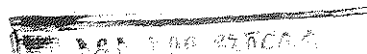


A STUDY OF THE WOOD ANATOMY OF THE VERNONIA LEOPOLDII

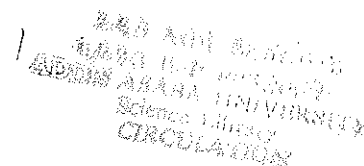
COMPLEX WITH THE IMPLICATIONS ON ITS TAXONOMY



A Thesis submitted to

The School of Graduate Studies

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In Partial Fulfilment of

the Requirements for the Degree of

Masters of Science in Biology.

By

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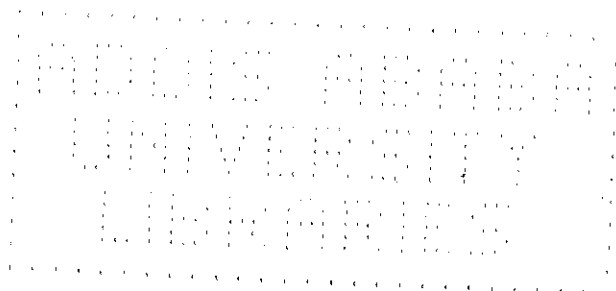
ABSTRACT

A systematic study has been made on the '*Vernonia leopoldii* complex' (Compositae) with the objective of determining the taxonomic status of the species involved in this complex. Two species were recognized as distinct, namely, *V. leopoldii* (Sch. Bip.) Vatke and *V. bipontini* Vatke.

V. leopoldii is distinguished as having leaves with pale brownish tomentum with the epidermal surfaces visible. The trichomes in this species are predominantly T-shaped with terete, lobed or unequal short arms. The petioles have five vascular traces and the leaves have a uniseriate epidermis.

V. bipontini, however, has densely whitish-tomentose leaves with the epidermal surfaces hardly visible. The trichomes are predominantly T-shaped, longhorn type, with equal to slightly subequal, long, terete, filiform arms. The petioles have three vascular bundle traces and the leaves often have a biseriate epidermis. This species was found to be highly variable and hence three varieties were recognized.

Both species have a chromosome number of 36 and pollen with subechinolophate, tricolporate, micropunctate tectum, usually with a continuous tectum cover and spines on the muri. Wood anatomical features are similar in both species and hence did not yield any characters with taxonomic implications to the '*Vernonia leopoldii*



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1

INTRODUCTION

The genus *Vernonia* belongs to the family Compositae, tribe Vernonieae. About 66 species of *Vernonia* are listed by Cufodontis (1967) for both Ethiopia and Somalia. Recent preliminary studies based on material in the herbaria in Ethiopia and at Kew, London (Dr. Mesfin Tadesse, Pers. comm.) indicated that there are about 40 - 45 species in Ethiopia.

The Old World species of the genus *Vernonia* Schreb. have received renewed interest in various research fields such as agronomy, natural products chemistry and industry, not only in Africa but also abroad (cf. Perdue et al. 1986, Berhanu Abegaz, Pers. comm., Gilbert 1986). This has been as a result of the discovery of epoxy-oleic acids and Vernolic acid (cis-12,13-epoxy-cis-9-octadecenoic acid) in *Vernonia anthelmintica* (L.) Willd., from India, first isolated by Gunstone in 1954. These natural epoxy acids were shown to be better substitutes in the manufacture of plasticizers and stabilizers for the paint and plastics industries (Perdue 1986). Of the African species of *Vernonia* screened for the presence of these acids, a variety of *V. galamensis* (Cass.) Less. from Ethiopia, namely, *V. galamensis* ssp. *galamensis* var. *aethiopica* M.G. Gilbert, was found to have about 30% more vernolic acid than the best improved varieties of *V. anthelmintica*. It contained 41.5% oil with 72.6% vernolic acid, substantially better than any selection of *V. anthelmintica*, which at

best contained 31% oil and 75% epoxy acid, according to Princen's findings of 1979(cited in Perdue 1986).

Many *Vernonia* species have wide use medicinally in some countries for treating a variety of diseases (Kokwaro 1976, Harbourn and Williams 1977, Castro 1986). Kupchan et al. (1968, 1969a,b) isolated vernolepin and vernomygdin which have anti-tumor properties, from the leaves of *V. hymenolepis* A. Rich.. Laekeman et al. (1983) found the same active substance in the fruit of *V. amygdalina* Del.. The above species as well as *V. galamensis* ssp. *galamensis* var. *aethiopica* M.G. Gilbert, occur in Ethiopia. This is therefore an indication of the potential natural products present in this genus, hence suggesting the need for further comprehensive research on the genus.

While looking for a suitable and manageable species group for study for an M.Sc. project within the genus *Vernonia*, the '*Vernonia leopoldii* complex' was identified with the help of noted authorities on the genus, namely, Mr. Charles Jeffrey (Kew, London), Mr. Mike Gilbert (Kew, Ethiopian Flora Project) and my advisor. The names included within this complex are *V. leopoldii* (Sch. Bip.) Vatke (1875), *V. bipontini* Vatke (1875), *Cyanopsis hypoleuca* Sch. Bip. (1846) or *Vernonia leopoldii* var. *hypoleuca* Chiov. (1939).

In the first Flora of Ethiopia, A. Richard (1848) cited two species under the genus *Cyanopsis* (currently a synonym of the genus

Vernonia) named by Schultz Bipontinus. These were *Cyanopsis leopoldii* Sch. Bip. and *C. hypoleuca* Sch. Bip. named in 1840 and 1844 respectively but 'published' in 1843 and 1846 respectively. Vatke, in 1875, transferred *C. leopoldii* to the genus *Vernonia* as the generic name *Cyanopsis* Bl. was considered illegitimate and superfluous. This was because the type species for this genus was found to be similar to that of *Cyanthillum*, that is, *Cyanthillum moluccensis* Bl. from Mollucas. Based on the variations in size of heads, presence and amount of resin glands on the florets and achenes as well as in the indumentum of the leaves, he segregated *Vernonia bipontini* from *V. leopoldii* in the same year. Oliver and Hiern (1877) gave *Cyanopsis hypoleuca* as a synonym under *Vernonia leopoldii* and also cited *V. bipontini* under the synonymy noting that *V. leopoldii* is a very variable species. Chiovenda, in 1939, reduced *Cyanopsis hypoleuca* of Schultz Bipontinus to a variety within *Vernonia leopoldii*. Cufodontis, in 1967, agreed with Oliver and Hiern (1877) and reduced *Cyanopsis hypoleuca* to a synonym of *Vernonia leopoldii*.

When these names were published, the taxa to which they were ascribed to were thought to be distinct. However, the large amounts of later collections of specimen of them showed overlaps in the diagnostic characters, especially in those of the achene, phyllary and leaf morphology. Consequently, some taxonomists treat these species as a 'complex' of taxa needing further studies while others still consider them as separate and distinct.

Given the above considerations, a thorough systematic study of the '*Vernonia leopoldii* complex' was made with the objective of seeking for additional diagnostic characters useful in determining the relationships within the complex. Palynological, anatomical, cytological and micromorphological studies were conducted on representative specimens of this complex to supplement the standard herbarium and field macromorphological studies. During the progress of this work, this approach was found to closely match with the observations made by other taxonomists who have worked on the genus, for example, Jones (1981:59) who wrote '... the purpose of the study was to delimit biologically meaningful groups within *Vernonia* , thereby creating smaller 'natural' groups of manageable size for subsequent revisionary studies, which eventually lead to a refinement of the classification. Without the system proposed, it would be difficult if not impossible to examine effectively such a wide and unwieldy genus , ... hence an attempt to bring order out of the chaos that currently exists in *Vernonia*'.

2. LITERATURE REVIEW

The Compositae have for a long time drawn the attention of many synantherologists as a well marked but highly variable group (Cronquist 1955). The tribe Vernonieae within this family was delimited by Lessing in 1829 (Jones 1979). The next major reorganization of the tribe was made by Bentham in 1873 in Bentham and Hooker's *Genera Plantarum*. New genera and species have, however, been described in recent years but no modern synopsis of the tribe is available and few revisions or generic monographs have been published in the last 110 years. The tribe has approximately 1,450 species and about 70 genera, 37 of which are monotypic (Jones 1979). This tribe is highly diversified but is basically characterized by discoid heads, basally sagittate anthers and long hirsute styles, flattened on the inner sides (Jones 1977b). About 1,000 species are found in the large genus *Vernonia* Schreb. which forms the core of the tribe. About 200 of these species are found in Africa, particularly in the savanna vegetation type south of the Sahara (Jones 1977b). The genus *Vernonia* was 'published' in Bentham and Hooker's *Genera Plantarum* in 1873 with the type species as *V. novaboracensis* (L.) Willd. from North America.

Although the importance of the genus *Vernonia* to the classification of the tribe is clear, there has been no comprehensive re-evaluation of the genus since the work of De Candolle in 1836 and Bentham in 1873 (Jones 1979). The current delimitations of the sections, subsections and series were described by Smith (1971) as

'nebulous and are clearly superficial'. Ekman, in 1914, had previously noted that the delimitations of the taxonomic units within Vernoniaeae is extremely difficult both at specific and generic levels due to the extensive intergradation of diagnostic features. Natural hybrids have been noted to be common among species in *Vernonia* making classification at this level difficult. This situation is further aggravated by the huge size and wide distribution of the genus (Jones 1979). This has therefore led to uncertainty as to whether a holistic or a piece-meal approach would be best suited for tackling the taxonomic problems in this genus.

Oliver (1877), in his treatment of the Compositae of Tropical Africa, recognized seven subsections in the genus *Vernonia*, namely, *Lepidella*, *Tephrodes*, *Cyanopsis*, *Xipholepis*, *Decaneurum*, *Stengelia* and *Strobocalyx* based on Bentham's (1873) classification.

The '*Vernonia leopoldii* complex' under study was kept under section *Cyanopsis* which was delimited as having persistent inner phyllaries without a terminal appendage, outer pappus made up of setae or these sometimes minute or wanting, and achenes that are (3-)4-6-costate. However, the species grouped under these sections were found by subsequent workers (cf. Jones 1981, Jeffrey 1988) to be heterogenous when other characters and character-states were considered.

With the availability of a wider range of taxonomic characters from other fields, namely, chemotaxonomy (Harborne and Williams 1977), palynology (Keeley and Jones 1979) and cytotaxonomy (Jones 1979), Jones, in 1981, distinguished New World and Old World *Vernonia* as distinct subgenera. The New World *Vernonia* (subgenus *Vernonia*) is distinguished as having a basic chromosome number of $x=17$ and sesquiterpene lactones of a simpler type. Pollen types recognized by Jones (loc. cit.) as B and D are typical of this subgenus, while types A and C are common to both subgenera. The subgenus *Orbisvestus* is tribasic with $x=9$ or 10 , has more complex sesquiterpene lactones and pollen types E and F are exclusive to this subgenus. The subgenus *Orbisvestus* is divided into four sections, namely, *Orbisvestus*, *Stengelina*, *Tephrodes* and *Azureae* each of which is divided into subsections. These sections are strikingly different from those proposed by Oliver (1877). Species belonging to the '*Vernonia Leopoldii* complex' are kept under sections *Orbisvestus* and *Hilliardinae*. Jones (1981), however, noted that the section *Orbisvestus* is a large one and merited further study.

In his paper on the Vernonieae of East Africa, C. Jeffrey (1988) stated that this tribe is well defined but its subdivision into subtribes and genera is still very uncertain. Based on data from chemistry, cytology and palynology, he noted that the distinction between basically Old World and New World taxa in the tribe goes deeper than merely subgeneric level and that there may be two major groups at the tribal level within it. Since the type species of the

genus *Vernonia*, *V. novaboracensis* (L.) Willd. is a New World species, the logical conclusion may seem to be that none of the Old World species should be referred to as *Vernonia*. He stated that 'it is impossible to escape the conclusion that major changes in the generic concepts in Vernonieae will occur in the future and this being the case, it is prudent to perpetrate as few nomenclatural changes as possible at present' (Jeffrey 1988:196). He divided the East African Vernonieae into five groups, each subdivided into subgroups. No taxonomic rank is attached to them. Since the taxa in the '*Vernonia leopoldii* complex' are not found in East Africa, they are not included in Jeffrey's account. However, the generic name *Cyanopis* Bl. to which *C. leopoldii* Sch. Bip. (= *Vernonia leopoldii* (Sch. Bip.) Vatke) and *C. hypoleuca* (= *Vernonia bipontini* Vatke) belong, is kept under synonymy in Group 2 subgroup C. Also the subsections *Orbisvestus* and *Hilliardinae*, erected by Jones (1981) are cited as synonyms under this group by Jeffrey (loc. cit). The citation of this synonyms is thought to be indicative of the possible affinity of the '*Vernonia leopoldii* complex' to the Group 2 Subgroup C.

External pollen morphology has been previously studied on different species of *Vernonia* by Wodehouse in 1928, Stix in 1960 and Skvarla and Turner in 1966 (all cited in Kingham 1960). Smith, in 1969, first observed differences in the pollen morphology of the Old World members of the section *Stengelia* and later emphasized the heterogeneous nature of this section. Keeley and Jones (1977) subsequently demonstrated the usefulness of pollen morphology in the

classification of the West Indian *Vernonia*. In her study of the African Vernonieae, Kingham (1976) distinguished six types of pollen grains in the tribe, from lophate grains with regular mural patterning and increasing tectum cover to echinate grains. The pollen types were described as follows: Type I - Grains lophate, triporate, micropuncta absent; Type II - Grains echinolophate, triporate, micropuncta present; Type III - Grains lophate, tricolporate, micropuncta absent; Type IV - Grains echinolophate, tricolporate, micropuncta present; Type V - Grains echinolophate, tending to subechinolophate, tricolporate, micropuncta present and Type VI: Grains subechinolophate tending to echinate, tricolporate, micropuncta present.

Jones (1981), in his synoptic treatment of the Old World Vernonieae, recognised similar groups which he referred to as Groups A to E. These were described as follows : Type A - echinate to subechinolophate, tricolporate with a continuous, micropunctate tectum, spines on the ridges or muri of the subechinolophate grain; Type B - echinolophate, tricolporate with discontinuous micropunctate tectum, germinal furrows elongated and separated at the poles by coincident muri, with spines generally pronounced on muri, but occasionally reduced, lacunae regularly or irregularly spaced, no polar lacunae present (paired poral lacunae may occur on this type as on type C); Type C - echinolophate, tricolporate, with a discontinuous micropunctate tectum, germinal furrows pronounced, spines on the muri or reduced in some, lacunae irregularly spaced, polar lacunae prominent, paired poral lacunae occur in some grains;

type D - echinolophate, triplicate, with a discontinuous micropunctate tectum, spines generally pronounced on the muri, occasionally reduced, lacunae regularly spaced, some of unequal size, germinal pores surrounded by a ridge ; found only in the New World; Type E - lophate or subechinolophate, semi-TECTATE with elevated geometrically arranged muri, supported by conspicuous collumellae, lacunae regularly spaced, germinal pores without distinguishing features and Type F - echinolophate to lophate, semi-TECTATE with geometrically patterned elevated muri, with conspicuous elevated columellae, lacunae regularly spaced, germinal pores with interrupted biparted muri.

It is on these classifications of pollen types that Jones' (1981) and Jeffrey's (1988) treatments of *Vernonia* are based.

Anatomical studies on the African species of *Vernonia* are scanty as much of the work has mainly been done on the New World species. Carlquist (1964) studied the wood anatomy of Vernonieae and the African species included in his work are *V. conferta* Blake and *V. colorata* Drake. Both species were collected from Ghana. In general, he observed that the data from wood anatomy of the tribe tend to give a measure of support to those who hold that Vernonieae contains a large number of characters that are considered as primitive within the Compositae. This conclusion is based on the presence of relatively long, wide vessel elements, without marked tendencies towards narrowness and shortness; absence of vascular tracheids; non-specialization of helical sculpture and minimal grouping of vessels.

storying is observed to be rare, or expressed only in rare ways; the rays are relatively unspecialized and uniseriate rays abundant. However, he noted that the great length of vessel elements in some species, the high wide primary-xylem-like rays and the abundance of erect cells in multiseriate rays could probably be an indication of paedomorphosis in accordance to a previously proposed theory (cf. Carlquist 1962) not primitiveness, per se.

Yohannes (1988), conducted comparative anatomical studies on *Vernonia galamensis* (Cass.) Less. and *Guizotia abyssinica* (L.f.) Cass., both of which are annuals. His observations on *Vernonia galamensis* concurred with the previous findings of Carlquist (1964) on other species of *Vernonia*.

Trichomes are among the most useful of all anatomical features for systematic comparison of angiosperms due to their variety, wide occurrence, ease of preparation for study and sometimes, their close correlation to various patterns among taxa (Carlquist 1961). Uniseriate trichomes as well as a variety of multicellular glandular and non-glandular trichomes are widely distributed in *Vernonia* (Solereider 1908). Hunter and Austin, in 1967, demonstrated the hybrid origin of a species of *Vernonia* by comparing the trichomes of two parental species and their hybrid progeny and they also suggested that further study of other trichomes of other species of *Vernonia* might be of taxonomic significance (cited in Faust and Jones 1973). Trichomes were also found useful in the revision of the genera *Centratherum* and

Phyllocephalus of the tribe, to review by Kirilova (1981) and in the investigation of 63 erlangeoid taxa in South tropical Africa by Pope (1983).

Relatively few chromosome numbers have been reported for the genus *Vernonia* when compared with other genera of Compositae. Jones (1974) attributed this to the comparative difficulty in counting chromosomes in *Vernonia*. Turner and Lewis (1965, cited in Jones 1974) worked on 16 species of African *Vernonia* and reported basic numbers of 9, 10, 16, and 17. They also stated that the cytological variation present in the genus is interesting and of taxonomic and evolutionary value. Jones (1974) made a summary of the 24 species known chromosomally and concurred with previous findings. In 1977, Jones noted that the majority of the Old World species are $n=9$, 10, 18 and 20 whereas the New World *Vernonias* have $n=8$, 17, 34, 51 and 68. However, Jones (1982) studied, among others, *V. amygdalina* Delile, *V. zuznellae* S. Moore and *V. thomsoniana* Oliver and Hiern and found that all the three species have $2n=30$.

Chromosome numbers, together with taxonomic and palynological data have been used in speculating evolutionary trends in *Vernonia* (Jones 1979a,b; 1981). Much information has accumulated regarding the biology of the New World species of *Vernonia* but relatively little is known about the Old World species (Jones 1977b). Based on work on several African species of *Vernonia*, Smith, in 1971, suggested that hybridization as well as a high degree of geographical variability

lead to the recognition of too many varieties, which are in most cases given specific rank. Results from work on narrow leaved species of North American *Vernonia* led Jones (1966) to conclude that the evolutionary significance of hybridization depends on the conditions where it occurs, in that if it occurs in an unstable, rapidly changing environment, some of the segregates may be better adapted to the new environment than were the parental types. Stebbins (1950) had earlier stated that *Vernonia* is one of the several genera in which forms that are widely divergent morphologically or ecologically lack development of extensive isolating mechanisms allowing hybridization and the production of fertile hybrids.

Jones (1977b) studied the reproductive biology and the crossing behaviour within seven Old World species namely, *V. anthelmintica* (L.) Willd., *V. cinerea* (L.) Less., *V. pauciflora* Less. (= *V. galamensis* subsp. *galamensis* var. *galamensis* M.G. Gilbert), *V. abyssinica* Sch. Bip. ex Walp., *V. adoensis* Sch. Bip., *V. melleri* Oliver and Hiern and *V. hymenolepis* A. Rich.. He observed that viable hybrids were generated between these stengeloid species of *Vernonia*. He concluded that hybridization could have played an important role in creating new genetic combinations among African species with the same chromosome numbers while differences in chromosome numbers were effective isolating mechanisms to preclude crossing should Old World and New World species come into contact.

1. MATERIALS AND METHODS

1.1 MATERIALS

The materials used for this study were obtained from the National Herbarium, Ethiopia (ETH), The East African Herbarium in Nairobi, Kenya (EA), and the Herbarium of the Royal Botanic Gardens, Kew, in England (K) (abbreviations based on Holmgren, Kueken and Nicholfeld 1981). Type specimens were obtained on loan from The Institute of Systematic Botany Herbarium, Uppsala, Sweden (UPS) and Muséum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, France (P). Both species were also studied in the field in Bahir Dar, Wellega, Gojjam and Keffa Provinces in Ethiopia and samples together with voucher specimen were collected. Slides prepared for anatomical, palynological and cytological studies are kept at ETH. Pollen preparations from a few specimens, prepared at the Palynological Laboratory in Stockholm, Sweden, were also studied at ETH.

Scanning Electron Microscope (SEM) studies of the leaf, achene, pappus and pollen surfaces were conducted at the Scanning Electron Microscopy and the Palynology and Palaeobotany Laboratories (EA) in Nairobi, Kenya. For study, samples were mounted on double-sided tape on stubs and coated with gold using a JEOL - Fine Coat Ion Sputter, JFC-1100. These were then examined using a JEOL-T100 Scanning Electron Microscope at 15kv and a working distance of 20mm.

A calibrated Olympus BH Binocular Microscope was used for Light Microscope (LM) studies. LM photographs were taken at the Traditional Medicine Unit of the Ministry of Health, Addis Ababa, Ethiopia. A Zeiss Axiophot photomicroscope with a magnification range of 25-1000x and equipped with two automatic cameras was used.

Methods for calculating the magnifications for both scanning and light microscope photographs are given in the appendices 3 and 4.

3.2 GROSS MORPHOLOGY

Specimens belonging to the '*Vernonia leopoldii* complex' were sorted out into groups that represented some degree of similarity in external morphology. Measurements of the vegetative and reproductive parts were then taken from specimens with mature floral and/or fructiferous capitula in each group. The size of the middle leaves and the mature capitula were measured directly from the herbarium sheets using a hand ruler calibrated in millimeters. The floral parts were prepared for study by boiling in water for 2 to 5 minutes. A minimum of three measurements were then taken from each part. The Bausch and Lomb stereomicroscope equipped with a finely scaled 10x ocular and with a magnification of upto 30x was used. Ranges of the measurements of the floral morphological characters for both species are given in Appendices 1 and 2.

3.3 PALYNOLOGY

Following the morphological studies and the subsequent distinction of two species within the '*Vernonia leopoldii* complex', samples of mature capitula were collected from specimens representing variation from both species, for pollen analysis. The grains were acetolysed following Erdtman's (1969) technique. For LM studies, acetolysed pollen was mounted in Kaiser's glycerol gelatin and sealed with wax. A minimum of 25 measurements per slide were taken for equatorial and polar diameters whereas a minimum of 15 measurements per slide were taken for the spine length, exine and sexine thickness. Light Microscope photographs were then taken from representative slides.

For SEM studies, the acetolysed pollen grains were kept in 70% alcohol and left to allow the alcohol to evaporate. The grains were then brushed onto double sided tape mounted on stubs, gold coated and then studied. Unacetolysed pollen grains were also studied for comparison.

The pollen fertility status of unacetolysed grains was estimated by determining the percentage of pollen stained with 1% aniline blue in lactophenol. A minimum total of 500 pollen grains were counted from each slide and the number of grains stained was expressed as a percent of this total.

4 CYTOLOGY

Cytological studies were made on somatic cells from the root tips of *Vernonia bipontini* Vatke and *Vernonia leopoldii* Vatke. Seeds were germinated on petri-dishes using Potassium nitrate treatment. Roots were collected a few hours after watering and pretreated in 0.002M 8-hydroxyquinoline solution for 4 hours. They were then transferred to 1:9 HCL:Orcein, warmed and cooled repeatedly four times and finally left to cool for 20 minutes. The roots were then transferred to 45% aceto-orcein and left overnight. The tips of the roots were then excised, squashed and chromosome counts done. Photographs were taken and used to confirm the count.

3.5 ANATOMY

Fresh samples of stems, petioles and leaves of the two species were collected from the field and fixed in Formaldehyde-Acetic acid-Alcohol (FAA) mixture (Cutler 1979). These were then dehydrated in a graded series of alcohol:acetone solutions and then cleared in chloroform. Gradual infiltration was done using chloroform:wax combinations and the sections were then embedded in Paraffin wax with a melting point of 55°C according to the procedures outlined by Sass (1958), Gray (1958) and Cutler (1978). Transverse, radial and tangential longitudinal sections were made from young and mature stems, serial transverse sections taken from petioles and transverse sections taken from the middle portion of the leaves.

Sectioning was done using an Optical 'A820' rotary microtome calibrated at 18 or 19 microns for stems and 10, 12 or 15 microns for petioles and leaves. The paraffin sections were attached to the slides using Haupt's adhesive (Wiley 1971), flooded with 4% formalin, warmed and dried overnight in a paraffin oven at 45°C.

The sections were stained using safranin- fast green differential staining technique adapted from Wiley (1971). The staining duration in safranin was however reduced from overnight to one hour. The sections were then mounted in Euparal after clearing in xylene. A minimum of 15 measurements were taken per selected specimen for leaf and petiole sections. Xylem vessel diameters are based on 50 measurements per specimen whereas 20 measurements per specimen were taken for fibre and vessel lengths.

For trichome studies, leaves fixed in FAA were transferred to 50% alcohol then 70% alcohol. They were then bleached in commercial 'hypochlorite' bleach and epidermal scrapes done. These were attached to the slides using Haupt's adhesive, flooded with 4% formalin, warmed, stained in safranin- fast green and mounted in Euparal.

3.6 MICROMORPHOLOGY

Leaf, phyllary and achene surfaces of samples from both species were studied by Scanning Electron Microscopy. Species thought to be related to those of the '*Vernonia leopoldii* Complex' were also studied for comparison.

Given the above considerations, a thorough systematic study of the '*Vernonia leopoldii* complex' was made with the objective of seeking for additional diagnostic characters useful in determining the relationships within the complex. Palynological, anatomical, cytological and micromorphological studies were conducted on representative specimens of this complex to supplement the standard herbarium and field macromorphological studies. During the progress of this work, this approach was found to closely match with the observations made by other taxonomists who have worked on the genus, for example, Jones (1981:59) who wrote '... the purpose of the study was to delimit biologically meaningful groups within *Vernonia*, thereby creating smaller 'natural' groups of manageable size for subsequent revisionary studies, which eventually lead to a refinement of the classification. Without the system proposed, it would be difficult if not impossible to examine effectively such a wide and unwieldy genus, ... hence an attempt to bring order out of the chaos that currently exists in *Vernonia*'.

Oliver (1877) accepted *V. leopoldii* but gave *V. bipontini*, *C. hypoleuca* and *C. leopoldii* as synonyms. He, however, did not cite Schimper 1542 as a type for *V. bipontini*. Hooker and Jackson (1895) in *Index Kewensis* cited *V. bipontini* as synonym of *V. leopoldii*. Cufodontis (1967) cited only *V. leopoldii* and kept *V. bipontini*, *V. leopoldii* var *incana* Avetta (1889), *V. leopoldii* var *hypoleuca* Chiovenda (1939), *C. hypoleuca* and *C. leopoldii* as synonyms. He cited Schimper 9 and 246 as the types for *V. leopoldii* and noted that the leaf indumentum is very variable within this taxon.

A survey of the three type specimens showed that the specimens Schimper 246 and 1542 were similar whereas Schimper 9 was quite distinct. Schimper 9 was collected on 26. 10.1837 from Tigray, Adwa, Mt. Scholoda and labelled '*Cyanopsis (Eucyanopsis) leopoldii* C.H. Schultz-Bipont.'. Schimper 246 was collected on 5.11.1837 and labelled '*Cyanopsis leopoldii* C.H. Schultzs-Bipont.'. However, this specimen is anonymously annotated as '*C. hypoleuca* in Sch. It. Abyss. Sect. III 1942'.

The third type specimen, Schimper 1542, was collected on 18.11.1842 and labelled '*Cyanopsis hypoleuca* C.H. Schultz-Bipont.'. The collection notes for this specimen are '*Nova species commixta et commutata cum C. leopoldii* in Sect. I. nr. 246, a qua differt achaeniis et floribus glabris (in *C. leopoldii* punctis resinosis munitis), involucro superne purpurascente, in *C. leopoldii* ad venas tomentosis, et insuper punctis resinosis adpersis'. It is apparent

from these Latin notes that Schultz-Bipontinus did not observe similarity between Schimper 246 and 1542.

In the current study, based on the morphological features of these type specimens and supported by herbarium and field studies, it was decided that the three type specimens represent two distinct species, hence, *V. leopoldii* (Sch. Bip.) Vatke (*C. leopoldii* Sch. Bip. of Schimper 9) and *V. bipontini* Vatke (*C. hypoleuca* Sch. Bip. of Schimper 246 and 1542). The delimitation by Vatke (1875) was therefore recognized as valid. Consequently, in the following text, these two species are treated as separate and distinct. Their diagnostic features are discussed in the following text.

4.2 GROSS MORPHOLOGY

4.2.1 HABIT AND LIFE FORM

Vernonia Leopoldii Vatke and *V. bipontini* Vatke are similar in habit and tend to occupy similar ecological niches. At one locality (54 km. from Ambo on the road to Nekemte, in Shewa Region, Ethiopia) they are found growing together yet exhibiting distinctive morphology. This is an indication of their distinctiveness, as implied by Davis and Heywood (1963:82), who observed that '...if they grow in the same area (sympatric) and particularly when they grow in the same habitat; and the plants continue to be distinct, it is fair to assume that there is some reproductive barrier between them'.

Both species are shrubs or perennial herbs with a more or less woody base. The branches are ascending from near the base (Fig. 1A,B). They grow up to a height of 2m. especially in open disturbed habitats such as roadsides where they are common. However, *V. bipontini* can also be a low lying suffrutescent perennial, growing only to 0.5m high with a woody base and a much branched crown (Fig. 2B) when found in unnatural habitats such as gutter walls. *V. leopoldii* growing under similar conditions still attained a height of up to 1.5m. (Fig. 2A).

The stem is terete, striate, densely brownish-, golden, greyish- or purplish- tomentose, with appressed T- shaped hairs.

4.2.2 LEAF ARCHITECTURE

The terms used below for leaf architectural studies are based on Hickey (1979).

The leaves of both species are alternate, petiolate, and decrease in size acropetally. They are dorsiventrally flattened, simple, symmetrical and ovate to ovate-lanceolate with the leaves of *V. bipontini* tending to be more narrowly- to linear-lanceolate. The apex is usually acuminate, sometimes attenuate, while the base is cuneate to decurrent. The margins are doubly serrate with regular spacing. The apical angle of the teeth is acute, the basal side mainly straight, apical side concave and sinuses are rounded. The petiole is winged and varies in length. Sometimes it is indistinct due to the decurrent leaf base.

The venation is reticulodromous, with stout straight primary veins. The secondary veins have a moderately acute angle of divergence. This angle is more acute in the upper secondary veins than in the middle ones. The curvature of this secondary veins is uniform and the intersecondary veins are composite. Tertiary veins are orthogonal reticulate, approximately at right angles to the midvein and predominantly alternate in arrangement. Quaternary veins are orthogonal and higher orders of venation than this are not distinct. The areoles are well developed, pentagonal and medium in size.

Studies of the epidermal scrapes from leaves of both species showed differences in the cell types of the two surfaces. The adaxial epidermal cells are polygonal, 5-6(-8) sided, regular, with straight walls, as seen with the light microscope. The abaxial epidermal cells are highly irregular and sinuous in outline (Fig. 3B). Similar observations from epidermal scrapes were made on *V. cinerea* (L.) Less. by Castro (1986). The stomata are simple, elongate in outline, with a raised rim. The guard cells are unornamented and are on the same level with the epidermal surface. The stomata on the teeth, however, are sunken (Fig. 4D). Distinct subsidiary cells are not evident. The cells surrounding the guard cells and the other abaxial epidermal cells have striae extended as lateral wings but the cells of the adaxial surface are unornamented (Figs 3A, 4A). The leaf surfaces of *V. hochstetteri* Sch. Bip. and *V. karaguensis* Oliv. & Hiern which occur in the same habitat were also examined (Fig. 3C-F). The main difference observed is in the ornamentation of cell surfaces. *V. hochstetteri* and *V. karaguensis* are not as densely striate as *V. leopoldii* or *V. bipontini*. The stomata appear larger in size in *V. karaguensis* and *V. hochstetteri* when compared to *V. leopoldii* and *V. bipontini*.

Despite the similarity in the epidermal cell shapes and surfaces, *V. leopoldii* and *V. bipontini* are easily distinguished from each other by the density of the indumentum and hair type (Fig. 5). The abaxial leaf surfaces as well as those of the stem, penduncle and phyllaries of *V. bipontini* are densely whitish tomentose, with the epidermal surfaces hardly visible. The trichomes are so densely

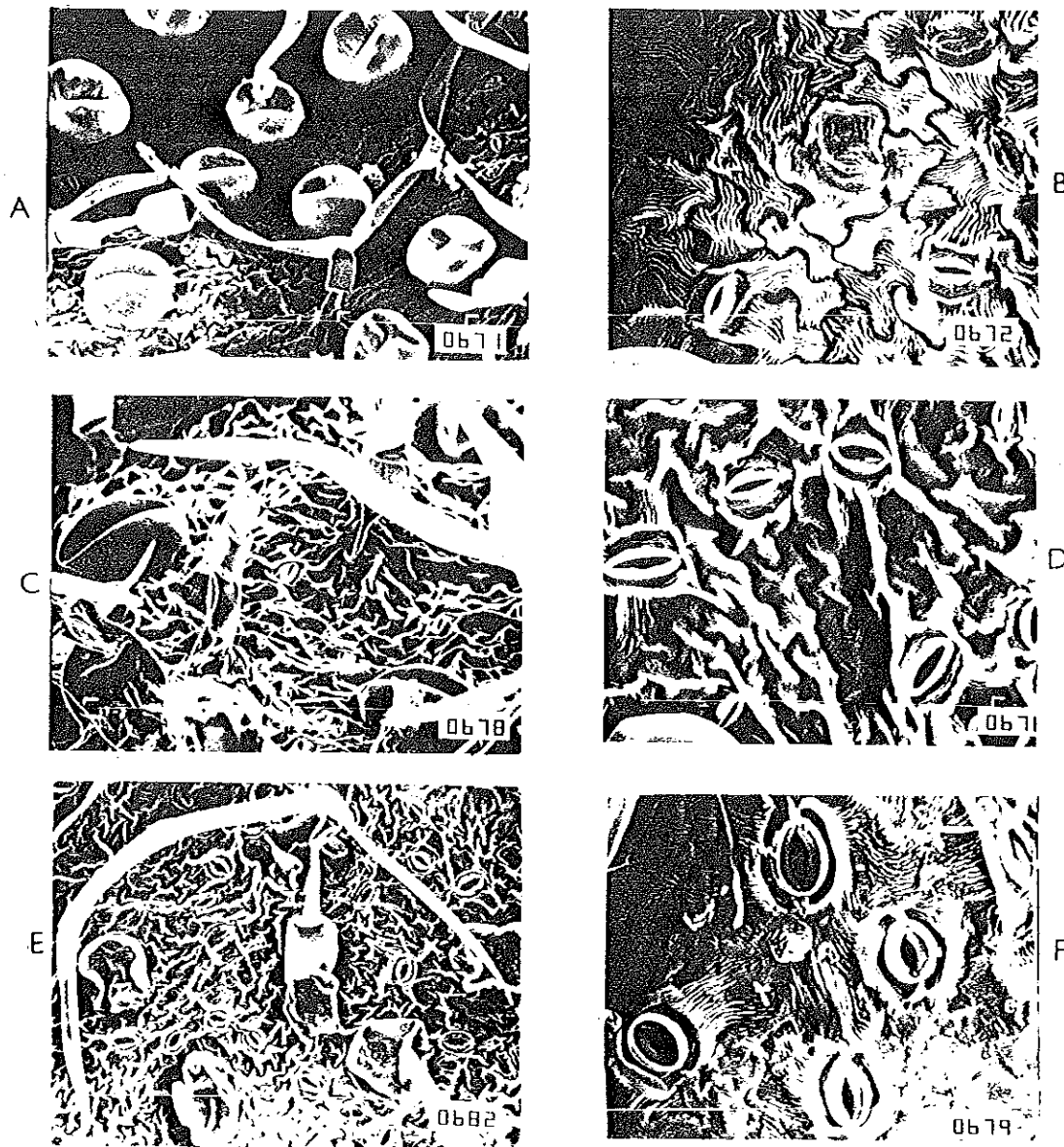


Fig. 3. Abaxial epidermal surfaces of leaves in *Vernonia*. (A:x160, C,E:x255, B,D,F:x510). A-B: *V. leopoldii* (Sch. Bip.) Vatke (Stella W. 46) C-E: *V. hochstetteri* Sch. Bip. (Stella W. 50) F: *V. karaguensis* Oliv. & Hiern (Stella W. 69).

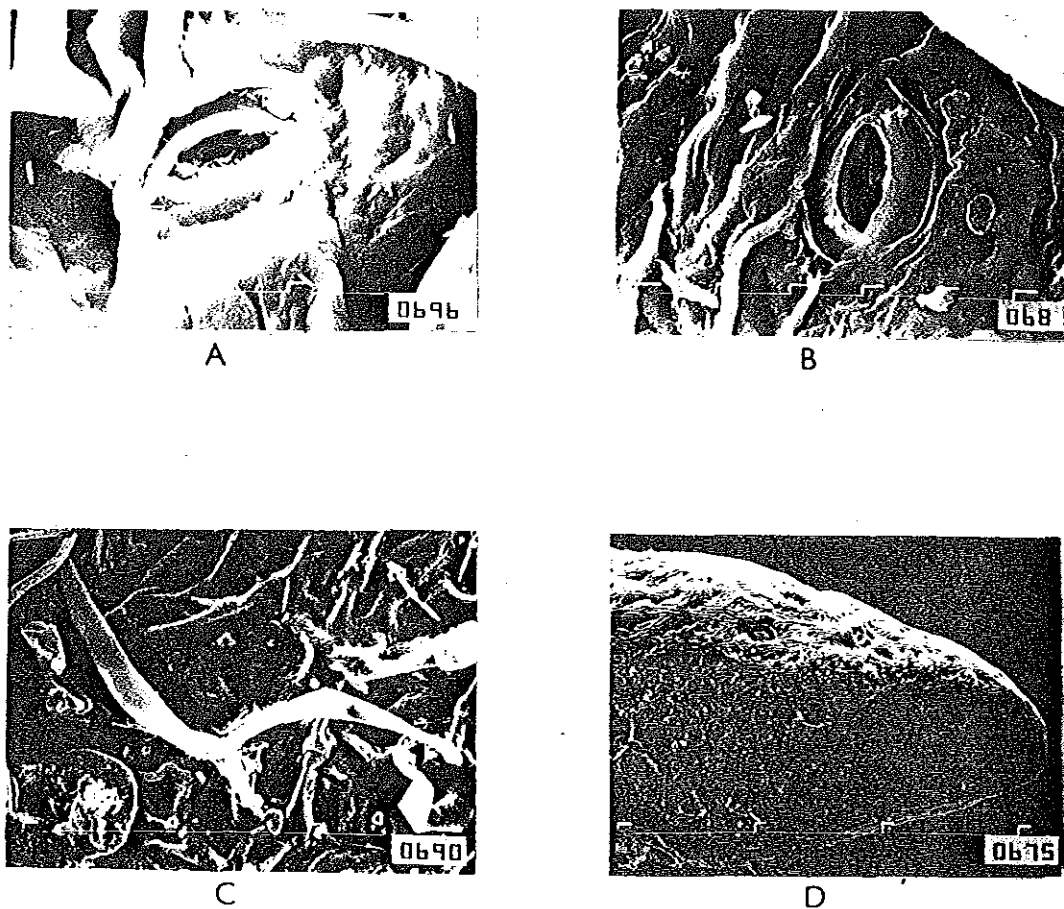
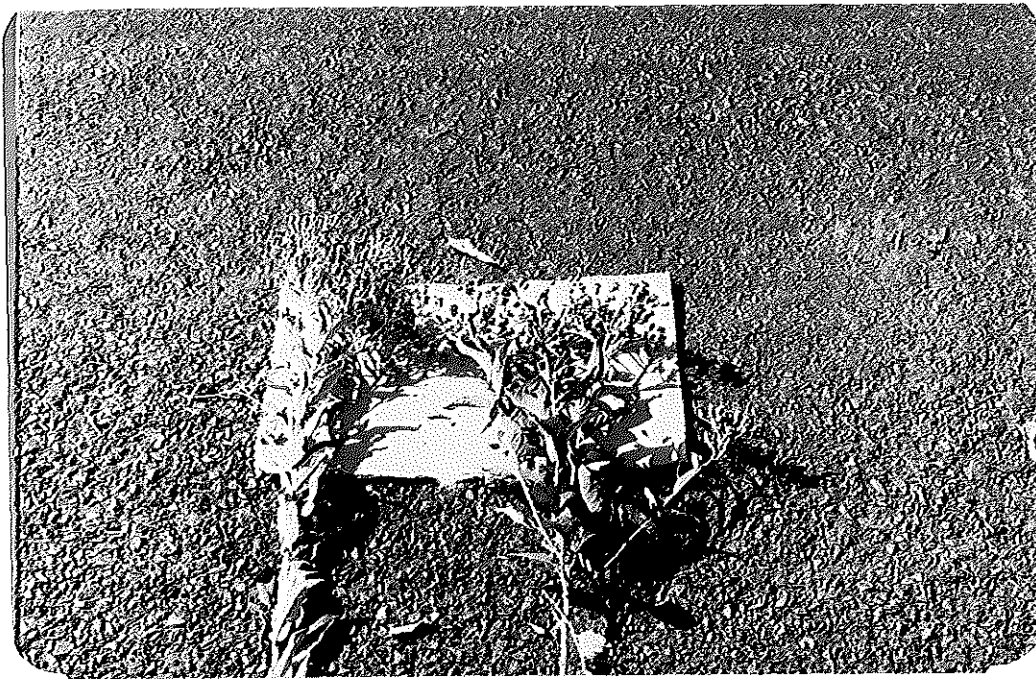
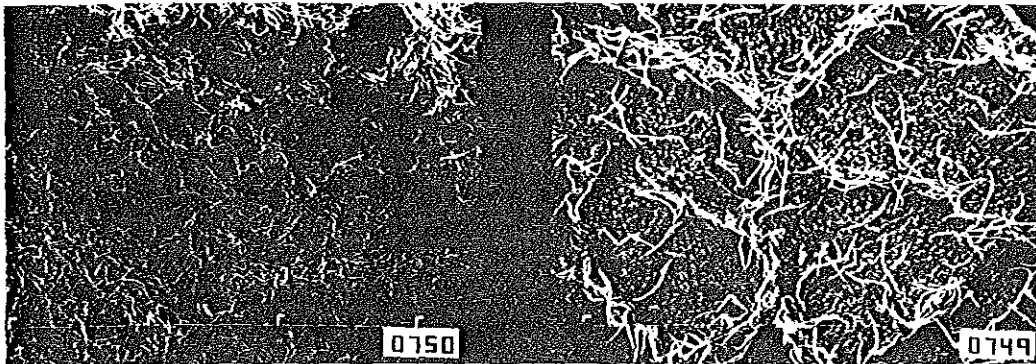


Fig. 4. Adaxial epidermal surfaces of leaves (A-C) and tooth on leaf margin (D) in *Vernonia*. A: *V. leopoldii* (Sch. Bip.) Vatke from Stella W. 101 (x1800) B: *V. hochstetteri* Sch. Bip. from Stella W. 50 (x1000) C: *V. bipontini* Vatke from Stella W. 48 (x390) D: *V. bipontini* Vatke from Stella W. 44 (x180).



A



B

Fig. 5. Differences in the leaf indumentum in *Vernonia*. A: *V. bipontini* on the left and *V. leopoldii* on the right B: Scanning Electron Micrographs of abaxial surfaces of *V. bipontini* from Stella W. 44 (left) and *V. leopoldii* from Stella W. 101 (right). {Both x18}.

interwined making it impossible to discern the individual hairs (Fig. 5A). In *V. leopoldii*, the leaf surfaces are thinly pale brownish tomentose, the epidermal surfaces are visible and the hairs are discernable as shown by the S.E.M. micrograph (Fig. 5B). This difference in the indumentum cover is thus considered to be of taxonomic value.

Six different types of trichomes could be distinguished from the leaf surfaces of these two species. These are:

1. Glandular, simple, unbranched hairs:

- 1a. Uniseriate, bilobed - Fig. 3A.
- 1b. Uniseriate, capitate - Fig. 6C,D.
- 1c. Uniseriate, multicellular - Fig. 6A,B,G.
- 1d. Multiseriate, multicellular - Fig. 6E,F,H.

2. Non-glandular, 2-armed, uniseriate hairs:

- 2a. T-shaped hairs with terete, lobed or short more or less equal arms - Figs. 7A,B and C respectively.
- 2b. Longhorn hair type according to Jones (1973), with the arms terete, more or less equal and filiform - Fig. 7D.

Vernonia bipontini has predominantly trichome type 2b whereas *V. leopoldii* can be distinguished by the presence of trichome type 2a. Trichome types 1a-d are common in both species but biseriate trichomes

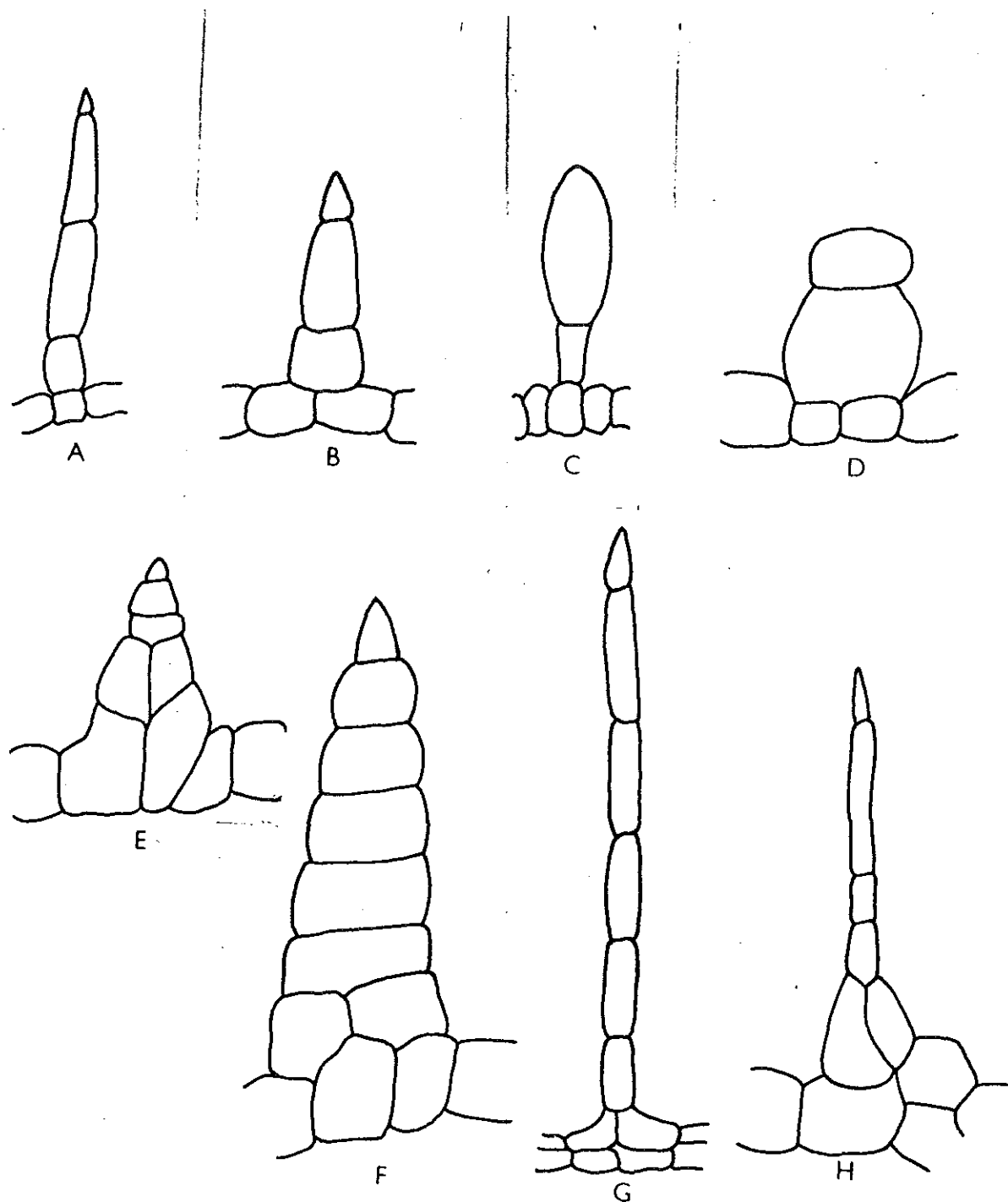


Fig. 6. Trichome types in *Vernonia leopoldii* and *V. bipontini* (A,B,D,E,H: x1000; C,F: x400; G: x100). A,B,G: Uniseriate, multicellular C,D: Uniseriate, capitate E,F,H: Multiseriate (at base), multicellular.

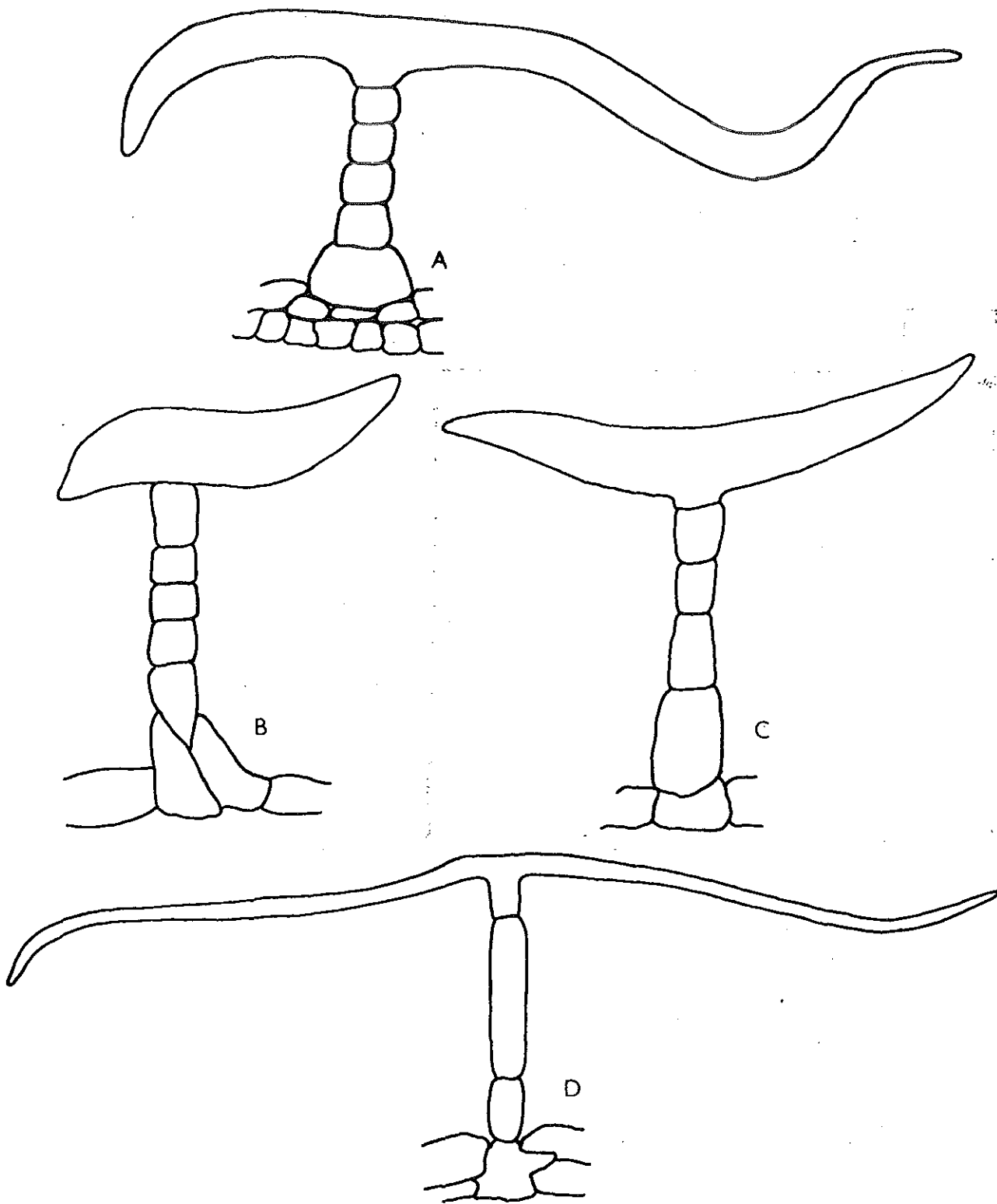


Fig. 7. Trichome types in *Vernonia leopoldii* and *V. bipontini* (x400). A: T-shaped with terete arms B: Short T-shaped hair with unequal equal arms C: T-shaped with lobed arms D: Longhorn T-shaped hair with the arms terete, subequal and filiform

lead to be more abundant in *V. Leopoldii* than in *V. bipontini*. As such trichome distribution is of diagnostic value in the two species.

Similar trichomes have been observed and used diagnostically in *Vernonia* (Jones, 1973); in erlangeoid taxa of Compositae (Pope, 1983); in *Centratherum* and *Phyllocephalum* of Tribe Vernonieae (Kirkman 1981) and in *Bidens*, of the Tribe Heliantheae (Mesfin 1984). The trichome type 1c was described as flagelliform by Kirkman (1981). Pope (1983) distinguished the T-shaped trichomes Type 2a as terete, lobed, and short armed. He described trichome Type 2b as T-shaped with filiform arms.

4.2.3 CONFLORESCENCES

The capitula of *V. Leopoldii* and *V. bipontini* are aggregated into loose clusters without a common involucre cover. Leppik (1977) terms these as conflorescences. The conflorescence shapes in both species are either compound corymboid, paniculate or subscorpioid cymes (Fig. 8), with the number of capitula varying from 20-200, rarely more. The simple units of these compound cymes, which can be described as simple cymes, have a terminal capitula, which is subtended by a peduncle that is shorter than those of the lateral capitula, and matures earlier than the later. The capitula are haplomorphic, discoid, homogenous, being composed of identically coloured tubular florets. The shape of the involucre varies from subcylindric to urceolate, but it is more pronouncedly urceolate in *V. bipontini*. The immature capitula of *V. bipontini* are turbinate with



A



B

Fig. 8. Conflorescence types in *Vernonia*. A: *V. bipontini* Vatke B: *V. leopoldii* (Sch. Bip.) Vatke. (Photo: Stella W. Nov. 1989)

reflexed phyllaries whereas those of *V. leopoldii* are globose-oblyhnetric usually with appressed phyllaries

The involucre size varies from 3 to 9mm in both species. The apitular length at anthesis is 8 to 11mm and 6 to 9mm when in fruit. however, in *V. bipontini*, the ranges are up to 14mm at anthesis and up to 11 mm in fruit.

The receptacle in both species is slightly convex in longitudinal section and the surface areolate. The areoles are separated by membranous fringe and the central part which forms contact with the base of the achene is raised.

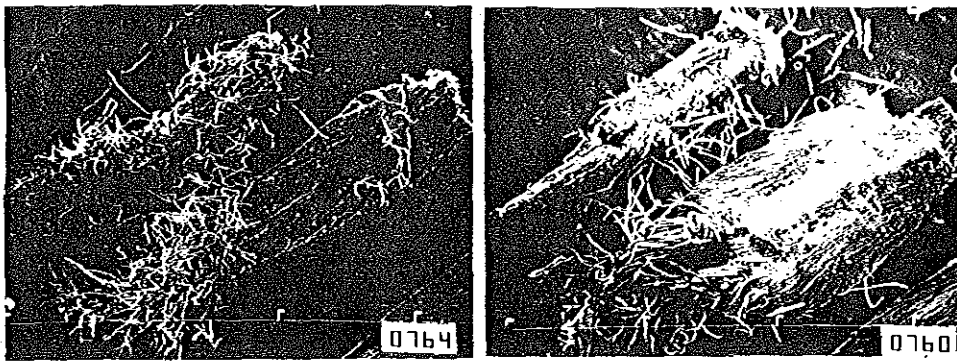
4.2.4 PHYLLARIES

The phyllaries are uniform, 5-6 seriate, increasing in size from the outermost to the innermost. The phyllaries of the different series however differ in shape, and in this study, they were classified as outermost, middle and innermost, to represent the range of variation.

The outermost phyllaries (Fig. 9B) are filiform (in *V. bipontini*), linear to ovate lanceolate (in both species) or triangular (in *V. leopoldii*). The apex is acute-apiculate. In *V. bipontini*, the apex is sometimes elongated to almost the same length as the capitula. The apex in this species is in most cases reflexed. The surface is sparsely to densely tomentose in both species (Fig. 10C, D) and papillate. The phyllaries are mostly green with a purple tinge towards



A



B

Fig. 9. Immature confluence (A) and outer surfaces of outermost and middle phyllaries (B) in *Vernonia*. A: *V. bipontini* ; (Photo: Stella W. Oct. 1989) B: *V. bipontini* (left); *V. leopoldii* (right) {Both x18}.

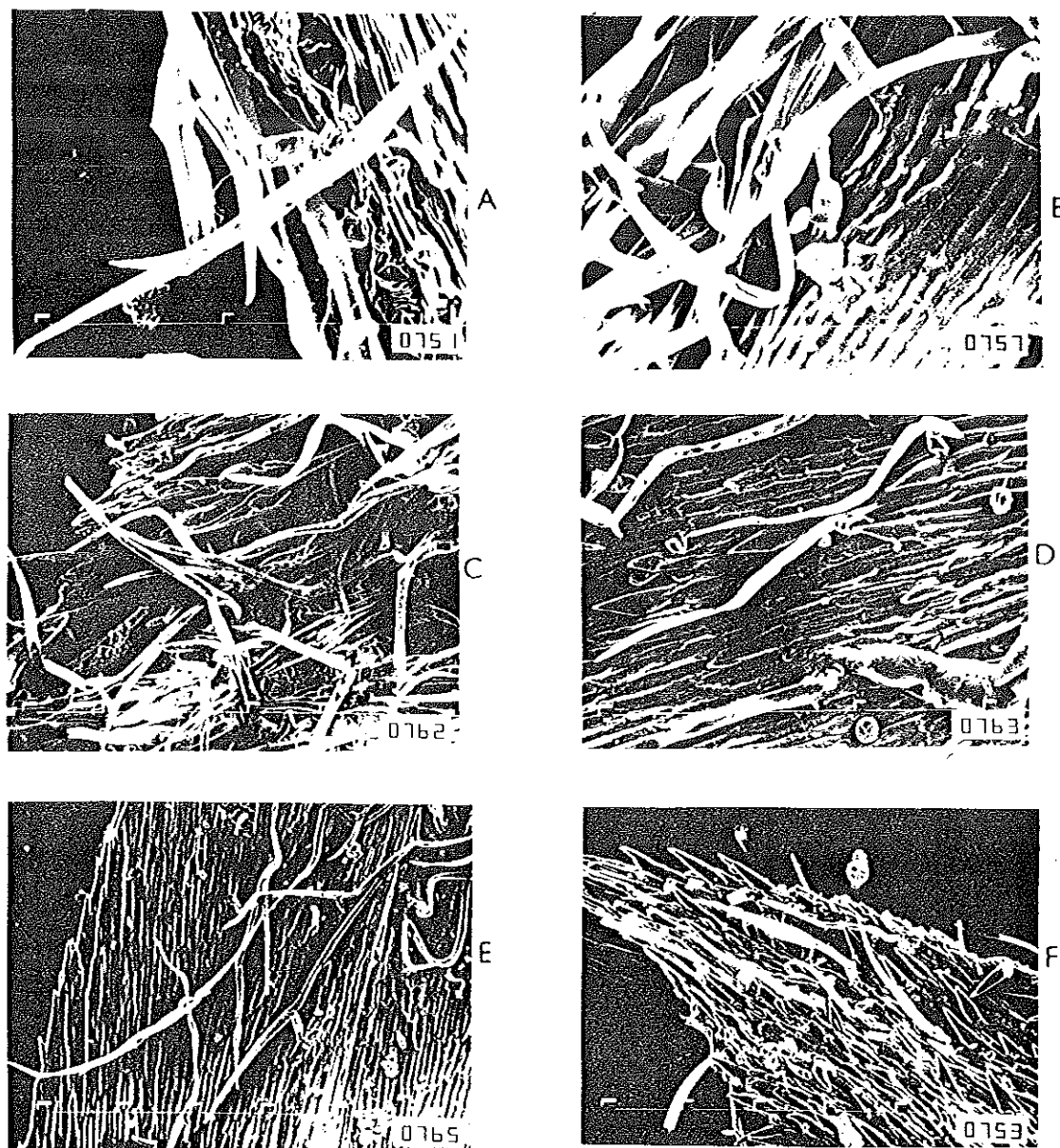


Fig. 10. Surfaces of phyllaries in *Vernonia*. A: *V. leopoldii* - Inner surface of outermost phyllary (Stella W. 102; x260) B: *V. bipontini* - Inner surface of middle phyllary (Stella W. 44; x380) C,D: *V. leopoldii* - Outer surface of innermost phyllary (Stella W. 48; x180) E: *V. bipontini* - outer surface of innermost phyllary (Stella W. 44; x100) F: *V. leopoldii* - inner surface of innermost phyllary (Stella W. 102; x100).

the apex and the margins are entire. The variation in size within each species is considerable: in *V. bipontini*, size varying from 1.0 to 3.4(5.4)mm and in *V. leopoldii*, from 1.0 to 3.2mm. The width of the phyllaries in both species ranges from 0.2 to 0.8mm.

The middle phyllaries are highly variable in shape and size. They are, in both species, oblong-elliptic to lanceolate or sometimes oblanceolate. The apex is acute to acuminate, reflexed sometimes elongate to 2.5mm (in *V. bipontini*) or appressed. They are membranous, pale green on unexposed parts, purple on exposed surfaces and 3-striate. The purple tinge is shortly continuous on the striations to the pale green zones and on the chartaceous translucent margins. The outer surface is tomentose on the exposed parts and glabrous on the non exposed parts, both surfaces being papillate. The inner surface is glabrous and papillate, except for a few scattered trichomes on the apical zone (Fig. 10B). The size is 3.0-5.0 X 0.7-1.7 mm in *V. bipontini* and (2.5-)3.0 X 0.6-1.6 mm in *V. leopoldii*.

The innermost phyllaries are similar in surface morphology to the middle phyllaries but differ in shape(Fig. 10C-F). They are mainly oblong-, or elliptic-lanceolate to oblanceolate and are 4.0-7.1 X 0.6-1.4(-1.6)mm in *V. bipontini* and 3.6-6.1 X 0.6-1.4mm in *V. leopoldii*. The apex is acuminate and sometimes produced to an elongate reflexed apicule to 0.6mm in *V. bipontini*.

Simple unbranched, bilobed trichomes and papillae are found on the surfaces of these phyllaries in both species. Unique to *V. leopoldii*, are L-shaped hairs with unequal arms (Fig. 10A,C,D,F) and few to many celled stalks. *V. bipartita*, however, has T-shaped trichomes with subequal to equal, long, filiform arms (Fig. 10B,E), thus the longhorn type of Jones (1973). The trichomes on the phyllaries of the two species are therefore also found to be of diagnostic value.

4.2.5. FLORETS

The florets are homogeneously tubular with five equal lobes at the apex. These florets are predominant in the subfamily Tubuliflorae of Compositae, to which the tribes Vernonieae, Eupatorieae and Cardueae belong. Leppik (1979) postulated that the radiate and labiate corollas could have been derived from tubulate structures. Hence, the sole presence of this type of florets indicates a degree of primitiveness in the tribe Vernonieae, to which these two species belong.

There are about 30 to 50 florets per capitula. These tubular florets are purple in colour, campanulate and have lobes that are obtuse at the apex. They vary slightly in length, with a range of about 4.5 to 8.5mm and the width about 0.4 to 0.6mm. The lobes are about 1.1-2.2 x 0.4mm. The only trichomes present on the corolla lobes are of the simple, unbranched bilobed type and the surface is microscopically striate (Fig. 11A).

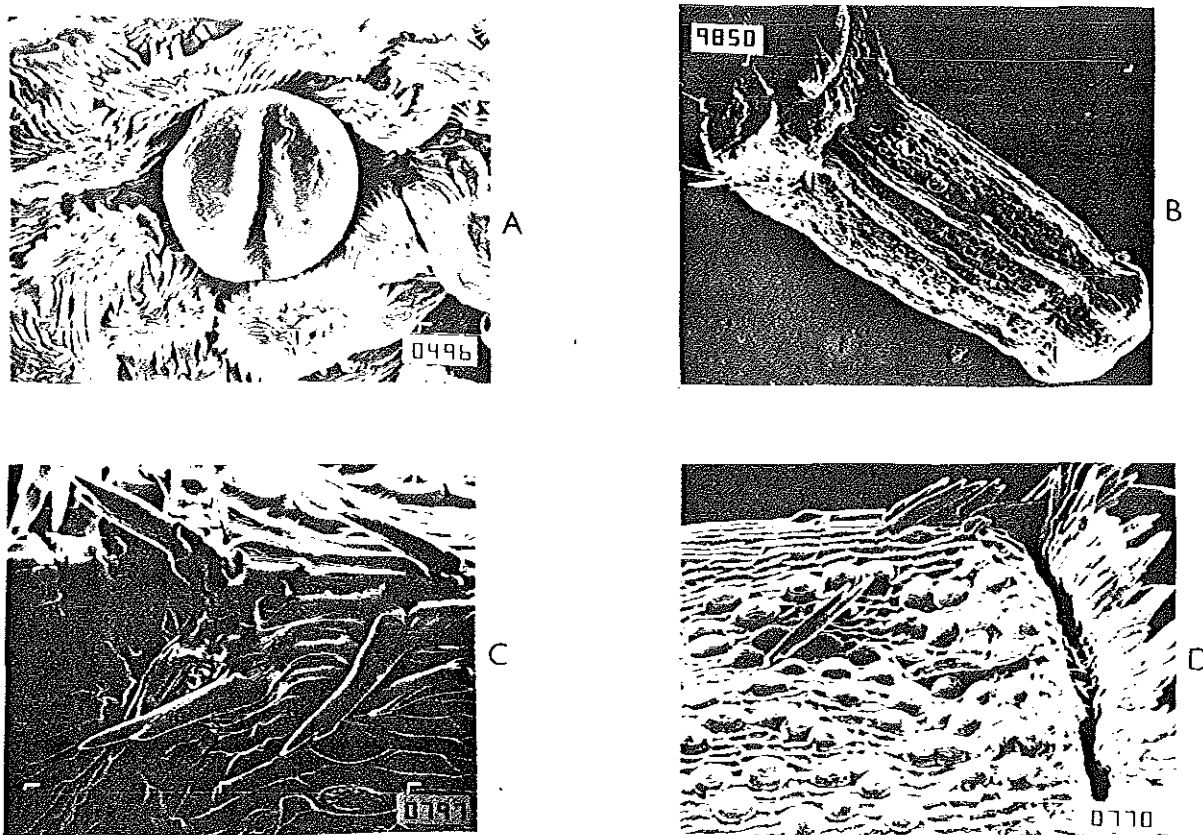


Fig. 11. Floret (A) and achene surfaces (B-D) in *Vernonia*. A: *V. leopoldii* (Mesfin and Kagnew 1618; x510) B: *V. bipontini* (Mesfin and Kagnew 1995; x51) C: *V. bipontini* (Stella W. 44; x260) D: *V. leopoldii* (Stella W. 102; x180).

The style is swollen at the base and bifurcate apically. It is terete, purple in colour and densely hispid on the arms which are usually exerted at anthesis. The style length in both species varies from 4.5 to 8.7mm in length with the arms being about 1.5 to 3.4mm long.

The anthers are yellowish in colour, sagittate at base, with acute basal lobes and ovate triangular apex. They are 2.0 to 4.2mm long. As noted by Leppik (1977), the anthers cohere to form a hollow cylinder and dehisce introrsely, filling the cylinder with pollen before the floret opens. The growing style brushes the pollen out of the anther cylinder by means of the hairs on its outer surface.

4.2.6 ACHENES

The achenes are cylindric-oblong to obpyramidal in shape (Pope 1983). The base is callus thickened and the apical rim is prominent and quadrangular (Fig.11B). The achenes usually have a stylophore at the apex and the walls are 4-6 ribbed, with a tuberculate surface except on the ribs. Simple, unbranched, bilobed hairs are distributed all over the surface, but the other trichomes, namely, hair-like subulate trichomes (Pope 1983), with one arm greatly reduced in some cases (Fig.11B-D); are mostly restricted to the upper half of the achene and are scantily distributed. The size range is from 1.0 to 2.2mm by 0.4 to 0.7mm in *V. leopoldii* and 1.4 to 2.4mm by 0.4 to 0.7mm in *V. bipontini*.

The pappus is biseriate with the outer series greatly reduced to form a toothed border, upto 0.4mm long. The inner series is elongate, barbellate, caducous and about 4.0 to 5.4mm long.

4.3 PALYNOLOGY

The pollen grains of *V. leopoldii* and *V. bipontini* are radially symmetrical, isopolar and spheroidal or circular (Fig. 12A-D). The Polar (P) to Equatorial (E) diameter ratio ranges from 0.958 to 1.045. Both species have echinolophate grains that are tricolporate, usually with a continuous micropunctate tectum and spines on the muri (Fig. 12). There are slight variations, however, in the continuity of the tectum. In most cases, the tectum is continuous but occasionally it is discontinuous with indistinctly shaped lacunae that are not prominent (Fig. 12E,F). There is no distinct variation in the size of the micropunctae on the tectum per grain. The pores and the colpi vary too in size and shape (Fig. 12C,D). In some grains, the colpi are well developed and converge at the polar axis whereas in some they are less well developed and end about halfway to the polar axis from the equatorial plane.

The spines are always conical, broadened at the base and with a sharp apex. They vary in length from 1.77 to 3.94 microns. Based on their shape, the pollen grains of *V. leopoldii* and *V. bipontini* can be said to belong to pollen Group VI of Kingham (1976) and pollen Type A of Jones (1981). This placement is supported by the fact that Kingham

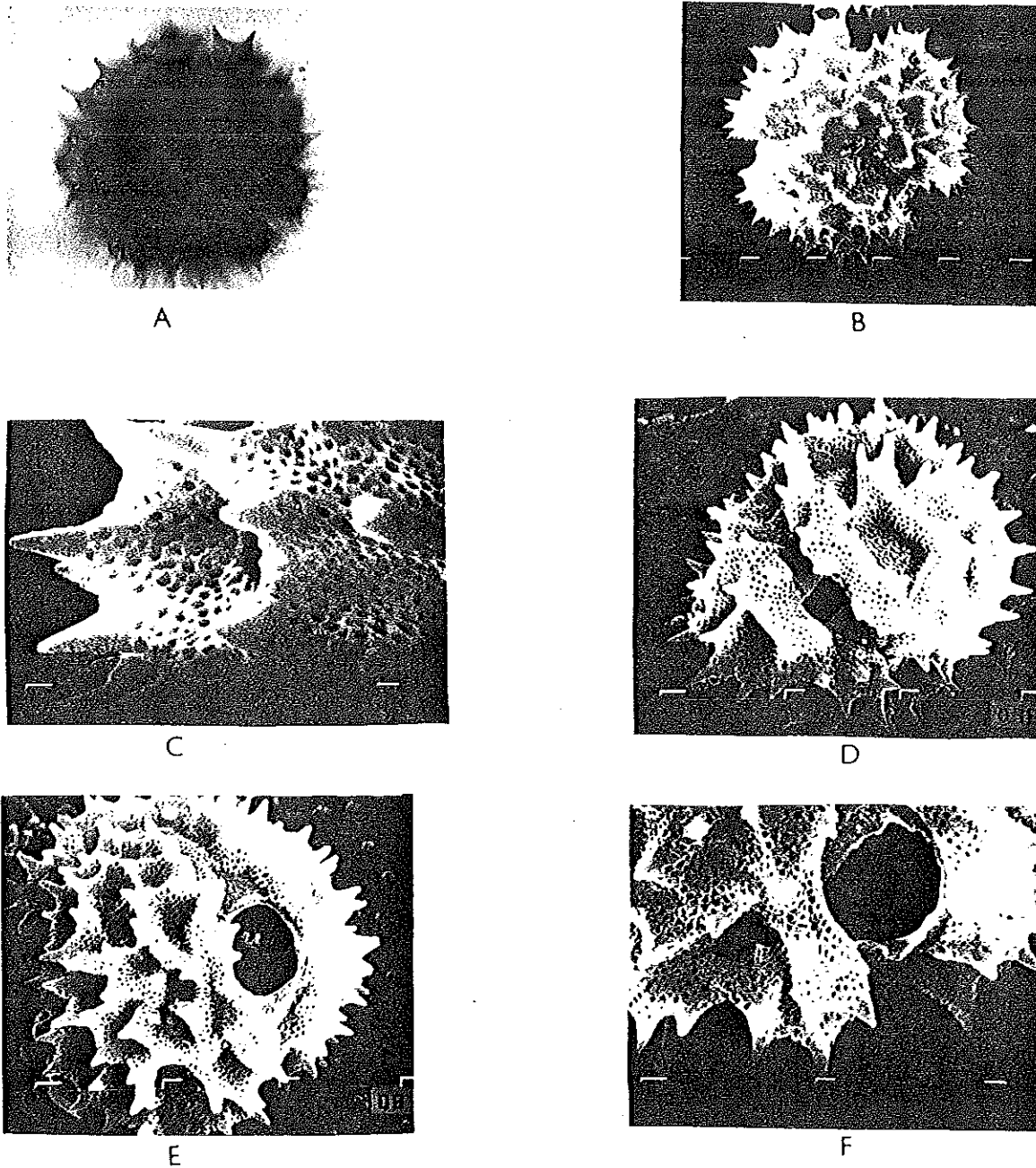


Fig. 12. Light (A) and scanning micrographs of pollen grains of *Vernonia*. A: *V. leopoldii*, x1000 (Evans and Lythgoe 307) B-F: *V. bipontini*:- B: Polar view, x1000 (Stella W. 44) C: Equatorial view, x1900 (Lundstrom 221A) D: Equatorial view, x1800 (Stella W. 47) E: Spine and tectum ornamentation, x5200 (Stella W. 44) F: Tectum and pore, x2500 (Stella W. 44).

(1976) studied *V. leopoldii* (Mooney 8853, from Ethiopia) and identified it as belonging to Group VI of her classification.

Jones (1981), studied among others, *V. leopoldii* and *V. bipontini*. The specimen cited under *V. leopoldii* is Gillett 5346 (from Somalia, kept at Kew), and that under *V. bipontini* is Ash 73 (from Ethiopia, kept at Athens Herbarium, Georgia-GA). One specimen, Mooney 5250, (from Ethiopia, kept at Kew), was studied under *V. natalensis* Sch. Bip. ex Walp.. In my present study, this specimen has been kept under *V. bipontini*. The pollen from Gillett 5346 and Mooney 5250 were classified as belonging to Type A, while pollen from Ash 73 was classified as belonging to Type B. Though Jones (1981) correctly identified the pollen type of *V. leopoldii* as Type A, which fits in with the results of the current study, it is most likely that the specimen, Gillett 5346, from Somalia was incorrectly identified since *V. leopoldii* is apparently endemic to the highlands of Ethiopia. *V. bipontini* pollen seems to be incorrectly classified as the grains in this species do not have distinct lacunae as is typical of the pollen Type B (Jones 1981 pp. 62), though they tend to have scattered regions of discontinuous tecta.

The polar diameter of the grains (excluding the spines) varies from 30.5 to 53.44(-59.6) microns whereas the range for the equatorial diameter is 31.8 to 54.4(-57.8)microns (Table 1). These pollen grain sizes are larger than those observed by Kingham (1976). In her survey of the pollen grains of Tropical Africa and certain other Vernonieae,

TABLE 1.

E = Equatorial diam

All measurements ar

Species, Collector	
<u>V. leopoldii</u>	
Namru 18	
Schimper 428	
Evans & Lythgoe	
De Wilde	8956
Schimper	9
Stella W.	46
Stella W.	101
<u>V. bipontini</u>	
Friis et al.	
Friis et al.	
Hepper 5881	
Nievergelt 1078	
Mooney 5250	
Mesfin & Kagnev	
Mesfin & Kagnev	
Mesfin & Kagnev	
Stella W.	44
Stella W.	47

Kingham (loc. cit.) recorded grain size range of (24.1-26.5/- 27.5) microns for *V. leopoldii* based on the collection of Mooney number 8858. However, this observation is not quite in discrepancy with the results of the current study as quantitative morphological studies showed that this specimen varied from the typical *V. leopoldii*. It has much smaller capitula, achenes and florets. Woodhouse (1928, cited in Kingham 1976), suggested that pollen grains may be used as an approximate measure of the chromosome number so that the difference in size could be a reflection of the level of ploidy. If this holds true, then the small size of the pollen of Mooney 8858 could indicate a lower level of ploidy. However, confirmatory studies could not be made due to the scanty herbarium material available and lack of similar field specimen. A fertility status showed that this particular plant (Mooney 8858) was fertile (Table 2).

Though Woodhouse (1928, cited in Kingham 1976), observed that the tribe Vernonieae is a group whose pollen pattern is sufficiently complex to permit such a wide range of expression that closely related species could be easily identified from each other, the current studies have shown that this is not the case. A similar conclusion was made by Kingham (1976:20) who stated that 'the present investigation shows that closely related species often infact show similar pollen characteristics'.

The pollen fertility for both species is found to be high (Table 2). This high percentage of fertility shows that each of these species

Species, Collect

V. lecpoldii

Stella W. 13

Stella W. 14

Stella W. 20

Stella W. 101

Stella W. 102

Evans & Lythgo

Mesfin & Kagne

Mooney 8858

V. bipontini

Mooney 6282

Mesfin & Kagne

Ash 2713

Friis et al.

Sebsebe D. 416

Berhanu A. 052

Stella W. 44

Friis et al. 4

is distinct and that there are no hybrids. Hence, though these two species are very closely related and occur in similar habitats, it is speculated that they are distinct species that have evolved specific isolating mechanisms.

The subechinolate to echinate pollen grains (Type VI of Kingham, 1976) are thought to be the most primitive of the pollen types of *Vernonia* (Kingham 1976, Jones 1981). This could be indicative of the fact that *V. leopoldii* and *V. bipontini* are among the primitive species in the genus *Vernonia*. However, other character states need to be studied before any valid conclusions can be made.

4.4 ANATOMY

4.4.1. LEAF ANATOMY

LAMINA. The leaves of both *V. leopoldii* and *V. bipontini* are dorsiventrally flattened. In *V. leopoldii*, the adaxial epidermis is uniseriate (Fig. 13A) and 12-26 microns thick. In *V. bipontini*, the adaxial epidermis is usually biseriate, rarely uniseriate and 9-45 microns thick. The epidermal cells in both species are transversely elongated or oblique, isodiametric, bullate or rectangular. The outer periclinal walls are convex, papillate, to 2 microns thick in *V. leopoldii* and up to 4 microns thick in *V. bipontini*. The thickened epidermal walls are of ecological importance as these plant species grow in open, dry habitats. The anticlinal walls are 1-2 microns thick in both species, and are straight, convex or undulating. The cuticle

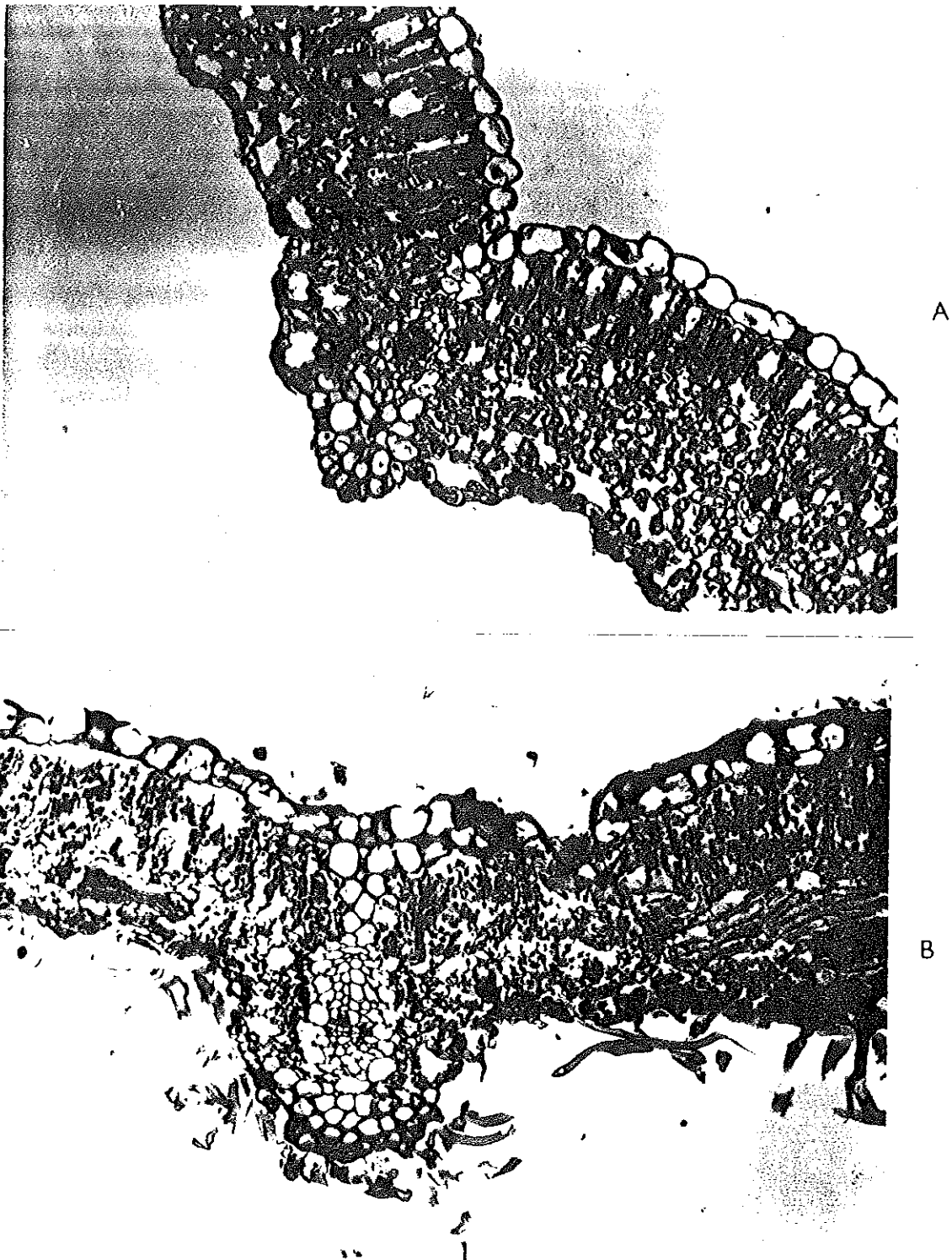


Fig. 13. Leaf transverse sections of *Vernonia* (x2000). A: *Vernonia leopoldii* showing secondary vein (Stella W. 8) B: *V. bipontini* showing primary vein (Stella W. 44)

is 1-3 microns thick. The adaxial epidermal cells are in general about three times the size of the abaxial cells.

The mesophyll is mainly bifacial in both species (Fig. 13A,B), with distinct palisade and spongy mesophyll layers. The palisade layer is uniseriate, sometimes biseriate (Fig. 14B) or discontinuous (in *V. leopoldii*-Fig. 14A). This is not abnormal as MetCalfe (1979:66) noted that 'the number of layers of palisade cells also varies, not only from species to species but sometimes in different specimen of a single species or even in different individual leaves from a single plant.' This layer is 10-80 microns thick in *V. bipontini* and 35-85 microns thick in *V. leopoldii*. When the palisade layer is biseriate, the cells making up the inner layer are usually shorter than the outer ones. The cells are transversely elongated, rectangular in shape and densely packed with chloroplasts along the wall.

The spongy mesophyll is compact, 15-100 microns thick in *V. bipontini* and 40-105 microns thick in *V. leopoldii*; thicker especially in regions where the secondary and tertiary veins are embedded in the medulla. The cells are isodiametric to irregular and densely packed with chloroplasts. The air spaces are small but in *V. leopoldii*, the substomatal chambers are prominent (Fig. 14A). Adjacent to the stomata on the abaxial epidermal surface, they are up to 20 microns deep into the spongy mesophyll. These are however not prominent in *V. bipontini*.

In *V. leopoldii*, the abaxial epidermis is uniseriate, wavy in outline, protracted from the main lamina especially at the stomatal

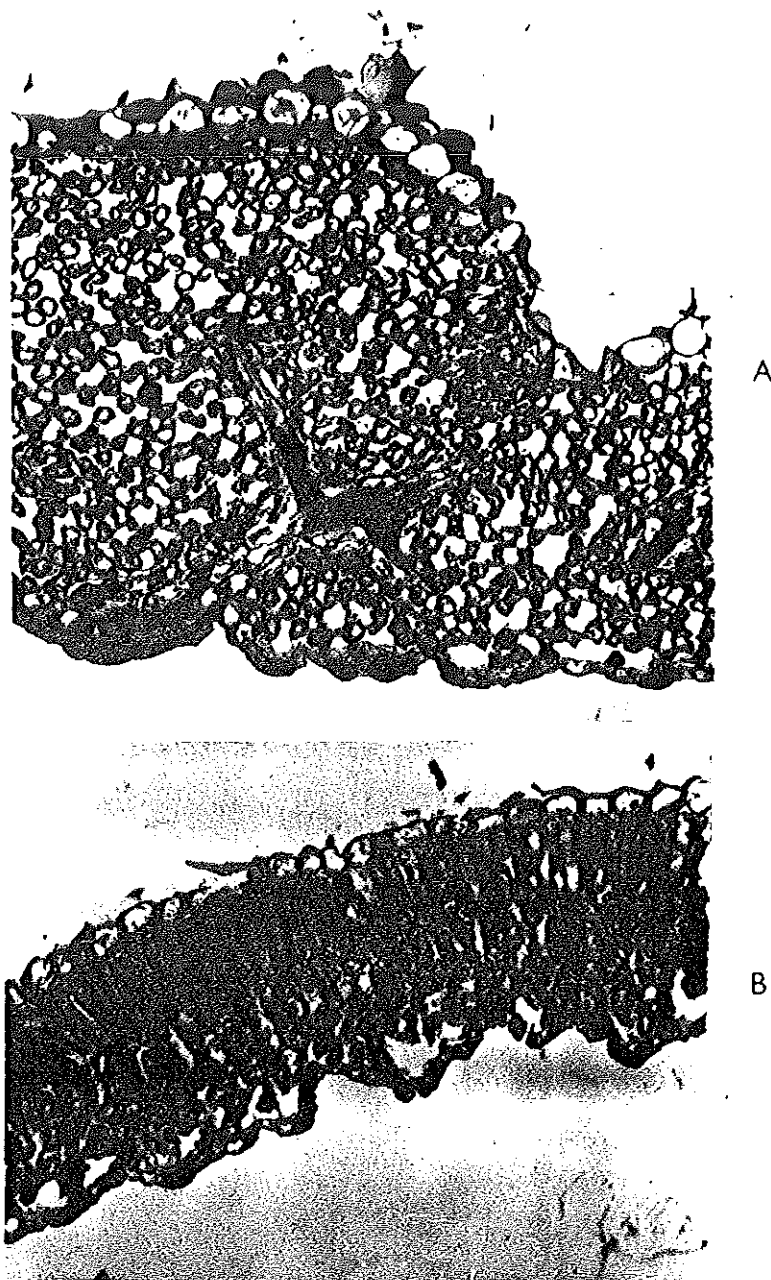


Fig. 14. Transverse sections of *Vernonia leopoldii* showing variations in the mesophyll layer (Stella W. 8; x2000). A: without the palisade layer B: with bifacial mesophyll and some parts with biseriate palisade layer.

regions, 6-15 microns thick (Fig. 14B). In *V. bipontini*, however, the epidermal layer is not distinctly protracted from the main leaf tissue, and the layer is 5-11 microns thick (Fig. 13B). This layer is highly piliferous in *V. bipontini* (Fig. 15B), but not in *V. leopoldii* (Fig. 15A). In both species, the cells are obliquely arranged or elongate transversely. The walls are sinous, sometimes straight or convex and the outer periclinal walls are papillate.

There are simple unbranched bilobed trichomes in both species, with their bases located in grooves on both surfaces (Fig. 15B, arrow). Scattered multiseriate, multicellular trichomes are present in *V. leopoldii*, whereas in *V. bipontini*, uniseriate, multicellular and T-shaped hairs are predominant.

The stomata are anomocytic, with the guard cells on the same level as the epidermal cells.

MIDVEIN. The epidermal layer around the midribs in both species is uniseriate, with the cells thickened on the outer periclinal walls, papillate, elongate vertically and rectangular to isodiametric or sometimes bullate.

The cortex is made up of both parenchymatous and collenchymatous tissues (Fig. 16A). The collenchymatous part is 2-5 cell layers thick. The cells are isodiametric, have angular thickening and they increase in size towards the parenchymatous cortex. The parenchymatous section

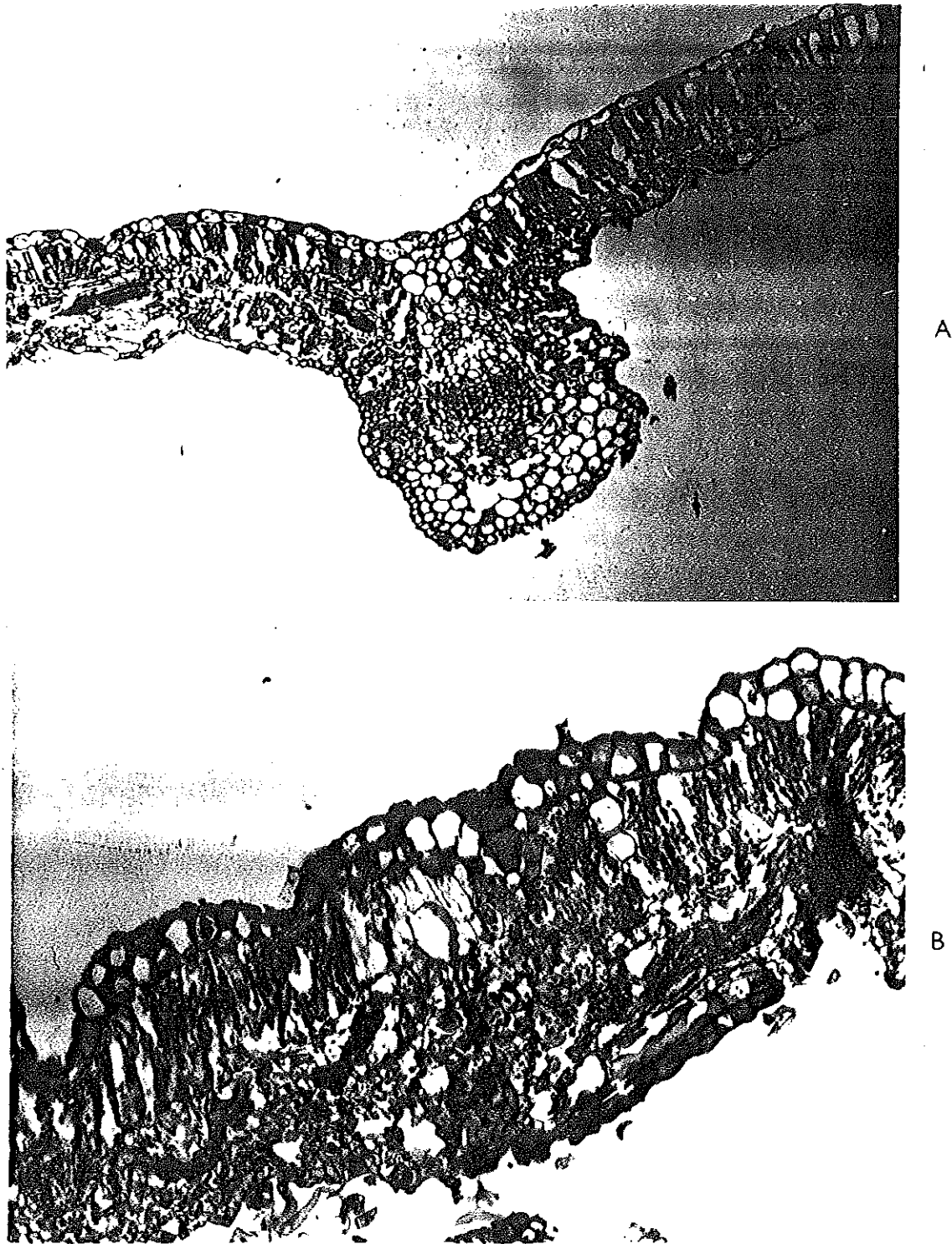


Fig. 15. Transverse leaf sections of *Vernonia*. A: *V. leopoldii* showing vein distribution (Stella W. 8; x1000) B: *V. bipontini* (Stella W. 44; x2000)

as isodiametric to polygonal cells that are about twice the size of the collenchymatous cells (Fig. 16B).

The central vascular bundles are fused (sometimes free in *V. leopoldii*) forming an arc in the medulla, with one free small rib race at each end of the arc. The bundles are collateral, with the phloem being abaxial to the xylem and with the parenchymatous cells surrounding them. A cap of sclerenchymatous tissue is found at the adaxial and abaxial ends of the vascular bundles of the midrib of *V. bipontini*.

Similar leaf anatomical characteristics have been observed by Johannes (1988) in *Vernonia galamensis* Cass. and by Castro (1986) in *Vernonia cinerea* (L.) Less. among others. However, Castro (1986) observed the abundance of druses in the mesophyll, a feature which was not observed in *V. leopoldii* and *V. bipontini*.

In general, anatomical studies of the leaves of *V. leopoldii* and *V. bipontini* show qualitative variation as discussed above, but no diagnostic quantitative differences were observed (Table 3).

4.4.2 PETIOLE ANATOMY

The adaxial epidermis is uniseriate in both species, 7-22 microns thick in *V. leopoldii* while it is 11-24 microns thick in *V. bipontini*. The cells in both species are elongated vertically and isodiametric to irregular. Periclinal walls are convex, rarely

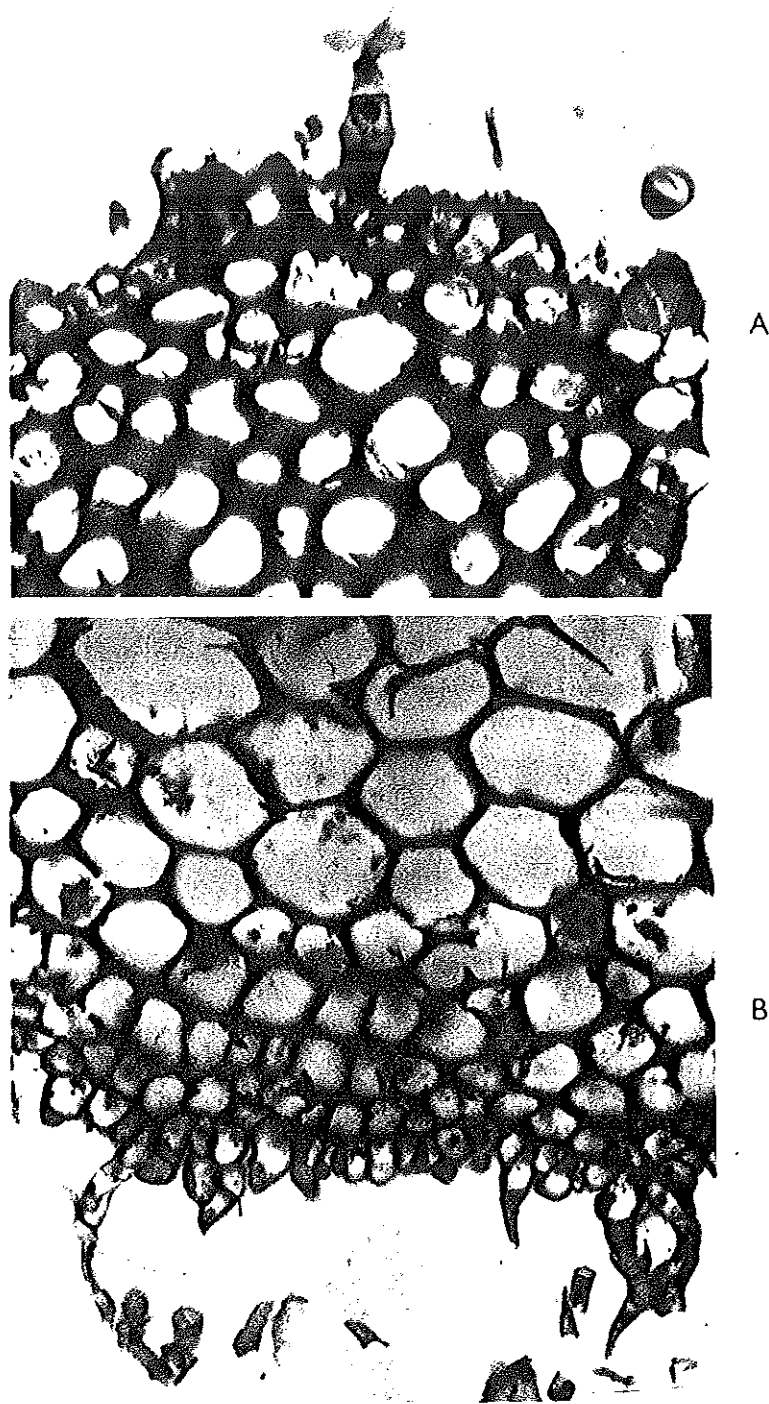


Fig. 16. Epidermal and cortical regions of leaf transverse sections of *Vernonia* (x4000). A: *V. leopoldii* - Adaxial layers (Stella W. 8) B: *V. bipontini* - Abaxial layers (Stella W. 17).

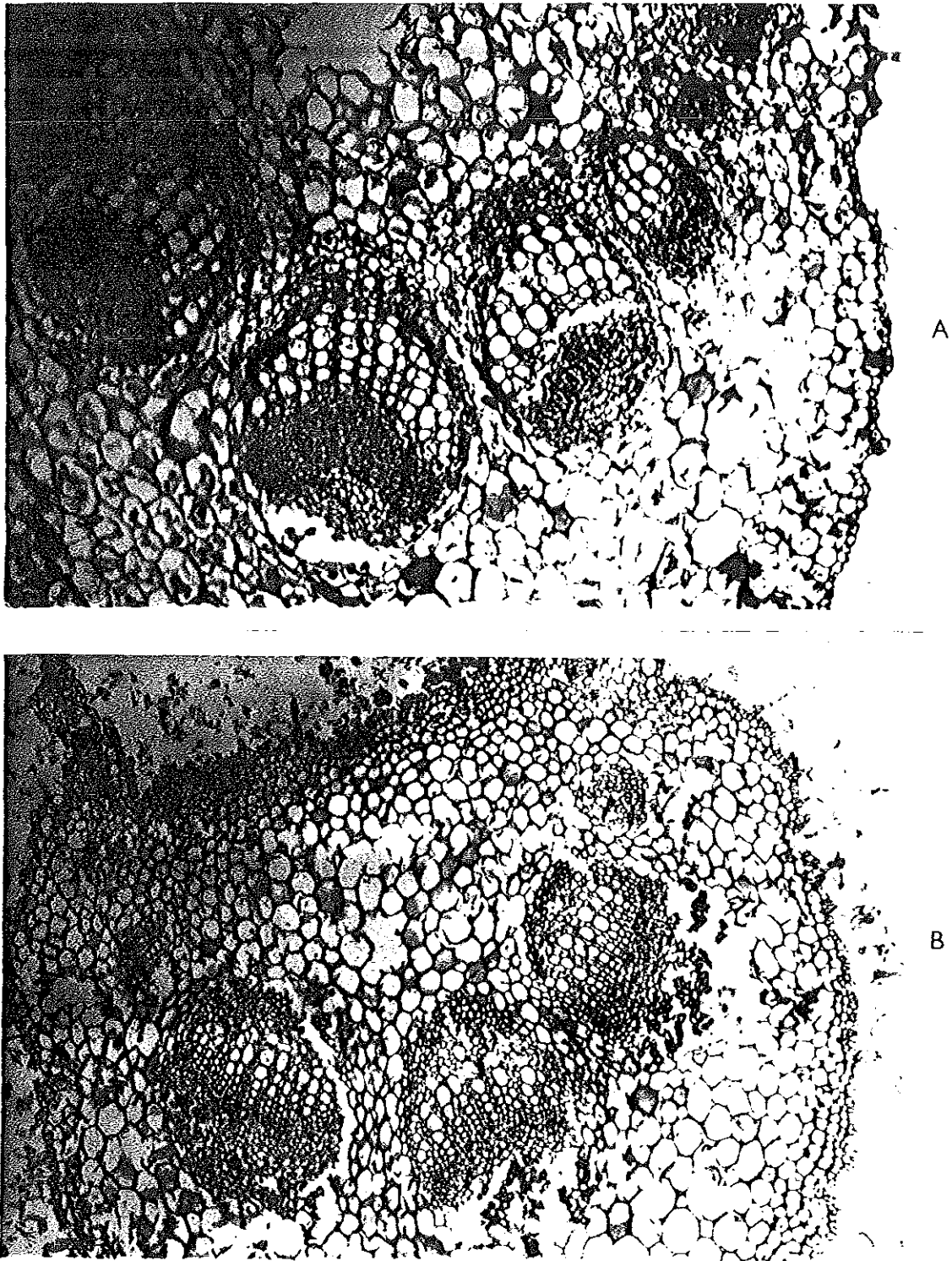


Fig. 17. Transverse sections of petioles of *Vernonia*. A: *V. leopoldii* (Stella W. 11; x2000) B: *V. bipontini* (Stella W. 17; x1000).

The abaxial epidermis is similar to the adaxial one in structure, and is 7-28 microns thick in *V. leopoldii* but 10-18 microns thick in *V. bipontini*. Both the adaxial and the abaxial epidermis are piliferous in both species but are more so in *V. bipontini*. Both the glandular and the non-glandular hairs are present.

Quantitative data from both species does not show any diagnostic differences but only continuous variation between them (Table 4).

4.4.3 STEM-NODE-LEAF CONTINUUM.

A study of hand sections of the nodes showed the presence of three gaps hence suggesting trilacunar nodes in both species. In *V. leopoldii*, however, the petioles consistently have five free bundles, with two small rib traces. In the leaf midrib, the five bundles fuse to form an arc while the small rib traces remain free.

According to Howard's (1979) classification of nodal patterns, the *V. leopoldii* node can be described as 3-3, bundles free, with the lateral traces dividing to form five traces (Fig. 17A). A similar situation is shown in the genus *Pedilanthus* (Euphorbiaceae) (Howard loc. cit.). In *V. bipontini*, the bundles are consistently three, free throughout the petiole and fuse to form a central arc in the medulla of the midrib. Hence, the nodal pattern can be described as 3-3, bundles free, 3-trace, free throughout the petiole according to Howard (1979) (Fig. 17B).

Stellia W. 11	(20)	(21)	(27)	(23)	(19)
7 - 21	16 - 45	18 - 55	20 - 34	7 - 20	

with lacunar thickening. These cells are elongate tangentially and are about three times as long as wide.

The parenchymatous cells are polygonal near the collenchyma but tend to be more or less isodiametric towards the cylinder of vascular bundles. The walls are thin and sinous. In mature stems, the cells are elongate transversely and are about 1 to 4 times as long as wide, increasing in size towards the medulla. The parenchyma cell walls are thickened.

Medullary rays

The medullary rays of early wood are 5-7 cells wide, widening towards the pith. The cells are polygonal, elongate radially but becoming elongate transcurrently towards the pith (Fig. 20B). In mature wood, the walls of the cells become secondarily thickened, with simple pits.

Vascular bundles

In transverse sections, the collateral bundles form a ring with each vascular bundle being accompanied by a large crescent shaped cap of fibres in the pericyclic region (Fig. 20A). This is typical of the Compositae as is indicated by Metcalfe and Chalk (1950). The sclerenchyma caps become more developed in mature stems and sclerified cells become more abundantly scattered in the phloem.

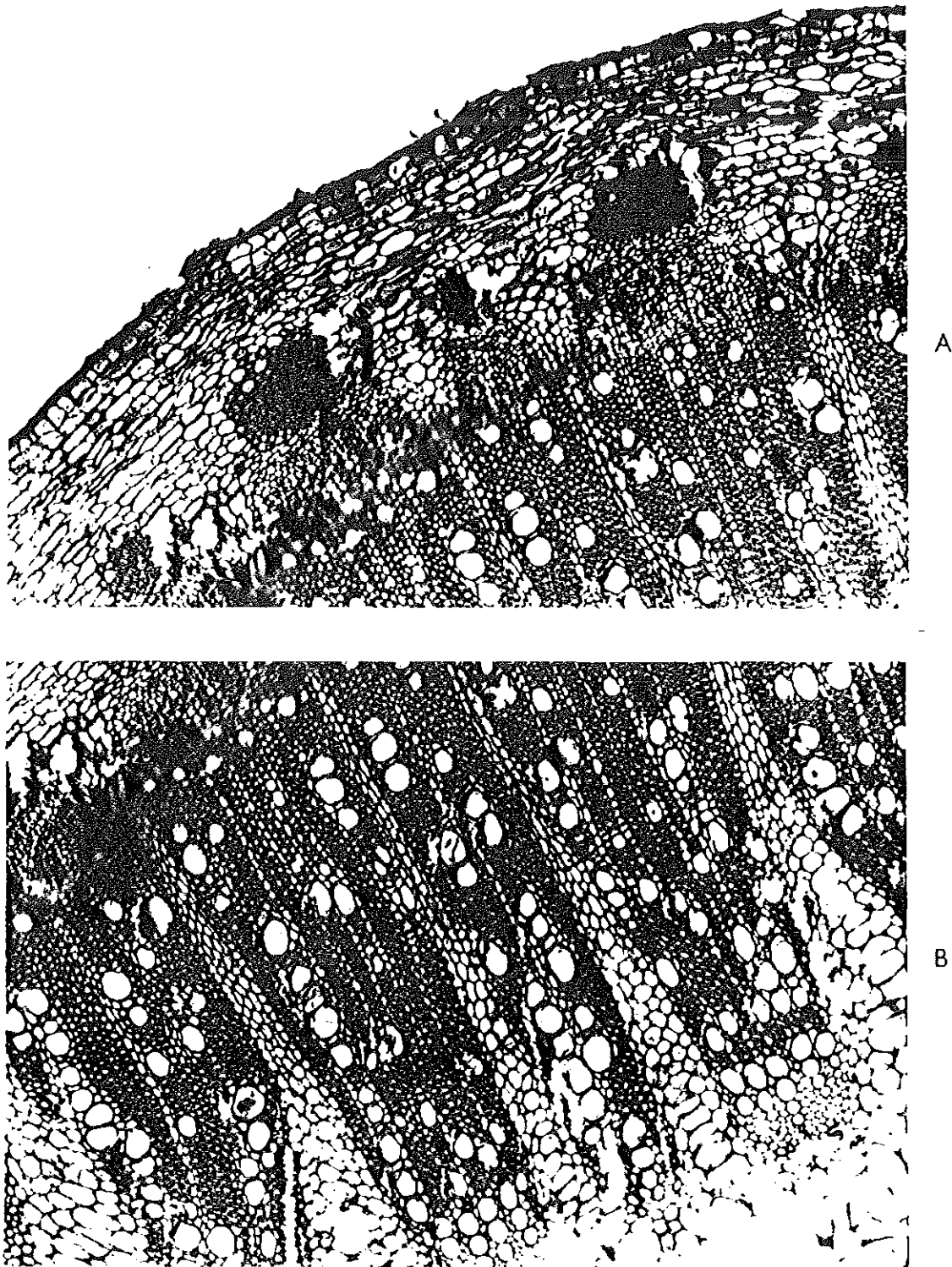


Fig. 20. Transverse sections of *Vernonia bipontini* stem (Stella W. 17; x1000). A: Cortex - bundles; B: Bundles - pith.

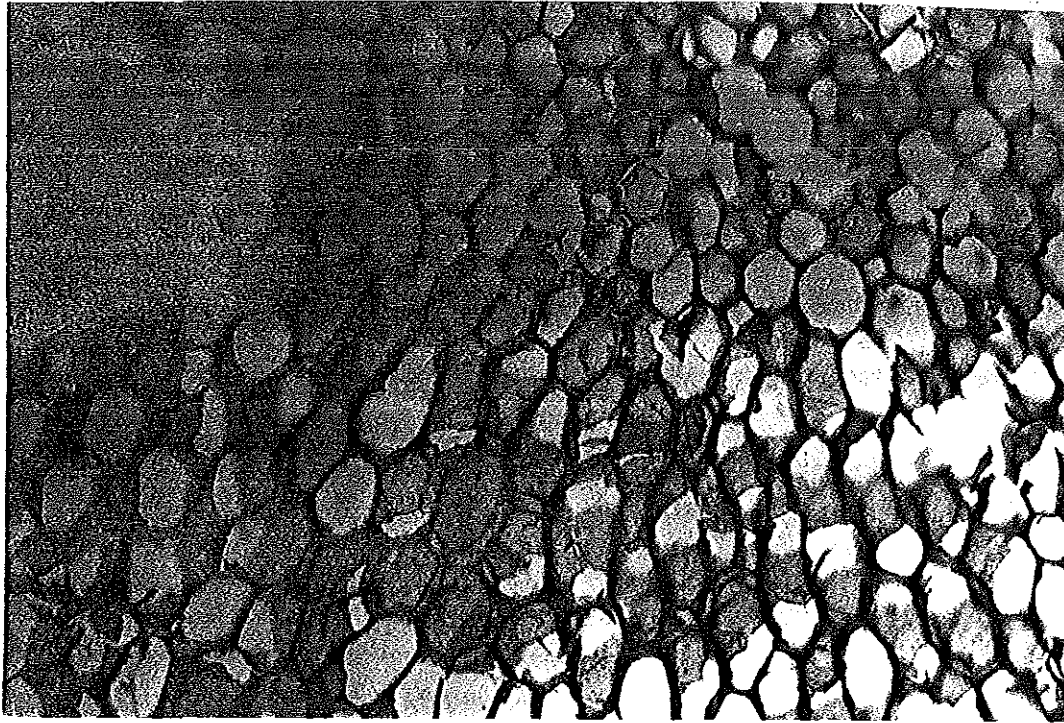
The pith is distinct with parenchymatous cells, elongated radially just beneath the bundle and polygonal, 6-8-sided, but regularly hexagonal at the centre. The persistence of the pith, mainly a water storage tissue, may be related to the mesic-tropical habitat of these two species.

4.4.5. WOOD ANATOMY

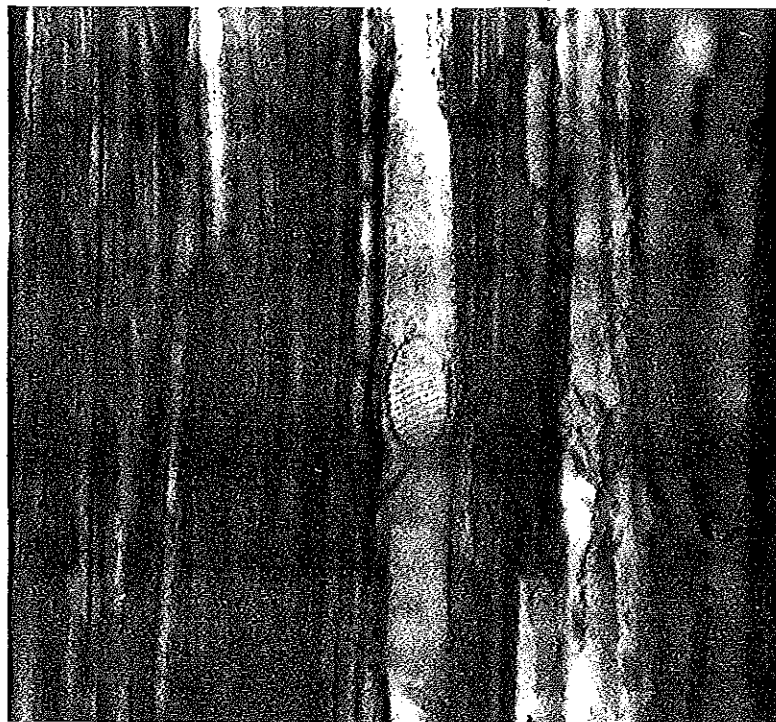
Vessels

The vessel elements in both species were measured from tangential sections. They are 22-125 microns in *V. leopoldii* and 30-60 microns in *V. bipontini*. The average diameters are 58.1 microns and 41.7 microns for *V. leopoldii* and *V. bipontini* respectively. The vessel element lengths are 190-420 microns in *V. leopoldii* with the average length being 297 microns. In *V. bipontini*, the range is 150 to 350 microns, with an average of 207 microns. Hence both species have small elements that are relatively long (Table 5). This is not unusual as Carlquist (1964) observed that in contrast with the other tribes of Compositae, short vessel elements are unusual in *Vernonia*. Carlquist (loc. cit.) further observed that the lack of exceptionally short vessel elements in Vernonieae must be considered as lack of great specialization and may help account for the fact that tracheids are not evident in any Vernonieae.

Unlike most Vernonieae, the vessel elements of these two species have multiperforate plates in which many (10-20) bars are present.



A



B

Fig. 21. Pith (A) and vessel showing perforation plate (B) in *Vernonia*. A: *V. leopoldii* (TS)- (Stella W. 11; x1000) B: *V. bipontini* (LS)-perforation plate on element at centre (Stella W. 17; x4000).

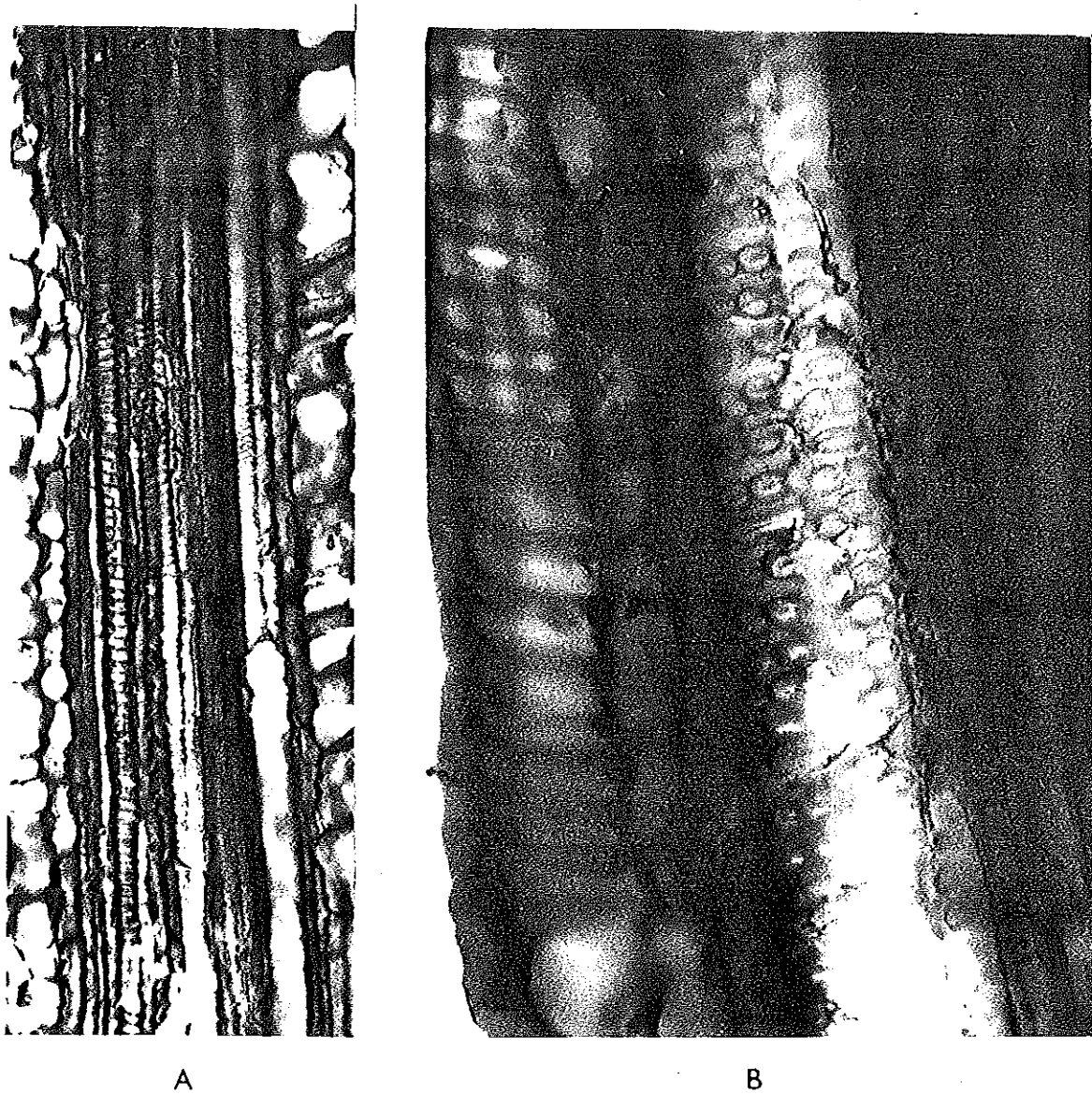


Fig. 22. Wall thickening and pitting on xylem vessels in *Vernonia leopoldii* (Stella W. 17; x2000). A: Annular and helical thickening and near-scalariform pitting on the walls B: Scalariform-transitional pitting with longer pits on walls and helical thickening.

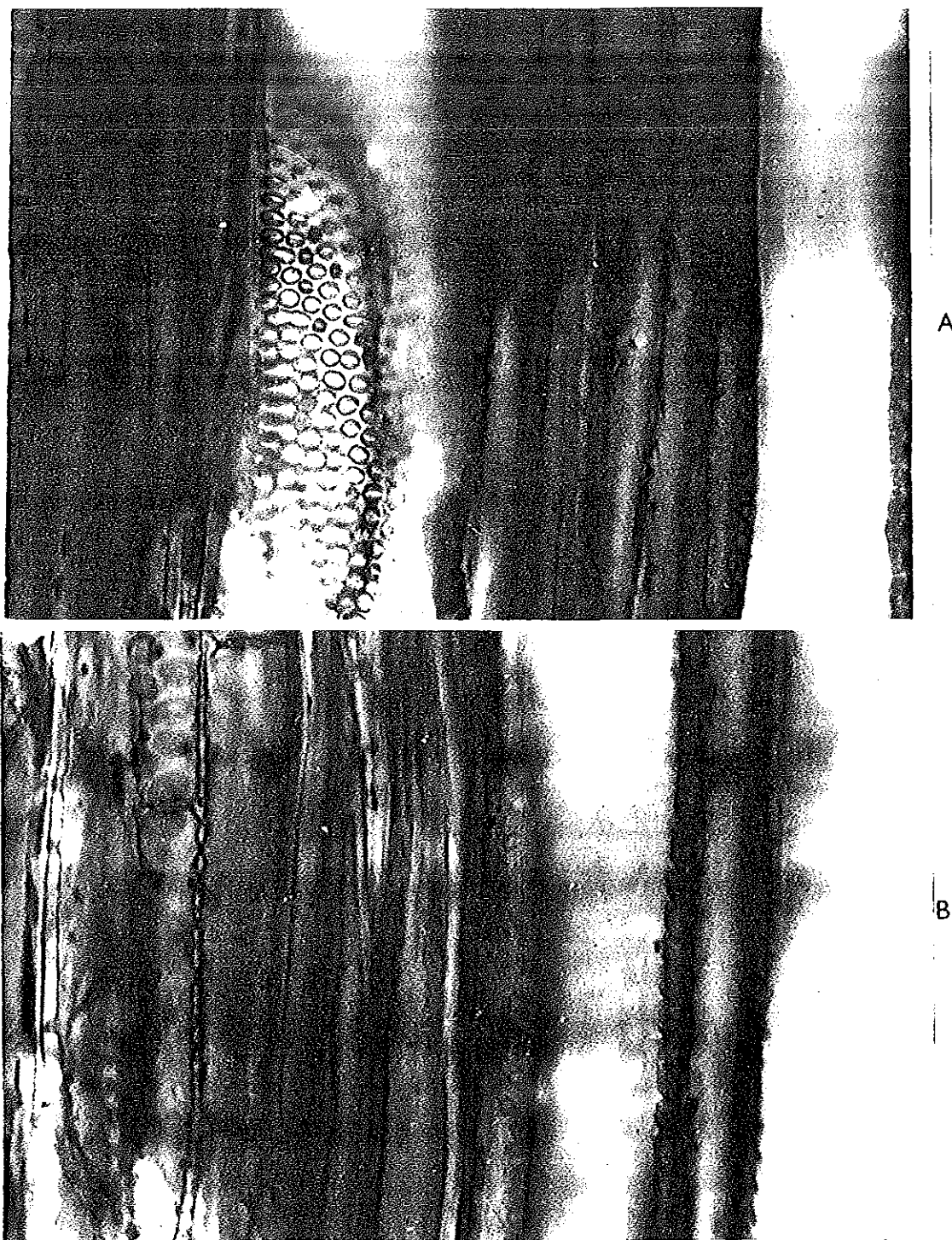


Fig. 23. Intervascular pitting on vessel walls in *Vernonia bipontini* (TLS)-(Stella W. 17; x10,000). A: Alternate elliptic bordered pits with interconnecting grooves B: Simple pits (left) and half bordered pits (right).

The vessels are grouped in clusters of 3-8 cells (Fig. 18A, 20), especially in the secondary xylem, but are in radial rows of up to 8 cells in the primary xylem (Fig. 24B). In general, there are very few solitary pores. This is unlike what has been previously observed for *Vernonieae*, as they have very few grouped vessels (Carlquist 1964).

The leaf trace bundles are distinct from the other vascular bundles in that the primary xylem vessels are well developed, as seen in radial pore rows in transverse sections but the secondary xylem vessels are not developed all, or may only be scanty (Fig. 24B).

Fibres

The libriform fibres are dominant in the xylem of both species. These fibres are mainly thin-walled, with the walls smaller in size than the lumen in most cases. The cells taper sharply at the ends and have small vertically elongated pits. Septate fibres are present. The variation in fibre length in both species is given in Table 5. The fibre lengths are 220-580 microns in *V. leopoldii*, with the average length being 401.2 microns. In *V. bipontini*, they are 150-540 microns and the average length is 316 microns. When compared with fibre lengths of other African species of the genus *Vernonia* (Table 5), they are relatively shorter (cf. *V. conferta* Blake and *V. colorata* Drake). On the whole, these figures for the fibre lengths correlate well with the vessel element lengths. These observations also fit well with those of Carlquist (1964) on other species of *Vernonia* and other

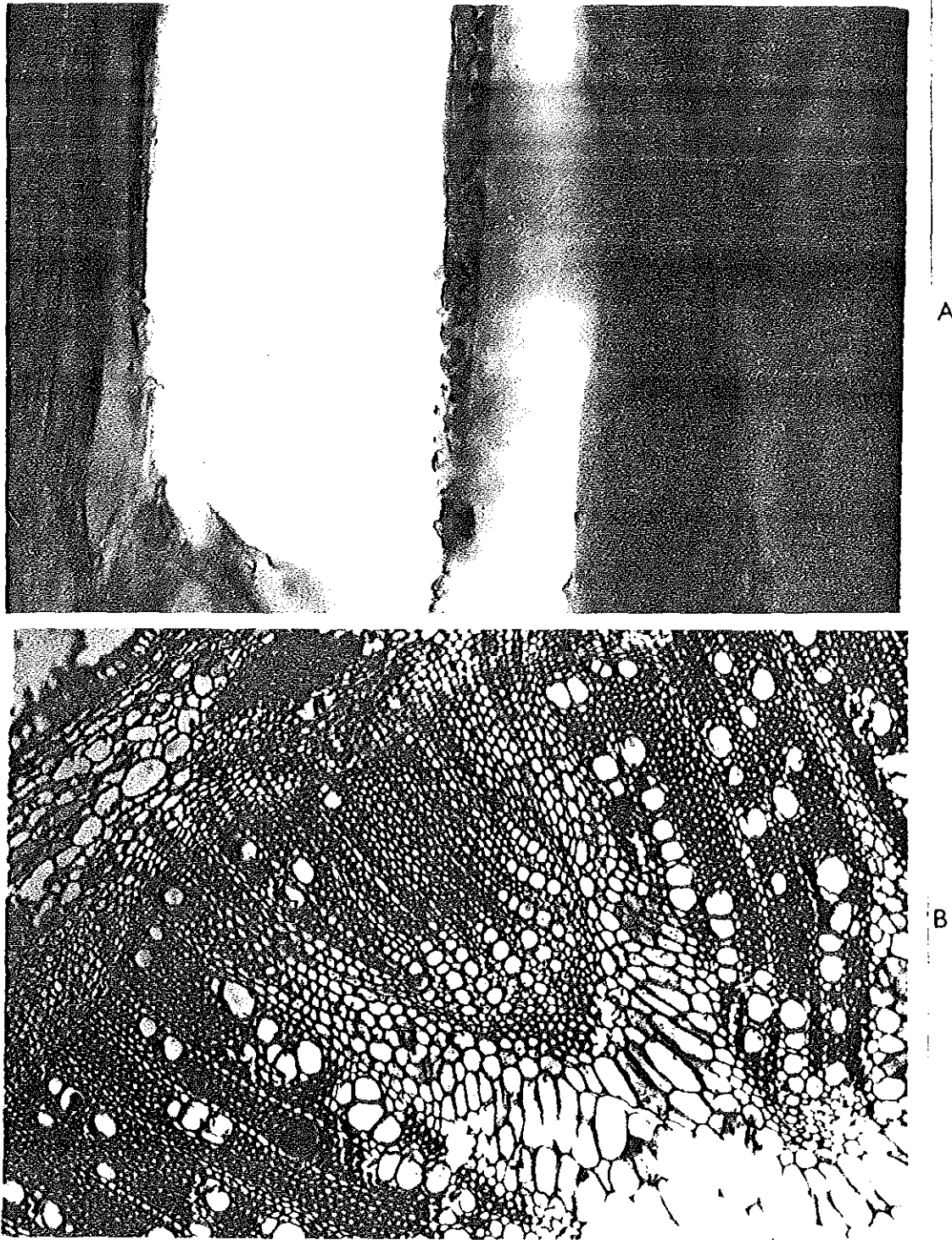


Fig. 24. Stem sections of *Vernonia bipontini* (Stella W. 17). A: TLS showing bordered pits in vessel-vessel pitting (x10,000) B: TS showing leaf trace bundle (x1000).

genera of the tribe Vernonieae, namely, *Lychnophora*, *Oliganthes*, *Eptocarpha* and *Proteopsis*.

Axial parenchyma

Vasicentric parenchyma is common, forming a complete sheath around the vessel or vessel groups. Ordinarily, they occur in strands of 1-3 cells thick. This is a common feature of the Compositae (MetCalfe and Chalk 1950) and is typical of the Vernonieae (Carlquist 1964).

Vascular rays

Uniseriate rays are scanty in both species, but when present, they are composed mainly of erect cells. High, wide, multiseriate rays are predominant, with abundant erect cells enclosed by a distinct uniseriate sheath of erect cells that are much more elongated axially. Erect cells present as wings on the rays are not common. The central region of the ray is composed of oblique and procumbent cells. This is generally not typical of other *Vernonia* as the genus is normally represented by rays with abundant procumbent cells (Carlquist 1964). The majority of the Compositae, however, have erect ray cells predominantly, as is shown in Heliantheae (Carlquist 1958).

The ray cells, as is typical of Vernonieae (Carlquist 1964), are relatively thin walled but secondary walls are lignified.

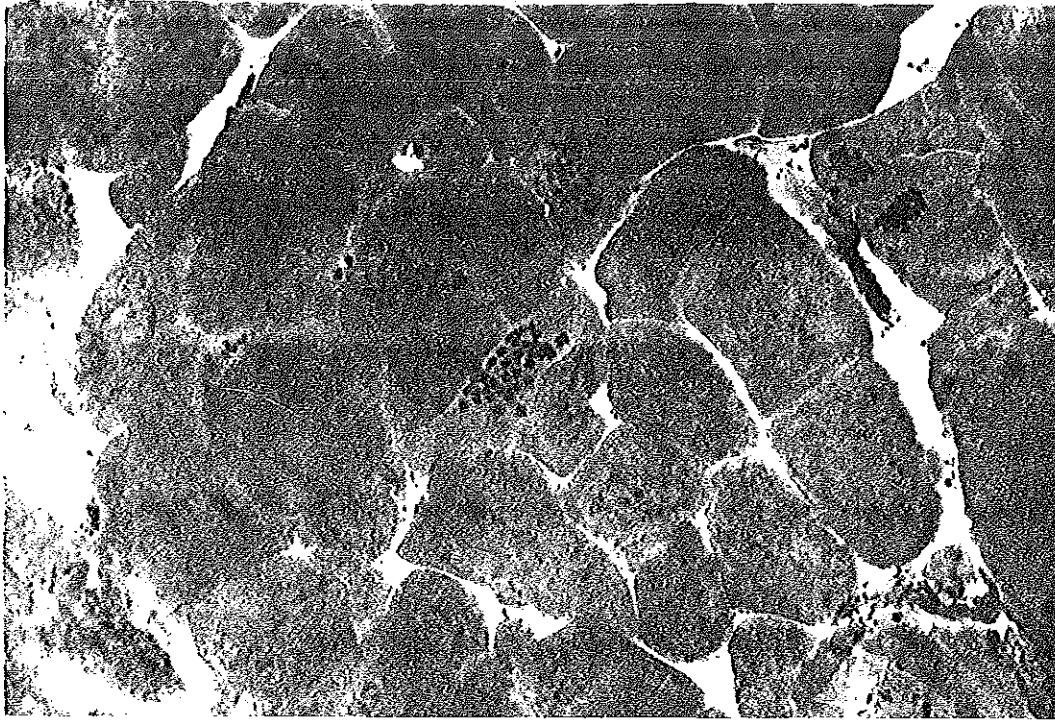
The high, wide, primary-xylem-like rays in these two species may be an indication of paedomorphosis (Carlquist 1962) as they represent juvenile character states of herbaceous stems.

The growth rings are not markedly pronounced, nor is the storying of the wood. This is typical of Vernonieae, unlike other Compositae (Carlquist 1964).

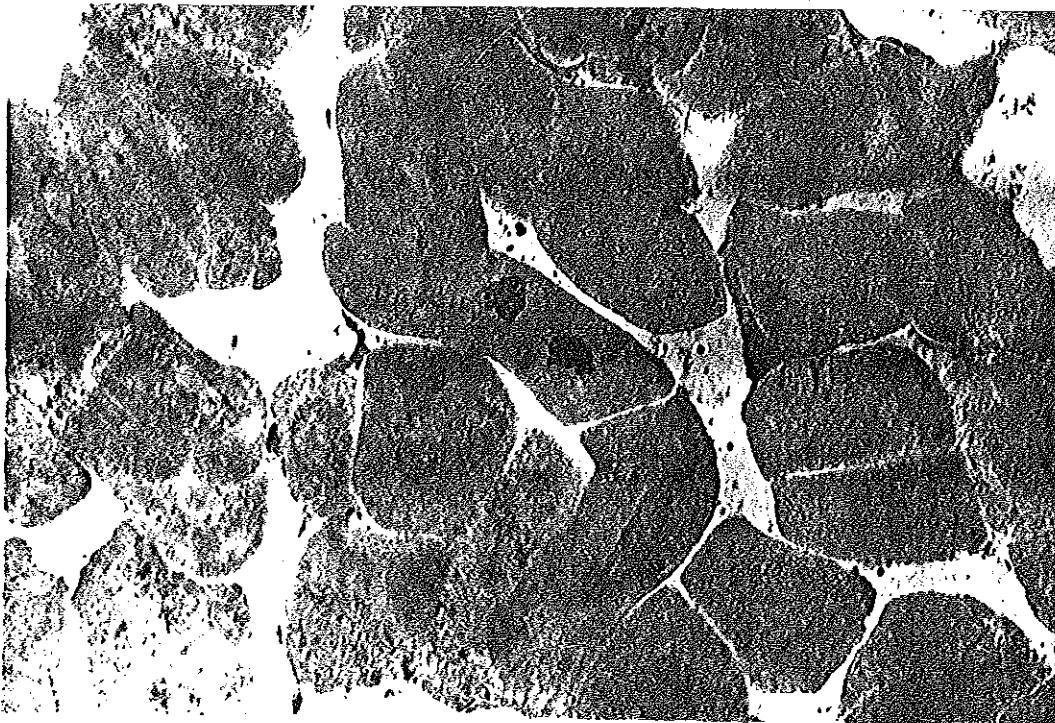
4.5 CYTOLOGY

The chromosomes of both *V. leopoldii* and *V. bipontini* are very small, about 1 micron in size and hence very difficult to count. The mitotic metaphase count from the somatic cells of the root tips indicated a chromosome number of 36 in both species (Fig. 25).

The basic chromosome number for most Old World species of *Vernonia* is $x=9,10$ (Jones 1981). Jones (1974) had previously noted that the African species of the section *Stengelina* (Genus *Vernonia*) have $n=10$, while other African species have $n=9$ or $n=10$. Based on this conclusion, it follows then that *V. leopoldii* and *V. bipontini* are tetraploids with $n=9$. However, in the systematic review of Vernonieae, Jones (1977a:511) stated that 'the Old World species have $n=9, 10, 18, 20$ '. This implies then that these two species could either be diploids with $n=18$ or tetraploids with $n=9$. It was, however, not possible to do a meiotic chromosome count, which would have facilitated verification of the level of ploidy.



A



B

Fig. 25. Chromosomes in *Vernonia bipontini* (Stella 44; x10,000). A: Mitotic metaphase B: Mitotic anaphase.

SPECIMEN	CHRO
<i>V. abyssinica</i> Sch.Bip.ex Walp	n=
<i>V. adoensis</i> Sch. Bip.	n=
<i>V. afromontana</i> R.E.Fries	n=
<i>V. amygdalina</i> Del.	2n
<i>V. arborea</i> Bach. Ham.	n=
<i>V. aurantiaca</i> (O.Hoffm.) N.E.brown	n=
<i>V. bainesii</i> Oliver & Hiern	n=
<i>V. bellinghamii</i> J. Moore	2n
<i>V. brachycalyx</i> O.Hoffm.	2n
<i>V. cinerea</i> [L.] Less.	n=
<i>V. cissifolia</i> O.Hoffm.	n=
<i>V. glabra</i> (Steetz) Vatke	n=
<i>V. holstii</i> O. Hoffm.	n=
<i>V. melleri</i> Oliver & Hiern	n=
<i>V. natalensis</i> Sch. Bip.	2n
<i>V. oligocephala</i> (DC.) Sch. Bip.	2n
<i>V. oxyura</i> O. Hoffm.	n=
<i>V. petersii</i> Oliver & Hiern	n=
<i>V. praemorsa</i> Muschler	2n
<i>V. smithiana</i> Less.	2n
<i>V. thomsoniana</i> Oliver & Hiern	2n
<i>V. tusnellae</i> S. Moore	2n
<i>V. galamensis</i> [Cass.] Less.	2n
<i>V. bipontini</i> Vatke	x=
<i>V. leopoldii</i> Vatke	x=

The chromosome counts for these two species are relatively high when compared with those of other African species of *Vernonia* (Table 6), especially those that are often confused with *V. leopoldii* and *V. bipontini*, namely: *V. smithiana* Less., *V. nazalensis* Sch. Bip. and *V. oligocephala* (DC) Sch. Bip..

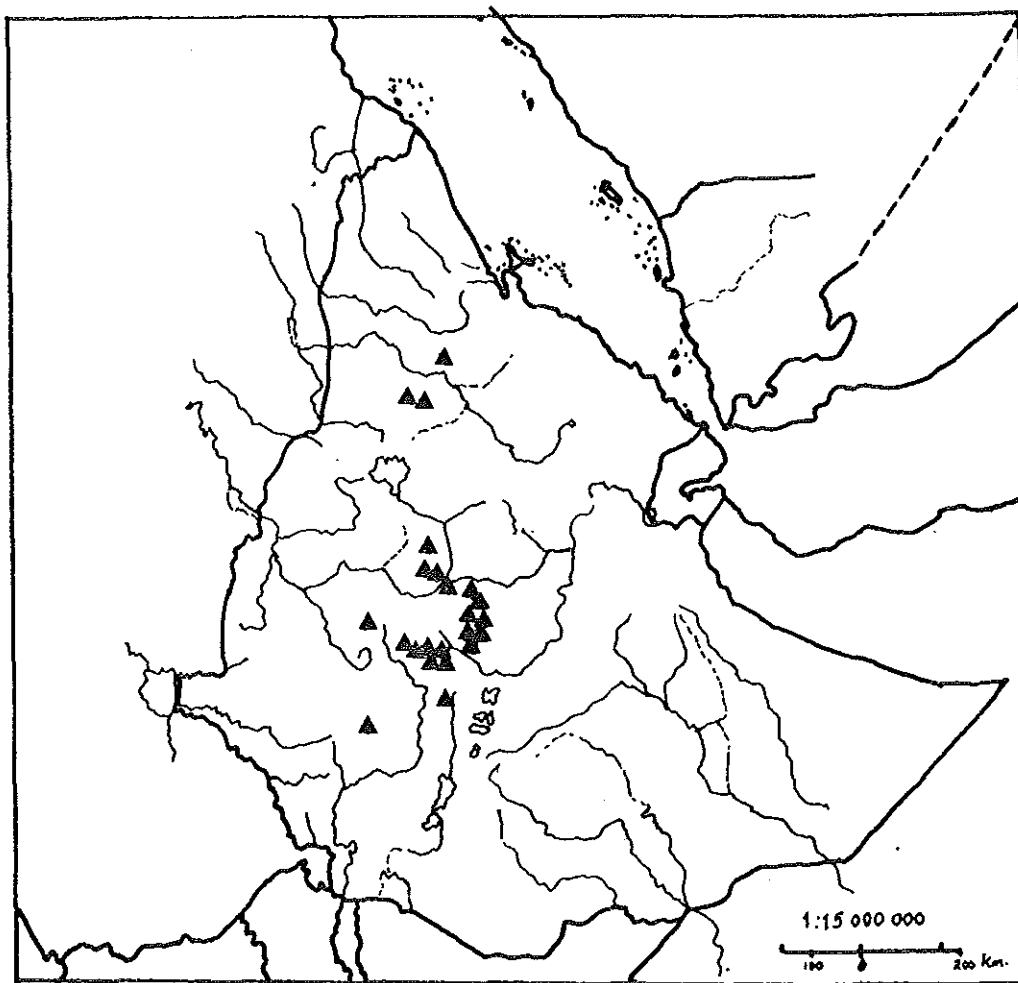
The possession of a similar chromosome number by both *V. leopoldii* and *V. bipontini* and yet different phenotypic expression supports the distinction of these two as different taxa.

4.6 PHYTOGEOGRAPHY

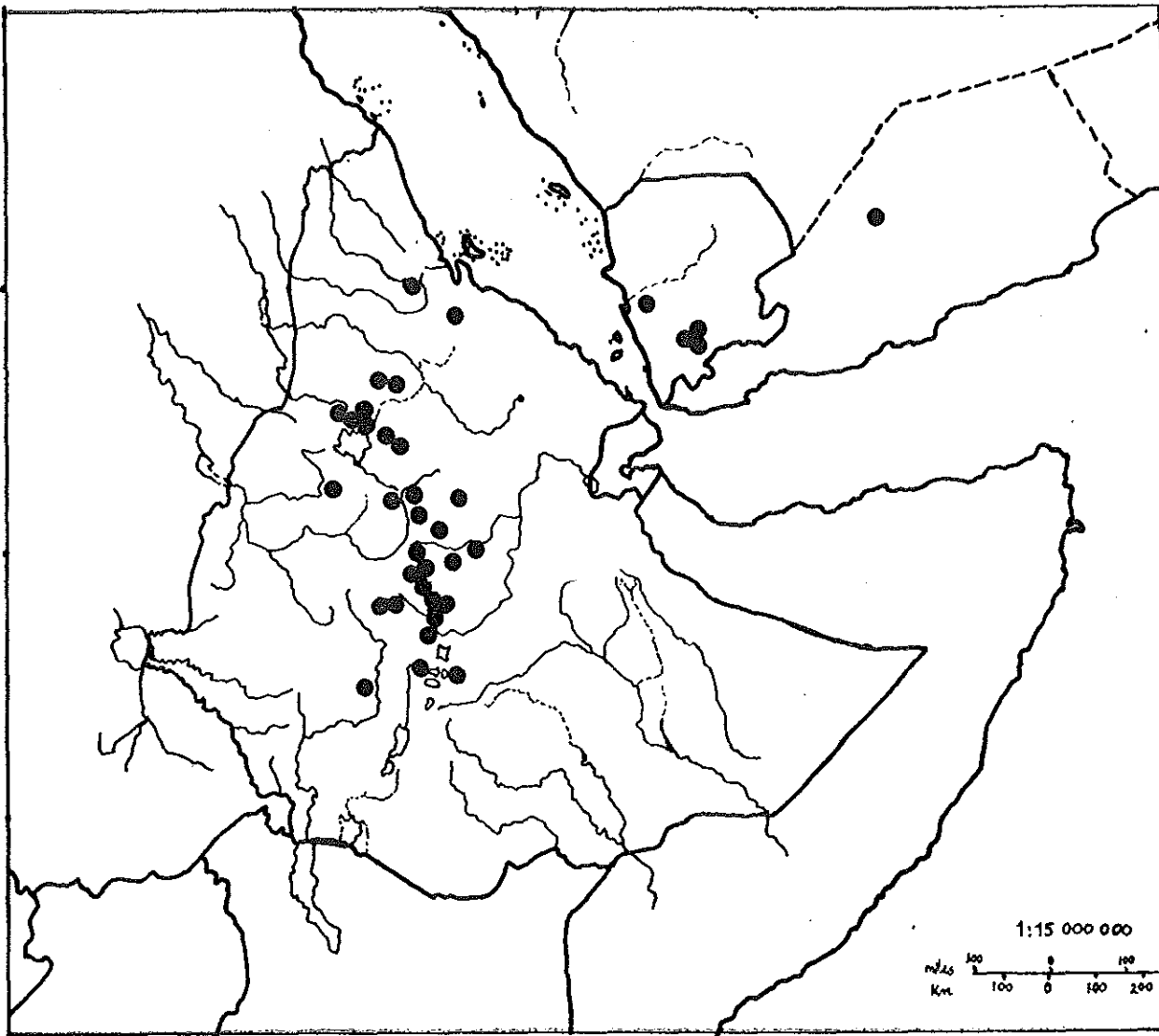
The two species, *V. leopoldii* and *V. bipontini* are both highland species, predominant on the Ethiopian Central Plateau. However, in as much as they tend to occur in similar localities, *V. leopoldii* is dominant between 1800-2500m above sea level. This species is endemic to Ethiopia and is found mainly in Shoa and Gojjam but is occasional in Wellega, Keffa, Gonder and Tigray (Fig. 26).

Vernonia bipontini has almost similar distribution as *V. leopoldii*, but tends to be more northerly in its distribution and extends into the Yemen Arab Republic (Fig. 27).

Vernonia bipontini has a wider altitudinal and latitudinal range than *V. leopoldii*. It is also apparent that the former has higher ecological tolerance than the latter as it is known to occur in



Map 1. The distribution of *Vernonia leopoldii* in Ethiopia.



Map 2. The distribution of *Vernonia bipontini* in Ethiopia and Yemen

habitats ranging from wet areas, such as river banks, to dry, exposed areas such as slopes and cliffs.

It is possible that these two species could have previously been more frequent on the Ethiopian highlands than is the case at present. This is because these highlands are heavily cultivated and only a few scattered patches of natural vegetation are left. As a result both species tend to be confined to roadside clearings and wastelands and occasionally in abandoned scattered patches of natural vegetation.

4.7 DESCRIPTIONS

VERNONIA Schreb. in Gen. Pl. 11. 541 (1791). Type: *V. novaborencis* (L.) Willd. (North America).

Herbs, shrubs or trees with alternate simple leaves and usually terminal corymbs of heads; involucre various, of many rows of phyllaries; receptacle naked; florets all bisexual, blue, white or purple, very rarely yellow or orange, exceeding the involucre at anthesis; achenes columnar, often angled or ribbed; pappus usually of two series, outer scales and inner bristles, sometimes of many rows of bristles, rarely of one row.

Key for *Vernonia leopoldii* and *V. bipontini*.

Leaves thinly pale-brownish tomentose with the epidermal surface visible, trichomes predominantly T-shaped, terete or lobed, with unequal short arms; petioles with five vascular traces; leaf adaxial epidermal layer always uniseriate 1. *V. leopoldii*

Leaves densely whitish-tomentose beneath with the epidermal surface not visible; trichomes predominantly T-shaped, longhorn type, with subequal to equal terete, filiform arms; petioles with three vascular traces; leaf adaxial epidermis usually biseriate 2. *V. bipontini*

4.7.1 *Vernonia leopoldii* (Sch. Bip.) Vatke in Linnaea, 39:478 (1875); Cufodontis, Enum. Pl. Aeth.: 1967, excl. *Cyanopsis hypoleuca* (1967).

Cyanopsis leopoldii Sch. Bip. ex Walp., Walpers Repert. Bot. Syst., 2:949 (1843); A. Rich., Tent. Fl. Abyss., 381 (1848) excl. Schimper 246. Orig. Coll. : Ethiopia, Tigray, Adwa, Mt. Scholoda, 26.IX.1837, Schimper 9 (lectotype P!, isoelectotypes K!, UPS!).

Map 1, Fig. 26, 27A-D, 28, 29, 30, Appendix 1.

Shrubs or rarely woody herbs, 0.5-2.5m high; stems with ascending branches from near the base. Indumentum brownish-grey, with short appressed T-shaped hairs that have unequal arms. Leaves alternate, simple, petiolate, with the petiole (0.2-)0.3-0.6(-0.8)cm long; lamina 9.0-15.5 x 5.0-7.0cm, ovate-lanceolate, lanceolate or elliptic lanceolate, glabrescent, pilose or shortly strigose above, tomentose especially on the veins beneath; base obtuse to decurrent; margins subentire to coarsely serrate; apex acute to acuminate. Inflorescence of terminal to subterminal corymboid or lax paniculate cymes; capitula 0.8-1.1cm at anthesis, 0.6-0.8cm long in fruit; receptacle areolate, convex to flattened; involucre cylindric, campanulate or turbinate, 0.3-0.7 x 0.4-0.6cm. Phyllaries 5-6 seriate; outermost phyllaries green, usually appressed, linear lanceolate to ovate lanceolate, 1-nerved, (1.2-)1.5-2.7(-3.2) x (0.3-)0.4-0.6(-0.8)mm, margins entire, outer surface densely tomentose, inner surface glabrescent, papillate, apex acute-acuminate;

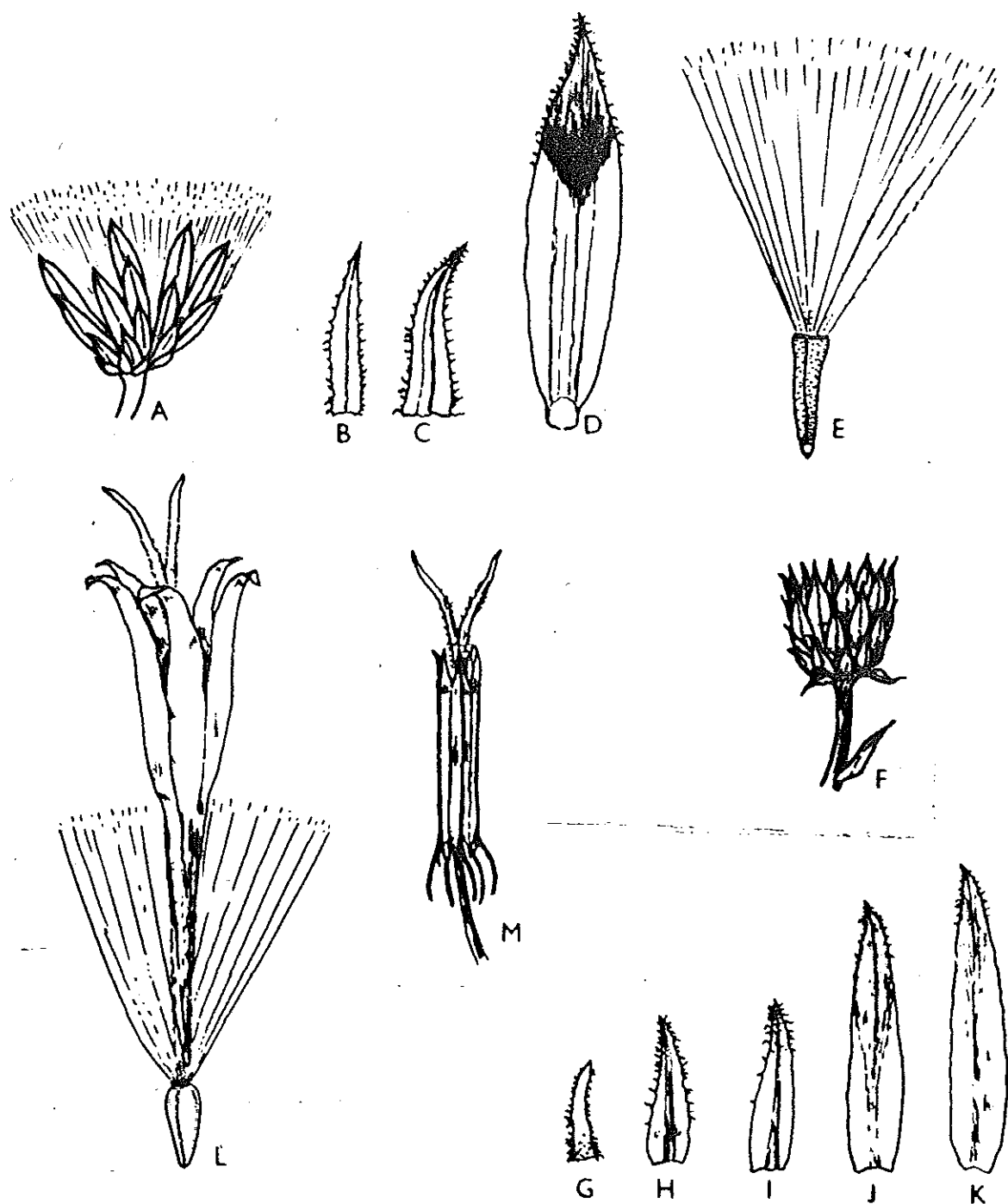
middle phyllaries green along the midrib and base, purple tinged on the scarious margins, acicular, appressed, oblong-lanceolate, oblanceolate or elliptic-lanceolate, (2.5-)3.5-5.5(-5.8) x (0.6-)0.8-1.4(-1.6)mm, apex gradually to abruptly narrowed, acute to acuminate, margins entire to minutely toothed at the apex, outer surface tomentose at the apex, inner glabrous or glabrescent, papillate; innermost phyllaries pale green, purple tinged at the apical region continuing on the exposed parts of the scarious margins, appressed but the apiculate tip slightly reflexed, narrowly elliptic-lanceolate to oblanceolate, 3-nerved, (3.7-)4.2-6.5(-6.6) x (0.6-)0.7-1.6mm, margins entire to minutely toothed at the apex, outermost surface tomentose at the apex, inner pilose and papillate, glabrous towards the base. Florets tubular, campanulate, purple, glabrous, 4.6-6.6 x 0.4-0.9mm, hermaphrodite, 5-lobed at the apex; anthers yellow, 2.3-3.2mm long, base sagittate, apex acute; style purple, 4.5-6.5mm long, stigmatic surface bifid, 1.5-2.9mm long, hispid, exserted at anthesis. Achenes pale to dark brown, (1.0-)1.35-2.3 x 0.5-0.7mm, glabrous or sparsely pilose on the upper half of the achene, with bilobed glandular hairs, oblong obovoid to turbinate, (4-)5(-6) ribbed, pappus biseriate, inner set setiform, barbellate, 3.3-5.6mm long, caducous, outer set reduced, forming a coroniform rim, 0.1-0.35 mm long, white.

Pollen grains subechinolophate, tricolporate, micropunctate with a continuous tectum cover and spines on the muri, with an average diameter of 33.2-59.9 microns. Chromosome number = 36.

VARIATION: *V. leopoldii* is not very variable in its vegetative character states. Most of the variation in the floral parts is continuous, such as is shown in Fig.31-33. The phenotypic variation is apparently



Fig. 26. *Vernonia leopoldii*. A: Habit (Mesfin T. 7259) B: variation in leaf (Mooney 8858) (x0.65).



DAMTEN T.

Fig. 27. Details from capitula. *Vernonia leopoldii*:- A: capitulum x3, B-D: outermost, middle and innermost phyllaries x10; *Vernonia bipontini* E: achene x10, F: capitula x3, G-K: phyllaries x10 - G. outermost, H-J. middle K. innermost, L: whole floret x10, M: stamen x10 (A from Mesfin T. and Kagnev Y. 2049, B-D from Mesfin T. 7259, E Evans 436, F-K from Friis et al. 3820, L-M from Afeworki G. and Mehret A. 12)

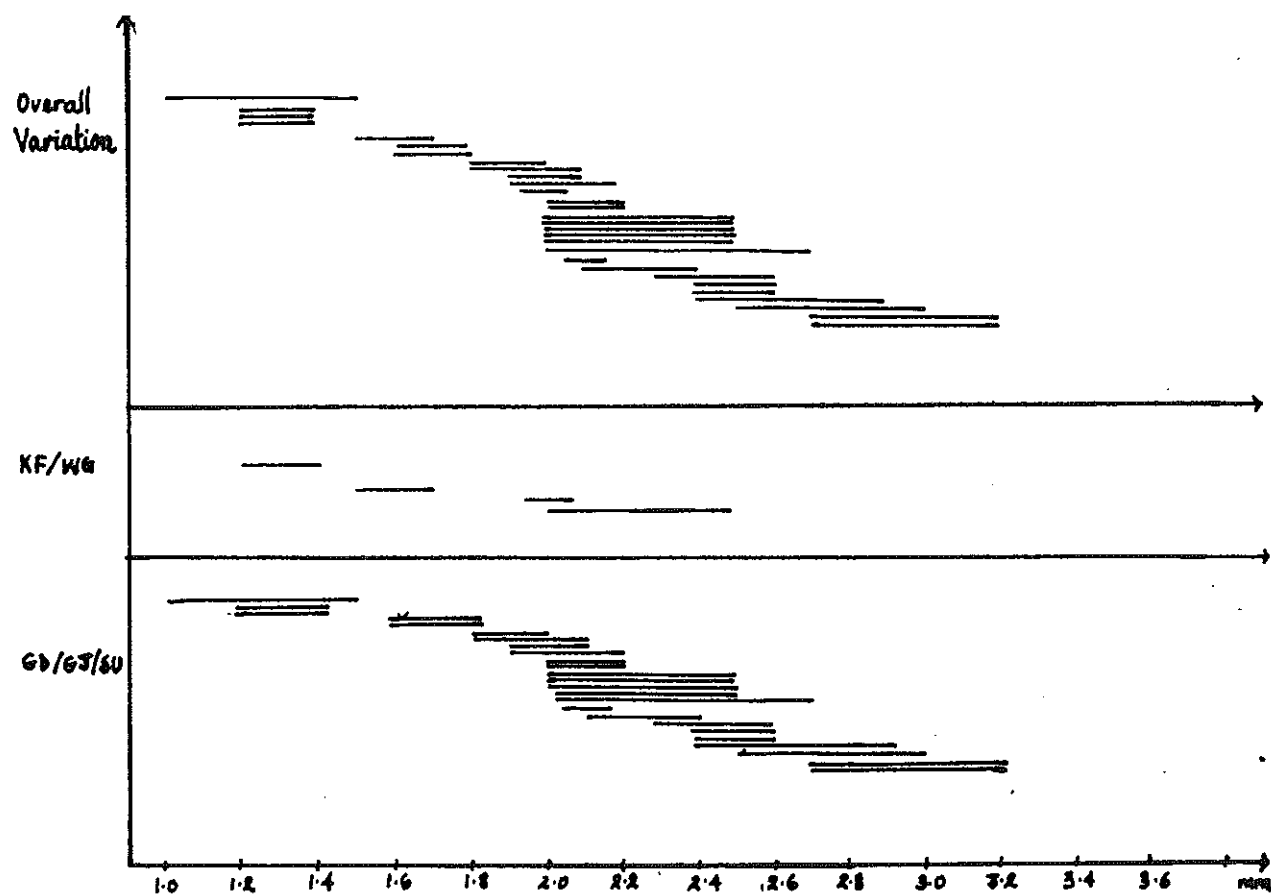


Fig. 28. Variation in the outermost phyllary lengths in *Vernonia leopoldii*.

(Abbreviations for regions on vertical axis:- GD = Gonder, GJ = Gojam, KF = Keffa, SU = Shewa, WG = Wellega)

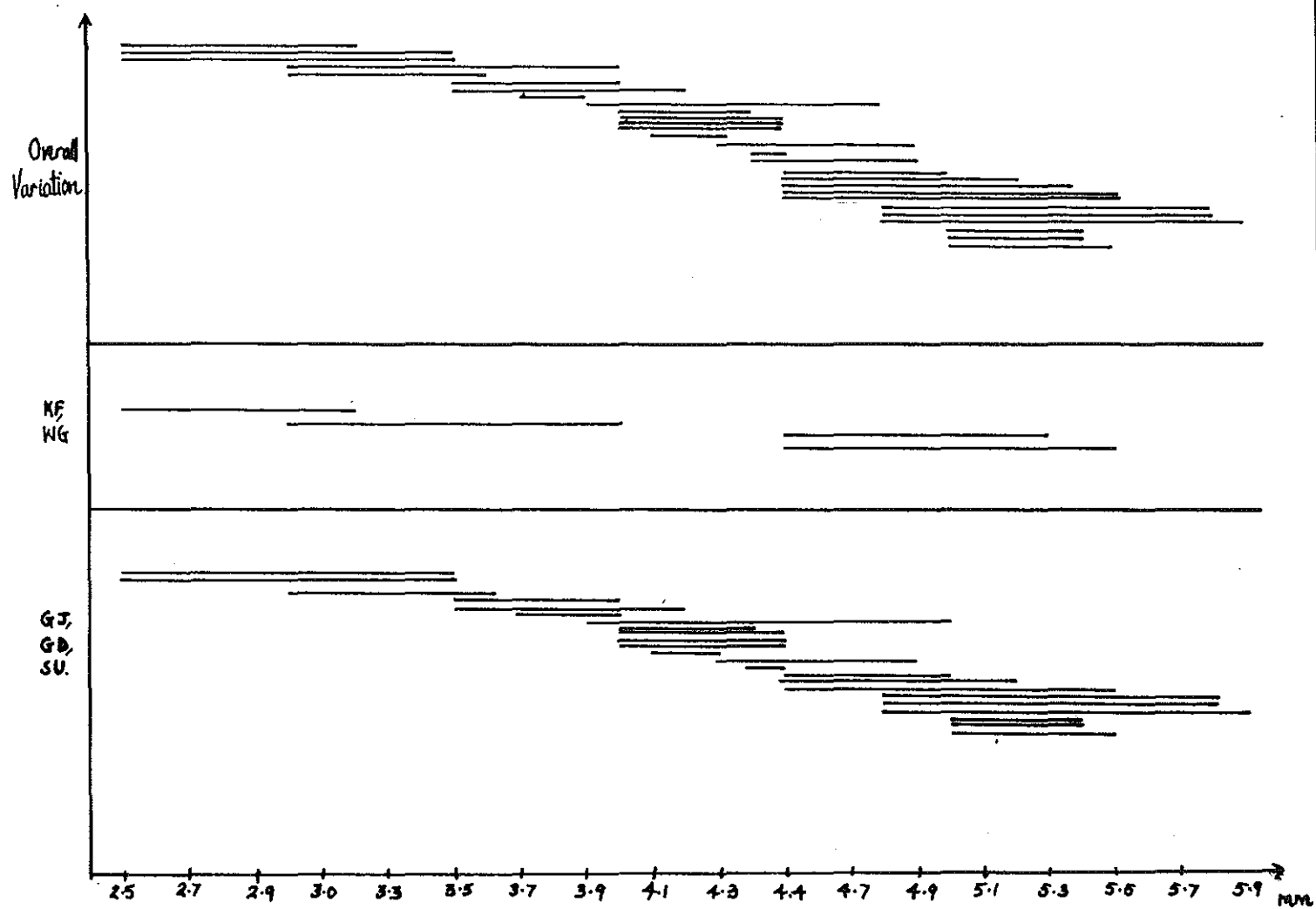


Fig. 29. Variation in the middle phyllary lengths in *Vernonia leopoldii*
(GD = Gonder, GJ = Gojam, KF = Keffa, SU = Shewa, WG = Wellega)

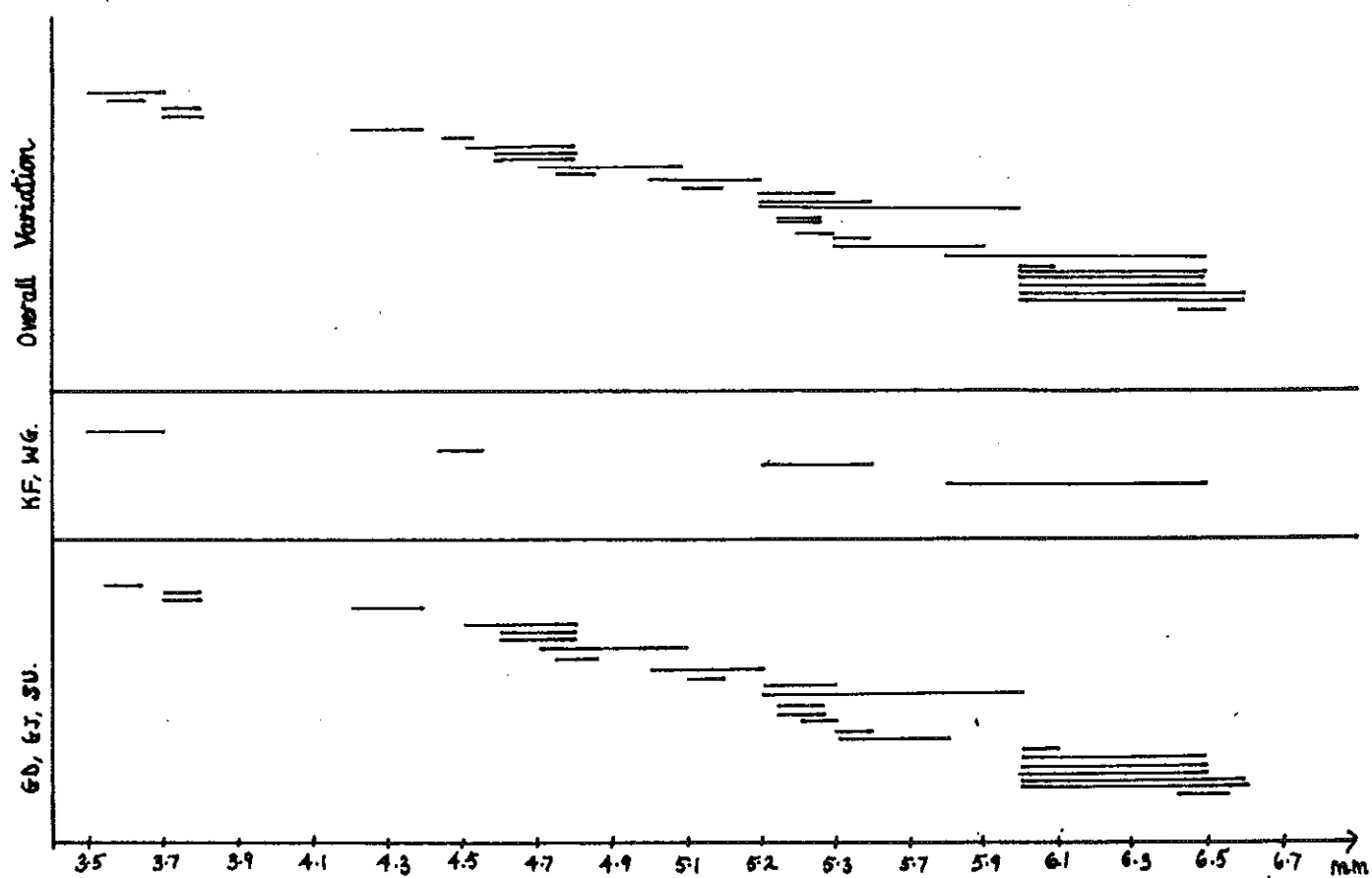


Fig. 30. Variation in the innermost phyllary lengths in *Vernonia leopoldii*
(GD = Gonder, GJ = Gojam, KF = Keffa, SU = Shewa, WG = Wellega)

related to the environmental variations. Populations in open broad-leaved bushlands, a typical habitat for this species, tend to have well developed capitula usually with many (50-200) capitula per confluence. However, those from cooler and wetter habitats such as forest margins have capitula that are reduced in size as well as number (cf. *Mooney* 8858 and *Mesfin* and *Kagnev* 1889 - Appendix 1). In these plants, the vegetative parts tend to be well developed (Fig. 26B), with sparse indumentum, while the purple pigmentation on the phyllaries is not well developed as these are mainly shade plants.

DISTRIBUTION: Endemic to Ethiopia, being found in the following regions:- Gonder (Simien Awraja); Gojam (Choke mts., Debre Markos Awraja); Shewa (Addis Ababa, along Ambo road, Bole Valley, Debre Libanos, Entoto Hills, Goha Tsion, Guder-Gheddo road, along Jimma road, Menagesha State Forest); Wellega (Amarti Valley); Keffa (Wushwush).

ECOLOGY: In scrub on dry to wet hillsides, gorges or roadside thickets, wastelands to forest margins, usually associated with *Acacia abyssinica* Hochst. ex Benth., *Maytenus pulterlickioides* (Loes.) Exell and Mendonca, *Hibiscus* spp., *Phytolacca dodecandra* L'Herit., *Rosa abyssinica* Lindley, *Carissa edulis* (Forssk.) Vahl., *Salix subserrata* Willd., *Myrica salicifolia* Hochst. ex A. Rich. and *Rumex nervosus* Vahl.. This species generally grows on shallow soils and rocky ground: Alt. 1850-2850m.

SPECIMENS STUDIED: ETHIOPIA

GONDER; Simien, Limalimo, 3.11.81, *Mesfin* and *Kagnev* 1889(ETH).
GOJAM; Choke mts., 23.5.87, *Evans* and *Lythgoe* 307(ETH), Debre Markos,

29.10.81(ETH), *Mesfin* and *Kagnew* 1610(ETH), s.l. 5.11.85, *Mercier* 2755(ETH), Dejen, 29.10.81, *Mesfin* and *Kagnew* 1618(ETH). SHEWA; Addis Ababa: 19.11.53, *Mooney* 5015(ETH), 3.11.71, *Jackson* 695(ETH), 21.11.65, *De Wilde* 8956(ETH), Menagesha State Forest: 27.12.79, *Sebsebe* 314(ETH), 1.12.69, *Lundstrom* 221A(EA), 19.11.72(ETH), *Friis* et al. 1285(ETH), Entoto Hills: 31.12.65, *De Wilde* 9521(ETH), 14.11.72, *Friis* et al. 1167(ETH), Ambo road, 27.11.65, *De Wilde* 8974(ETH), Goha Tsion: 8.11.81, *Mesfin* and *Kagnew* 2043(ETH), 28.10.81, *Mesfin* and *Kagnew* 1559(ETH), L. Wonchi, 17.2.74, *Gilbert* and *Tewolde* 3233(ETH), Ginji, 22.12.84, *Mercier* 1969(ETH), Babich, 20.11.88, *Mesfin* 7063(ETH), Kersa river valley, 17.11.84, *Friis* et al. 3823(ETH), Yeke Arsano, 20.11.88, *Mesfin*, 7260, 7261, 7262(ETH), Jibat, 29.10.85, *Sebsebe* and *Ensermu* 1658(ETH). WELLEGA; 150km. west of Guder, 2.11.62, *Albers* 62473(ETH), Jimma road, 24.12.62, *Tekle Hagos* 28(ETH).

4.7.2 *Vernonia bipontini* Vatke in Linnaea, 39:478(1875).

Cyanopsis leopoldii Sch. Bip., Walpers Repert. Bot. Syst. 6:98 (1843); A. Rich., Tent. Fl. Abyss. 2:381 (1847) in part. Orig. Coll. : Ethiopia, Tigray, Adwa - Mt. Scholoda, 5.XI.1837, *Schimper* 246 (lectotype P!, isolectotypes K!, UPS!).

C. hypoleuca Sch. Bip., Walpers Repert. Bot. Syst. 6:98 (1846); A. Rich., Tent. Fl. Abyss. 2:382 (1847). Specific epithet nonvalid for *Vernonia*. Type: Ethiopia, Tigray, near Axum, 18.11.1842, *Schimper* 1542 (holotype P!, isotypes K!, UPS!).

Map 2, Fig. 27E-N, 31-34, Appendix 2.

Small shrubs, erect to straggling woody herbs, 0.6-1.5m high; stems with ascending branches from near the base. Indumentum of densely appressed greyish-white to brownish-grey T-shaped hairs with equal to subequal filiform arms. Leaves alternate, simple, petiolate; petiole 0.2-0.5cm long; lamina 4.5-10.0 x 0.8-4.5cm, ovate lanceolate to narrowly lanceolate, base decurrent, pilose, scabrous or tomentose above, densely whitish-tomentose to velvety beneath, margins subentire, finely to coarsely serrate, apex acute to acuminate. Inflorescence of terminal to subterminal corymboid, paniculate or subscorpioid cymes. Capitula 0.8-1.4cm long at anthesis, 0.5-1.1cm long when fruiting; peduncles 0.2-1.5cm long, densely brownish - whitish velvety tomentose; receptacle areolate, convex to flattened, glabrous. Involucre turbinate or oblong-cylindric, 0.4-0.9cm long; phyllaries (4-)5-6-seriate; outermost green, linear, linear lanceolate to narrowly triangular, 1-nerved, (1.1-)1.5-3.4(-5.3) x (0.3-0.5(-0.9))mm, apex attenuate - apiculate, reflexed, margins entire, outer surface densely appressed whitish-grey tomentose except on the apicule, inner surface glabrous except at the apex, apicule 0.3-1.0cm long; middle phyllaries green along the midrib and base, purple tinged on the exposed parts, acicular, ovate-, oblong-, or elliptic lanceolate to oblanceolate, 2.5-5.3(-6.5) x 0.5-1.1(-1.7)mm, apex acute to acuminate, reflexed, margins sometimes minutely toothed, outer surface densely appressed whitish-grey tomentose on all exposed parts, inner papillate, pilose at apex, apicule 0.3-0.6mm long; innermost phyllaries pale green, purple tinged on exposed parts, appressed but apiculate tip

reflexed, narrowly elliptic, lanceolate to oblanceolate, 3-nerved, 4.3-6.0(-8.5) x 1.2(-1.6)mm, acute to apiculate at the apex, apicule 0.2-0.6mm long, margins entire to minutely toothed at the apex, outer surface densely whitish-grey tomentose on exposed parts, inner surface papillate and pilose at the apex, glabrous towards the base. Florets purple, tubular, campanulate, glabrous, (3.0-)5.0-8.0(-10.8) x (0.6-)0.8-1.1mm, hermaphrodite, 5-lobed at the apex; anthers yellow, (1.5-)2.0-3.8(-4.2)mm long, base sagittate, apex acute; style purple, (3.0-)4.7-7.2(-8.7)mm long, stigmatic surface bifid, (1.0-)1.6-2.4mm long, hispid, exerted at anthesis; achenes pale to dark brown, (1.3-)1.6-2.2(-2.6) x (0.35-)0.4-0.7(-0.9)mm, glabrous or pilose on the upper half mainly oblong-obovoid to obpyramidal, 4-5(-6)-ribbed; Pappus biseriate, inner set setiform, barbellate, (3.6-)3.9-6.0(-7.0)mm long, caducous, outer set much reduced, forming a coroniform border, 0.1-0.4mm long, white.

Pollen grains subechinolophate, tricolporate, with continuous micropunctate tecta and spines on the muri, 30.48-59.24 microns in diameter. Chromosome number =36.

VARIATION: This species is highly variable in its morphology and this is possibly why its taxonomic status has not been very easy to define. Commenting on the variability within *Cyanopsis hypoleuca* Sch. Bip. (sensu stricto), A. Richard (1847) stated that 'it is a very variable species, sometimes nearly glabrous, it appears to me that it is quite distinct from *V. leopoldii*'. Indeed it is quite distinct from *V. leopoldii*, yet the intraspecific variation is so much, that one is tempted to ascribe specific ranks to the varying populations. This high



Fig. 31. Habit (A) and leaf variation (B-F) in *Vernonia bipontini*. A: Mercier 2778 B: Afeworki and Mehret 12 C: Friis et al. 3820 D: Mesfin T. and Zerihun W. 2835 E: Mesfin T. 7268 F: Sebsebe D. 416 (all x0.65).

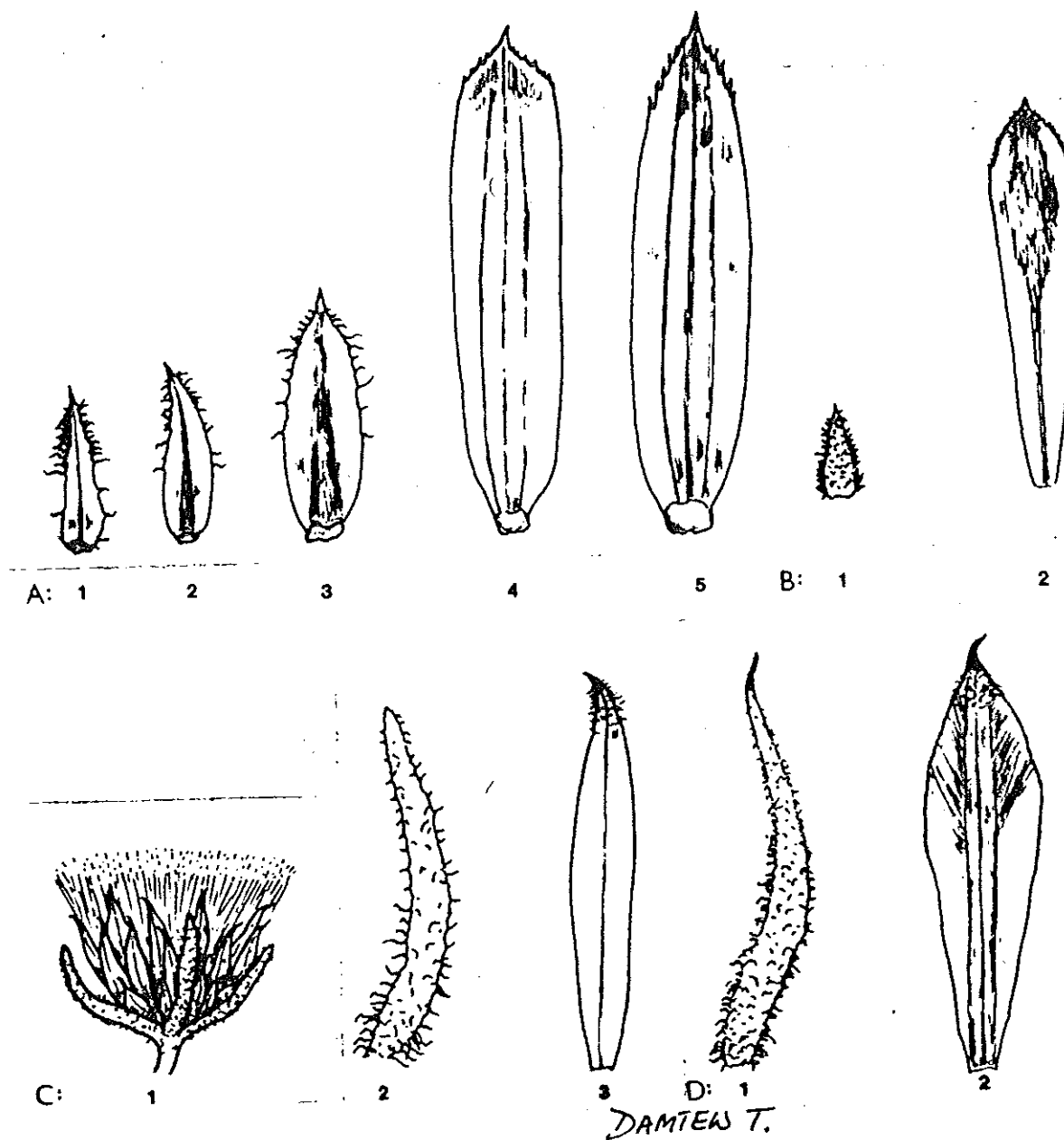


Fig. 32. Variation in phyllary forms in *Vernonia bipontini*. Var. A, A1-5: outermost, middle and innermost phyllaries x10 (Mesfin T. and Zerihun W. 2835), B1-2: outermost and innermost phyllaries x10 (Afeworki G. and Mehret A. 12); Var. B, C1-3: 1. capitula x3, 2-3. outermost and innermost phyllaries (Sebsebe D. 416); Var. C, D1-2: outermost and innermost phyllaries x10 (Ash 2713)

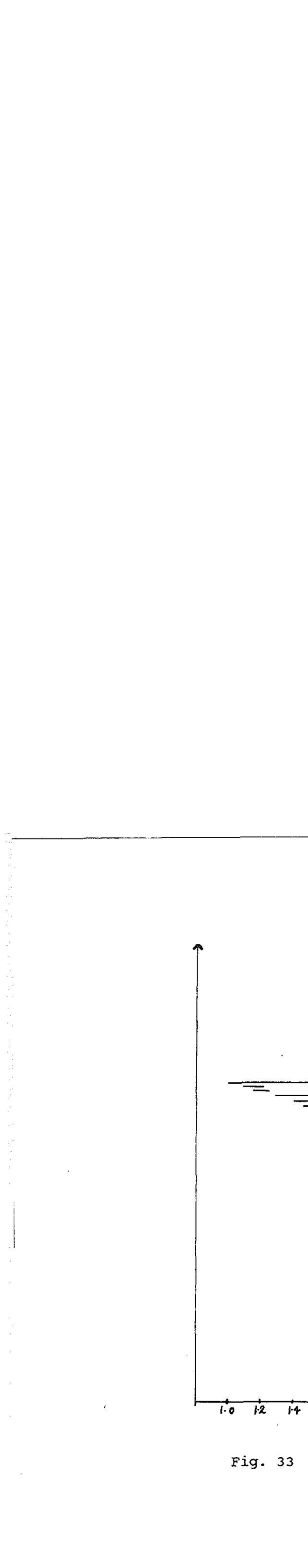


Fig. 33

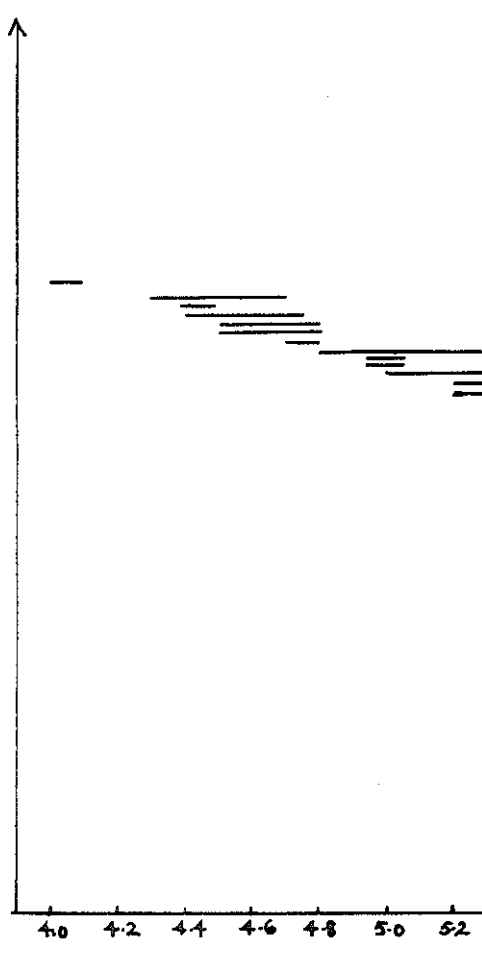


Fig. 34. Overall

variability within this species seems to be attributable to the high ecological tolerance that it displays

Three varieties have been recognized in this study and have been temporarily termed as Var. A, Var. B and Var. C.

Key to the varieties in *V. bipontini*

1. Outermost phyllaries lanceolate, 1.2-2.1mm long; leaf margins distinctly serrate or crenate Var. A
- Outermost phyllaries linear, 2.3-5.3mm long; leaf margins indistinctly to very finely serrate 2.
2. Capitula subtended by a set of phyllary-like bracteoles that are densely tomentose; Innermost phyllaries less than 6mm long Var. B
- Capitula not subtended by a set of phyllary-like bracteoles; innermost phyllaries greater than 6.3mm long Var. C

4.7.2.1 *V. bipontini* var. A

For synonymy, see under the species.

Fig. 27E-M, 31A-E, 32A-B.

Leaves ovate to ovate-lanceolate, margins serrate or crenate, upper surfaces subscabrous with multiseriate, multicellular glandular and T-shaped hairs; outermost phyllaries 1.1-2.1mm long, lanceolate, innermost

phyllaries 5.2-7.6mm long, oblong-elliptic or oblanceolate; sphenes 1.6-2.5mm long. Inner sphenes 1.3-6.0mm long.

DISTRIBUTION: ETHIOPIA; Showa, Gojjam, Gonder, Tigray, Eritrea.

ECOLOGY: Dry shrubby woodlands, broad-leaved woodlands, roadside bushlands and disturbed habitats. Alt. 1650-2800m.

NOTES: The variation in this taxon is related to the altitude and the ecology of the habitat. Populations from high altitudes and exposed areas such as slopes with thin soil tend to have longer inner phyllaries, greater than 7.0mm long (Fig. 31D). The phyllaries are tomentose only at the apex, unlike the other populations from lower altitudes (<2600m) which predominantly occur in broad-leaved bushlands. The latter have dense tomentum on all the exposed parts. Populations typical of dry habitats with very thin soils tend to have linear to linear-lanceolate leaves (cf. *Ash* 105 and *Friis* et al. 3820 - Appendix 2) with phyllaries that are much narrower (Fig. 27F-K, 31C).

SPECIMENS STUDIED: ETHIOPIA

ERITREA; About 5km from Senafe, Deb Deb village, 19.11.86, *Friis* et al. 4530, (ETH), Bet-Ghiorgis, Asmara, *Afeworki* and *Mehret* 12(ETH). GONDER; Debre Tabor Awraja, About 8km north of Emed Ber, 6.11.81, *Mesfin* and *Kagnew* 1995(ETH), Geech, Simien, 5.2.65, *Lemma* 648(ETH), Debre Tabor Awraja, 40km east of Hammusit, 22.12.83, *Mercier* 1671(ETH), Simien Awraja, Limalimo, 25.11.82, *Mesfin* and *Zerihun* 2835(ETH). GOJJAM; Mota Awraja, Sabara deldey, Abbay valley, 6.11.85, *Mercier* 2778(ETH). SHEWA; Manz, 30km west of Mahel Meda, 27.1.85, *Mercier* 2170(ETH), Mt. Yerer, 3.11.54, *Mooney* 6282(ETH), Bole Gorge, about 50km north of Addis Ababa,

12.11.72, *Friis* et al. 1113(ETH), Tagula Awraja, 5km north of Ankober,
 26.10.85, *Mercier* 2691(ETH), Yerer-Balchi, 17.11.83, *Mercier* 1529(ETH),
 Yeke Arsano, town between Guder and Cheddo, 20.11.88, *Mesfin*
 7259, 7268(ETH), Wegidi, on the slopes of the Kersa river valley, below
 the Muger Cement Factory, 17.11.84, *Friis* et al. 3820(ETH), Akaki river,
 west side, about 1km north of the highway bridge, 17km north of Addis,
 13.11.67, *Meyer* 7457(ETH), Cement factory at end of branch road, on left
 off Debre-Markos road, about 45km north of Addis, 6.12.69, *Ash* 105(ETH).

4.7.2.2 *V. bipontini* Var. B.

For synonymy, see under the species.

Fig. 32C.

Stems unevenly hoary white; Leaves ovate to ovate-lanceolate,
 margins subentire with minute even serrations, upper surface subscabrous
 with multiseriate, multicellular and uniseriate, glandular trichomes as
 well as T-shaped hairs; capitula subtended by phyllary-like, long,
 filiform bracteoles that are densely white-feltish tomentose, 2.3-5.3mm
 long, almost the same length as the involucre, innermost phyllaries
 lanceolate, 5.3-5.8mm long; achenes 1.3-2.1mm long, setae 4.0-5.1mm long.

DISTRIBUTION: ETHIOPIA; Shewa, Gonder.

ECOLOGY: Along river banks or in cultivation, rarely in open
 bushlands. Alt. 2090-2600m.

NOTES: This variety is homogeneous, being easily distinguished by the presence of the filiform, phyllary-like bracteoles subtending the capitula.

SPECIMENS STUDIED: ETHIOPIA;

GONDER; 8km from Azezo town, on the way to Setit Humera, 4.11.81, *Mesfin* and *Kagneu* 1919(ETH), Gonder Awraja, ca. 4km north of Gonder, on Setit-Humera road, 2.11.81, *Mesfin* and *Kagneu* 1835(ETH), closer to Tseda town, about 20km from Gonder to Bahir Dar, 24.10.80, *Sebsebe* 416(ETH), Gonder Public Health College, cultivated for medicinal plants project, 7.12.82, *Sebsebe* and *Nigatu* 1206(ETH), SHEWA; Aleltu valley before its confluence with Kessem, 24.9.72, *Tewolde* 1189(ETH), upper reaches of the Koromi river, 17.11.84, *Friis* et al. 3825(ETH).

4.7.2.3 *V. bipontini* Var. C.

For synonymy, see under species.

Fig. 32D

Leaves ovate lanceolate, margins minutely serrate with the bases of the teeth indistinct, upper surface pilose with uniseriate, glandular and T-shaped hairs; outermost phyllaries 3.1-5.3mm long, linear, outermost and middle phyllaries with apices elongated to about half the length of the involucre, apices purple, filiform, reflexed, innermost phyllaries 6.5-6.8mm long, oblong- to elliptic-lanceolate, apices slightly produced into reflexed tips; achenes 1.3-2.4mm long, setae 5.4-5.8mm long.

DISTRIBUTION: ETHIOPIA; Shewa, Gonder.

ECOLOGY: On shallow soils in open grasslands or rock crevices. Alt. 2700-3350m

NOTES: This variety is restricted to the Central Ethiopian Plateau, Eastern Shoa. It is a high altitude plant, found above 2700m, generally higher than *V. leopoldii* and any of the other varieties of *V. bipontini*. It is easily distinguished by its phyllaries that have greatly elongated, reflexed, filiform apices.

SPECIMENS STUDIED: ETHIOPIA:

ARSI: Mt. Cacca, 25.12.53, *Mooney* 5250(ETH), SHEWA: L. Arakit, near Dila village on Hossana road, 2.11.74, *Ash* 2713(ETH), KEFFA; Mt. Maigudo, 41km from Jimma-Addis road on the Omo-nada track, 25.11.82, *Frlis* et al. 1429(ETH).

4.8 CONCLUSION

From the current study, it is shown that the '*Vernonia leopoldii* complex' consists of two distinct species, namely *V. leopoldii* (Sch. Bip.) Vatke and *V. bipontini* Vatke. Three varieties have also been recognized within *Vernonia bipontini* and these have been designated as var. A, var. B and var. C.

The diagnostic characters used in distinguishing between the two species have been obtained mainly from trichome studies, with support from leaf and petiole anatomy. The two species were, however, observed to have similar wood structure. As such, a study of the wood anatomy of the members of this 'complex' did not provide any diagnostic features that could have been of significance in the systematics of the taxa included.

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APPENDIX 1: MORPHOL

All measurements ex

Specimen	Invo leng
Mooney 8858	0.3-
Mesfin &	
Kagnew 1889	0.3-
Evans &	
Lythgoe 307	0.4-
Mesfin 7063	0.4
Friis et al.	
3823	0.4-
Tekle H. 28	0.7
Mooney 5015	0.6-
Sebsebe 314	0.6-
Jackson 695	0.7-
Albers 62473	0.6-
De Wilde 8956	0.6-
De Wilde 8974	0.6-
De Wilde 9521	0.6-

Friis et al.

1167

Friis et al.

1285

Mesfin &

Kagnew 1618

Gilbert &

Tewolde 3233

Mesfin &

Kagnew 1610

Mesfin &

Kagnew 1559

Mesfin &

Kagnew 2043

Mercier 1969

Mesfin 7260

Mercier 2766

Mesfin 7259

Mesfin 7261

Sebsebe &

Ensermu 1653

APPENDIX 2: MORPHO

All measurements e

Specimen	Inv len
Var. A	
Mesfin &	
Kagnew 1995	0.6
Mercier 1529	0.4
Mooney 6282	0.6
Pappi 75	0.5
Ash 105	0.6
Mercier 1671	0.6
Mesfin 7268	0.6
Friis et al.	
3320	0.6
Mercier 2778	0.6
Mercier 1575	0.5
Mercier 2095	0.4
Mercier 2170	0.8

De Wilde 8657	0.6	2.1	3.7-4.6	5.3-5.5	1.6-1.8	4.6-5.0
Friis et al.						
4530	0.6-0.7	1.5-1.7	4.6-4.8	5.2-5.6	2.3-2.5	5.2-5.8
Mesfin &						
Zerihun 2835	0.6-0.9	1.9-2.1	4.4-4.6	7.5-8.5	2.3-2.6	6.5-7.0
Jemna 648	0.8-0.9	1.9-2.1	4.4-6.7	7.5-8.5	2.3-2.6	6.5-7.0
Mercier 2691	0.6	1.3-1.5	4.5-5.5	5.5-5.7	2.0-2.2	4.5-5.5
Afeworki &						
Mehret 12	0.6-0.7	1.5-2.0	4.5-5.5	5.9-6.0	1.5-1.9	4.5-5.0
Friis et al.						
1113	0.5-0.6	1.5-1.6	1.0-1.3	5.0	1.9-2.1	4.0-5.0
Var. B						
Sebebe &						
Nigatu 1206	0.6-0.7	3.0-3.4	4.0-5.0	5.2-5.5	1.9-2.1	4.5-5.1
Sebebe 416	0.6-0.7	3.0-3.4	4.7-5.0	5.3-5.5	1.9-2.1	4.9-5.1
Mesfin &						
Kagneu 1919	0.7-0.8	4.5-5.3	5.0-5.4	5.3-5.6	1.3-1.6	4.8-5.0
Tewolde 1189	0.7-0.8	4.5-5.3	5.0-5.4	5.3-5.6	1.3-1.6	4.8-5.0
Friis et al.						

3825 0.

Mercier 2931 0.

Mesfin & 0.

Kagnew 1518 0.

Var. C

Ash 2713 0.

Mooney 5250 0.

APPENDIX 3. SCANNING ELECTRON MICROSCOPY.

Obtaining the magnification:

Example: When the measured value of D on the micrograph is 1.5 cm, and scale D is 10 μm :

$$\text{Magnification} = \frac{1.5 \text{ cm}}{10 \mu\text{m}} = \frac{15,000 \mu\text{m}}{10 \mu\text{m}} = 1,500\times$$

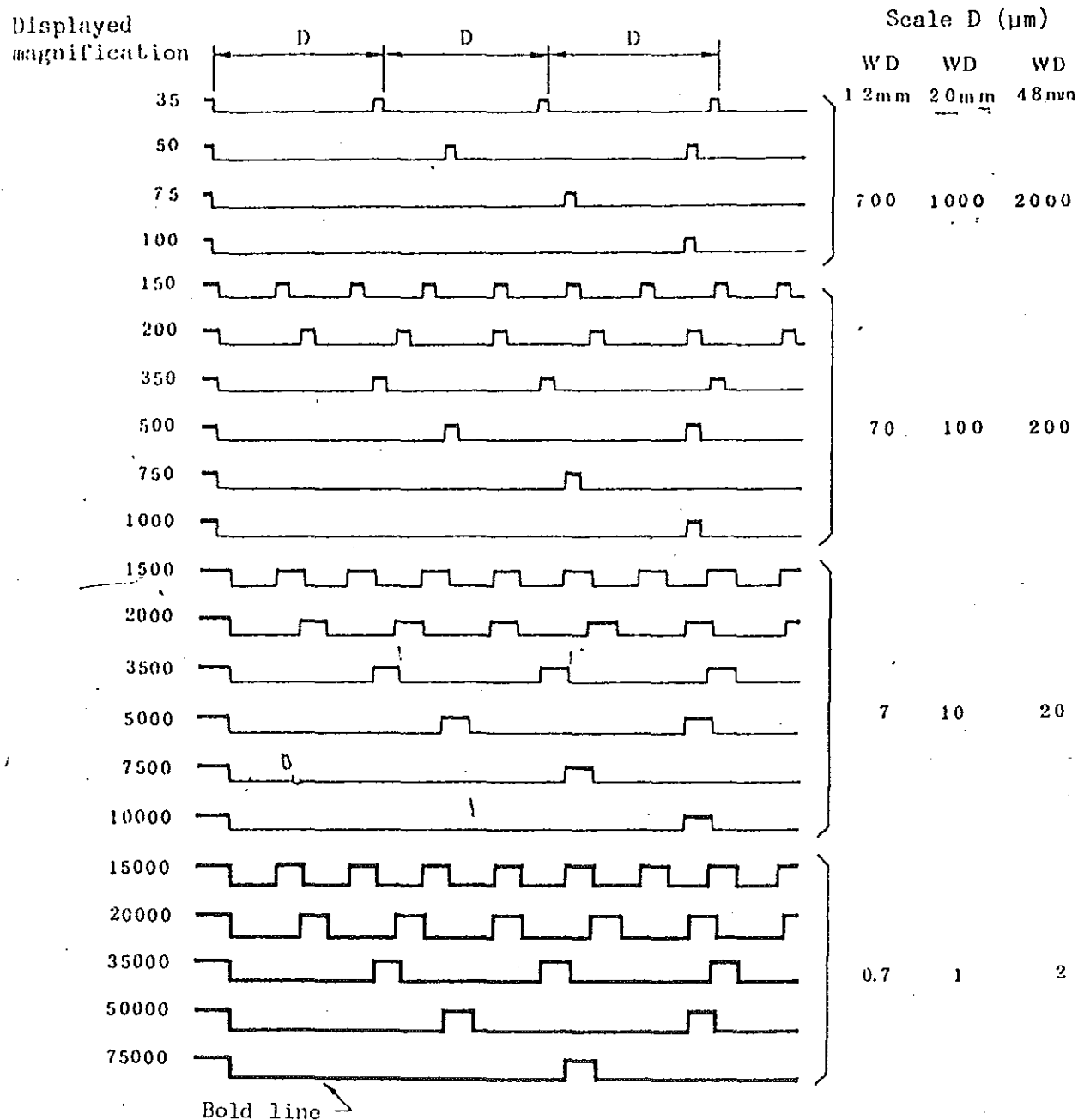


Fig. 4.8 Magnification mark and scale

T100

APPENDIX 4. LIGHT MICROSCOPY

Obtaining the magnification, using the Axiophot Photomicroscope.

Image scale on the film = Objective magnification X 2.5 for 35mm film.

= X10 for large format 9 X 12cm or 4 x 5 inches.

Declaration.

I, the undersigned, declare that this thesis is my original work, and has not been presented for a degree in any other university.

Name: Stella Naliaka Wattimah

Signature:

This thesis has been submitted for examination with my approval as university advisor.

Name: Mesfin Tadesse, Ph.D.

Signature:

Place and date of submission.

Addis Ababa university

June 1990