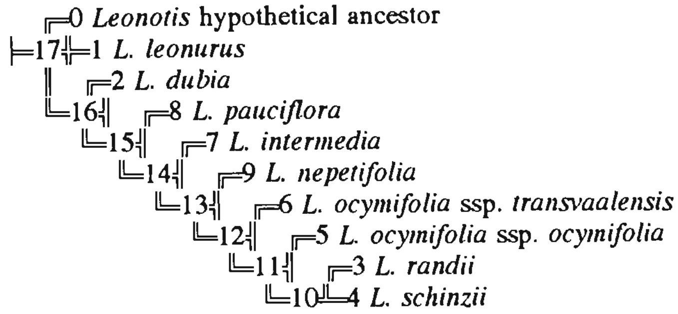


Figure 37. Cladogram of *Leonotis.*

Discussion and conclusion

Leonotis is a monophyletic group of closely related ornithophilous species. The similar essential oil profiles obtained for the majority of species studied (Chapter 11) support this claim.

The lack of floral divergence in perennial species is an indication of the success of ornithophily (Chapter 12). However, the autogamous annual, *L. nepetifolia*, is equally successful and is not dependent on sunbird pollinators. In addition *L. nepetifolia* has attained a pan-tropical distribution. The numerous autapomorphies displayed by *L. nepetifolia* such as a short corolla, 2-3 basal rings of corolla trichomes and hexose-rich nectar, associated with a switch to facultative autogamy, indicate a highly derived condition for this species.

L. nepetifolia does not show xeric adaptations and does not frequent high lying areas subject to frost. Consequently, it is vegetatively unspecialized and allied to the more mesic perennial species. The anatomy of *L. nepetifolia* differs from that of the perennial species as discussed in Chapter 4.

The proposed phylogeny is reasonably compatible with phytogeography (Chapter 13). Plesiomorphic species located basally on the cladogram are widespread and synapomorphic species located apically are more limited in distribution.

The basal position of *L. leonurus* on the phylogenetic tree correlates to its wide distribution and probable antiquity. *L. dubia* is also basal on the tree with plesiomorphic leaf characters associated with its forest habitat.

Plant habit (Chapter 13, Figure 36) and leaf size (Chapter 3) correlate with the proposed phylogeny. *L. ocymifolia* ssp. *transvaalensis* occupies an intermediate position on the cladogram between the big-leaved, tall species and the small-leaved, short species and may approximate the core species from which xeric species were derived. *L. ocymifolia* ssp. *transvaalensis* also occupies an

intermediate position, in the Transvaal (Chapter 13, Figure 34 A), between the East African and southern African species.
The terminal clade consisting of *L. schinzii* and *L. randii* implies a close relationship and recent derivation of these two species which frequent high lying areas subject to frost and low rainfall (Chapter 13). These species display synapomorphic characters associated with xeric habitats such as a low growth habit and small, hairy leaves. Similarly, *L. ocymifolia* ssp. *ocymifolia* displays xeric morphology (Chapter 3) but grows in nutrient-poor soils where rainfall is higher.

The majority of taxa have broadly ovate leaves, however, primitive species (*L. leonurus*) and derived species (*L. schinzii* and *L. randii*) display lanceolate leaves, indicating a possible reversal of leaf shape in the latter two species.

Calyx and inflorescence morphology provide some indication of phylogenetic polarity. Basal species on the cladogram (*L. leonurus* and *L. dubia*) have blunt calyx lobes and derived species have pungent lobes. Spinescence which is known to limit browsing (Cooper and Owen-Smith, 1986), reaches a peak in the annual species (*L. nepetifolia*) which has the highest fruit set (Chapter 12). Similarly, advanced species display many-flowered compact verticillasters, which may limit the lateral predation of nectar and afford better protection for developing nutlets than the few-flowered loose verticillasters of plesiomorphic or basal species (namely *L. leonurus* and *L. dubia*).

Chapter 15

Formal taxonomy

The genus *Leonotis*

Leonotis (Pers.) R. Br., Prodr. Fl. Nov. Holl. 504 (1810); in Ait. f., Hort. Kew. edn. 2,3: 409 (1811); Benth., Lab. 618 (1834); Spach, Hist. Nat. 9: 210 (1840); Benth. in DC., Prodr. 535 (1848); Benth. and Hook. f., Gen. Pl. 2: 1214 (1876); Briq. in Natürl. PflFam. 4,3a: 246 (1896); Bak. in Flora of Tropical Africa 5: 490 (1900); Skan in Flora Capensis 5,1: 374 (1910); Morton in Flora of West Tropical Africa 2: 470 (1963); Launert and Schreiber in Flora of South West Africa 123: 15 (1969). Lectotype species: *L. leonitis* R. Br., included here in *L. ocymifolia* (Burm. f.) Iwarsson *pro parte.*

Phlomis L. sect. *Leonotis* Pers., Syn. Pl. 2: 127 (1807), the rank of this taxon was not indicated.

Hemisodon Raf., Fl. Tellur. 3: 88 (1837). Type species: *H. leonurus* (L.) Raf.

Annual or suffrutescent perennial herbs or sub-woody shrubs up to 6 m tall, erect, seldom scandant, decumbent, procumbent or mat-forming, single-stemmed or strongly branched. Stems quadrangular, minutely puberulous to tomentose, seldom villous, usually with sessile glands, becoming cylindrical and glabrous. **Leaves** lanceolate to broadly ovate, seldom orbicular, glabrescent, puberulous or tomentose, with sessile glands, or discolorous due to silvery-white trichomes below, decurved or spreading, sometimes conduplicate, seldom sub-membranous; base attenuate, truncate or cordate; apex rounded to acuminate; margin crenate to serrate, sometimes revolute and or undulate, 3--60-toothed; petiolate. **Verticillasters** 3--11 per flowering stem, spherical or turbinate, loose or compact; flowering stems erect, 4-angled and 4-grooved, angles rounded or ridged, glabrescent, puberulous, tomentose or slightly scabrid, green; floral leaves usually smaller and narrower than the foliage leaves, pendant or spreading, caducous or persistent; bracts linear to subulate, blunt or pungent; pedicel up to 8 mm long. **Calyx** puberulous to velutinous; tubular, distal third of tube deflexed, seldom straight; 10-nerved; 8--10-lobed, lobes blunt or pungent; adaxial lobe 3-nerved, usually broader and longer than the remaining lobes, straight or flexed, remaining lobes usually 1-nerved, straight, spreading or reflexed, opposing medial lobes often imbricate, the lowest 3 abaxial lobes often deflexed. **Corolla** whitish, covered in non-glandular trichomes of various shades of orange to scarlet, rarely yellow or white, glabrescent within except for 1--3 basal rings of hairs; decurved; tubular, cylindrical, distally dilated, usually exserted; 2-lipped; adaxial lip entire, fringed; abaxial lip 3-lobed, reflexed and or twisted after anthesis, medial lobe usually slightly longer than the lateral lobes. **Androecium** stamens 4, didynamous, abaxial pair longer, inserted at or below the throat, included within the adaxial corolla lip; anthers 2-thecous, often with sessile glands near the filament junction. **Disc** abaxially enlarged. **Style** slightly bifid, abaxial lobe

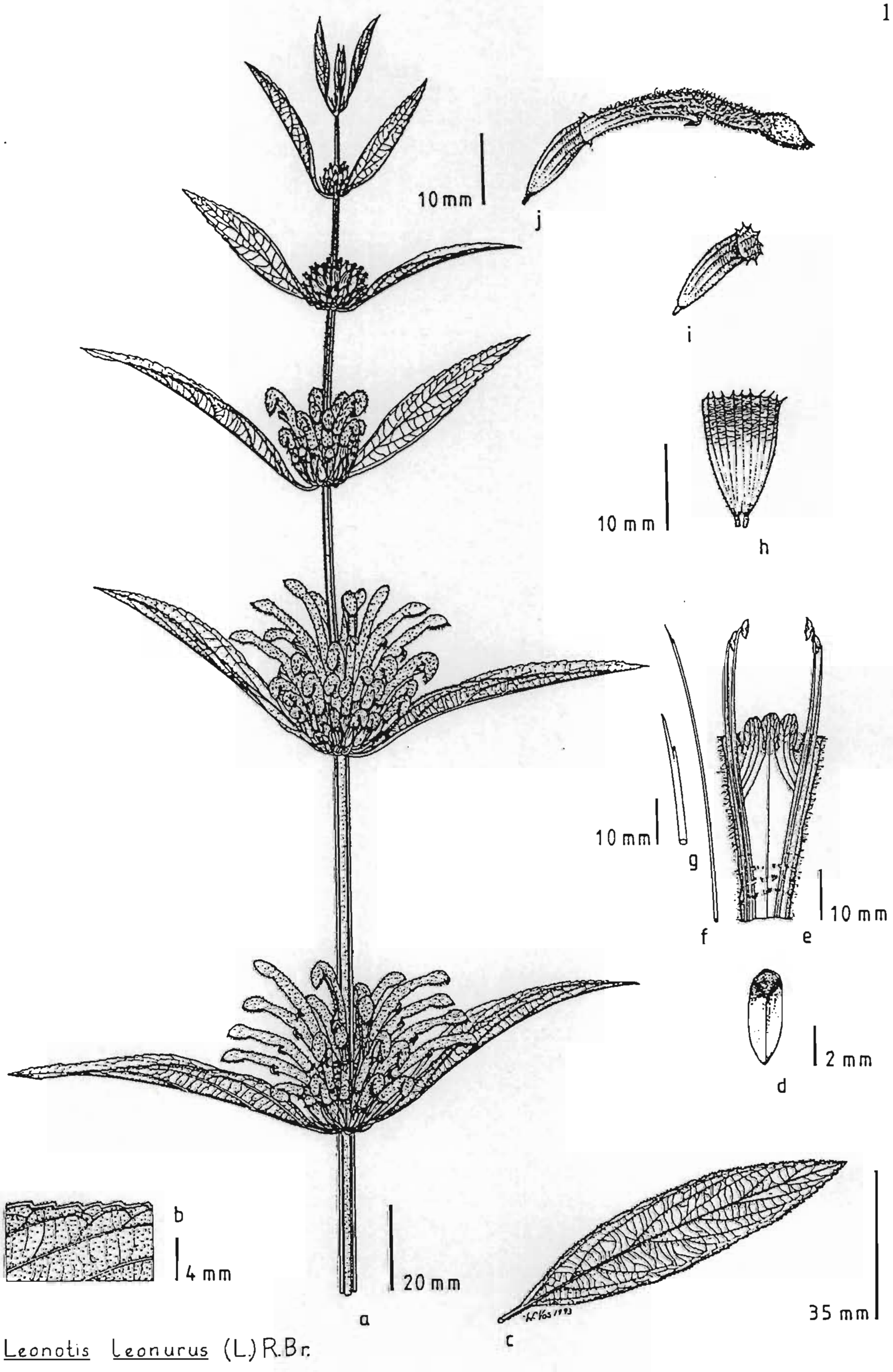


Figure 38. *Leonotis leonurus* (L.) R. Br. (a) flowering branch, (b) leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal rings of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla), (f) stigma and style (scale of f as for e), (g) stigma and distal part of style, (h) flattened calyx, (i) lateral view of calyx (scale of i as for j) and (j) calyx and corolla. Voucher: *Vos 78.*

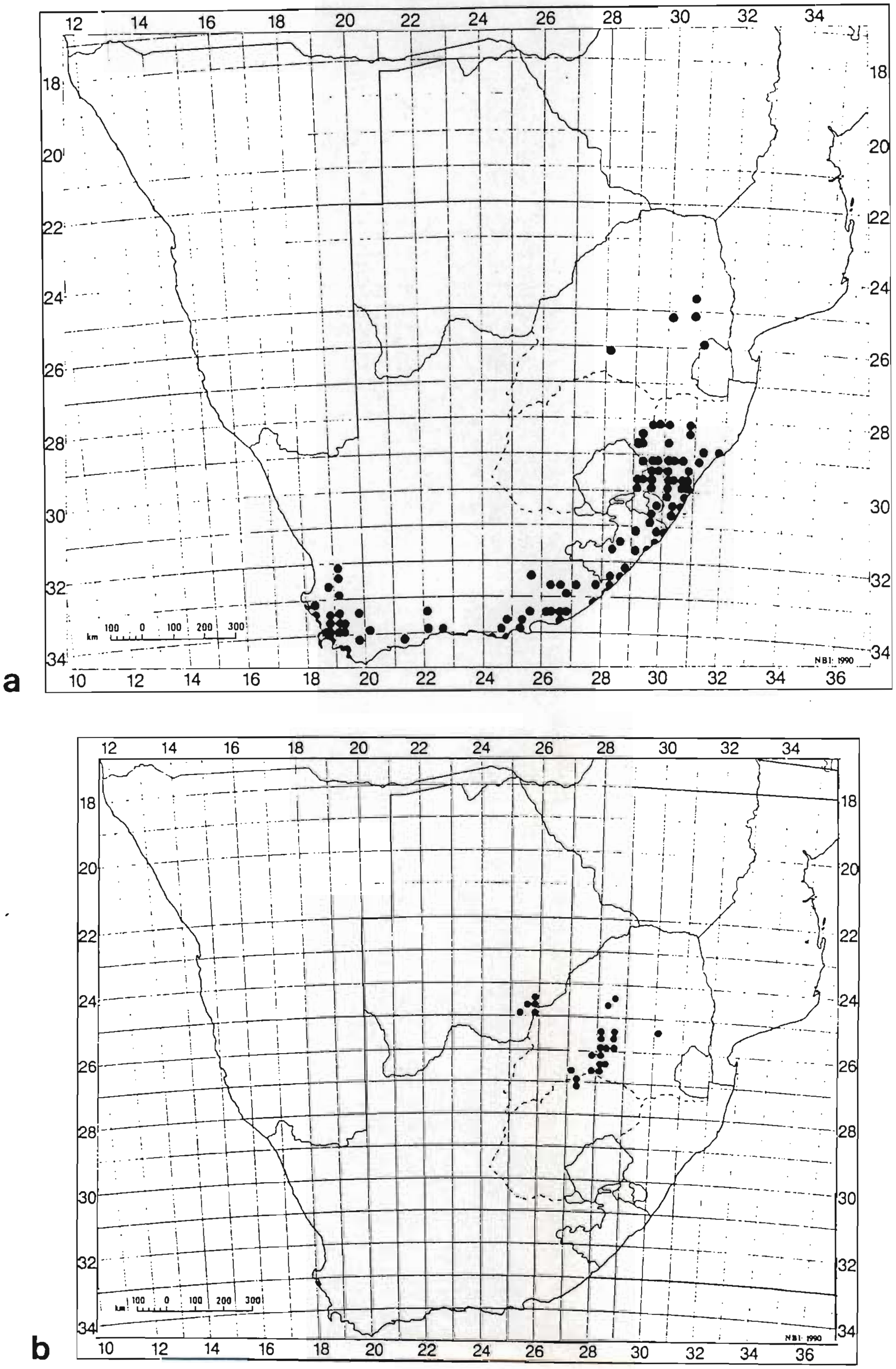


Figure 39. Recorded distribution of (a) *Leonotis leonurus* and (b) *Leonotis randii*.

reduced. **Nutlets** 3-angled in transverse section, obovate or oblong; distally glandular, truncate, obtuse or irregularly rounded; glabrous; usually brown to blackish and glossy.

Etymology: *Leonotis* is Greek for lion's ear and according to Hooker (1839) was adopted by Linnaeus due to the superficial resemblance of the fringed adaxial corolla lip to a lion's ear. A more appropriate name used by the Zulu tribe of South Africa is "uTchwala uBezinyoni" meaning "the beer of the birds", a reference to the copious nectar produced by this plant which is relished by sunbirds.

Key to the species of *Leonotis*

1a Calyx lobes 10, blunt, subequal; abaxial corolla lobes separate, subequal ...1. *L. leonurus*
1b Calyx lobes 8 (or less), pungent, adaxial lobe usually twice as long as the remaining lobes; abaxial corolla lobes fused, medial lobe slightly longer than the lateral petals ...2

2a Leaves narrowly obovate or narrowly ovate to lanceolate ..3
2b Leaves broadly ovate, elliptic or orbicular ...4

3a Leaves narrowly obovate to oblanceolate, glabrescent or sparsely pubescent and slightly scabrid, 10--35 x 4--12 mm, petiole 3--10 mm long; verticillasters 40--60 mm in diameter; Orange Free State, Transvaal, southern Botswana and Zimbabwe ...2. *L. randii*
3b Leaves narrowly ovate to lanceolate, tomentose, seldom glabrescent, 30--65 x 10--25 mm, petiole 8--20 mm long; verticillasters 30--45 mm in diameter; highlands of Namibia ...3. *L. schinzii*

4a Annual herb with shallow fibrous roots ...4. *L. nepetifolia*
4b Perennial herbs or shrubs with woody base ...5

5a Leaves usually 8--30 mm long, 5--13 teeth per margin ...6
5b Leaves usually more than 30 mm long, 7--26 teeth per margin ...7

6a Plants 0.5--1.5 m tall; lateral branches to 0.12 m long, leafy; Cape; 0--1500 m above sea level ...5a. *L. ocymifolia* ssp. *ocymifolia*
6b Plants 1--3 m tall; lateral branches to 2 m long, leafless except for the apical regions; Transvaal ...5b. *L. ocymifolia* ssp. *transvaalensis*

7a Pedicel (4--) 5--8 (--11) mm long, leaves sub-membranous, lax, usually glabrescent, petiole (7--) 30--90 (--110) mm long; floral and foliage leaves similar, spreading; in mist belt and coastal forest margins ...6. *L. dubia*
7b Pedicel 0.5--3.5 (--7) mm long, leaves not sub-membranous or lax, seldom glabrescent, petiole (4--) 10--50 (--70) mm long; floral leaves smaller and narrower than foliage leaves, pendant; common in grassland and on rocky outcrops ...8

8a Leaf base usually cordate; (15--) 28--45 (--60) flowers per verticillaster; calyx usually pungent; north-eastern Cape, northern Natal, Orange Free State and Lesotho ...7. *L. pauciflora*
8b Leaf base usually attenuate; (22--) 40--125 (--185) flowers per verticillaster; calyx blunt or pungent; Cape, Transkei, Natal, Orange Free State, Transvaal and Swaziland ... 8. *L. intermedia*

Species' descriptions:

1. **Leonotis leonurus** *(L.) R. Br.* in Ait. f. Hort. Kew. edn. 2,3: 410 (1811); Benth., Lab. 620 (1834); in E. Mey., Comm. 1: 243 (1837); Krauss in Flora 28: 66 (1845); Skan in Flora Capensis 5,1: 375 (1910). Type: Cape of Good Hope, Herb. *Linnaeus 740.19* (LINN, lecto.).

Phlomis leonurus L., Sp. Pl. 586 (1753); Mant. 2: 412 (1767); Bergius, Descr. Pl. Cap. 151 (1767); Thunb. Prodr. 2: 95 (1800); Sims in Bot. Mag. (Curtis) 478 (1800); Pers. Syn. Pl. 2: 127 (1807). *Hemisodon leonurus* (L.) Raf., Fl. Tellur. 3: 88 (1837). Type as above.

Leonurus africanus Mill., Dict. 768 (1768). No type material known.

Leonurus grandiflorus Moench, Meth. 400 (1794). No type material known.

Leonotis leonurus (L.) R. Br. var. *albiflora* Benth. in E. Mey., Comm. 1: 243 (1837); in DC., Prodr. 12: 537 (1848); Skan in Flora Capensis 5,1: 376 (1910). Type: Hexrivier, *Drège s.n.* (K!, lecto.; S, W). The specimens at Kew have the number *4829*.

Perennial shrub, 1.0--3.0 (--5.0) m tall, erect, weakly branched; lateral branches up to approximately 0.8 m long, leafless except for the apical regions. **Leaves** lanceolate, oblanceolate or narrowly elliptic, lamina (31--) 40--110 (--148) x 4--20 (--31) mm, puberulous or tomentose, older leaves discolorous due to silvery-white trichomes below; base acute or cuneate; apex acute; margin sub-entire or obscurely serrate to crenate distally, slightly revolute, (4--) 8--24-toothed; petiole (0.5--) 2--10 (--15) mm long. **Verticillasters** (3--) 5--8 (--11) per flowering stem, spherical or sub-spherical, 20--37 (--40) mm in diameter, compact, (12--) 35--55 (--89) flowers per verticillaster; cyme branches reduced; flowering stem 55--250 (--380) mm in length, grooved, tomentose; internodes (10--) 30--80 (--95) mm long; floral leaves lanceolate to oblanceolate, 40--90 x 4--15 mm, spreading, persistent, petiole 7--30 mm long; bracts linear to subulate, 5--27 mm long, pungent, curved upwards around the inflorescence; pedicel (1.5--) 2--4 (--5) mm long. **Calyx** 10--16 mm long, glabrescent to puberulous, tube linear or distal third slightly deflexed; 8--10-nerved; 8--10-lobed, lobes blunt, adaxial lobe equivalent to remaining lobes, acute to subulate, 0.5--2 (--4) mm long, sub-equal, patent or reflexed. **Corolla** orange to reddish, rarely creamy white, (35--) 40--53 (--60) mm long; tube (20--) 24--33 (--40) mm long with 1--3 incomplete inner basal rings of trichomes, throat dilated; adaxial lip 18-22 mm long; abaxial lip 5--7.5 x 6.6--8.5 mm, 3-lobed, lobes separate, lateral lobes 3--4.5 x 3--4 mm, obtuse, medial lobe 3.5--5 x 2.5--3.5 mm, spatulate, cucullate, apex obtuse, truncate, lip reflexed after anthesis. **Nutlets** oblong, 4.1--6 x 1.0--1.9 mm, flanks brown and glossy (Figure 38).

Recorded distribution: Cape, Ciskei, Transkei, Natal, Transvaal (Figure 39 a), Zaire, Angola, Zambia, Malawi and Tanzania.

L. leonurus was one of the first South African plants cultivated overseas by Jacob Breynius in 1663 (Batten and Bokelmann, 1966) and has subsequently become a popular garden subject in many parts of the world.

Habitat: grassland, savanna, scrub vegetation, forest margins and rocky slopes.

Flowering: mainly between March and May.

Allied species: three tropical African species, *L. pole-evansii*, *L. decadonta* and *L. goetzei*, have a similar calyx but differ in that the calyx is densely hairy with comparatively long, straight lobes. The leaves of these three species are broader than those of *L. leonurus* and the inflorescences have fewer verticillasters.

Etymology: *L. leonurus* is Greek for lion's tail, presumably the fancied resemblance of the inflorescence to a lion's tail. The vernacular name "wild dagga" ("dagga" is Afrikaans for marijuana) is inappropriate as the plant is seldom, if ever, smoked by African people.

Southern African material of *Leonotis leonurus* examined

South Africa

---**2430** (Pilgrim's Rest): Mariepskop (--DB), *Van der Schijff 4588* (PRE).
---**2530** (Lydenburg): Draaikraal (--AA), *Burgoyre 2205* (M); 3km NNE of Draaikraal (--AA), *Meeuse 10324* (M, PRE, S); Sabie (--BB), *Rogers 14672* (BOL).
---**2531** (Komatipoort): Barberton (--CC), *Thorncroft 19188* (MO, NBG, S).
---**2628** (Johannesburg): Germiston (--AA), *Harvey 25* (NU); near Germiston (--AA), *Pillans 8450 (PRE).*
---**2829** (Harrismith): Nolens Volens Farm E of Van Reenen's Pass (--AD), *Jacobsz 1549* (PRE); Tabamhlope Mtn. (--BA), *West 179* (PRE); Biggarsberg (--BB), *Rehmann 7058* (Z); Cathedral Peak, Mikes Pass (--CA), *Baxter s.n.* (NU); hill above Little Switzerland Hotel (--CB), *Anderson 287* (PRE).
---**2830** (Dundee): Indumeni (--AA), *Truscott 90* (PRE); Pomeroy district, Jacobskop, summit of plateau (--CA), *Venter 1813* (PRE).
---**2831** (Nkhandla): Eshowe (--CD), *Lawn 1542* (NH); Mtunzini (--DD), *Lawn 1539* (NH).
---**2929** (Underberg): Giant's Castle Game Reserve (--AB), *Trauseld 385* (NU); 20 km from Hlatikulu Vlei on road to Nottingham Road (--BA), *Edwards 913* (NU); entrance to Moor Park Nature Reserve (--BB), *Beaumont 98* (NU); Carter's Nek, Nottingham Road (--BC), *Hilliard 8224* (NU); Kamberg (--BD), *Wright 1793* (NU); Loteni Nature Reserve (--DA), *Phelan 379* (NU); Sunset Farm (--DC), *Rennie 4* and 281 (NU); Sunset Farm (--DC), *Vos 538* (NU).
---**2930** (Pietermaritzburg): Mooiriver (--AA), *Isherwood s.n.* (BM); near Rietvlei (--AB), *Nicholas* and *Isaacs 1291* (K, MO, PRE); Nottingham Road (--AC), *Brierley 92* (BM); Nottingham Road (--AC), Dunisa, *Button 79* (NU);

Tweedie (--AC), *Mogg 1058* (NU); Drayton, Lion's River (--AC), *Wright 1505* (NU); Greytown district (--BA), *Lawn s.n.* (NH); Greytown (--BA), *Newmark 15* (NU); Nsuze (--BD), *Strey 7527* (K, M); scrub on the road to Boston (--CA), *Maclean 796* (PRE); Town Hill (--CB), *Ahrens 13* (NU); Durban road, 6,43 km from Pietermaritzburg (--CB), *Keppler 6* (NU); Cascade Falls (--CB), *Lawson 120* (NU); Mountain Rise (--CB), *Levey 16* (NU); Pietermaritzburg (--CB), *Fitzsimons 26263 (PRE);* new botanical gardens (--CB), *Roetz 18* (NU); Byrne turn about (--CC), *Strey 11269* (MO, NH); Table Mtn. (--DA), *Killick 700* (NU); Table Mtn. vicinity, 1 km from Rietspruit, Behn/Chinn Estate (--DA), *Vos 78 and 300* (NU); Nagle Dam (--DA), *Wells 1561* (NU); Inanda (--DB), *Wood 164* (BM, K, NBG); Botha's Hill (--DC), *Akitt 12* (NU); Hillcrest (--DD), *Owen 2540* (NU).
---**2931** (Stanger): Thring's Post (--AA), *Moll 2274* (NU, PRE); Bluff near Durban (--CC), *Meebold 12850* (M).
---**3029** (Kokstad): Ibisi Cutting (--BD), *Ward 6276* (NU); Ngele forest (--DA), *Wirminghaus 1276* (NU); 8 km SW of Fort Donald between Emaqusheni and Bizana (--DC), *Lewis s.n.* (PRE).
---**3030** (Port Shepstone): Ixopo, Eastwolds road (--AA), *Huntley 354* (MO); Vernon Crookes Nature Reserve (--AD), *Duff 28* (NU); Vernon Crookes Nature Reserve (--AD), *Mooney 13* (NU); Vernon Crookes Nature Reserve (--AD), *Paige 1* (NU); Amamzimtoti (--BB), *Clarkson 56* (NU); Isipingo (--BB), *Pennifather 5* (NU); Isipingo Beach (--BC), *Ward 887* (NU); Scottburgh (--BC), *Goosens 1768* (PRE); Port Shepstone (--CB), *Weeks s.n.* (BM); Sunwich Port, Henderson's Estate (--DA), *Morgan 3* (NH).
---**3128** (Umtata): Umtata Mouth (--BC), *Johnson 68* (PRE); Baziya, Tembuland (--CB), *Baur 160* (NU).
---**3129** (Port St. John's): near Omsamvubu (--AA), *Drège s.n.* (BM); 40 km from Bizana on the road to Spesbona (--BB), *Van Wyk 1535* (PRE); Libode (--CA), *Barker 8235* (NBG); Manteku (--DA), *Strey 8941* (NH, NU, S).
---**3130** (Port Edward): S of Port Edward (--AA), *Bayliss 2215* (NBG, Z).
---**3218** (Clanwilliam): banks of the Olifantsrivier (--DB), *Galpin 11113* (PRE).
---**3219** (Wuppertal): Khamiesberg (--AA), *Pearson 5373* (K); Matjesrivier, Cedarberg (--AC), *Wagener 362* (PRE); Theerivier, Citrusdal (--CC), *Hanekom 2042* (MO, PRE).
---**3225** (Somerset East): Stockenstroom (--DD), *Schirach 285* (NBG).
---**3226** (Fort Beaufort): Fort Hare College, Tyumie River Bridge (--DD), *Griffen 460* (PRE).
---**3227** (Stutterheim): Tor Doon (--CA), *Archibald 95* (GRA); Forestry Department arboretum, Hogsback (--CA), *Johnson 1143* (PRE); Keiskammahoek, lower E slopes of Wolf Ridge (--CA), *Story 3488* (GRA); Komga, Prospect Farm (--DB), *Flanagan 251* (NBG); Komga (--DB), *Flanagan s.n.* (NU).
---**3228** (Butterworth): Old Fyfe-King Bridge, Willowvale (--AD), *Wood 64* (NU); The Haven (--BB), *Gordon-Gray 1167* (NU); Mazeppa Bay (--BC), *Phillipson 310* (MO); near Kentani (--CB), *Pegler 368* (BM, PRE); Kobongaba (--CB), *Taylor 3577* (NBG); Evelon (--CC), *Commins 1570* (PRE).
---**3318** (Cape Town): Hopefield (--AB), *Bachmann 1282* (Z); 10 km SE of Darlington (--AD), *Booysen 133* (NBG); Swartland (--BD), *Ecklon* and *Zehyer*

s.n. (BOL); Atlantis, Buffelsrivier Farm (--CB), *Boucher 4328* (PRE); Durbanville (--CD), *Police Department s.n.* (PRE); Lions Rump (--CD), *Burchell 108* (K); Table Mtn. (--CD), *Cormick s.n.* (BM); Devil's Peak (--CD), *Ecklon 48* (K); Cape Peninsula (--CD), around Cape Town (--CD), *Oldenburg 131* (BM); *Humbert 9422* (PRE); Wellington (--DB), *Thompson 178* (PRE); Rosendal (--DC), *Rehm s.n.* (M); Constantia (--DC), *Wallich s.n.* (BM); Jonkershoek (--DD), *Krausel 404* (M); Vlottenberg, near Stellenbosch (--DD), *Krausel 475* (M); without precise locality, *Drège s.n.* (K).
---**3319** (Worcester): Tulbagh road, river bank below station (--AC), *Smith 2694* (PRE); Hexrivierskloof (--BD), *Drège s.n.* (S); Hex River Pass (--BD), *Vos 334* (NU); Paarl side of Du Toit's Kloof (--CA), *Walters 1356* (NBG); Hexriver (-CB), *Drège 4829* (K); Wemmershoek (--CC), *Smuts 1117* (PRE); Waterval, Villiersdorp (--CD), *Rycroft 2208* (MO).
---**3320** (Montague): Montague Baths (--CC), *Page 83* (PRE).
---**3322** (Oudtshoorn): Schoemanskloof near Kango Caves (--AC), *Van Breda 4183* (PRE); Robinson's Pass (--CC), *Heginbotham 311* (NBG); Duiwels Kop Pass (--DC), *Rourke 445* (NBG).
---**3324** (Steytlerville): Zwartkops (--DB), *Ecklon 6* (M); kloof between Patensie and Mistkraal (--DB), *Lewis s.n.* (PRE); near Port Elizabeth on road to Seaview (--DC), *Rodin 1003* (BOL, MO).
---**3325** (Port Elizabeth): Zuurberg Mtns. (--BC), *Bayliss 6106* (PRE); Zuurberg, near the sanatorium (--BC), *Schonland 3239* (GRA); Springfields (--CB), *Paterson 3304* (GRA); Helpmekaar (--CB), *Schroeder 8* (NU); Van Staden's Nature Reserve (--CC), *Nkhotyana 1* (GRA).
---**3326** (Grahamstown): 5 km from Grahamstown Highlands road, roadside (--AC), *Brink 619* (GRA, PRE); Howieson's Poort (--AD), *Bayliss 7428* (MO, S); Grahamstown Nature Reserve (--BC), *Richardson 14* (GRA); Port Alfred road near Blackwoods Farm gate (--BC), *Van Wyk s.n.* (GRA); Artillery Dam (--BC), *Britten 1459* (PRE); between Kaffir Drift Police Station and Trappes Valley (--BD), *Burrows 3326* (GRA); slopes of Moutain Drive (--DA), *Daly* and *Cherry 943* (GRA); Grahahamstown (--DA), *Jacot Guillarmod 8564* (GRA).
---**3327** (Peddie): East London (--BB), *Sim s.n.* (NU).
---**3418** (Simonstown): Wynberg (--AB), *MacOwan s.n.* (GRA); Simonstown (--AB), *Meebold 12154* (M); Point and Smitswinkel Bay (--AB), *Phillips s.n.* (NBG); Hout Bay (--AB), *Wall s.n.* (S); Cape Flats (--BA), *Ecklon s.n.* (S); Stellenbosch Berg, behind Coetzenburg sportsfield (--BB), *Bos 26* (M, PRE); triangle at Van der Stel (--BB), *Smith 4686* (PRE).
---**3419** (Caledon): kloof near Mosselrivier (--AC), *Smith 4237* (PRE); Fern Kloof Nature Reserve (--AD), *Orchard 139* (MO); Sonderend River (--BB), *Hutchinson 3157* (BM, K); Uilenkraal E of Tafelberg (--CB), *Hugo 807* (PRE).
---**3421** (Riversdale): Riversdale (--AB), *Muir 5293* (PRE).
---**3423** (Knysna): (--AA), *Bayliss 1382* (G, Z); Vandervats (--AB), *Burchell 5288* (K); Keurbooms River, roadside (--AB), *Vos 292* (NU).
---**3424** (Humansdorp): Clarkson (--AB), *Thode A982* (K, PRE); Kabeljaaw's River (--BB), *Cruden 364* (GRA).

Without precise locality

Woody ravine, *Schmidt 160* (M); The Heights Farm, *Wiss 526* (M); *Miller s.n.* (BM); Uitenhage district, *Cooper 1499* (Z).

Non-southern African material of *Leonotis leonurus* examined

Tristan da Cunha Island
---**3712** (Tristan da Cunha): settlement garden *ex. hort.* (--BA), *Mejland 1644* (BM).

Madeira Island
---**3216** (Madeira Island): gardens at Funchal *ex. hort.* (--AA), *M'Cormick s.n.* (BM).

Zaire
---**1127** (Katanga): Elisabethville (--DA), *Rogers 26304* (BM).

Without precise locality
(North Katanga): Niembe River, *Kassner 3008* (BM).

Malawi
---**1133** (Mzimba/ Rhumpi): Chikangawa/Luwawa road near Mzimba road (--DA), *La Croix 3306* (MO); Rhumpi, Majimbula road, Nyika plateau (--DC), *Pawek 9982* (MO); North Nyasa, Nyika plateau (--DC), *Brass 17152* (BM, MO).
---**1134** (Nkhata Bay): 10 km S of Chikangawa (--CB), *Phillips 3419* (MO); Vipya Link road, Mzimba River (--CB), *Pawek 7270* (MO).

Angola
---**0916** (Malanje): Hochland Von Quela (--AC), *Nolde 163* (BM).

Without precise locality
Cambo Niederung, *Von Mechow's Expedition 498* (W); Rio Ludica at Baca varaquanha, *Gossweiler 1730* (BM).
(Benguela): Cuito River near Quipeio, *Exell* and *Mendonca 1887* (BM); Calupiango, headwaters of Cuito, *Gossweiler 12329* (BM).

Zambia
---**0830** (Northern): Abercorn (Mbala), Kambole road (--DD), *Richards 15275* (MO); Abercorn (--DD), *Burtt 6014* (K).
---**1328** (Copper Belt): Ndola, Mwekera stream crosses Ndola/ Mufulera road (--BA), *Linley 167* (MO).

Tanzania
---**0335** (Mbulu): Zambe plain (--DC), *Sanane 910* (K).
---**0538** (Iringa): Amani (--BA), *Emson 385* (K).
---**0631** (Mpanda): Uruwire plateau, Mpanda, on riverside (--AC), *Smith 1198* (K).

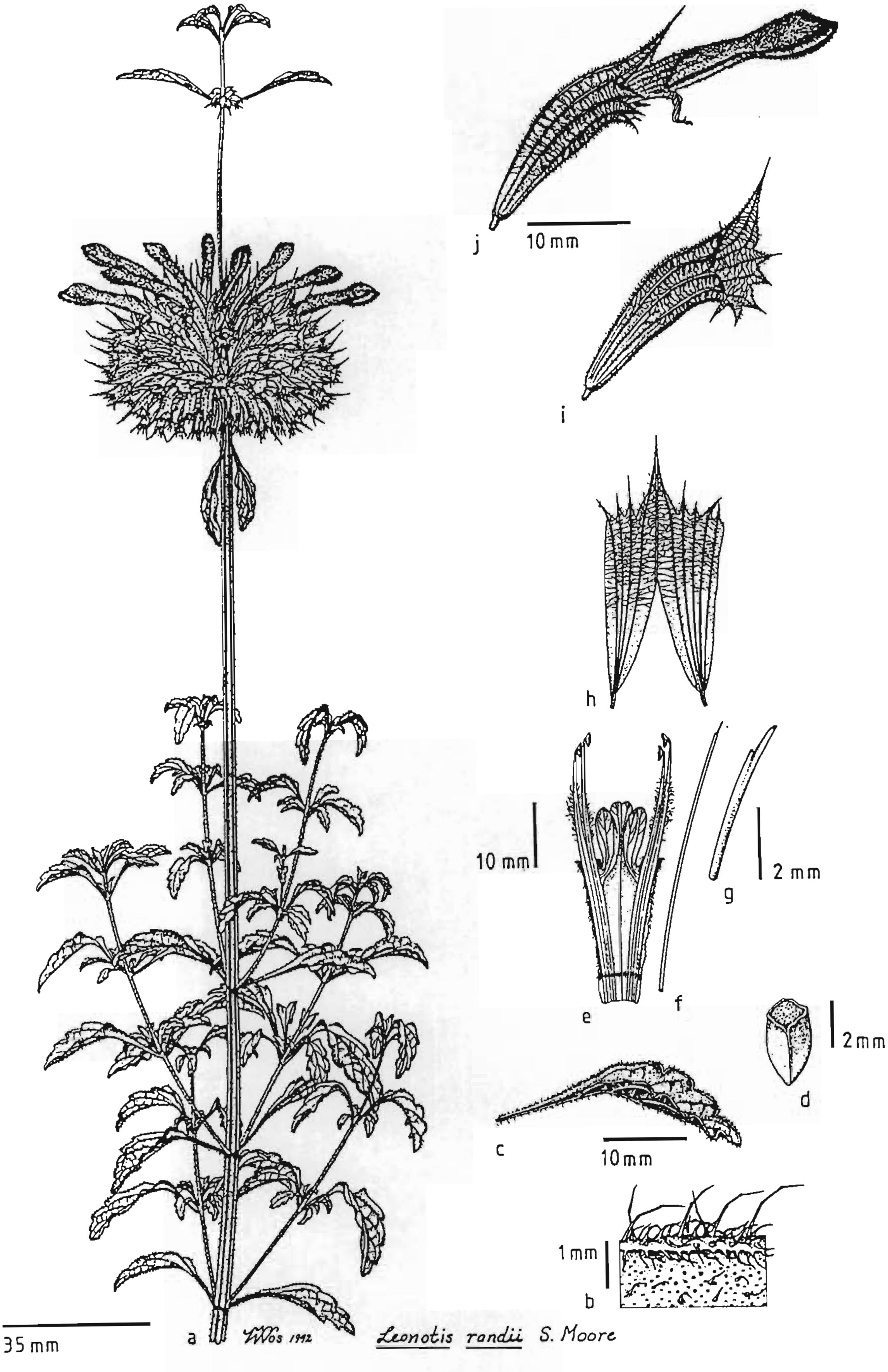


Figure 40. *Leonotis randii* S. Moore. (a) flowering branch, (b) abaxial leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla), (f) stigma and style (scale of f as for e), (g) stigmatic lobes, (h) flattened calyx (scale of h and i as for j), (i) lateral view of calyx and (j) calyx and corolla. Voucher: *Vos 268*.

---**0731** (Sumbawanga): Malonji Farm, Sumbawanga (--BA), *Richards 16810* (K); 14 km NNE of Sumbawanga in marshy ground, Nzika stream (--DC), *Mwasumbi, Mohamed* and *Kajula* 13192 (K).
---**0833** (Mbeya): Poroto Mtns. (--CD), *Richards 9727* (K); Poroto Mts. (--CD), *Richards 9729* (K).

2. **Leonotis randii** *S. Moore* in Bot. Linn. Soc. 38: 465 (1900). Type: Zimbabwe, Bulawayo, *Rand 165* (BM!, holo.; GRA!).

Leonotis microphylla Skan in Flora Capensis 5,1: 377 (1910); Dyer *et al.*, Wild Flowers of the Transvaal: 284 (1962); Van Wyk and Malan, Field Guide to the Wild Flowers of the Witwatersrand and Pretoria Region: 278 (1988). Type: Transvaal, Johannesburg, Jeppestown Ridges, *Gilfillan 161* in Herb. Galpin (K!, lecto.; BOL!, GRA!).

Perennial shrub, 0.3--0.8 (--2.0) m tall, erect or decumbent, strongly branched basally, seldom mat-forming; lateral branches up to 0.31 m long, leafy. **Leaves** narrowly obovate or oblanceolate, seldom ovate, lamina (5--) 10--35 (--53) x 4--12 (--17) mm, glabrescent, puberulous, often scabrid, glossy above, decurved, conduplicate; base narrowly attenuate; apex obtuse to rounded; margin coarsely serrate to crenate, revolute, 3--7 (--10)-toothed; petiole (1.5--) 3--10 (--18) mm long; apical leaves fascicled. **Verticillasters** 1--2 (--5) per flowering stem, spherical, (30--) 40--60 (--75) mm in diameter, compact, 31--85 (--144) flowers per verticillaster; (7--) 13--15 cyme branches, 5--27 mm long, 6--12 flowers per branch; flowering stem 110--330 (--600) mm long, shallowly grooved, puberulous to tomentose; internodes 65--220 (--250) mm long; floral leaves narrowly obovate, 8--43 x 3--7 mm, petiole 2--8 mm, pendant, caducous; bracts linear to subulate, (3--) 5--14 (--17) mm long, pungent, often curved around the verticillaster; pedicel (0.5--) 1--3.5 (--6) mm long. **Calyx** (12--) 18--27 (--30) mm long, glabrescent or puberulous, distal third of tube deflexed; 10-nerved; 8-lobed, lobes usually pungent, adaxial lobe acuminate, 4--9 (--14) mm long, flexed slightly upwards, remaining lobes acute to acuminate, (1.5--) 2--4 (--6) mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** rusty orange to reddish; 34--44 mm long; tube 14--26 mm long with 1 complete inner basal ring of trichomes; adaxial lip 14--24 mm long; abaxial lip 6--8.7 x 4--7 (--10.5), 3-lobed, lobes fused distally, lateral lobes 2--3.5 x 1.5--2.5 (--4) mm, sub-elliptic, apices acute to obtuse, medial lobe 2.5--4 x 2--3 mm, spatulate, apex obtuse, truncate to emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 3--3.5 x 1--2.5 mm, flanks dark brown and glossy (Figure 40).

Recorded distribution: Transvaal, Orange Free State and Botswana (Figure 39 b). The type specimen of *L. randii* (*Rand 165*) was collected in southern Zimbabwe near Bulawayo.

Habitat: Bankenveld, Sourveld and Mixed Bushveld and dry rocky hillsides.

Flowering: mainly between October and February.

Allied species: resembles *L. ocymifolia* ssp. *ocymifolia* but differs in the following: leaves narrowly obovate or oblanceolate, slightly scabrid, often sub-sessile. *L. randii* and *L. ocymifolia* ssp. *ocymifolia* are allopatric.

Etymology: named in honour of R.F. Rand (1856-1937). *L. randii* commonly occurs on rocky hills, hence the Afrikaans name "klipdagga" which literally translated means "rock marijuana".

Southern African material of *Leonotis randii* examined

Botswana

---**2425** (Gaberone): Kopong (--BD), *Turton* and *Norman 75* (GAB); Kanje, Pharing (--CD), *Hillary* and *Robertson 527* (PRE); Kanje, Ga-Ngwaketse (--CD), *Keoloale s.n.* (GAB); Kolobeng River, 27 km W of Gaberone (--DA), *Mett 146* (GAB); base of Makolodi Hills, roadside (--DB/DD), *Hansen 3492* (GAB, K, PRE); Lekkerlach, Marico (--DD), *Louw 304* (PRE).

South Africa

---**2428** (Nylstroom): 7 km SW of Geelhoutkop (--AD), *Leistner 156* (PRE); Sterkrivierdam Nature Reserve (--BC), *Jacobsen 2580* (PRE).

---**2528** (Pretoria): Zoutpan Experimental Farm, ± 50 km N of Pretoria (--AC), *Clarke 1174* (PRE); Sybrandskraal (--BC), *Repton 5742* (PRE); Wonderboompoort (--CA), *Leendertz 8557* (PRE); Meintjies Kop, *Merxmüller 115* (--CA) (BM, K, M); hills near Pretoria (--CA), *Scott Elliot 1405* (K); Pretoria, between Louis Botha's home and Zoogrounds, rocky hillslopes (--CA), *Smith 1238* (PRE); between Meintjieskop and Reservoir (--CA), *Smith 2839* (PRE); Meintjieskop, at quarry above Government Avenue (--CA), *Smith 3328* (PRE); Meintjieskop behind Union Buildings (--CA), *Vos 268* (NU); Murrayfield suburb, rocky outcrops (--CA), *Stephen 390* (PRE); Irene (--CC), *Rogers 24485* (PRE); between Pretoria and Warmbaths, 1 km before Babaleigie turnoff (--CD), *Van Wyk 441* (PRE); 32 km E of Pretoria (--DA), *Mauve s.n.* (NU); Premier Mine (--DA), *Rogers 20850* (PRE); Bekker Farm (--DC), *Phillips 478* (PRE).

---**2530** (Lydenburg): without precise locality (--AC), *Krynauw 129* (PRE).

---**2627** (Potchefstroom): 4 km NE of Krugersdorp, hills of sourbushveld, (--BB), *Acocks 18731* (PRE); Roodepoort, Transvaal Botanic Gardens (--BB), *Behr 363* (NBG); Krugersdorp (--BB), *Jenkins 9249* (PRE); Krugersdorp, Jack Scott Private Nature Reserve (--BB), *Wells 2392* (PRE); Losberg (--CA), *Botha 2863* (PRE); Boskop Hotel, base of ridge (--CA), *Louw 542* (PRE); Zandfontein, on route to Witkoppiesfontein (--CA), *Ubbink* and *Van Wyk 547* (PRE); Koedoeslaagte, on road to Venterskroon Koppies (--CD), *Ubbink 627* (PRE); 8.84 km from Vereeniging (--DB), *Mogg 20973* (MO).

---**2628** (Johannesburg): Johannesburg (--AA), *Galpin 6169* (GRA); Houghton Estate, sides of hill (--AA), *Bryant 48* (PRE); Jeppe's Town ridges (--AA), *Gilfillan 161* (K); Johannesburg (--AA), *Leendertz 6189* (PRE); Melville koppies, upper northern slope, below rock ledges (--AA), *Macnae 1290* (NBG); Melville Koppies Nature Reserve, old nature trail (--AA), *McMurtry 2457* (PRE); Doornfontein Farm, koppies and mountains (--AA), *Prosser 1194* (PRE); Kliprivieresberg, S of Rosettenville, rocky hills (--AC), *Wasserfall 894* (PRE); Heidelberg (--AD), *Leendertz 1035* (K, NBG); Milner Park kopjies (--AD), *Moss 6013* (BM); Zoo kopjies (--AD), *Moss 8369* (BM); Heidelberg (--AD), *Robertson 13709* (BM); Heidelberg (--AD), *Thode s.n.* (PRE);

Suikerbosrand, Nolte se Kloof (--CA), *Bredenkamp 444* (PRE).
---**2727** (Kroonstad): 18 km from Scandonovias Drift on road to Schoemans drift (--AB), *Lumley 144* (NBG).

Non-southern African material of *Leonotis randii* examined

Zimbabwe
---**1629** (Karoi): Mwami river bank (--DA), *Rand 148* (BM).
---**2028** (Bulawayo): Bulawayo Commonage (--BA), *Hopkins s.n.* (BM); Bulawayo, *Rand 165* (--BA), (BM (holo), GRA).

3. **Leonotis schinzii** *Gürke* in Bot. Jb. 22: 143 (1895). Type: Namibia (S.W.A.), Homeib, without precise locality, *Schinz 40* (Z!, lecto.; B†).

Leonotis ocymifolia (Burm. f.) Iwarsson var. *schinzii* (Gürke) Iwarsson in Fl. S. Afr. 28,4: 35 (1985). Type: Namibia, Nomeib, *Schinz 40*, (Z!, lecto.; B†).

Leonotis dinteri Briq. in Bull. Herb. Boissier ser. 2,3: 1090 (1903). Type: Namibia (S.W.A.), Hereroland, near Okahandja, Tabakstuin, *Dinter 249* (Z!, lecto.).

Leonotis hereroensis Briq. in Bull. Herb. Boissier ser. 2,3: 1092 (1903). Type: Namibia (S.W.A.), Hereroland, *Nels s.n.* (Z!, lecto.).

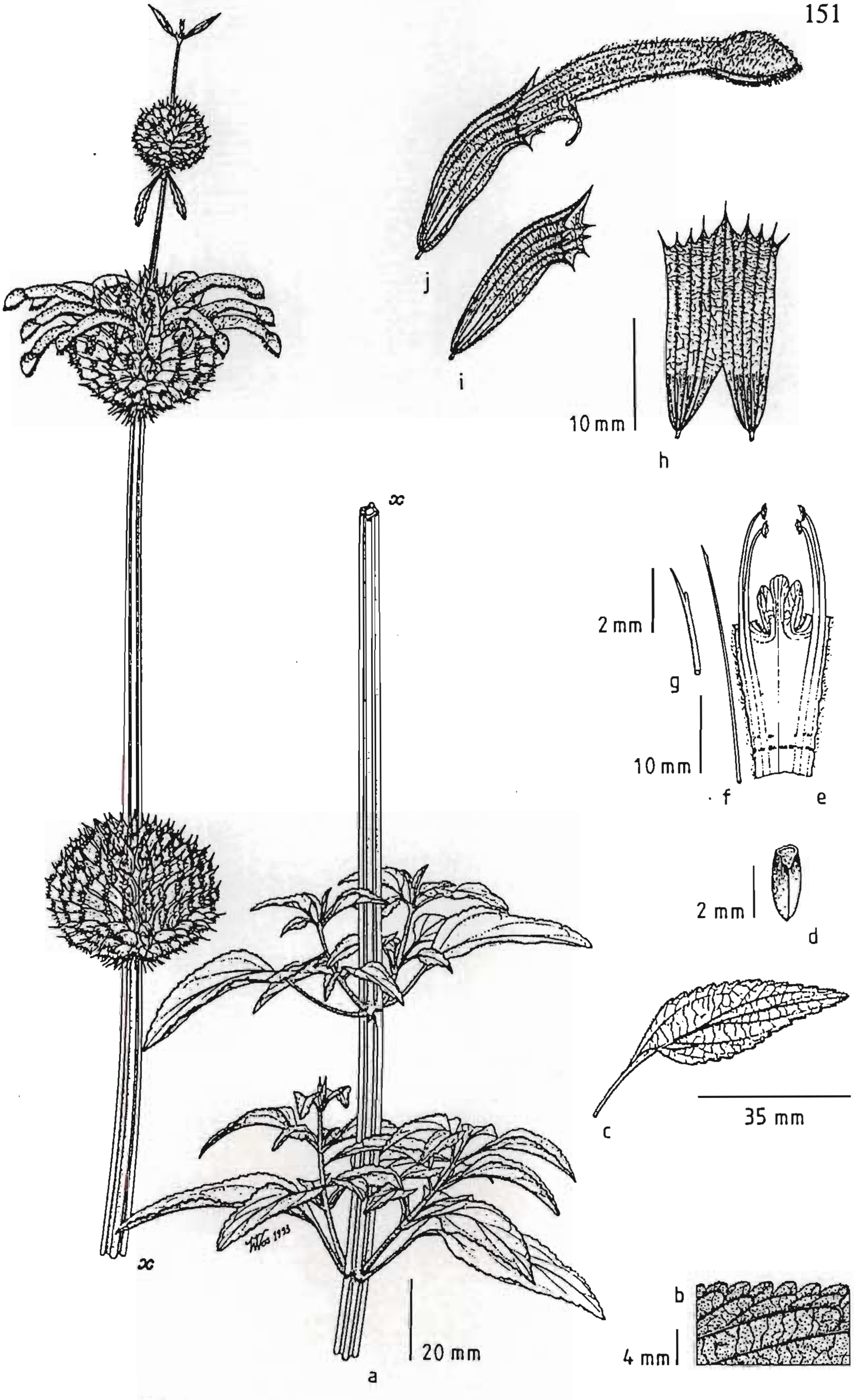
Perennial shrub, 0.5--1.0 (--3) m tall, erect, strongly branched basally; lateral branches up to 0.35 m long, leafy. **Leaves** ovate, narrowly ovate or lanceolate, lamina (20--) 30--65 (--80) x (5--) 10--25 (--30) mm, glabrescent, puberulous or tomentose, decurved, conduplicate; base shortly attenuate; apex acuminate or obtuse; margin serrate to crenate, (4--) 6--14 (--19)-toothed; petiole (3--) 8--20 (--35) mm long; apical leaves fascicled. **Verticillasters** 1--3 (--5) per flowering stem, spherical, 30--45 (--58) mm in diameter, compact, (15--) 38--68 flowers per verticillaster; 6--9 cyme branches up to 13 mm long, 6--10 flowers per branch; flowering stem (113--) 210--630 (--700) mm long, grooved, glabrescent to tomentose, often hollow at maturity; internodes (35--) 60--190 (--270) mm long; floral leaves narrowly ovate to oblanceolate, 12--38 (--48) x 3--12 mm, pendant, caducous, petiole up to 9 mm long; bracts linear, subulate to oblanceolate, 4--15 x 0.5--2 mm long, pungent, spreading; pedicel 0.5--3 (--6) mm long. **Calyx** 15--26 mm long, puberulous, velutinous or villous, distal third of tube deflexed; 10-nerved; 8-lobed, lobes blunt or pungent, adaxial lobe acute to acuminate, (2.5--) 3--7 mm long, flexed slightly upwards, remaining lobes acuminate, 0.5--3.5 mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** orange, (24--) 32--39 mm long; tube (11--) 15--20 mm long with 1 complete inner basal ring of trichomes; adaxial lip 12--18 mm long; abaxial lip 6--9 x 6--7 mm, 3-lobed, lobes fused distally, lateral lobes 1.5--3.5 x 2--3 mm, sub-elliptic, apices obtuse, seldom acute, medial lobe 2.5--3.5 (--4.5) x 2--3.5 mm, spatulate, apex truncate to emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 3.5 x 1.3--1.9 mm, flanks dark brown to blackish, glossy (Figure 41).

Recorded distribution: Namibia (Figure 42 a).

Habitat: savanna, highland savanna, semi-desert and savanna transition, grassland, scrub, dry water courses, rocky hillsides and disturbed sites.

Flowering: mainly between January and April.

Allied species: *L. randii* has similar leaves but these are considerably smaller and have fewer marginal teeth. These two species are allopatric.



Leonotis schinzii Gürke

Figure 41. *Leonotis schinzii* Gürke . (a) flowering branch, (b) leaf margin (*Dinter 90*), (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla) (*De Winter 2612*) (scale of e as for f), (f) stigma and style, (g) stigma and distal part of style, (h) flattened calyx, (i) lateral view of calyx (scale of i and j as for h) and (j) calyx and corolla. Voucher: *Dinter 5449*.

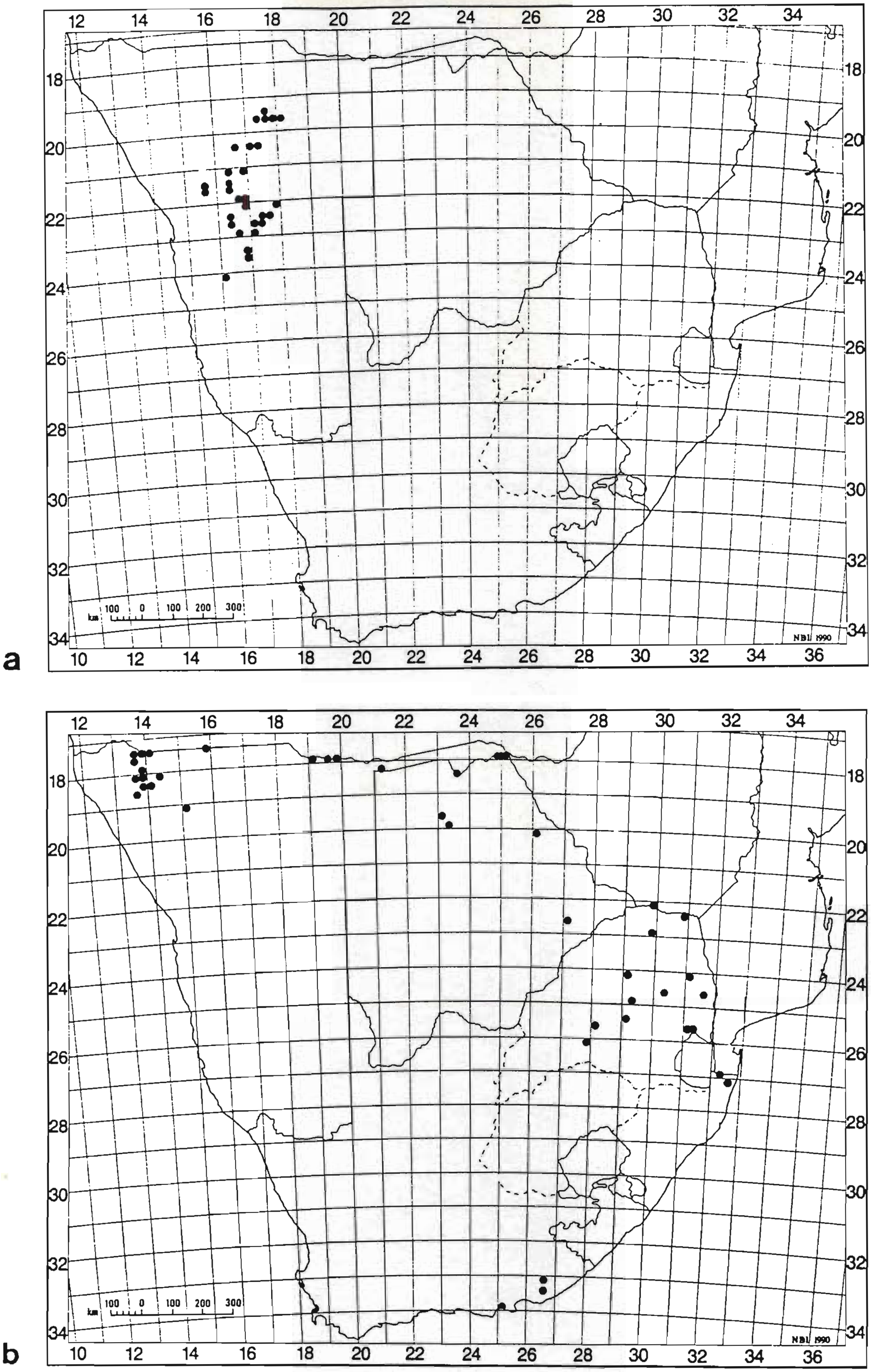


Figure 42. Recorded distribution of (a) *Leonotis schinzii* and (b) *Leonotis nepetifolia*.

Etymology: *L. schinzii* was named in honour of the late H. Schinz (1858-1941).

Southern African material of *Leonotis schinzii* examined

Namibia (South West Africa)

---**1917** (Tsumeb): Ghaub (--BC), *Dinter 2457* (NBG); Otavi (--CB), *Dinter 1726* (NBG); Otavifontein (--CB), *Dinter 5449* (BOL, G, NBG, NU, PRE); Grootfontein, Elefantenberg Halt, Kumkauas Farm (--CB), *Kinges 2895* (PRE, M); 15 km from Otavi along road to Tsumeb (--CB0, *Kolberg* and *Maggs 553* (NU); 10 km before Otavi travelling from Otjivarongo (--CB), *Wanntorp 475* (S); Kombat Farm, GR 656 (--DA), *Giess 8567* (M, PRE, WIND); Talsohle, Auros Farm GR 595 (--DA), *Merxmüller* and *Giess 30133* (M, WIND); Grootfontein, Kombat, next to road (--DA), *Merxmüller* and *Giess 2170* (PRE, M, WIND); Uitsab Mine (--DB), *Naegelsbach 72* (M).
---**1918** (Grootfontein): N of Grootfontein (--CA), *Schoenfelder 498* (PRE).
---**2016** (Otjiwarongo): Waterberg (--BC), *Kinges 2559* (PRE); Waterberg (--BC), *Liebenberg 4776* (PRE, WIND); Waterberg (--BC), *Schelpe 186* (BOL).
---**2017** (Waterberg): Omuramba, Otjenga (--AC), *Launert 1404* (M); near Waterberg in Waterberg Mts. (--AC), *Rodin 2581* (BOL, MO, PRE); Waterberg, Omuverume Plateau (--AC), *Rutherford 37* (WIND); Okarikuwisa, Waterberg Plateau Park (--AD), *Jankowitz 512* (WIND). ---**2115** (Karibib): Omaruru (--BD), *Hardy 2031* (WIND); Ombu Farm OM 130 (--DA), *Giess 8423* (M, WIND).
---**2116** (Otjimbingwe): Otjiwarongo, Mt. Etjo Safari Lodge (--AB), *Immelman 468* (WIND); 80 km W of Windhoek on the road to Otjimbingwe Reserve (--AD), *De Winter 2612* (M, PRE, WIND); 18 km NW of Seeis, Voigtskirch Farm (--AD), *Kers 2519* (M); Okahandja, Tabakstuin (--BB), *Dinter 249* (Z); Khomas Hochland, Fieldnau Farm (--CB), *Sassner 96* (M); Ongombombero Farm, 40 km before Okahandja travelling from Karibib (--DC), *Wanntorp 852* (K, RBG, S); Okahandja (--DD), *Dinter 90* (NBG).
---**2214** (Swakopmund): Dammara land, coast due W of Windhoek, without precise locality, *Een s.n.* (BM).
---**2217** (Windhoek): Voigtskirch Farm 135, 40 km from Kapps Farm (--AD), *Wanntorp 214* (K, S); Okakua (--BB), *Von Koenen 547* (WIND); Windhoek Bergland, Bodenhausen (--BC), *Seydel 2708* (M, WIND, MO); Kruin road to Bergland (--CA), *Giess 153* (M); Regenstein Farm WIN 32 (--CA), *Giess 11647* (M, WIND); Windhoek, 6.76 km W of Neudam College (--CA), *Vuuren 998* (M, W, WIND); Windhoek (--CA), *Wilman 15267* (BOL); Finkenstein (--CB), *Seydel 3843* (M); Immental Farm (--CB), *Von Koenen s.n.* (WIND); Lichtenstein Farm (--CC), *Merxmüller* and *Giess 1246* (M, PRE, WIND).
---**2316** (Nauchas): Spitzkop Farm (--BD), *Giess, Müller* and *Hub 11550* (M, WIND); Nomeib (--DB), *Schinz 40* (Z).
---**2416** (Maltahohe): Naukluft Mts., between Goas and Kabiras (--AA), *Pearson 9087* (BOL).

Without precise locality

---**1918** (Grootfontein): Ossa Farm, Diessel, *Walten 611* (WIND).
---**2217** (Windhoek): Avis, *Seydel 1709* (MO, S, WIND); Avis, Avisrivier; Otjihaenena, Omuramba (--B?), *Volk 533* (M).
Rietfontein, Felshany-fraint, *Leippert 4284* (M); *Nels s.n.* (Z); small Bergriver, Windhoek Bergland, Avis, *Seydel 3456* (G, M, MO).

4. **Leonotis nepetifolia** *(L.) R. Br.* in Ait. f., Hort. Kew. edn. 2, 3: 409 (1811); Ker-Gawler in Bot. Reg. t. 281 (1818); Benth., Lab. 618 (1834); Hook. in Bot. Mag. 6, 65: 3700 (1839); in DC., Prodr. 12: 535 (1848); Bak. in Flora of Tropical Africa 5: 491 (1900); Morton in Flora of West Tropical Africa 2: 470 (1963); Launert and Schreiber in Flora of South West Africa 123: 16 (1969). Iconotype: plate p. 117 in Hermann, Horti Academi Lugduno-Batavi Catalogus (1687), figured from a plant raised from seeds originally from Surinam (lecto.).

Phlomis nepetifolia L., Sp. Pl. 586 (1753); Willd., Sp. Pl. 3: 128 (1800); Pers., Syn. Pl. 2: 127 (1807). Iconotype: plate p. 117 in Hermann, Horti Academi Lugduno-Batavi Catalogus (1687), figured from a plant raised from seeds originally from Surinam (lecto.).

Leonotis kwebensis N.E. Br. in Kew Bull. 3: 132 (1909). Type: Botswana, Kwebe Hills, *Lugard* 222 (K!, holo.).

Single stemmed annual, (0.5--) 1--3.0 m tall, erect, strongly branched; lateral branches often exceed 1 m in length, leafless except for the apical regions, apical nodes often sparsely hirsute. **Leaves** ovate to broadly ovate, lamina (20--) 50--125 (--245) x (12--) 40--80 (--100) mm, glabrescent or puberulous, sub-membranous; base cordate, truncate or attenuate; apex acute to acuminate; margin coarsely and irregularly crenate, seldom dentate, slightly revolute, 9--34-toothed; petiole (6--) 15--60 (--90) mm long. **Verticillasters** 1--3 (--5) per flowering stem, spherical, (30--) 40--60 (--65) mm in diameter, compact, (18--) 25--167 (--210) flowers per verticillaster; 9--18 cyme branches, 2--16 mm long, 8--21 (--28) flowers per branch; flowering stem (90--) 220--650 (--1500) mm long, stout, deeply grooved often with dark green lines in the furrows, glabrescent to puberulous, internodes 20--270 mm long; floral leaves narrowly obovate to oblanceolate, 28--70 (--104) x 5--30 mm, petiole (6--) 15--90 mm long, pendant, persistent; bracts linear to subulate, 1--19 mm long, pungent, angled downwards at ± 45 degrees; pedicel 0.5--2 mm long. **Calyx** (13--) 18--25 (--32) mm long, glabrescent, puberulous or villous; distal third of tube deflexed; 10-nerved; 8-lobed, lobes strongly pungent, especially when brown and dry, adaxial lobe acuminate, 6--11 mm long, flexed slightly upwards, remaining lobes acute to acuminate, 1--4 mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** orange to scarlet, rarely light orange, 19--32 mm long, somewhat pendulous; tube 9--18 mm long, usually with 2--3 complete inner basal rings of trichomes; adaxial lip 11--18 mm long; abaxial lip 3.5--6 x 3.5--6 mm, 3-lobed, lobes fused medially or distally, lateral lobes 1.5--2 x 1.5--3 mm, sub-elliptic, apices obtuse, medial lobe (1.5--) 2--3 x 1.5--2 mm, spatulate, apex obtuse, truncate, lip spreading or reflexed after anthesis. **Nutlets** obovate, 3.0--4.3 x 1.0--1.9 mm, flanks marmorate dull grey to cream and brown (Figure 43).

Recorded distribution: pantropical and southern African (Figure 42 b).

Habitat: various vegetation types and disturbed sites.

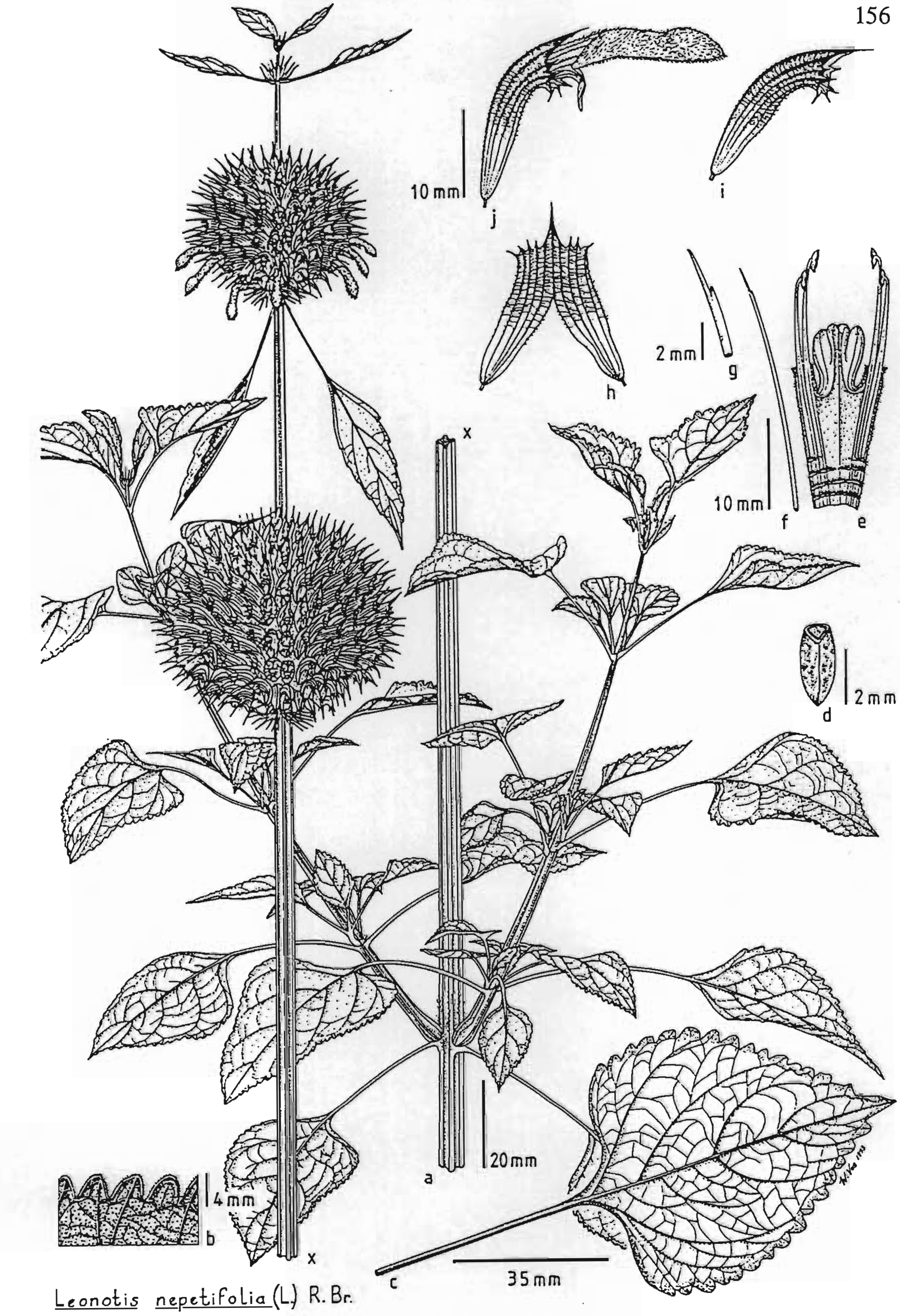


Figure 43. *Leonotis nepetifolia* (L.) R. Br. (a) flowering branch, (b) leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal rings of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla) (scale of e as for f), (f) stigma and style, (g) stigma and distal part of style, (h) flattened calyx (scale of h and i as for j), (i) lateral view of calyx and (j) calyx and corolla. Voucher: *Vos 174*.

Flowering: mainly between February and June.

Allied species: *L. nepetifolia* is the only annual species in the genus and has a shallow, fibrous root system compared to the remaining species which are suffrutescent. The leaves are similar to those of *L. dubia* in shape and texture, however it is easily distinguished by its densely packed, spinescent verticillasters, and flowers which have short corolla tubes with three basal rings of hairs.

Etymology: *Nepeta* Riv. ex L. or catmint is a member of the Lamiaceae which bears similar leaves to *L. nepetifolia.*

Southern African material of *Leonotis nepetifolia* examined

Namibia (South West Africa)

---**1713** (Swartbooisdrif): Koakoveld (--BD), *Giess 9323* (M); 25 km W of Ruacana Falls, (--BD), *Rodin 9188* (MO); Otjitambi, Hondoto River (--DA), *Giess 3159* (M, PRE).

---**1813** (Opuwo): flat-topped mountain about 4.82 km NNE of Ohopoho (--BA), *De Winter* and *Leis 5283* (M, PRE); 48.27 km S of Ohopoho (--BB), *Hall 361* (NBG); around Ohopoho (--BB), *Merxmüller* and *Giess 1522* (M); 48 km S of Ohopoho (--BD), *Hall 362* (NBG).

---**1814** (Otjerunda): 33.78 km E of Ohopho (--AB), *Merxmüller* and *Giess 30373* (M, PRE).

---**1822** (Kangara): Bonga (--CB), *Schlechter 12655* (BM).

Without precise locality

---**1821** (Andara): along road from Andara to Bagani (--A?), *Merxmüller* and *Giess 1987* (M).

Botswana

---**1923** (Maun): island Boro floodplain (--CA), *Biggs s.n.* (PRE); in garden 300 yards from river (--CD), *Lambrecht 85* (PRE).

---**2026** (Nata): Nata River Delta (--AA), *Ngoni 490* (MO).

---**2227** (Palapye): Palapye, Malete (--CA), *De Beer 695* (PRE).

South Africa

---**2229** (Waterpoort): Parkfield (--DD), *Raal 422* (PRE).

---**2230** (Messina): Mutale River, Maalgate (--BD), *Van Rooyen 3277* (PRE).

---**2429** (Zebediela): Arabie, Lebowa, camp H1, roadside, Olifants River (--CD),
Ellery 414 (PRE).

---**2430** (Pilgrim's Rest): 0.5 km SE of Mineralbad turnoff on the R36 main road (--BD), *Vos 419* (NU); Spekboom River Bridge, 3.22 km N of Burgersfort, riverside (--DB), *Storey 054* (PRE).

---**2431** (Acornhoek): on road 10 km S of Phalaborwa, Water Board, Shiela 10 KU (--AA), *Retief 576* (PRE); Seweweekspoort (--AD), *Lewis s.n.* (NBG); 10

km S of Satara, roadside (--BD), *Thrash s.n.* (NU); Manyaleti Game Reserve (--DA), *Bredenkamp 1579* (PRE).
---**2528** (Pretoria): Menlyn drive near Constantia Primary School, roadside (--CA), *Joffe 37* (PRE); intersection of Menlyn and Eybers drive, Pretoria (--CA), *Vos 174* (NU).
---**2529** (Witbank): Maloeksekop, near Derielton (--AC), *Codd 9905* (BM).
---**2531** (Komatipoort): The Gorge, Kruger National Park (--CA), *Van der Schijff 2345* (PRE); 3 km W of Malelane, beside watercourse (--CB), *Codd 2538* (PRE).
---**2627** (Potchefstroom): Transvaal Botanic Garden (--BB), *Behr 404* (NBG).
---**2632** (Bela Vista): Ndumo Game Reserve, below red cliffs (--CD), *Pooley 597* (NU).
---**2732** (Ubombo): Tembe Elephant Park (--BA), *Ward 2001* (NH).
---**3318** (Cape Town): Kirstenbosch Botanic Gardens (--CD), *Anon s.n.* (NBG).
---**3325** (Port Elizabeth): New Brighton (--DC), *Tsuane s.n.* (PRE).
---**3326** (Grahamstown): Victoria Rd. (--BA), *Boor s.n.* (GRA); Gunfire Hill (--BC), *Bishop 44* (MO).

Without precise locality
Natal University Botanic Gardens (Pietermaritzburg) (*ex hort.*), seed from the Botanical Research Institute of Pretoria, *Vos 420* (NU).

Non-southern African material of *Leonotis nepetifolia* examined

Africa
Congo
---**0028** (Kalehe): Ile Fshegera, Lake Kivu (--DD), *Germain 3307* (K).
---**0229** (Lake Kivu): Idjwi Island, Lake Kivu (--AA), *Loveridge 646* (K); Kivu North, Goma (--AA), *Stauffer 3* (K).

Uganda
---**0031** (Mwanga): without precise locality (--BD), *Swynnerton 45495* (NBG).
---**0032** (West Mengo): Gayaza Road (--CB), *Ruaburindore 704* (MO).

Kenya
---**0037** (Central): Kirerwa (--DD), *Dummer 336* (NBG).

Rwanda
---**0229** (Butare): Gihindamuyaga (--DA), *Raynal 20349* (K).

Cameroon
Without precise locality
---**0312** (Aconolinga): Koza, 15 km NNE of Mokolo, *Letouzey 6956* (K).

Burundi
---**0329** (Bubanza): Bubanza province, 20 km from plaine Rusizi (--AD),

Reekmans 11128 (MO).

Tanzania
---**0430** (Buha): Buha near Kakonko (--AB), *Smith 857* (K).
---**0636** (Dodoma): Ikova reservoir (--AA), *Mhoro* and *Backens 1963* (K).

Ethiopia
---**0737** (Alalia): Alalia, Omo Valley (--CB), *Turton 71* (K).

Sudan
---**0933** (Jongol's Post): near Jongol's Post (--BA), *Sherif 3995* (K).
---**1229** (Kordofan): Dilling (--DC), *Patel* and *El Kheir 3* (K).

Malawi
---**1334** (Salima): near railway line (--CD), *Balaka 1110* (NBG).

Senegal
---**1417** (Rufisque): Rufisque, Sangalkam (--BD), *Adam 414* (MO).

Angola
---**1714** (Ruacana Falls): 25 km W Ruacana Falls, Kwanyama, Eetilovalodi (--AC), *Rodin 9188* (M, PRE).
---**1715** (Ondangwa): Etilovalodi, Omatiovalodi (--BD), *Loeb 348* (PRE).
---**1719** (Rundu): 43.2 km E of Rundu along main road (--DD), *Merxmüller* and *Giess 408* (M).

Zambia
---**1725** (Livingstone): Kasane (--CC), *Mott 280* (PRE).

Madagascar
---**2246** (Fianaranatsoa): Zazafotzy (--AB), *Croat 30382* (MO),

Mozambique
---**2532** (Maputo): Namaacha (--BB), *Marques s.n.* (NBG); Umbeluzi, Sol do Savo (--CA), *De Carvalho 895* (NBG); Namaacha, base of Lebombo Mts. (--CC), *Marques 1981* (NBG).

Asia
Sri Lanka (Ceylon)
---**0779** (Puttalam): Chattychena (--BB), *Sumithraarchchi 709* (K).
---**0780** (Matale): Dambulla (--BC), *Cramer 4851* (K).

Thailand (Siam)
Without precise locality
---**1898** (Chiang Mai): Chawmtawng, *Garrett 902* (K),

India

Without precise locality
---**3176** (Punjab): Karnal Jungle, *Drummond 25945* (K).

Australia
---**13130** (Darwin): Blackfellow Creek, Daly River Road (--DB), *Rankin 2901* (K).
---**33157** (New South Wales): La Perouse (--CC), *Coveny* and *Powell 6428* (K).

Mexico
Without precise locality
---**1999** (Mexico): Rancho del Flores near San Pablo, *Happ 229* (MO).
---**25100** (Nuevo Leon): Canon de Huajuco, *Barkley s.n.* (MO).

Central and South America
Colombia
Without precise locality
---**0477** (Buga): Rio Guadalajara riverbank, *Murphy 588* (K).

Venezuela
---**0871** (Qda. Idea): Paraguana, 3 km S of Pueblo Nuevo (--DA), *Wingfield 7289* (K).

Lesser Antilles
Without precise locality
---**1261** (?): Langshurt, *Stoffers 505* (K).

Honduras
---**1486** (El Zamerane): 32 km E of de Tegucigalpa (--CD), *Sosa 2* (MO).

Guatemala
Without precise locality
---**1590** (?): Sayaxche, bordering Rio Pasion, *Contreras 9567* (MO).

Brazil
Without precise locality
---**1846** (Minas Gerais): Viscosa, Fazenda de Bon Jardim Reserva, *Mexia 5429* (K).

Porto Don Pedro II, *Dusén 880a* (MO).

Argentina
---**2554** (Prov. Misiones): Dep. Iguazú, Parque Nacional del Iguazú (--DA), *Ferrucci, Radovancich* and *Vanni 489* (K).

5. **Leonotis ocymifolia** *(Burm. f.) Iwarsson* pro parte.

Phlomis ocymifolia Burm. f., Prodr. Fl. Cap. 16 (1768). Type: Cape of Good Hope, Herb. N. L. *Burman s.n.* (G, holo.!).

(a) **Leonotis ocymifolia** ssp. **ocymifolia** *W.T. Vos and T.J. Edwards* ssp. nov.

Leonotis ocymifolia (Burm. f.) Iwarsson. *Phlomis ocymifolia* Burm. f., Prodr. Fl. Cap. 16 (1768). Type: Cape of Good Hope, Herb. N. L. *Burman s.n.* (G, holo.!).

Leonurus minor Boerh. Ingdb. 1, p. 180. Mill. Dict. t, 162. f. 2. in: Linnaeus 1767. Mantissa Plantarum vol. 1, p. 83. Type: no type material known.

Phlomis leonotis L., Mant. 1: 83 (1767); Thunb., Prodr. 96 (1800); Willd., Sp. Pl. 3: 128 (1800), as *"P. leonitis"*; Pers., Syn. Pl. 2: 127 (1807), as *"P. leonitis"*. *L. leonitis* R. Br. in Ait. f., Hort. Kew. 3: 410 (1811); Skan in F. C. 5,1: 377 (1910). *L. obovata* Spreng., Syst. Veg. 2: 744 (1825). *L. capensis* Raf., Fl. Tellur. 3: 88 (1836).

Leonotis parvifolia Benth., Lab. 619 (1834). Type: Cape of Good Hope, *Masson s.n.* in Herb. Banks (BM, lecto!).

Leonotis mollis Benth. in E. Mey., Comm. 1: 242 (1837); Skan in F. C. 5,1: 378 (1910). Type: Cape, Nieuweveldsbergen near Beaufort West, *Drège 7953* (K, lecto!).

Leonotis hirtiflora Benth. in DC., Prodr. 12: 536 (1848). *L. leonitis* R. Br. var. *hirtiflora* (Benth.) Skan in F. C. 5,1: 378 (1910). Type: Cape, Cape Town, "Ludwigsburg" *ex. hort.*, *Zehyer 206* (K, lecto.!; BM!).

Perennial shrub, 0.5--1.5 m tall, erect or procumbent, seldom mat-forming, strongly branched basally; lateral branches 0.02--0.12 m long, leafy. **Leaves** broadly ovate to orbicular, lamina (5--) 8--26 (--37) x (3--) 6--18 (--30) mm, tomentose, puberulous or glabrescent; base truncate to shortly attenuate; apex obtuse to rounded; margin crenate, often revolute, 5--8 (--10)-toothed; petiole (2--) 6--24 (--37) mm long. **Verticillasters** 1--2 per flowering stem, spherical, (26--) 30--45 (--56) mm in diameter, compact, (11--) 18--55 (--175) flowers per verticillaster; 6--12 cyme branches, 2--12 (--19) mm long, 7--16 flowers per branch; flowering stem (30--) 70--240 (--460) mm long, shallowly grooved, glabrescent or puberulous; internodes 40--160 (--120) mm long; floral leaves elliptic, ovate, obovate or lanceolate, 8--20 (--32) x 4--11 mm, petiole 6--14 mm, pendant, caducous or persistent; bracts linear to subulate, 4--16 mm long, pungent, pendant or curved around the verticillaster; pedicel 1--2.5 mm long. **Calyx** (12--) 15--22 mm long, glabrescent, puberulous or hispid, distal third of tube deflexed; 10-nerved; 8-lobed, lobes blunt or pungent, often pungent, adaxial lobe acuminate, 2.5--7.5 mm long, remaining lobes acute to acuminate, 0.5--4 mm long, unequal, straight, lowest 3 lobes often deflexed.

Corolla rusty orange to reddish, rarely creamy white; (28--) 32--45 (--47) mm long; tube (13--) 17--26 mm long with 1 complete inner basal ring of trichomes; adaxial lip 16--23 mm long; abaxial lip 7--9 x 6--8 mm, 3-lobed, lobes fused distally, lateral lobes 1.5--3 x 2--3 (--4) mm, sub-elliptic, apices acute to obtuse, medial lobe 3--3.5 x 2.5--3.5 mm, spatulate, apex obtuse, truncate to emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 2.6--4.5 x 1.3--2 mm, flanks dark brown and glossy (Figure 44).

Recorded distribution: Cape (Figure 45 a).

Habitat: fynbos, False Macchia, grassland, scrub, karroid and secondary dune vegetation, rocky slopes and outcrops, forest margins and streambanks.

Flowering: sporadic or non-seasonal.

Allied taxa: resembles *L. randii* but differs in the following:
leaves broadly ovate to orbicular, never scabrid, never sub-sessile. *L. ocymifolia* ssp. *ocymifolia* and *L. randii* are allopatric. *L. ocymifolia* ssp. *transvaalensis* has similar leaves but is a tall shrub with long, decumbent, lateral branches and occurs 1--2000 m above sea level.

Etymology: *L. ocymifolia* is Greek for basil-like leaves. *Ocimum*, commonly known as basil, is spelt *Ocymum* in old literature.

Southern African material of *Leonotis ocymifolia* ssp. *ocymifolia* examined

South Africa
---**3219** (Wuppertal): Donkerkloof, Baden Baths (--AC), *Walgate s.n.* (BOL).
---**3222** (Beaufort West): Nieuweveldsberg, near Beaufort West (--BA), *Drège 7953a* (K); Molteno Pass, roadside (--BA), *Shearing s.n.* (PRE).
---**3226** (Fort Beaufort): Hogsback (--DB), *Giffen 1438* (BOL, MO); Amatole Mtns., near the top of Mitchell's Pass (--DB), *Phillipson 1214* (PRE; MO).
---**3227** (Stutterheim): Henderson Heights, Cathcart (--AB), *Kemp s.n.* (NBG); Inverthorn, Cathcart (--AC), *Barker 3466* (NBG); banks of Casta stream below the village (--CA), *Phillipson 297* (MO); Pirie Forest (--CC), *Grant 3190* (MO).
---**3319** (Worcester): Prince Albert (--DC), *Krige 12963* (BOL); Prince Albert, Drooge Kloof, rocky slope (quartzites) (--DC), *Marloth 11289* (PRE).
---**3320** (Montague): Prinspoort (--BC), *Walgate 336* (BOL, NBG); Kogmans Kloof (--CC), *Barker 5418* (NBG); Montague (--CC), *Salter 1118* (BM); Kogmans Kloof (--CC), *Taylor 360* (BOL); Donkerkloof (--CC), *Lewis s.n.* (NBG); Kogmans Kloof (--CC), *Steyn 5418* (NBG); Tradouw Pass (--DC), *Thorns s.n.* (NBG).
---**3321** (Ladismith): Ladismith (--AD), *Bayliss 2818* (NBG); Seweweekspoort (--AD), *Bond 8606* (NBG); Seweweekspoort (--AD), *Compton 4261* (BOL); Seweweekspoort (--AD), *Compton 8606* (NBG);
between Storm Valley and Ataquaskloof (--DD), *Drège 7952* (K, S).
---**3322** (Oudtshoorn): Baviaanskloof (--AC), *Bayliss s.n.* (MO); Cango Valley,

just S of road to Fontein Farm, Kalksteen Kop (--AC), *Hugo 35* (PRE); Meiringspoort (--BC), *Hafsrom* and *Acocks 1331* (S); Meiringspoort, Swartberge (--BC), *Van Wyk 1846* (PRE); Meiringspoort, Groot Zwarteberg (--BC), *Wall 53* (S); Langekloof (--CB), *Drège 7954* (K); Huisriver Pass (--DA), *Compton 20329* (NBG); 86 km E of Willowmore (--DB), *Bayliss 5667* (MO).

---**3323** (Willowmore): Winterhoekberge (--BC), *Ecklon* and *Zeyher s.n.* (P); Onzer (--CD), *Drège s.n.* (S); Baviaanskloof, roadside (--DB), *Bos 957* (M); Baviaanskloof, Dam se Kloof, Mountain View (--DB), *Van Jaarsveld 7855* (NBG).

---**3324** (Steytlerville): Kougarivier, Winterhoekberge (--CC), *Ecklon* and *Zehyer s.n.* (P); Suuranysberge (--CC), *Van Jaarsveld 6871* (NBG); Steytlerville (--CD), *West 371* (GRA); Zuurbron, Hankey (--DD), *Fourcade 2567* (BOL).

---**3325** (Port Elizabeth): near H.F. Verwoerd Airport (--AA), *Walters 2066* (NB G); high point of the Kariega Valley (--AD), *Van der Walt 471* (PRE); Zuurberg, Gower's Kloof (--BC), *Archibald 7329* (GRA); Zuurberg State Forest (--BC), *Long 725* (GRA, PRE); arid area (--BD), *Bayliss s.n.* (PRE); Groendal Wilderness Reserve, rocky, Fynbos/forest (--CC), *Scharf 1267* (PRE); Van Staden's Pass (--CC), *Barker 6907* (NBG); mountains around Van Staden's River (--CC), *Ecklon 9* (S); between Van Stadensberg and Bethelsdorp (--CC/CD), *Drège 79* (E); Bethelsdorp (--CD), *Bolus s.n.* (BOL, NBG); Uitenhage (--CD), *Pappe s.n.* (NBG); Addo (--DA), *Drège 7953b* (K); near Addo between Zontags and Boshermansman's Rivers (--DA), *Ecklon 41* (S); Addo (--DA), *Ecklon* and *Zeyher 1349* (P, W); Addo Heights (--DB), *Long 973* (GRA, PRE); building plots around Port Elizabeth and Walmer (--DC), *Dahlstrand 336* (MO); Zwartkops River (--DC), *Krauss s.n.* (G, M); Humewood (--DC), *Long 412* (GRA); Bethelsdorp, Redhouse (--DC), *Paterson 139* (PRE); Humewood (--DC), *Paterson 2301* (GRA); road toward Seaview, near Port Elizabeth (--DC), *Rodin 1004* (BOL, K, MO, S, W); Sim's Pass (--DC), *Dix 232* (GRA).

---**3326** (Grahamstown): 16 km W of Grahamstown (--AD), *Compton 23394* (NBG); Highlands (--AD), *Rogers 3871* (GRA); military base, near relieve 202, quartzite outcrop (--BA), *Palmer 1390* (PRE); Botha's Ridge (--BA), *Wells 2619* (GRA); Ecca Pass, 10 km NE of Grahamstown (--BC), *Baxter s.n.* (NU); Sugarloaf Hill (--BC), *Booi 13* (GRA); Woest Hill, Albany, karroid hillside (--BC), *Bayliss 4503* (MO); hills above Grahamstown (--BC), *Bayliss 7355* (MO); Albany Museum, flower table (--BC), *Britten* and *Shumane s.n.* (PRE); hill above Botanic Gardens (--BC), *Daly* and *Cherry 952* (K); Gunfire Hill (--BC), *Rennie* and *Rennie* 539 (BOL); Grahamstown (--BC), *Schlechter 2665* (Z); 38.61 km E of Grahamstown (--BD), *Barker 7020* (NBG); hills above Grahamstown (--BD), *Scott Elliot 746* (E, K); Oribi Reserve, round hill (--BD), *Wirminghaus 78* (GRA); between Sundays and Bushmans Rivers (--CB), *Ecklon* and *Zeyher 79* (G, NBG); Port Alfred (--DB), *Hayton s.n.* (K).

---**3418** (Simonstown): Belmont valley (--BB), *Britten 1575* (GRA).

---**3419** (Caledon): Riviersonderend (--BB), *Baxter s.n.* (NU, PRE); Bushman's River Mouth (--DA), *Archibald 4356* (GRA); Rietfontein Poort, (--DA), *Schlechter 9689* (K); near Elim (--DB), *Bolus 8583* (BOL, K); SE end of Zoetendalsvlei, Fynbos (--DB), *Sidey 1829* (PRE, S).

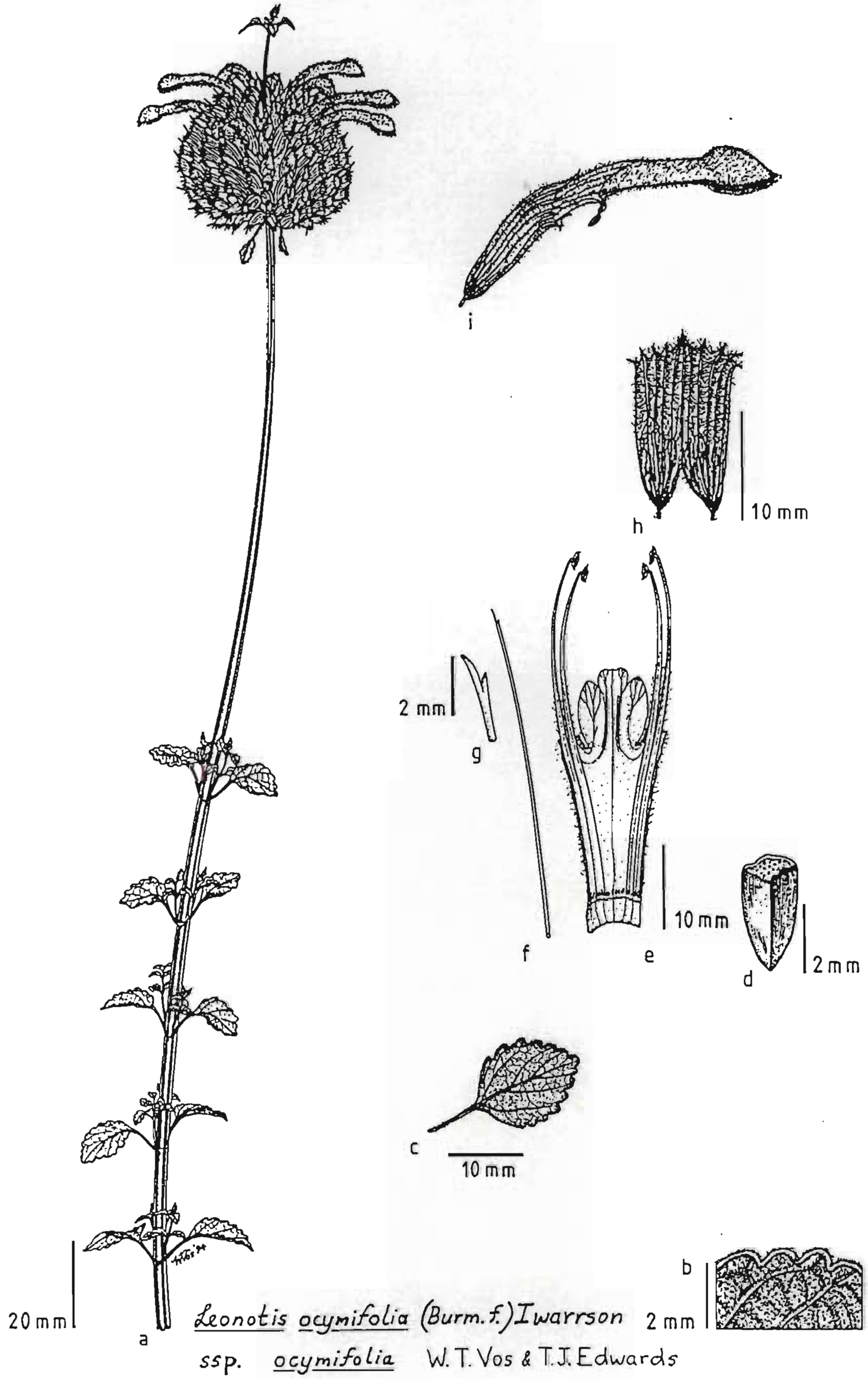


Figure 44. *Leonotis ocymifolia* (Burm. f.) Iwarsson ssp. *ocymifolia* W.T. Vos and T.J. Edwards. (a) flowering branch, (b) leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla), (f) stigma and style (scale of f as for e), (g) stigma and distal part of style, (h) flattened calyx, (i) lateral view of calyx and (j) calyx and corolla (scale of i as for h). Voucher: *Taylor 1170.*

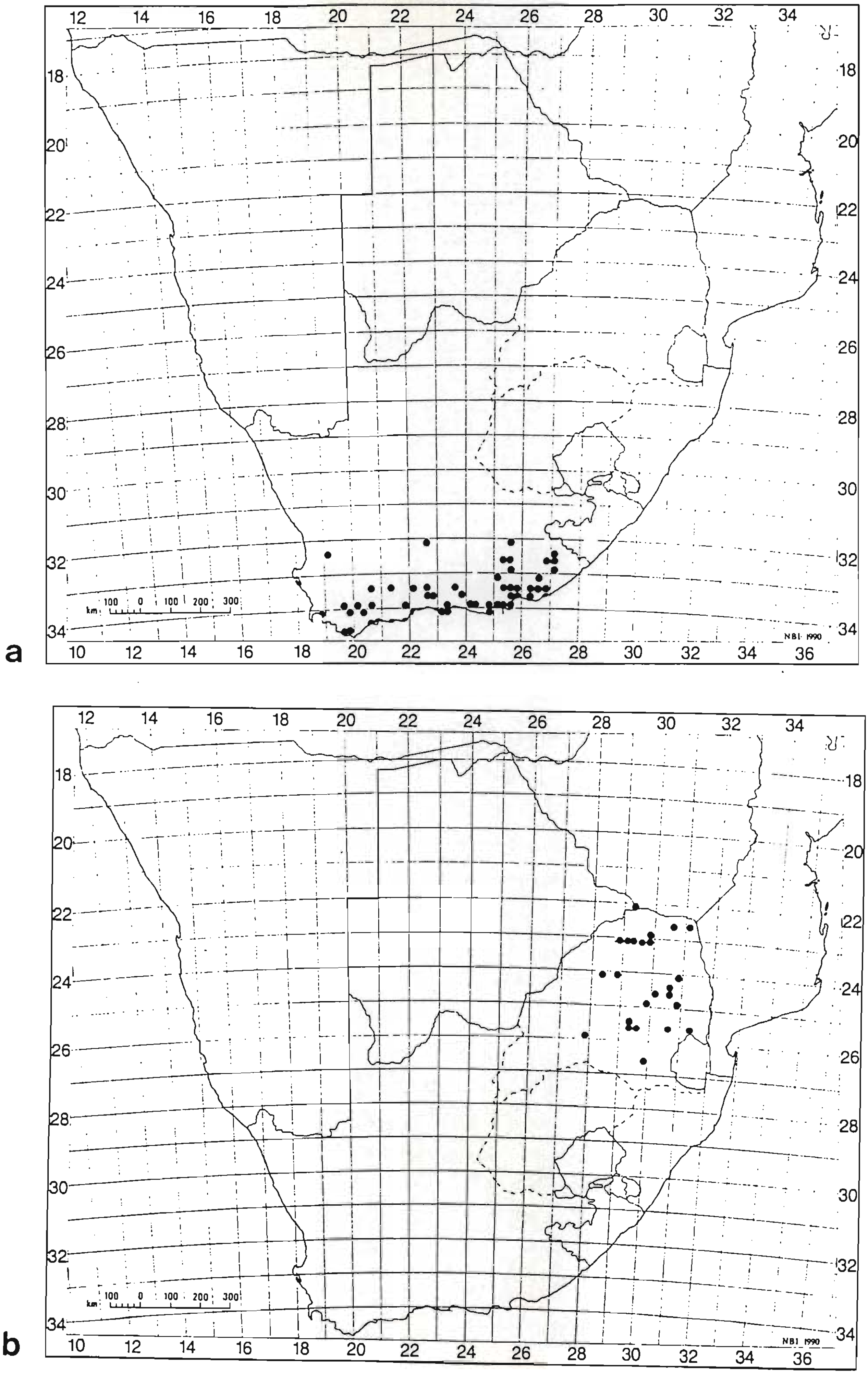


Figure 45. Recorded distribution of (a) *Leonotis ocymifolia* ssp. *ocymifolia* and (b) *Leonotis ocymifolia* ssp. *transvaalensis*.

---**3420** (Bredasdorp): Bontebok National Park (--AB), *Liebenberg 6438* (PRE); NW of The Poort (--DA), *Acocks 1773* (S); Rietfontein Poort (--DA), *Schlechter 1467* (PRE); Rietfontein Poort (--DA), *Schlechter 9689* (BM, G, K); Rietfontein Poort (--DA), *Smith 3057* (PRE).
---**3421** (Riversdale): Stilbaai, hill W of the bridge (--AD), *Bohnen 4143* (PRE); Stilbaai (--AD), *Horn s.n.* (PRE); Albertinia, Ystervarkpunt, old quarry on W border (--BD), *Willemse 187* (PRE).
---**3422** (Mossel Bay): Mosselbay (--AA), *Sidey 1732* (MO, S); NE of Mosselbaai, sandy slope (--AA), *Acocks 15388* (PRE); Mt. Pleasant (--AB), *Martin 118* (NBG); hillside above Sedgefield (--BB), *Leighton s.n.* (MO); Sedgefield, along national road (--BB), *Rousseau 25* (PRE).
---**3423** (Knysna): Knysna (--AA), *Breijer s.n.* (Z, G, PRE); N slopes of Knysna Heads (--AA), *Schonland 3477* (GRA); Hunter's Home (--AA), *Taylor 1170* (NBG); W part of Robberg Peninsula (--AB), *Acocks 21137* (PRE); Keurbooms River, roadside (--AB), *Vos 229* (NU); between Plettenberg Bay and Humansdorp (--AB), *Werdermane* and *Oberdi 1007* (PRE); Kabeljou (--BB), *Burtt Davy 12050* (BOL); (--BB), *Rogers 2916* (NBG).
---**3424** (Humansdorp): dunes near Jeffreys Bay Village (--BB), *Rogers 3962* (BOL).
---**3425** (Skoenmakerskop): Emerald Hill (--BA), *Paterson 2552* (BOL).

Without precise locality (often labelled C.B.S. or Cape of Good Hope):
---**3323** (Willowmore): Groot River, Knysna area (--B?), *Burman s.n.* (G); Groot River (--B?), *Fourcade 1242* (BOL).
---**3325** (Port Elizabeth): Addo, Bushmans River; *Ecklon s.n.* (P); Alexandria, Boshoek (--C?), *Galpin 10658* (BOL).

Commerson s.n. (G, BM); *Drège s.n.* (MO); Ludwigsburg's garden, *Drège* (BM); *Ecklon s.n.* (BM, K, S); *Ecklon 88* (M); *Ecklon* and *Zehyer s.n. (pro parte.)* (P); *Masson s.n.* (BM); *Thunberg s.n.* (S); *Verraux s.n.* (G); *Vertè s.n.* (S); Ludwigsburg's garden, *Zeyher 206* (BM, K).

(b) **Leonotis ocymifolia** ssp. **transvaalensis** *W.T. Vos and T.J Edwards* ssp. nov. Simulans *Leonotis ocymifolia* ssp. *transvaalensis* W.T. Vos and T.J. Edwards *ssp. nov.* sed differens ramis, extensis, longis et decumbentibus, foliis latioribus, caulibus florentibus brevibus exorientibus ex ramis lateralibus, repertis in marginibus sylvarum.

Type: ---**2430** (Pilgrim's Rest): Abel Erasmus Pass (--DA), *Vos 421* (NU, holo.; PRE)

Perennial shrub, 1--3 (--5) m tall, erect to decumbent, strongly branched; lateral branches up to 2 m long, leafless except for the apical regions. **Leaves** broadly ovate to orbicular, lamina (7--) 12--30 (--58) x (6--) 9--20 (--36) mm, puberulous or glabrescent; base cordate, truncate or shortly attenuate; apex obtuse to rounded; margin crenate or dentate, seldom revolute, often undulate, (4--) 6--13-toothed; petiole (3--) 6--25 (--37) mm long. **Verticillasters** 1--2 (--3) per flowering stem, spherical, (19--) 32--44 (--58) mm in diameter, compact, 20--110 (--150) flowers per verticillaster; 6--10 cyme branches, 8--13 (--20) mm long, 9--15 flowers per branch; flowering stem (23--) 45--170 (--380) mm long, shallowly grooved, glabrescent or puberulous; internodes (27--) 74--140 (--255) mm long; floral leaves elliptic, ovate, obovate or lanceolate, 8--20 (--32) x 4--11 mm, petiole 6--14 mm, pendant, caducous or persistent; bracts linear to subulate, 4--19 mm long, pungent, pendant or curved around the verticillaster; pedicel 1--2.5 (--3.5) mm long. **Calyx** (12--) 14-26 mm long, glabrescent, puberulous or velutinous, distal third of tube deflexed; 10-nerved; 8-lobed, lobes blunt or pungent, adaxial lobe acuminate, 3--9 mm long, remaining lobes acute to acuminate, 0.5--4 mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** rusty orange to reddish, rarely creamy white; 25--36 mm long; tube (11--) 14--18 (--20) mm long with 1 complete inner basal ring of trichomes; adaxial lip (14--) 16--20 mm long; abaxial lip 7--9.5 x 5--7 mm, 3-lobed, lobes fused distally, lateral lobes 1.5--3 x 2--3 mm, sub-elliptic, apices acute to obtuse, medial lobe 2--4 x 2.5--3.5 mm, spatulate, apex obtuse, truncate to emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 3--4 x 1.5--2 mm, flanks dark brown and glossy.

Recorded distribution: Transvaal (Figure 45 b), Zimbabwe, Tanzania and Kenya.

Habitat: grassland, mountainous areas, montane forest margin, rocky slopes and outcrops and disturbed sites.

Flowering: mainly between January and July.

Allied taxa: resembles *L. randii* but differs in the following:
tall plant with basally leafless stems up to 2 m long; leaves broader with more marginal teeth, never scabrid or subsessile. *L. randii* and *L. ocymifolia* are allopatric. *L. ocymifolia* ssp. *ocymifolia* has similar leaves but is a dwarf shrub with short, leafy lateral branches and occurs 0--1500 m above sea level.

Etymology: In South Africa, *L. ocymifolia* ssp. *transvaalensis* is restricted to the Transvaal.

Southern African material of *Leonotis ocymifolia* ssp. *transvaalensis* examined

South Africa
---**2229** (Waterpoort): Mapungubwe, Greefswald (--AB), *Eicker* and *students 209* (PRE); Zoutpansberg, Budworth Farm (--DD), *Mogg 28221* (PRE); Soutpansberg, upper slopes of Franz Hoek Peak (--DD), *Galpin s.n.* (BOL, K, NBG).
---**2230** (Messina): Sweetwaters, Klein Spelonken (--AC), *Schinz s.n.* (BOL); Savhani, Thengwe, Nwanedzi (--DA), *Van Wyk 5691* (PRE).
---**2231** (Pafuri): 4 km NW of Punda Milia, Kruger National Park (--CA),*Codd* and *De Winter 5547* (PRE).
---**2328** (Baltimore): Leipzig (--BB), *Strey* and *Schlieben 8472* (M, PRE);

Leipzig, Blouberg (--BB), *Van der Schijff 5337* (PRE).
---**2329** (Pietersburg): Soutpansberg, Blouberg Plateau (--AA), *Klopper 34* (PRE); Blouberg Kloof (--AA), *Strey* and *Schlieben 8600* (M, MO); Blouberg, above Ga-Makibi (--AA), Stirton and Edwards 12703 (NU); Blouberg, margin of *Podocarpus* forest below summit (--AA), *Vos 422* (NU); Soutpansberg (--AB), *Rogers 21155* (G); Soutpansberg, Letsjume Plateau (--AB), *Schlieben 10684* (NU, S); Soutpansberg, Letsjume Plateau, Bergplaas Farm (--AB), *Venter 6228* (PRE); Happy Rest (--BA), *Gerstner 6096* (PRE) Leipzig, Blouberg (--BB), *Van der Schijff 5337* (PRE); Blouberg (--BB), *Leeman 96* (PRE); Blouberg (--BB), *Van Wyk 892* (PRE).
---**2330** (Tzaneen): northern edge of Tzaneen, roadside (--CC), *Vos 413* (NU).
---**2428** (Nylstroom): Lehpalala River, Klipheuvel Farm (--AA/AB), *Breijer s.n.* (PRE); Mapela (--BB), *Breijer 21020* (PRE).
---**2429** (Zebediela): Sekhukhune, Schoonoord Farm (--DD), *Barnard, 403* (PRE).
---**2430** (Pilgrim's Rest): Abel Erasmus Pass, roadside (--BC), *De Winter 7728* (PRE); Onverwacht, near Steelpoort (--CA), *Van Jaarsveld 5980* (NBG); Abel Erasmus Pass (--DA), *Schlieben* and *Strey 8399* (PRE); Abel Erasmus Pass (--DA), *Vos 421* (NU, PRE); Blydepoort (--DB), *Van Wyk 297* (PRE); Mariepskop area (--DD), *Killick* and *Strey 2724* (PRE).
---**2527** (Rustenburg): 19 km W of Pretoria, Magaliesberg (--DD), *Schlieben 7044* (M).
---**2528** (Pretoria): Hornsnek, ± 19.30 km W Pretoria, *Schlieben 7044* (--CA) (M);
---**2529** (Witbank): Loskop Nature Reserve (--AD), *Mogg 30423* (BM, PRE); Loskopdam, W of Scheepersloop (--AD), *Theron 1321* (PRE); Olifants River Gorge, 37 km NW of Middleburg (--CA/CB), *Mogg 22433* (PRE); Middelburg, Doornkop 273J, Broodboomspruit (--CB), *Du Plessis 228* (PRE).
---**2530** (Lydenburg): roadside, rocky grassland (--DA), *Goldsworthy s.n.* (NU, PRE).
---**2531** (Komatipoort): Malelane (--CB), *Murphy 25* (PRE); Barberton (--CC), *Williamson 215* (PRE).
---**2629** (Bethal): Ermelo (--DB), *Leendertz 3058* (GRA).

Non-southern African material of *Leonotis ocymifolia* ssp. *transvaalensis* examined

Kenya

---**0036** (Naivasha/Nakuru): Eburu (--CA), *Humbert 9094* (P).
---**0130** (Machakos): Augen gneiss outcrop, Mt. Lukenya (--AC), *Vos 672* (EAH). ---**0136** (Naivasha/Masai): edge of Kedong Rift, 3.38 km NW of Mukutane, 8-12 km E of Limuru (--BA), *Verdcourt 3813* (K).
---**0137** (Machakos): Lukenya, hillside (--AC), *Napier 2588* (K); Lukenya, along river bed (--AC), *Lucas* and *Williams EA12352* (K).

---**0237** (Machakos/Masai): Chyulu South, on rocks on lava flow blowholes (--DB), *Bally 8375* (K).

Tanzania
---**0335** (Mbulu/Masai): Mt. Oldeani, lower N slopes, Olairobi (--AD), *Raynal 19370* (K).
---**0438** (Lushoto): peak 2.5 km NNE of Manolo, Western Usambaras (--CA), *Drummond* and *Helmsley 2779* (K, S).

Zimbabwe
---**1730** (Sindia): Umvukwe Range, near Mtorashangu Pass (--BA), *Rodin 4419* (MO); N of the Great Dyke, Mukwadzi River, Airey's Pass (--BC), *Schneller 124* (Z); Mazowe, summit of Iron Mask Ridge (--DB), *Eyles 462* (BM).
---**1831** (Marondera): Bromley district (--AB), *Bayliss 10382* (MO); Marandellas (--AB), *Dehn 555* (M).
---**1832** (Mutare): roadside, Rusape (--AC), *Vos 414* (NU).
---**2028** (Bulawayo): Bulawayo (--CA), *Cheesman 82* (BM).
---**2030** (Masvingo): 6.5 km N of Lundi River Bridge, near Madziviri dip (--DA), *Drummond 7910* (MO).

Without precise locality
---**1730** (Sindia): Mabubu Hill, Great Dyke (--B?), *Nyariri 203* (MO); Lomagundi, near Rod Camp mine, *Rutherford-Smith 323* (MO).
---**1832** (Mutare): summit of Matika's Mtn. (*pro parte.*), *Chase 2207* (BM).
---**2028** (Bulawayo): Matopo, Besner Kobila, *Miller 1644* (MO); Mazoe Dam near Bulawayo, *Moss 14844* (BM).
---**2131** (Victoria): *Monro 1063* (BM); Eyles 4912 (BOL); *Wilman s.n.* (BOL).

6. **Leonotis dubia** *E. Mey.* in Comm. 1: 242 (1837). Type: Cape, Witrivier, near Enon, *Drège 4831* (K!, lecto. designated here; PRE!).

Leonotis laxifolia MacOwan in Kew Bull. 73: 13-14 (1893). Type: Natal, Mt. Malowe, *Tyson 2766* in Herb. A.A. 1300 (GRA!, holo.; BM!, G!, K!, NBG!, PRE!, SAM!, W!, Z!).

Leonotis laxifolia MacOwan *forma pilosa* Gürke in Bot. Jb. 22: 144 (1895); Skan in Flora Capensis 5,1: 382 (1910). Type: Natal, Karkloof, *Rehmann 7374* (Z!, lecto.).

Leonotis urticifolia Briq. in Bulletin de L' Herbier Boissier Géneva. Seconde série 2,3: 1091 (1903). Type: *Cooper 1182* (as *Cooper 1152* in Briquet, 1903) (K!, lecto.; BM!, W!, Z!).

Leonotis galpinii Skan in Flora Capesis 5,1: 379 (1910). Type: Cape, near Queenstown, *Galpin 1825* (K!, holo.; Z!).

Leonotis mollis Benth. var. *albiflora* Skan in Flora Capensis 5,1: 378 (1910). Type: Cape, Boschberg, *MacOwan s.n.* (K!, lecto.).

Leonotis westae Skan in Flora Capensis 5,1: 382 (1910). Type: Cape, Port Elizabeth, *West 75* (K!, holo.).

Weakly perennial shrub, 1.5--3.0 (--6) m tall, erect, strongly branched; lateral branches often exceed 1 m in length, leafless except for the apical regions. **Leaves** broadly ovate, lamina (16--) 40--110 (--295) x (13--) 20--80 (--100) mm, glabrescent or puberulous, lax, sub-membranous; base cordate, truncate or attenuate; apex acute to acuminate; margin coarsely crenate to dentate, 8--21-toothed; petiole (7--) 30--90 (--110) mm long. **Verticillasters** 1--9 per flowering stem, often interspersed with non-flowering nodes, spherical or turbinate, (25--)30--50 (--54) mm in diameter, loose to compact, (9--) 18--47 (--60) flowers per verticillaster; up to 8 cyme branches although usually reduced, up to 11 mm long, 8--10 flowers per branch; flowering stem (160--) 210--1250 (--1900) mm long, slender, shallowly grooved, glabrescent or puberulous; internodes (25--) 30--70 (--200) mm long; floral leaves narrowly to broadly ovate, as large as the foliage leaves, spreading, persistent during flowering, petiole (7--) 30--90 (--110) mm long; bracts linear to subulate, 3--12 (--18) mm long, pungent, spreading; pedicel (4--) 5--8 (--11) mm long. **Calyx** (10--) 15--22 (--24) mm long, glabrescent to puberulous, tube almost linear or distal third slightly deflexed; 10-nerved; 8--10-lobed, lobes blunt or weakly pungent, adaxial lobe acute to acuminate, (1--) 3--5 (--7) mm long, flexed upwards or downwards, remaining lobes acuminate, 0.25--2.5 mm long, unequal, straight, lowest 3 lobes seldom decurved. **Corolla** rusty orange to reddish, rarely creamy white, (16--) 26--32 (--39) mm long; tube (11--) 13--16 (--20) mm long with 1 complete inner basal ring of trichomes; adaxial lip 15--21 mm long; abaxial lip 8--10 x 5--7.5 mm, 3-lobed, lobes fused distally, lateral lobes (1.3--) 2--2.5 x 2--3.5 mm, sub-elliptic, apices acute to obtuse, medial lobe 2--

3.5 x 2--4 mm, spatulate, apex obtuse, truncate to emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 3.5 (--4) x (1.3--) 1.8 mm, flanks dark brown and glossy (Figure 46).

Recorded distribution: Cape, Transkei, Natal and Swaziland (Figure 47 a).

Habitat: forest, forest margin and scrub vegetation.

Flowering: mainly between February and May.

Allied species: *L. intermedia* has similar shaped leaves but these are never sub-membranous and seldom as glabrescent as those of *L. dubia* and displays shorter petioles. Inflorescence, habit and habitat characters also differentiate these species.

Etymology: *L. dubia* means doubtful.

Southern African material of *Leonotis dubia* examined

South Africa

---**2731** (Louwsburg): 15 km from Ingwavuma on road to Gwalaweni Forest (--BB), *Botha* and *Van Wyk 955* (PRE).
---**2732** (Ubombo): Lembombo Mtns., Hlatikulu Forest (--AC), *Muir 1* (NH); approximately 3 km N of Mabiebie (--BC), *Ward 202* (NH).
---**2828** (Bethlehem): Royal Natal National Park, Rugged Glen, margin of montane forest (--DB), *Vos 417* (NU, PRE); Royal Natal National Park, Mahai streamside (--DB), *Vos 418* (NU).
---**2829** (Harrismith): Mont aux Sources, bush near The Gorge (--CB), *Hutchinson 45* (PRE); Qudeni, lower forest (--DC), *Hilliard 1368* (NU).
---**2830** (Dundee): top of Umhlumba Mtn. (--CD), *Acocks 13984* (PRE); Qudeni (Zululand) (--DB), *Gerstner 666* (PRE).
---**2831** (Nkhandla): main road through Nkhandla Forest (--CA), *Jorden 751* (PRE); Nkhandla Forest Reserve (--CA), *Van Wyk 7371* (M, NH).
---**2832** (Mtubatuba): Cape Vidal (--AB), *Pooley 2129* (NU); Mapelana (--AD), *Strey 5414* (PRE); Mapelana (--AD), *Ward 3389* (NH, NU); Banghazi fire tower (--BA), *Ward 7027* (NU).
---**2929** (Underberg): Giants Castle Game Reserve (--AB), *Morris 509* (NU); Injasuti Valley, 500 meters W of Battle Cave (--AB), *Vos 537* (NU); Hlatikulu, krantz (--BA), *Evans 532* (NH); 17 km E of Mooi River on Hlatikulu road (--BC), *Balkwill* and *Manning 495* (NU); Loteni Valley, forest patch below Pitoli (--BC), *Hilliard* and *Burtt 16147* (NU); Kamberg (--BD), *Wright 1732* (NU); Sipongweni Mtn. (--CB), *Grice s.n.* (NU); Cobham Forest Reserve, Sipongweni (--CB), *Hilliard* and *Burtt 14074* (NU); Cobham State Forest, Emeraldvale (--CB), *Hilliard* and *Burtt 18299* (K, NU); Loteni Nature Reserve (--DA), *Killick 3853* (NH, PRE); Sunset Farm (--DC), *Vos 58* (NU, PRE); Sunset Farm, Bulwer Mtn. (--DC), *Vos 559* (NU); Hlabeni forest (--DC), *Wirminghaus 1275* (NU); Donnybrook (--DD), *Shirley s.n.* (NU).
---**2930** (Pietermaritzburg): Mooi River (--AA), *Schlechter 6839* (BOL, GRA,

PRE); Silverdale, Lion's River (--AC), *Wright 1495* (NU); Lions River, 9.65 km from the Balgowan/Curry's Post turnoff (--AC), *Moll 888* (NU, PRE); 19 km from York on Rietvlei road (--AD), *Marais 351* (NU); Umgeni River (--AD), *Schlechter 2847* (PRE, S); Karkloof (--AD), *Rehmann 7374* (Z); Karkloof (--AD), *Vos 416* (NU); Karkloof (--AD), *Wirminghaus 819* (NU); Umvoti, Rietvlei road (--BB), *Marais 351* (PRE); Little Noodsberg (--BD), *Medley Wood 828* (BM); Taylors (--CA), *Bews 2537* (NU); Town Bush Valley (--CB), *Ward 46* (NU); Town Bush Valley (--CB), *Johnstone 89* (NU); Ferncliff Nature Reserve (--CB), *Vos 77* (NU, PRE); Byrne, mountain top (--CC), *Reid 8* and *9* (NU); at the gate of Keerom-Cottingham Farm (--CC), *Strey 8419* (MO, NU); Table Mtn., Amatulu Forest (--DA), *Killick 403* (NU); Mariannhill (--DD), *Forbes 1058* and *1150* (NH).

---**2931** (Stanger): Durban area (--CA), *Pappe s.n.* (NBG); Umgeni River Mouth (--CC), *Schlechter 2847* (GRA).

---**3029** (Kokstad): P.O. Cedarville, Mvenyani (--AC), *Bandert 163* (GRA); Mt. Currie (--AD), *Tyson 391* (BOL) and *1445* (NBG); in the woods of Mt. Malowe (--BD), *Tyson 2766* (BM, NBG, G, GRA, PRE, K); Kokstad area (--CB), *Coleman 309* (NH); Insizwa Forest (--CD), *Strey 10727* (PRE).

---**3030** (Port Shepstone): Dumisa station (--AD), *Rudatis 1393* (BM, G, K, PRE, S, W); Oribi Gorge (--CA), *Edwards 876* (NU, PRE); Timbankula Forest, Bantu location no. 6 (--CB), *Strey 8731* (S); in forest bush (--CB), *Strey 5883* (NU, PRE).

---**3126** (Queenstown): n'Qebenacht Forest, mountain sides, Queenstown (--DD), *Galpin 1825* (K, GRA, PRE).

---**3127** (Lady Frere): in forest, n'Zebanga Mtn., Glen Grey (--CC), *Galpin 8039* (BOL, PRE).

---**3129** (Port St. John's): near the Umzimvubu River (--AC), *Drège 4830* (K).

---**3225** (Somerset East): Cradock (--BA), *Rogers s.n.* (PRE); Bruintjies Hoogte (--CB), *Burchell 3008* (K); kloof behind the Episcop burial ground (--DC), *Scott Elliot 351* (E).

---**3226** (Fort Beaufort): Bedford (--CA), *Nicol 34* (K); Aukland Trust Forest, Hogsback (--DB), *Dahlstrand 2814* (MO); Lovedale (--DD), *Bennie 41* (GRA); Tyumie River, riverine fringe (--DD), *Gibbs Russell 3734* (BOL, GRA, MO, NU, PRE); Block Drift, Tyumie River, Fort Hare College (--DD), *Giffen 463* (PRE).

---**3227** (Stutterheim): northern aspect of Windvoelberg (--AC), *Roberts 1730* (PRE); Amatola Mts. below Hogsback (--CA), *Lewis s.n.* (NBG, PRE); Fort Cunningham (--CB), *Von Gadow 153* (GRA); Debe Nek (--CC), *Rogers 4468* (GRA); King Williamstown, Buffalo River (--CD), *Zeyher s.n.* (NBG); margin of woods near Komga (--DB), *Flanagan 671* (BOL, GRA, NBG).

---**3228** (Butterworth): near Kentani (--CB), *Pegler 355* (PRE, BM, GRA, NBG).

---**3324** (Steytlerville): Mistkraal, Baviaanskloof (--CB), *Lewis s.n.* (NBG); Witrivier above Cambria, Saasveld (--DA), *Geldenhuys 1266* (PRE).

---**3325** (Port Elizabeth): Enon, near Witrivier (--BC), *Drège 4831* (PRE, K); Loerie Plantation (--CC), *Bayliss 7418* (MO); Addo (--DA), *Ecklon* and *Zehyer 36.7* (M, MO, P, S); Cape, Port Elizabeth (--DC), *West 75* (K).

---**3326** (Grahamstown): Howieson's Poort (--AD), *Bayliss 7467* (G, M, MO,

S, Z); Kieskammahoek, Ghulu Kop, rock crevices (-BB), *Wells 3293* (GRA); Kowie East (--BC), *Dyer 2014* (GRA); forests around Grahamstown (--BC), *MacOwan 16410* (BM); Grahamstown (--BC), *Bayliss 6329* (PRE); Fort Selwyn, Gunfire Hill (--BC), *Richardson 6* (GRA); Alexandria Forest (--CB), *Marais 407* (GRA, PRE, MO); Boknesstrand, Alexandria (--DA), *Burrows 2899* (GRA); Kowie West (--DB), *Burtt Davy 7854* (PRE); near the coast, Kowie (--DB), *Levyns 3785* (BOL); Port Alfred (--DB), *Rogers 16642* (G); near Kowie River Mouth (--DB), *Phillips s.n.* (PRE); Kowie West (--DB), *Tyson 1300* (BM, G, MO).
---**3327** (Peddie): 48.23 km W of East London (--BA), *Taylor 5612* (NBG); East London (--BB), *Salter s.n.* (BM); Greenpoint, near boat landing on edge of forest (--BB), *Smith 3781* (PRE); East London, Second Creek (--BD), *Galpin 5734* (K, PRE).
---**3425** (Skoenmakerskop): Cape Recife (--BA), *Olivier 2372* (GRA).

Without precise locality
---**2732** (Ubombo): Ingwavuma district, *Ward 2372* (NU).
---**3029** (Kokstad): near Nalogha, *Krook 1713* (W).
---**3226** (Fort Beaufort): Dontsa Pass (--C?), *Sidey 618* (S).

Natal, Ismont, *Medley Wood 1837* (NH); Natal, *Cooper 1182* (BM, W); Natal, *Gueinzius s.n.* (G).

7. **Leonotis pauciflora** *W.T. Vos and T.J. Edwards* sp. nov. Simulans *L. intermedium* sed differens foliis angustioribus cum petiolis longioribus, basi saepius cordata quam attenuata, caulibus florentibus cum 2--5 verticillastris minoribus, pauciflorus, sub-pariter dispositis.

Type: ---3024 (De Aar): Chinaman's Hat W of Colesberg (--DB), *Acocks 17996* (PRE, holo.; M).

Perennial shrub, 0.5--1.5 (--1.8) m tall, strongly branched basally; stem puberulous to tomentose; lateral branches up to approximately 0.13 m long. **Leaves** broadly ovate to orbicular, lamina (22--) 32--60 (--124) x (13--) 20--45 (--65) mm, puberulous or velutinous; base cordate to truncate, seldom attenuate; apex acuminate to rounded; margin coarsely crenate or crenate to dentate, 7--18-toothed; petiole (7--) 18--45 (--70) mm long. **Verticillasters** (1--) 2--5 per flowering stem, spherical or turbinate, (29--) 31--45 (--52) mm in diameter, compact, (15--) 28--45 (--60) flowers per verticillaster; up to 10 cyme branches although usually reduced, up to 9 mm long, 6--11 flowers per branch; flowering stem (105--) 230--530 mm long, shallowly or deeply grooved, puberulous or tomentose; internodes (14--) 30--172 mm long; floral leaves ovate, obovate or elliptic, 14--36 x 7--22 mm, pendant, caducous or persistent, petiole 5--35 mm long; bracts linear or subulate, 4--16 mm long, pungent, spreading horizontally or downwards; pedicel up to 3.5 mm long. **Calyx** (12--) 14--23 (--26) mm long, glabrescent, puberulous or velutinous, distal third of tube deflexed; 10-nerved; 8-lobed, lobes usually pungent, adaxial lobe acute to acuminate, 3--9 mm long, flexed slightly upwards, remaining lobes acuminate, 0.5--3 mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** rusty orange to reddish, rarely creamy white, (26--) 32--42 mm long; tube (12--) 17--26 mm long with 1 complete inner basal ring of trichomes; adaxial lip 12--22 mm long; abaxial lip 6--9 x 6--8 mm, 3-lobed, lobes fused distally, lateral lobes 1.5--2.5 x 3--3.8 mm, sub-elliptic, apices obtuse, medial lobe 2.5--3 x 2--4 mm, spatulate, apex obtuse, truncate or emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 2--4 x 1.5--2 mm, flanks dark brown to blackish, glossy (Figure 48).

Recorded distribution: Orange Free State, Lesotho, Cape and Natal (Figure 47 b).

Habitat: grassland, (Highland Sourveld to *Cymbopogon-Themeda* Veld Transition and *Cymbopogon-Themeda* Veld (sandy), False Upper Karoo, scrub, mountain slopes and sandstone outcrops.

Flowering: mainly between December and April.

Allied species: resembles *L. intermedia* but differs in the following: leaves narrower with longer petioles, base more often cordate than attenuate; flowering stems with 2--5 verticillasters, verticillasters smaller, fewer flowered and sub-equally spaced.

Etymology: *L. pauciflora* means few-flowered.

Southern African material of *Leonotis pauciflora* examined

South Africa

---**2827** (Senekal): Ficksburg (--DC), *Fowkes* 167 (BOL).

---**2828** (Bethlehem): at Bethlehem (--AB), *Potgieter 2189* (PRE); 6.76 km SE of Bethlehem on Kestell road (--AB), *Scheepers 1563* (MO, S); Mt. Libanon, De Hoek Farm (--AC), *Vos 98* (NU, PRE); Kromdraai, Fouriesberg (--CA), *Watt* and *Breyer-Brandwyk 265* (PRE); Clarens, sheltered mountain slope (--CB), *Peyton 1* (PRE); Leribe, Mt. Hopes, Basutoland (--CC), *Dieterlen 106* (NBG, P, PRE); Leribe (--CC), *Phillips 519* (NBG); Royal Natal National Park (--DB), *Lewis s.n.* (NBG).

---**2829** (Harrismith): Harrismith (--AC), *Sankey 232* (MO); Van Reenen's Pass (--AD), *Kuntze s.n.* (K); Biggarsberg (--BB), *Rehmann 7057* (Z); without precise locality, *Smit 98* (PRE).

---**2926** (Bloemfontein): Mensvretersberg (--BB), *Peeters 307* (PRE).

---**2927** (Maseru): Above la Chaba (--BB), *Guillarmod 895* (PRE).

---**3024** (De Aar): Grasfontein, Phillipstown district (--AD), *Vahrmeÿer 2243* (PRE); Petrusville, Rolfontein Nature Reserve (--BB), *Jooste 225* (PRE); Wachbanks River (--CB), *Burchell 2732* (K); Chinaman's Hat W of Colesberg (--DB), *Acocks 17996* (PRE, M).

---**3026** (Aliwal North): Burgersdorp (--CD), *Thode A514* (PRE); Orange River, Sand Drift (--DA), *Burke s.n.* (BM, K).

---**3125** (Steynsburg): at Grootfontein (--AC), *Theron 390* (PRE).

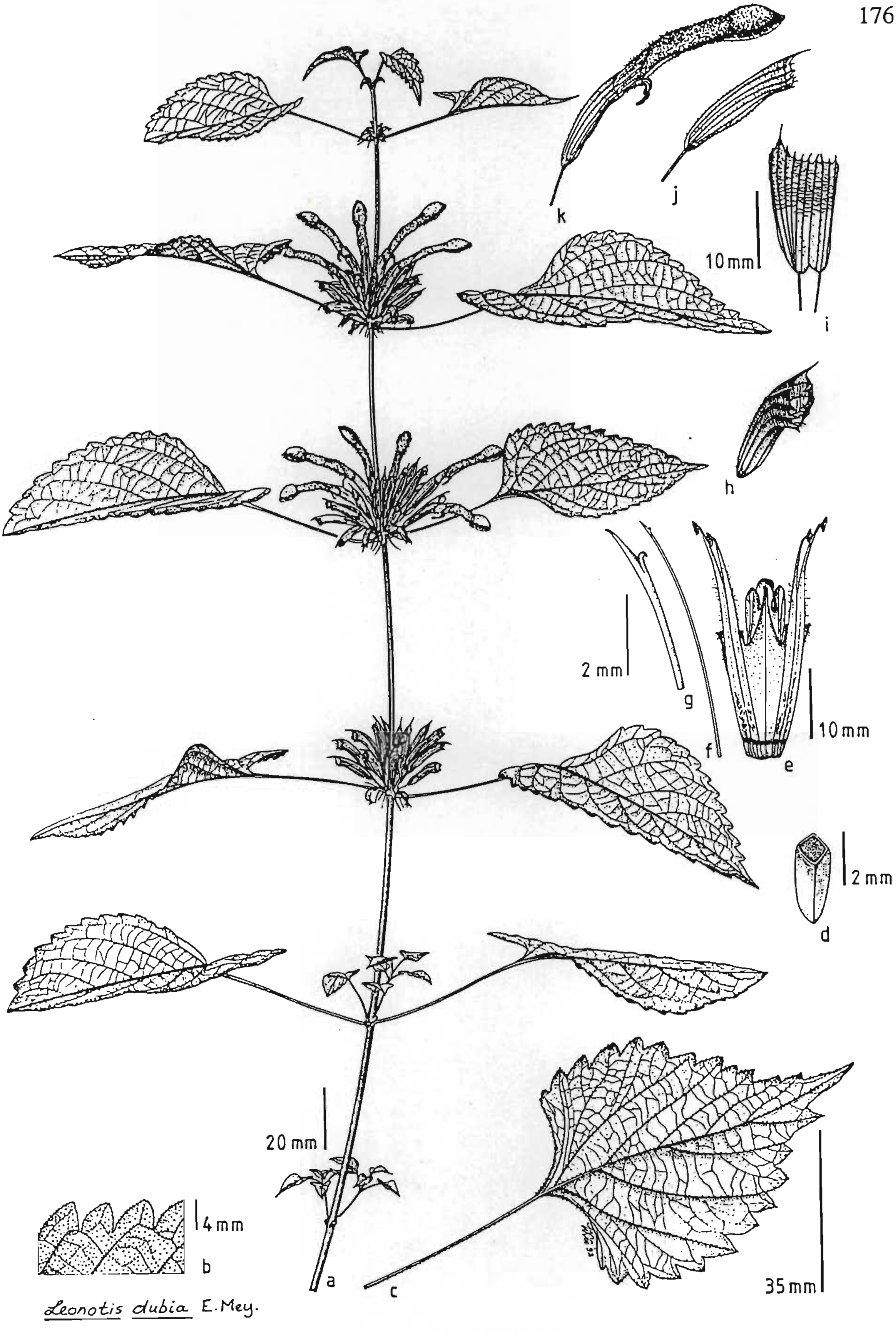


Figure 46. *Leonotis dubia* E. Mey. (a) flowering branch, (b) leaf margin, (c) abaxial leaf (*Tyson 2766*), (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla), (f) stigma and style (scale of f as for e), (g) stigma and distal part of style, (h) front view of calyx (scale of h, i and j as for k), (i) flattened adaxial calyx, (j) calyx and (k) calyx and corolla. Voucher: *Vos 77.*

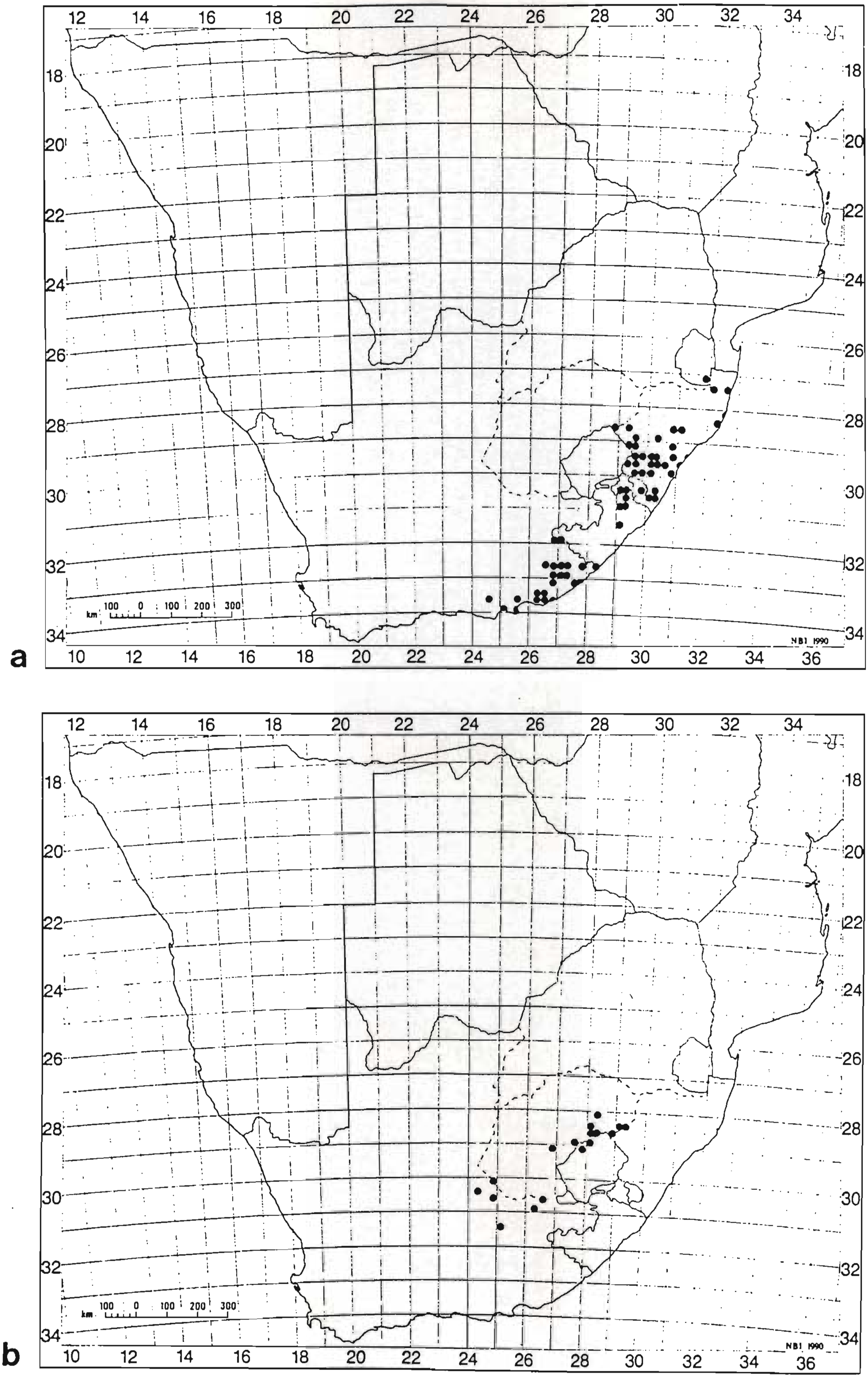


Figure 47. Recorded distribution of (a) *Leonotis dubia* and (b) *Leonotis pauciflora*.

8. **Leonotis intermedia** *Lindl.*, Bot. Reg. t. 850 (1824); Skan in Flora Capensis 5,1: 381(1910). Type: *ex hort.*, seeds from *Forbes s.n.*, Cape, Algoa Bay (erroneously as Delagoa Bay in Bot. Reg.) (CGE, holo.; BM!, BR, G-DC, K!).

Leonotis dysophylla Benth. in E. Mey., Comm. 1: 242 (1837); Skan in Flora Capensis 5,1: 380 (1910); Prain in Curtis's bot. Mag. t.8404 (1911); Launert and Schreiber in Flora of South West Africa 123: 15 (1969); Compton, Fl. Swaziland 493 (1976). Type: between Omsamwubo and Omcomas Rivers, *Drège 4832a* (K!, lecto.).

Leonotis malacophylla Gürke in Bot. Jb. 22: 142 (1895). Type: Clydesdale, *Tyson 2729*, in Herb. A.A. 1508 (K!, lecto.; GRA!, PRE!, SAM!, UPS!, W, Z!).

Leonotis bachmannii Gürke in Bot. Jb. 22: 143 (1910). Type: Transvaal, Barberton, *Galpin 922* (Z!, lecto.; GRA!, PRE!).

Leonotis brevipes Skan in Flora Capensis 5,1: 378 (1910). Type: Transvaal, Zoutpansberg, Medingen, *Burtt-Davy 2657* (K!, holo.).

Leonotis intermedia Lindl. var. *natalensis* Skan in Flora Capensis 5,1: 381 (1910). Type: Natal, near Durban, *Peddie s.n.* in Hb. Harvey (K!, lecto.).

Perennial shrub, 0.5--1.5 (--2) m tall, erect, strongly branched basally; lateral branches up to approximately 0.3 m long. **Leaves** broadly ovate, seldom sub-orbicular, lamina (19--) 30--90 (--170) x (8--) 10--50 (--70) mm, glabrescent, puberulous or velutinous, sometimes discolorous due to silvery-white trichomes below, base cordate, truncate or attenuate; apex acute to acuminate, seldom obtuse; margin coarsely crenate or crenate to dentate, sometimes undulate, (6--) 12--26-toothed; petiole (4--) 10--50 (--65) mm long; apical leaves narrowly ovate to lanceolate, sub-sessile and fascicled. **Verticillasters** 1--3 (--5) per flowering stem, spherical, (25--) 30--50 (--68) mm in diameter, compact, (22--) 40--125 (--185) flowers per verticillaster; 8--19 cyme branches, 6--28 mm long, 5--18 flowers per branch; flowering stem 180--600 mm long, shallowly or deeply grooved, glabrescent to tomentose; internodes 60--190 (--260) mm long; floral leaves narrowly;, ovate to oblanceolate, (5--) 15--30 (--45) x 5--12 (--17) mm, pendant, caducous, petiole 5--20 mm long; bracts linear, subulate or oblanceolate, 3--12 (--18) mm long, pungent, spreading horizontally or curved upwards around the inflorescence; pedicel 1--3 (--7) mm long. **Calyx** (11--) 13--22 (--26) mm long, glabrescent, velutinous or villous, distal third of tube deflexed; 10-nerved; 8-lobed, lobes blunt or pungent, adaxial lobe acute to acuminate, 1.5--6 (--9) mm long, flexed slightly upwards, remaining lobes acuminate, 0.5--4.5 mm long, unequal, straight, lowest 3 lobes often deflexed. **Corolla** rusty orange to reddish, rarely creamy white, (25--) 32--44 mm long; tube (13--) 15--23 mm long with 1 complete inner basal ring of trichomes; adaxial lip 12--23 mm long; abaxial lip (5.5--) 6--9 (--11) x 5--8.5 mm, 3-lobed, lobes fused distally, lateral lobes 1.5--2.5 x 2.5--3.5 mm, sub-elliptic, apices obtuse, seldom acute, medial lobe (2--) 3--4 x 2.5--3.5 mm, spatulate, apex obtuse, truncate, emarginate, lip reflexed and or twisted after anthesis. **Nutlets** obovate, 2.5--4 x 1.5--2.5 mm, flanks dark brown to blackish, glossy (Figure 49).

Recorded distribution: Cape, Transkei, Natal, Orange Free State, Transvaal, Swaziland (Figure 50), Angola, Mozambique, Malawi and Tanzania.

Habitat: grassland, savanna, scrub vegetation, rocky hillsides, stream banks and occasionally forest margins.

Flowering: mainly between January and June.

Allied species: *L. nepetifolia* has similar shaped leaves but is easily distinguished by its annual habit and flowers which have a short corolla and a corolla tube with three complete, inner basal rings of trichomes.

Etymology: Lindley (1824) noted that *L. intermedia* appears morphologically "intermediate" between *L. leonurus* and *L. nepetifolia.*

Southern African material of *Leonotis intermedia* examined

South Africa

---**2229** (Waterpoort): Soutpansberg, Soutpan Farm (--CD), *Obermeyer 229* (PRE); Wyllie's Poort (--DD), *Breijer 19521* (PRE); Soutpansberg, near Wyllie's Poort (--DD), *Vos 555* (NU).

---**2230** (Messina): Vendaland, Nzhelele River (--CD), *Van Wyk 2877* (PRE).

---**2329** (Pietersberg): Soutpansberg (--AB), *Mogg 9377* (K); near Sand River Bridge (--BA), *Meeuse 10208* (M, S); Louis Trichardt (--BB), *Breijer 22100* (PRE); approx. 0.5 km from Louis Trichardt on road to Messina (--BB), *Van Wyk 447* (PRE).

---**2330** (Tzaneen): ± 50 km from Louis Trichardt to Sibasa (--AB), *Van Wyk 924* (PRE); near Medingen Mission Station, Zoutpansberg (--CA), *Burtt Davy 2657* (K, PRE); Merensky Dam, along road to boathouse (--CA), *Scheepers 280* (M, PRE); Modjadji's Reserve near Duiwelskloof (--CB), *Krige 166* (PRE); Tzaneen estates (--CC), *Edwards s.n.*; part 16, Franschoek, Magoebaskloof (--CC), *Hanekom 2266* (MO); Kratzenstein (--CC), *Hoffmann 73* (PRE); New Agatha (--CC), *Rogers 18865* (G, PRE); 4 km from Tzaneen on the road to Duiwelskloof (--CC), *Van Wyk 486* (PRE); Magoebaskloof (--CC), *Verdoorn 2222* (PRE); near top of Magoebaskloof Pass (--CC), roadside, *Vos 423* (NU).

---**2429** (Zebediela): Zebediela (--AA), *Rogers 3317* (PRE); kloof above Hooggenoeg Aspestos Mine, Wolkberg/Strydpoort (--BB), *Moffet 1757* (PRE); Uitkyk Koppie, Glen Gowie, SW of Jane Furse Hospital (--DD), *Crosby 164* (PRE).

---**2430** (Pilgrim's Rest): Wolkberg 634, under a cliff on the NW side of Serala Peak (--AA), *Müller* and *Scheepers 127* (PRE); Shilouvane mission (--AB), *Junod 1141* (G); Shilouvane mission (--AB), *Junod 5018* (PRE); Skoonoord, Sekukulana district (--CA), *Van Warmelo 259* (PRE); Trichardspoort, rocky slopes at entrance of poort (--DB), *Bredell 19* (S, W); Bourkes Luck Potholes(--DB), *Thrash s.n.* (NU); Origstaddam Nature Reserve (--DC), *Jacobsen 2905* (PRE); at base of krantz near summit of Jubulie Peak (--DD), *Galpin 14454* (PRE).
---**2431** (Acornhoek): Acornhoek (--CA), *Roberts 26191* (PRE); (--CA), *Zambatis 1422* (PRE).
---**2528** (Pretoria): Pretoria (--CA), *Meebold 12155* (M); Rooiplaat, Pienaars River (--CB), *Leendertz 770* (BOL).
---**2529** (Witbank): Suikerboskop 361 JS, near beacon 5455 (--DB), *Fourie 2798* (PRE).
---**2530** (Lydenburg): Nooitgedacht (--AB), *Henrici 1378* (PRE); near Lydenburg town, Sterkspruit (--AB), *Wilms 1146* (BM, G, K, M, W); Steenkampsberg Nature Reserve (--AC), *Bloem 89* (PRE); Dullstroom, Wanhoop Farm 78 JT, on section E of road (--AC), *Drews 246* (PRE); Dullstroom, dolerite rockeries (--AC), *Galpin s.n.* (BOL); Skurweberg, Mokubulaan plantations (--BA), *Onderstall 1299* (PRE); 15 km from Sabie travelling to the Kruger National Park, roadside (--BA), *Van Wyk 498* (PRE); Sabie, Tweefontein Experimental Area (--BB), *Beruardi 8965* (G); Lydenburg, hillsides of Sabie Valley (--BB), *Galpin s.n.* (BOL); Sheba Farm 219 JT (--BB), *Krynauw 1199* (PRE); Sabie, Tweefontein experimental area (--BB), *Wager s.n.* (PRE); Schagen (--BD), *Liebenberg 2955* (PRE); 10 km from Nelspruit to Machadodorp (--BD), *Van Wyk 850* (PRE); (--CA), *Leendertz 8067* (PRE); Waterval Boven (--CB), *Moss 14977* (BM); Waterval Boven (--CB), *Rogers 14473* (PRE); Starvation Creek Nature Reserve (--DA), *Kluge 1299* (PRE); ± 50 km S of Barberton on road to Badplaas (--DC), *Edwards 824* (NU).
---**2531** (Komatipoort): 5 km S of Numbi gate (--AA), *Van der Schijf 127* (PRE); 4 km W of Pretoriuskop, Kruger National Park (--AB), *Codd 6016* (PRE); Pretoriuskop (--AB), *Van der Schijf 2626* (PRE); Kruger National Park, Wolhuter Trails Camp (--AD), *Thrash s.n.* (NU); hills of Barberton (--CC), *Compton 19770* (NBG); Piggs Peak, Havelock, near river, (--CC) *Compton 29994* (NBG); Barberton (--CC), *Edwards 64* (PRE); hillsides of Barberton (--CC), *Galpin 922* (GRA, PRE); Barberton (--CC), *Rogers 19188* (BM, G, S); Pedley's Bush, Barberton (--CC), *Thorncroft 2144* (PRE); 16 km E of Barberton, Zeist Farm (--CC), *Van der Merwe 324* (PRE); Agnes Mine (--CC), *Vos 558* (NU); Barberton (--CC), *Williams 3127* (NBG).
---**2628** (Johannesburg): near Heidelberg (--AD), *Wilms 1146* (BM, G).
---**2630** (Carolina): Badplaas/Lochiel road, 20 km from Lochiel (--BA), *Crosby 270* (PRE); 23 km from Panbult to Amersfoort, hilltop (--CC), *Crosby 316* (PRE); Kalkoenkrans, Kromhoek Farm, *Turner 740* (PRE); Nooitgedacht Research Station (--CD), *Balsinhas 2977* (MO); Iswepe (--DC), *Sidey 1611* (PRE).
---**2631** (Mbabane): Komati Bridge (--AA), *Compton 26815* (PRE, NBG); Komati Pass (--AA), *Compton 31520* (PRE); Forbes Reef (--AA), *Compton*

32072 (NBG, PRE); Hlambanyati Valley (--AC), *Compton 24945* (PRE, NBG); Ukutulu (--AC), *Compton 25114* (PRE); Usutu Forest (--AC), *Compton 25470* (NBG); Mbuluzi Valley (--BC), *Compton 28647* (PRE); Hlatikulu (--CD), *Stewart s.n.*(BOL); Hlatikulu (--CD), *Stewart 103* (K, NBG); Hlatikulu, edge of thick bush (--CD), *Stewart 182* (NBG); 3.2 km from Maputa on road to Ingwavuma (--DD), *Van Wyk 540* (PRE).

---**2632** (Maputo): Namaacha (--AA), *Correia* and *Marques 656* (NBG); Namaacha (--AA), *Marques 2472* (NBG); Lebombo Mts., Jilobi Forest (--CA), *Kemp 814* (MO); Namaacha (--CC), *De Gomes Sousa 410* (K).

---**2729** (Volksrust): Glen Atholl Farm, near Charlestown (--BD), *Smith 5627* (PRE); Driekoppe Farm, 42 km SE of Vrede on road to Verkykers (--CB), *Retief 2027* (PRE).

---**2730** (Vryheid): Wakkerstroom (--AC), *Beeton 228* (NBG); Wakkerstroom (Groothoek) Madlangampisieberg (--AC), *Killick 3921* (MO); Honeymoon Kloof (--AC), *Galpin 9799* (PRE); 2.5 km NW Wakkerstroom along road to Amersfoort (--AD), *Davidse 6750* (MO); Oshoek, Wakkerstroom (--AD), *Devenish 603* (PRE); Utrecht, retirement village (--AD), *Devenish 1714* (MO, PRE); Piet Retief, Mooihoek (--BB), *Devenish 634* (BM, M, MO, PRE); Municipal Waterworks, 6 km from Piet Retief to Wakkerstroom (--BB), *Van Wyk 2470* (PRE); Vryheid Nature Reserve (--DC), *Youthhead 130* (NH).

---**2731** (Louwsburg): Itala Game Reserve (--CD), *Baxter s.n.* (NU, PRE); Ngome, above forest near police post (--CD), *Hilliard* and *Burtt 9960* (MO, NU, S); Itala Game Reserve (--CD), *Hilliard* and *Burtt 10057* (MO, NU).

---**2732** (Ubombo): 16 km before Ingwavuma, travelling from Jozini (--AA), *Van Wyk 520* (PRE).

---**2828** (Bethlehem): Witsieshoek (--DB), *Junod 17315* (PRE); Royal Natal National Park (--DB), *Trauseld 36* (NU); Royal Natal National Park (--DB), *Trauseld 188* (NU, PRE).

---**2829** (Harrismith): Drakensberg Botanic Garden (--AC), *Jacobsz 2195* (NBG); E of Van Reenen, Nolens Volens Farm (--AC), *Jacobsz 1595* (NBG, PRE); 25.74 km S of Harrismith, Gravelotte Farm (--AC), *Van der Zeyde s.n.* (NBG); 29 km SE of Harrismith, steep rocky hill (--AD), *Marais 331* (PRE); Harrismith, King's Hill, township lands (--BB), *Van Zeyde s.n.* (NBG); Cathedral Peak, road to summit, grass along stream bank (--CC), *Halliwell 5076* (MO); Cathedral Peak Forest Reserve, tributary of Tseketseke (--CC), *Hilliard* and *Burtt 16281* (NU, PRE); between the Klip and Tugela Rivers (--DB), *Gerrard 393* (NH); Ladysmith (--DB), *Wilms 2111* (BM).

---**2830** (Dundee): Impati Mtn. (--AA), *Shirley s.n.* (NU); Weenen Nature Reserve (--CC), *Morley 18* (NH); Weenen thornveld near Nkhumba Mtn. (--CC/CD), *West 1448* (NH); near Buffels River, 30 km W of Tugela Ferry (--DA), *Vos* and *Crouch 536* (NU).

---**2831** (Nkhandla): Umfolozi Game Reserve (--BD), *Vos 636* (NU); along highway opposite the University of Zululand (--DA), *Vos 408* (NU, PRE); Umhlatuzi Valley (--DC), *Lawn 535* (NH).

---**2832** (Mtubatuba): Hluhluwe Game Reserve, top of Ntabayentombi Hill (--AA), *Phelan 694* (NU); Hluhluwe Game Reserve (--AA), *Ward 2235* (NH, NU); Lake St. Lucia (--AB), *Louw 1918* (PRE); dune forest above Lake Bhangazi (--AB), *Vos 415* (NU); St. Lucia estuary, recreation game park (--

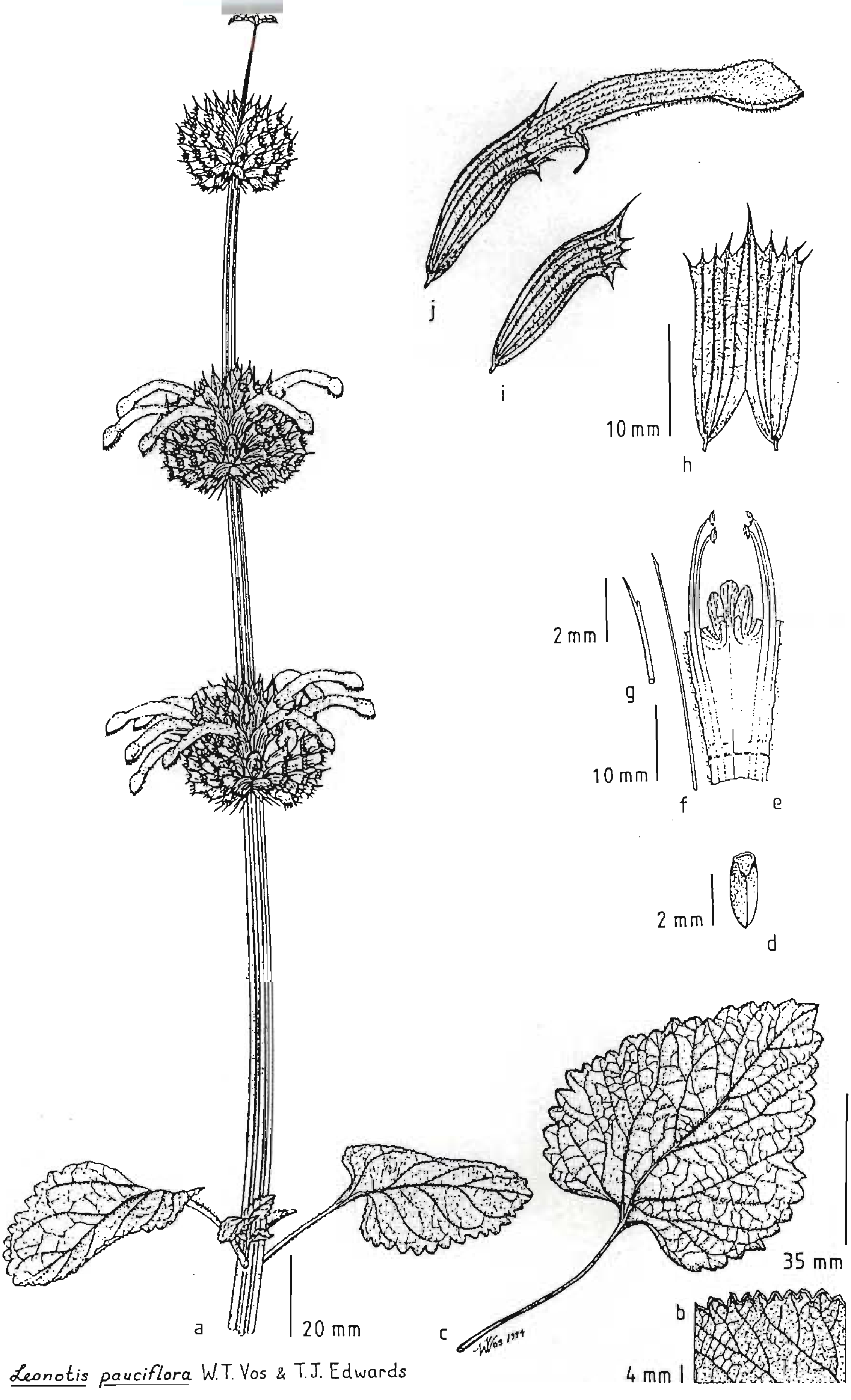


Figure 48. *Leonotis pauciflora sp. nov.* W.T. Vos and T.J. Edwards. (a) flowering branch (*Potgieter 2189*), (b) leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla) (scale of e as for f), (f) stigma and style, (g) stigma and distal part of style, (h) flattened calyx, (i) lateral view of calyx (scale of i and j as for h) and (j) calyx and corolla. Voucher: *Peeters et. al. 307.*

AD), *Pooley 1857* (NU); Mapelana (--AD), *Strey 5414* (NH); grassland, St. Lucia Nature Reserve, 5 km N of entrance (--AD), *Vos 409* (NU, PRE); Mapelana (--AD), *Ward 3389* (NU, PRE).

---**2929** (Underberg): without precise locality, *Grice s.n.* (NU); Cathkin Park, Drakensberg (--AB), *Galpin s.n.* (BOL); Giant's Castle Game Reserve (--AB), *McOwan 161* (NU); Ntabamhlope Research Station (--BA), *West 705* (PRE); Estcourt, Draycott Hill (--BB), *Acocks 11434* (PRE); Estcourt (--BB), *Acocks 10235* (PRE); entrance to Moor Park Nature Reserve (--BB), *Beaumont 97* (NU); Mulangane ridge, above Carter's nek, slope below cliff (--BC), *Hilliard* and *Burtt 18403* (PRE); Kamberg (--BD), *Wright 1685* (NU); Cobham State Forest (--CB), *Hilliard* and *Burtt 18299* (MO); Sani Pass (--CB), *Hilliard* and *Burtt 18* (NU); upper tributaries of Mkomazi River (--CB), *Hilliard* and *Burtt 15880* (NU); Sani Pass (--CB), *Hilliard* and *Burtt 17946* (NU); Umkomaas area, Nhlangeni Valley, Bird's Nest Cave area (--CB), *Hilliard and Burtt 18288* (NU); Cathedral Peak, Ndumeni Valley, Catchment XV (--CC), *Farrell 38* (NH); Cathedral Peak Forest Research Station (--CC), *Killick 1415* (NU); (--CD), *Mclean 660* (PRE, MO); Nkife Valley, Glengariff Farm (--DC), *Rennie 804* (NU); Sunset Farm, hilltop (--DC), N slope, *Vos 44* (NU).

---**2930** (Pietermaritzburg): Mooiriver (--AA), *Mogg 7202* (PRE); Meteor Ridge, Mooiriver (--AA), *Mogg 7082* (PRE); Balgowan (--AC), *Gordon-Gray 4620* (NU); 21 km from Merrivale on Boston road, Kunhardt's Farm (--AC), *Kunhardt 37* (NH); Tweedie (--AC), *Mogg 753* (S); Lion's River, Lidgetton, Lister's Farm (--AC), *Reid 10* (NU); Dargle State Forest, below look-out tower (--AC/CA), *Nicholas* and *others 1780* (NBG); Albert Falls (--AD), *Commins 349* (NU); York (--AD), *Graham 7* (NU); Karkloof (--AD), *Rycroft 183* (NU); Greytown (--BA), *Galpin 14713* (PRE); Greytown (--BA), *Galpin 14841* (PRE); Umvoti Valley, 16 km NW of Mpumulo (--BA), *Moll 1657* (NU); Greytown (--BA), *Wylie s.n.* (NH, NU); travelling N, 0.5 km past Table Mtn. turnoff (--CA), *Vos 410* (NU); Pietermaritzburg (--CB), *Goosens s.n.* (NU); Cedara State Forest (--CB), *Groenewald 132* (NH); World's View (--CB), *Reid 19* (NU); Hayfields, hill above Darville Sewerage Works (--CB), *Vos 59* (NU, PRE); top of Pollyshorts Hill (--CB), *Vos 411* (NU, PRE); Hela Hela hilltop near Richmond (--CC), *Hildyard 95* (PRE); Richmond, Byrne Mtn. (--CC), *Reid 3* (NU); roadside, Tollgate Bridge (--DA), *Vos 110* (NU); Botha's Hill, 5 km past Valley of a Thousand Hills Hotel (--DC), *Edwards 21* (NU); on Botha's Hill, grassland (--DC), *Mclean 11* (NU); Shongweni Dam (--DC), *Morris 788* (NU); Pinetown district, Kloof (--DD), *Gibson s.n.* (NU); Hillcrest (--DD), *Owen 2536* (NU); Isipingo Flats (--DD), *Ward 6828* (NH, NU,PRE).

---**2931** (Stanger): Amatikulu Nature Reserve (--BA), *Ward 174* (NH); Stanger (--CA), *Acocks 10352* (PRE); environment of Durban (-CC), *Humbert 14603* (P); near Durban (--CC), *Peddie s.n.* (K).

---**3029** (Kokstad): between Kokstad and New Market (--AD), *Krook s.n.* (W); Clydesdale, in cliffs (--BB), *Pegler s.n.* (G); Clydesdale, stony slopes of Umzimkulu River (--BB), *Tyson 2729* (NBG, PRE, RA, G, W); near Weza, Zuurberg (--BC), *Hilliard* and *Burtt 8068* (NU); Mt. Frere-Cedarville (--CC), *Strey 10794* (NH); Harding (--DB), *Hilliard* and *Burtt 16719* (NU).

---**3030** (Port Shepstone): 16 km from Ixopo on Donnybrook road, Lyn Avis Farm (--AA), *Crewe 92* (NU); Alfred district, 10 km E of Harding, Rooiwal

Farm (--AC), *Balkwill 2768* (M); Dumisa Station, Friedenau Farm (--AD), *Rudatis 629* (K, BM, G, W); Pennington (--BC), *Repton 1285* (PRE); Oribi Gorge (--CA), *Milstein 23* (NU, PRE); Port Shepstone (--CB), *Moss 7* (BM); Marburg, damp grassland (--CC), *Edwards 164* (NU); Paddock (--CC), *Mclean 260* (PRE); Palm Beach, campsite Greenhart (--CD), *Weigend 2312* (NU).
---**3128** (Umtata): along the Tsitsa River (--BB), *Strey 10697* (NH); 4 km from Umtata/Kokstad road, on road to Shawbury (--BB), *Van Wyk 7130* (NH); Baziya (--CB), *Baur s.n.* (K); between Mgandulu and Coffee Bay, near Kwaaiman post office (--DD), *Lewis s.n.* (NBG).
---**3129** (Port St. Johns): 11.83 km NE of Flagstaff (--AB), *Lewis 68165* (NBG); between Umsimvubhu and Umsicaba Rivers (--BA), *Drège 4832* (K); Msikaba Nature Reserve (--BA), *Vos 539* (NU); Tsitsa River (--BD), *Krook s.n.* (W); edge of forests (--DA), *Moss 340* (BM); Mkambati Nature Reserve, mouth of Mkambati River (--DA), *Smook 6147* (PRE); Ntafufu Hills (--DA), *Strey 8516* (NH, NU, PRE). ---**3130** (Port Edward): Umtamvuma Nature Reserve, Clearwater (--AA), *Abbott 1044* (NH); Umtamvuma Nature Reserve (--AA), *Botany 3 field trip 67* (M); Umzamba River Mouth (--AA), *Lewis 68164* (NBG).
---**3227** (Stutterheim): ridge above Evelyn Valley (--CA), *Acocks 15731* (PRE); King Williamstown (--CD), *Sim s.n.* (NU); King Williamstown (--CD), *Sim 235* (PRE); Erassa Hills near Komga (--DB), *Flanagan 585* (NBG, PRE, GRA); Blaney (--DC), *Sim 2538* (NU).
---**3228** (Butterworth): The Haven (--BB), *Gordon-Gray 419* (NU); The Haven, sandy shore of lagoon (--BB), *Gordon-Gray* 252 (GRA); Mazeppa Bay, hill E of river mouth (--BC), *Phillipson 321* (MO); Kentani (--CB), *Pegler 1514* (PRE).
---**3325** (Port Elizabeth): Algoa Bay (--DC), *Forbes s.n.* (BM, K); Baakens River Valley, Fairview (--DC), *Olivier 1269* (MO, NBG).
---**3327** (Peddie): Tower Hill, East London (--BB), *Compton 16990* (NBG).

Without precise locality
In the district of Swellendam and George, *Bowie s.n.* (BM): *Ecklon* and *Zehyer 79.2* (G, E); *Flanagan s.n.* (NBG); Bushmans River, *Gerrard 362* (NBG); *Cooper 1041* (BOL); Transvaal, *Creux 69* (G): Zululand, *Gerrard 596* (BM, W).

Non-southern African material of *Leonotis intermedia* examined

Tanzania
---**0934** (Njombe): Ruhudje, Lupembe (--AA), *Schlieben 7* (G); Milo, Livingstone Mtns. (--DC), *Rae 57* (BM).

Angola
---**1314** (Caconda): Higlands between Ganda and Caconda (--D?), *Hundt 900, 581* (BM).
---**1413** (Sá da Bandeira): Sá da Bandeira (--CD), *Humbert 16185* (BM).

Malawi

---**1535** (Mulanje): Mt. Mlanje, Chambe, W face (--DC), *Chapman* and *Chapman 7669* (K); Mt. Mulanje, Ruo Plateau (--DC), *Newman* and *Whitmore 611* (BM); Mount Mulanje, E of Tuchila hut (--DC), *Newman* and *Whitmore 23* (BM).

Zimbabwe
Without precise locality
---**1833** (Inyanga): without precise locality, *Heed 258* (BM).

Tropical to sub-tropical species of *Leonotis* examined.

Leonotis mollissima Gürke

Sudan
---**0433** (Equatoria): Mount Lotuke (--DC), *Jackson 1357* (BM).

Uganda
---**0136** (Kiambu): station Lamuru, Buschiges Hochland (--BA), *Scheffler 263* (E).
---**0332** (Mengo): Entebbe (Uganda) (--AB), *Bagshawe 829* (PRE); Mityana (--CA), *Downer s.n.* (BM).
---**0336** (Arusha): Oberhalt Momela (--BB/BD), *Geilinger 3870* (Z).

Without precise locality
Ruwenzori expedition, *Scott-Elliot 6950* (BM); Heide, *Geilinger 412* (Z).

Rwanda
---**0229** (Butare): Nyarutembe, Maraba Commune (--DA), *Radoux 27* (MO); Kigembe, Colline Ngoma (--DA), *Raynal 20362* (MO).

Burundi
---**0329** (Muramvya): Nyakibuye (--BC), *Reekmans 2667* (K).

Kenya
---**0330** (Kigoma): Marungu Station, Kilimanjaro (--DA), *Volkens 235* (BM).

Without precise locality
(Central): Aberdare range, *Greathead s.n.* (GRA).

Tanzania
---**0337** (Moshi): Kilimanjaro (--AB), *Johnston s.n.* (BM); Kilema, Kilimanjaro (--BC), *Volkens 1688* (BM); Kilimanjaro (--CD) *Schlieben 4333* (Z).
---**0933** (Mbeya): Station Kyimbila (--DA), *Stolz 834* (NBG).

Without precise locality
---**0538** (Tanga): Usambara (--B?), *Buchwald 19* (BM).
---**0835** (Iringa): Dabagga, Uheha Plateau, *Geilinger 1974* (Z).

Ethiopia
---**0638** (Sidamo): 80 km N of Kebre Mengist (--AD), *Friis, Gilbert, Rasmussen* and *Vollesen 1095* (K).
---**0636** (Bedero): Gemu Gofa, W of Felege Nevay (--DA), *Gilbert 4145* (K).

Congo
---**0724** (Mutombo): Mutombo Mukulu au mont Lambala (--CC), *Iuarve 2549*

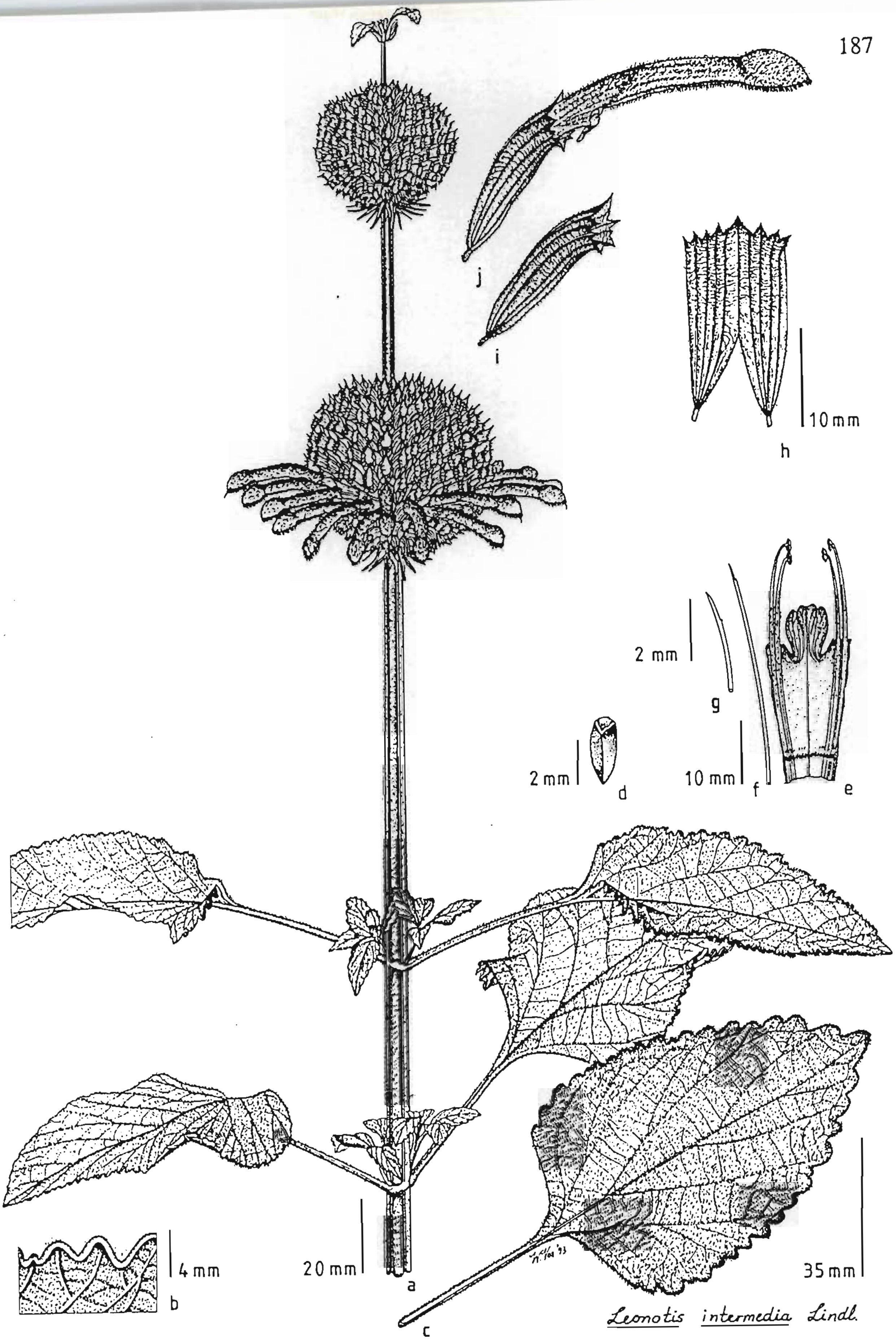


Figure 49. *Leonotis intermedia* Lindl. (a) flowering branch, (b) leaf margin, (c) adaxial leaf surface, (d) nutlet, (e) dissected corolla tube showing the basal ring of hairs and abaxial lip (the adaxial lip has been removed just above the throat of the corolla) (scale of e as for f), (f) stigma and style, (g) stigma and distal part of style, (h) flattened calyx, (i) lateral view of calyx (scale of i and j as for h) and (j) calyx and corolla. Voucher: *Vos 539*.

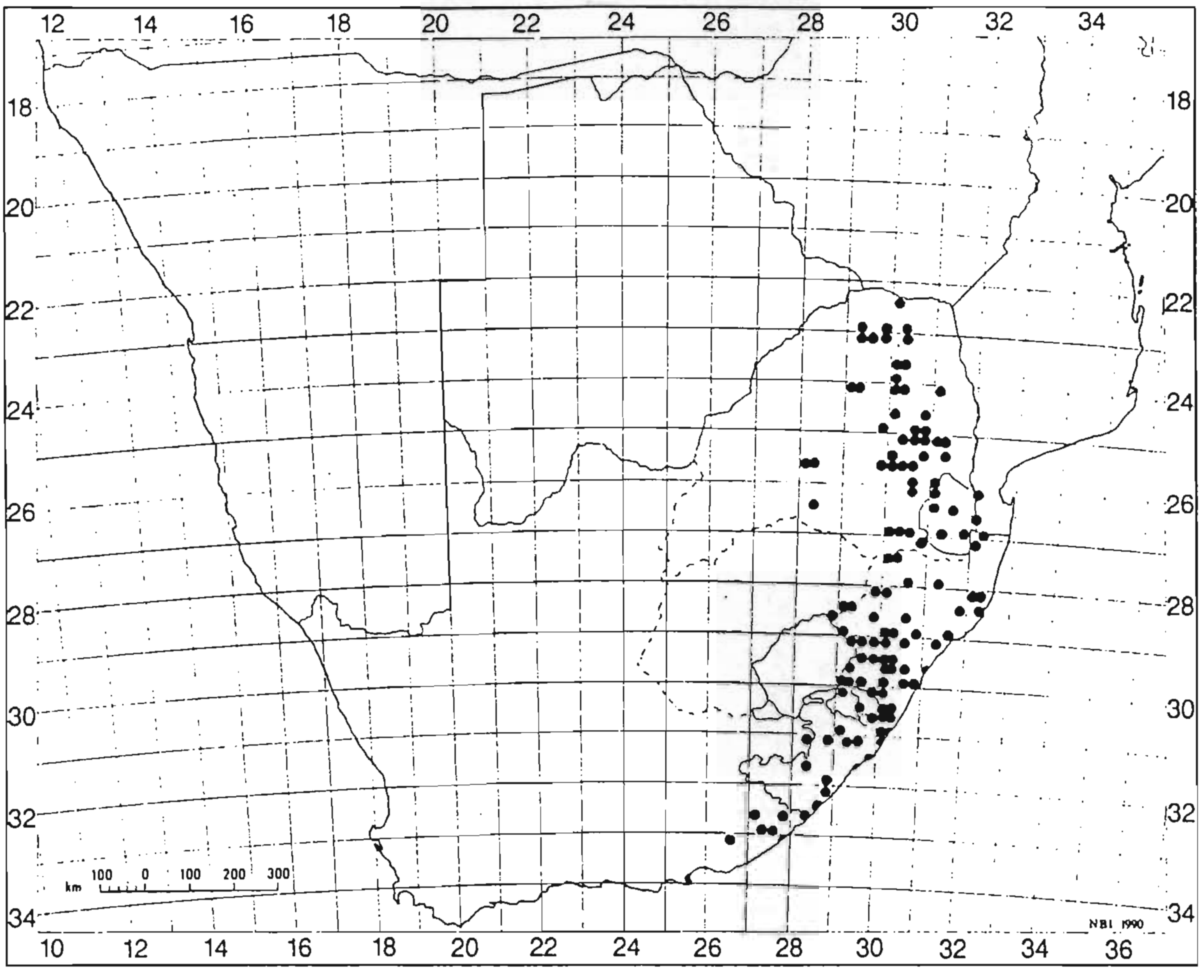


Figure 50. Recorded distribution of *Leonotis intermedia*.

(K).

Malawi
---**1033** (Chitipa): Manganja Hills (--BA), *Meller s.n.* (K).
---**1133** (Nkhata Bay): Chikangawa (--BB), *Phillips 2560* (Z); 6 km S of Chikangawa (--BB), *Phillips 3408* (Z); 6.76 km S of Chikangawa (--BB), *Phillips 3588* (Z).
---**1134** (Nkhata Bay): 85 km S of Nkhata Bay (--AC/CA), *Phillips 2259* (Z).
---**1535** (Blantyre/Mlanje/Zomba): Mt. Chiradzulu (--CA), *Whyte s.n.* (K); Ntonya Hill, Nsenjere stream (--DD), *Masiye 240* (Z).

Zambia
Without precise locality
Ludazi (Zambia), *Robinson 794* (K).

Mozambique
---**1737** (Zambédzia): Mts. do Curué, Rio Namuco (--AC), *De Koning 7470* (BM). ---**1834** (Gorongosa): Gorongosa Massif, Bar l Ranch (--CB), *Wright 565* (NU).

Zimbabwe
---**1832** (Mutare): Odzi, shade of streambed (--CD), *Eyles 8563* (K); Nuza Mtn. (--DB), *Gilliland 1757* (K, BM); Stapleford (--DB), *Hopkins 12468* (BM); Odzani River Valley (--DC), *Teague 243* (BOL); Vumba Mtn. (--DD), *Martin 1002* (NBG); Vumba Mtn. (--DD), *Rodger 1100* (NBG): Vumba Mtn. (--DD), *Simleit 20* (NU); *ex. hort.* National Botanical Gardens, Harare (--DD), *Vos 363* (NU).
---**1932** (Melsetter): Dangari Mtn., 10 km S of Mutare (--BA), *Chase 4667* (BM, MO); streamside below cliff (--DD), *Crook 77* (K); edge wattle plantation, foot of mountain (--DD), *Rutherford-Smith 172* (MO); Chimanimani Mtns. (--DD), *Swynnerton 2013* (BM).
---**2032** (Chipinge): NW portion of Rusitu River between Jansen's Hill and Silver Streams (--BB), *Chase 8587* (MO).

Leonotis longidens

Uganda
---**0032** (Mengo): Entebbe, Hama road (--CD), *Bagshawe* and *Camb 829* (BM).

***Leonotis pole-evansii* Hutch.**

Tanzania
---**0933** (Mbeya): Station Kyimbila, Nyassa Highlands (--DA), *Stolz 2115* (MO, NBG).

Malawi
---**1033** (Rumpi): Nyika Plateau, 19 km W of Chilinda (--DB), *Phillips 3395* (MO); Nyika Plateau, Businande (--DC), *Phillips 762 (MO),* Nyika Park, S of

Zovochipolo road (--DD), *La Croix 4636* (MO).

Zambia
Without precise locality
---**1330** (Kanona?): Serenje corner (--AA), *Hutchinson* and *Gillett 3711* (BM).

Leonotis decadonta **Gürke**

Tanzania
---**0933** (Mbeya): Station Kyimbila (--DA), *Stolz 835* (BM).
---**0532** (Tabora): Chunja Escarpment (--DA), *Richards 25885* (MO).

Malawi
---**1133** (Mzimba/ Rhumpi): Nyika plateau (--DC), *Benson 198* (BM).
---**1535** (Zomba): Zomba Plateau (--AD), *Banda* and *Salubeni 1557* (Z).

Without precise locality
Buchanan 202 (BM).

Leonotis goetzei **Gürke**

Tanzania
---**0934** (Njombe): Nkinga, Djilulu Mtn. (--BC), *Goetze 918* (BM).

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