A Revision of the Genus **Plectocephalus** *in Ethiopia.*

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ABSTRACT

A systematic study of *Plectocephalus varians* (A.Rich.) C.Jeffrey ex Cuf. was conducted with an objective of obtaining data that will contribute to its relation with other members of the genus and to the related genus *Centaurea* L. Special emphasis was given to characters of generic value. Representative specimens of the following taxa from Latin America were studied: *Plectocephalus americanus* Nuttal, *P. chilensis* Hook & Arnott, *Centaurea floccosa* Hook & Arnott, *C. bulbosa* Hook & Arnott, *C. atacamensis* (Reiche) Johnston, *C. tweediei* Hook & Arnott, *C. rothrockii* Greenm. and *C. cachinalensis* Phil. Although widely distributed in Ethiopia, the different populations of *P. varians* are found to constitute a single taxonomic species hence authenticating the previously established synonymy by Jeffrey (1968).

P. varians is also found to be strikingly different from any known taxon of *Centaurea* in Ethiopia.Based on data from morphology, anatomy and palynology, two ecologically differentiated populations of *P. varians* are recognized: grassland and forest populations. The grassland populations differ from forest populations in the degree of the presence of indumentum. They tend to have a higher degree of hairiness compared to forest populations. A high or low amount of hair reflects xeromorphic or mesic conditions, respectively.

Forest populations tend to have dark-green broad and large leaves with prominent brochidodromous venation, whereas grassland populations have small shiny, light green leaves with inconspicuous venation. In the forest populations studied, stem anatomy revealed presence of a hollow pith, but in the grassland populations, the pith is filled with parenchymatous cells. The significance of this is associated with either xeromorphic or mesic conditions. In grassland populations, the ray florets are entirely purple, but forest populations tend to have yellow or mauve ligulate flowers. The significance of this is not clear.

Pollen grains derived from grassland populations have much thicker exine layer (6.5-8.5 microns) and longer spines (3.0-4.5 microns), whereas those from forest populations have much thinner exine layer (5.5-8.0 microns) and spinules (1.5-4.0 microns).

A key to distinguish *P. varians* from the Latin American species of *Plectocephalus* is provided. In the key *Centaurea tweediei* is given as *Plectocephalus tweediei* because it shares many characters with *Plectocephalus*. In a recent communication about this taxon Jeffrey (in litt.) wrote that "... *Centaurea tweediei* H.& Arn. ...belongs to *Cheirolophus* Cass. not to *Plectocephalus*."

1. INTRODUCTION

Plectocephalus D.Don (1830 in Index Kewensis) is a taxon about which many botanists have differing views as regards to its rank within the tribe Cardueae (Syn: Cynareae) of the family Compositae. Some are of the opinion that *Plectocephalus* is a distinct genus and should be treated separately from *Centaurea* L.(1753), while others maintain that, since it is only slightly differentiated from *Centaurea*, it should be placed as a section under the later genus. According to Wagenitz (in Davis 1975:466), *Centaurea* is "taxonomically a very difficult genus which needs much more study ... some sections stand clearly apart and could be treated as genera ...."

"The tribe Cardueae Cass. (1819), which many authors, e.g. De Candolle (1838), Boissier (1875), Bentham(1873) and Hoffmann (1894), treated under the illegitimate name Cynareae,was recognized by its "typical Cynareae Style" with its thickened or hairy articulation and by the absence of female or ligulate ray florets" (Dittrich in Heywood, Harborne and Turner 1977:999). By Examining the stylar character of all taxa of the four traditional subtribes of Cardueae, that is Echinopsidinae, Carlininae, Carduinae and Centaureinae, one will note that the thickened or hairy style articulation is typical only of the Carduinae and Centaureinae. In the other two subtribes, Echinopsidinae and Carlininae the style is more or less cylindrical throughout its length, and the articulation is not thickened and is either covered with short or bristly hairs.

In the earliest studies on the Compositae of Ethiopia, it was noted that there is only one species of *Centaurea*, that is *Centaurea varians* A. Rich. under the section *Cyanus* (A. Richard, 1848). The description of this species was based on two specimens by A. Petit and Quartin-Dillon which were collected from northern Ethiopia.

Boissier (1856, in Oliver & Hiern 1877) described *Plectocephalus cyanoides* Boiss. and *P. abyssinicus* Boiss. Further studies on the Compositae of Africa by D.Oliver and W.D.Hiern (1877) listed eight species of *Centaurea*, of which three were recorded from the Ethiopian mountains. These are *C.varians* A. Rich; *C. abyssinica* Sch.Bip. ex Boiss. and *C. hochstetteri* Oliv. and Hiern, and *Plectocephalus* D.Don was given in the above as a synonym of *Centaurea* L. The names published under *Plectocephalus* from Ethiopia were also given as synonyms of *C.varians* A.Rich. and *C. abyssinica* Sch.Bip.ex Boiss. Similarly names published under *Plectocephalus* from other countries were given as synonyms of *Centaurea* (Jackson, 1895).

Cufodontis (1967), in his Enumeratio Plantarum Aethiopiae Spermatophyta, recognized *Plectocephalus* as a genus and gave *P. varians* (A.Rich) C.Jeffrey ex Cuf. as the only species occuring in Ethiopia, and indicated that it is an endemic species. Under this species, Cufodontis (loc.cit) recorded: *C. varians* A.Rich. , *P. abyssinicus* Boiss. , *P.cyanoides* Boiss. , *C.varians* var *macrocephala* Vatke and *C. abyssinica* (Boiss.) Sch.Bip.ex Oliv. and Hiern as synonyms. In the same work, he also recognized three species of *Centaurea* from Ethiopia, that is *C. melitensis* L., *C. praecox* Oliv. and Hiern (Syn: *C. rhizocephala* Oliv. and Hiern), *C. solstitialis* L. and one undefined *Centaurea* specimen. In a later study on Cardueae (given as Cynareae) in Tropical East Africa, C. Jeffrey (1968) concurred with Cufodontis (1967).

In his Enumeratio Plantarum Aethiopiae, Cufodontis (1967) gave only a list of the genera and species occuring in Ethiopia. Jeffrey (1968) on the other hand provided a key to distinguish between *Plectocephalus* and *Centaurea*. The distinction was based entirely on the character of the achenial pappus and that of the pollen. He also gave the phytogeographical distribution of the genus. According to Jeffrey (1968), one species is confined to southern USA, one northern Mexico, one in Ethiopia and the remaining few species in the temperate regions of southern America.

n a discussion on the pollen morphology of the Cynareae, Dittrich (in Heywood et al.1977) indicated *Plectocephalus* as a section of *Centaurea*.

t was in a disscusion on the position of *Plectocephalus* within the Cardueae between my advisor and Prof. B. Nordenstam (Natural History Museum, Stockholm, Sweden) where it was recommended that "a thorough study of the Ethiopian material of *Plectoceplalus* both in the field and herbarium was necessary, so as to provide basic information to the solution of its rank." It was on this basis that the research topic was selected.

2. LITERATURE REVIEW

The Compositae, with over 20,000 species, are a "natural" family with well established limits and a basic uniformity of floral structure imposed on all members by the common possession of characters such as aggregation of flowers into capitula, and the special features of the stamens and corolla (Heywood et al. 1977). Most of the names applied to the group such as Synanthereae, Androtomeae, Nervamphipetalae, Aggregatae refer to such features. The basic classification of the family Compositae as recognized today is little different from that established by Bentham in his treatment for Genera Plantarum (1873a) and further explained in his work "Notes on the classification, history and geographical distribution of Compositae" (1873b).

Bentham's circumscription of the family especially into tribes was largely based on the works of earlier authors, notably Cassini (1819), De Candolle (1838) and Lessing (1831) . Bentham (1873a) recognized the following tribes under Compositae: Vernonieae, Eupatorieae, Astereae, Inuleae, Heliantheae, Helenieae, Anthemideae, Senecioneae, Calenduleae, Arctotideae, Cynareae, Mutisieae and Cichorieae. Modifications to Bentham's tribal classification of Compositae by Hoffmann, in his account of the family in Engler and Prantl's die Naturlichen Pflanzenfamilien (1889-94), Dalla Torre and Harms (1907) in their genera Siphonogamarum and Melchior in the sixth edition of Engler's Syllabus (all cited in Heywood et al. 1977), forms the basis of the most current work. Although the 13 tribes recognized by Bentham and Hoffmann have been largely accepted to the present day, some more proposals of the modification of the system have been made (Heywood et al. 1977).

To mention a few examples, there is a growing recognition that Helenieae is an unnatural assemblage as indicated by Cronquist (1955, cited in Heywood et al. 1977). Also the position of the genus Liabum in the Vernonieae (Cassini) or Senecioneae (Bentham) is anomalous. The genus Echinopsis which Cassini recognized as forming a separate tribe, placed between Cardueae and Arctotideae, but which Bentham placed under the Cardueae is also puzzling (Heywood et al. 1977). Recently Wagenitz (1975 cited in Heywood et al. 1977) has surveyed the distribution of certain characters in the tribes of the Compositae and has revealed "the existence of two rather distinct groups of the tribes inside the Asteroideae, each characterized by several common characters and common tendencies. The two groups are:

I. Vernonieae, Liabeae, Mutisieae, Cardueae, Echinopeae and Arctotideae.

II. Eupatorieae, Heliantheae, Helenieae, Senecioneae, Calenduleae, Astereae, Inuleae and Anthemideae.

He noted that the affinities of Cichorioideae are closer to group I of the Asteroideae than to group II, agreeing to the division of Carlquist (1955, cited in Heywood et al 1977).

The tribe Cardueae (Syn: Cynareae) was delimited by Cassini in 1815. From Bentham (1873a) to Wagenitz (1964, cited in Heywood et al. 1977), in the latest edition of Englers "Syllabus", classification within the tribe Cynareae has remained unchanged (Jeffrey 1968). It is purely artificial, but has had the merit of some convenience and has therefore been retained. Jeffrey (1968), noted that insufficient further study has been made since Bentham's time to provide any reasonable basis for its improvement.

Jeffrey (1968), in the key to the genera of East Tropical African Cynareae, recognized 11 genera and discussed in detail and provided a key to what he termed "the Centaurea-group". The question of the limits of the genus Centaurea L. is one that has been much disputed by many botanists (Jeffrey 1968).

The earliest study on the Compositae of Ethiopia by A. Richard (1848) recognized only one species of *Centaurea* i.e. *C. varians* A. Rich. under the section *Cyanus*. The description was based on two specimens by A. Petit and Quartin-Dillon from northern Ethiopia. Later on, D. Oliver and W.D. Hiern (1877), in Flora of Tropical Africa, recognized 8 species of *Centaurea*, of which 3 were recorded from Ethiopia. These are *C. varians* A.Rich.; *C. abyssinica* Sch. Bip. ex Boiss; (both currently kept as synonyms of *Plectocephalus varians* (A.Rich.) C. Jeffrey ex Cuf.) and *C. hochstetteri* Oliv. & Hiern. Cufodontis (1967) listed only one species of *Plectocephalus* from Tropical Africa as *P. varians* (A.Rich.) C. Jeffrey ex Cuf. and noted that it is endemic to Ethiopia. He also recognized three species of *Centaurea* from Ethiopia as *C. melitensis* L.; *C. praecox* Oliv. & Hiern; *C. solstitialis* L. and a *Centaurea* sp. Jackson (1895), in Index Kewensis listed four species of *Plectocephalus* (Syn: *Centaurea*) as *P. abyssinicus* Boiss. (= *C. abyssinica* Sch. Bip. ex Boiss.); *P. abyssinicus* D.Don (= *C. americana* Spreng); *P. chilensis* Boiss. (= *C. chilensis* Berth. ex Bull.) and *P. cyanoides* Boiss. (= *C. varians* A.Rich.). The genus *Centaurea* L. has been given various circumscriptions from comparatively wide ones such as those of Baillon (1882), Bentham (1873), Hoffmann (1890) and of Philipson (1939) for the African species to narrower ones such as those of De Candolle (1838), Boissier (1875) and Klokov, Sosnovskii, Tsvelev and Cherepanov (1963), (all cited in Jeffrey 1968).

In the narrower sense there has been inconsistency between different authors as to which species should be kept under *Centaurea* and which should be excluded from it. To solve this problem studies were made on *Centaurea* species in the broader sense with special attention directed to floral architecture, particularly the type and distribution of pubescence, on the style arms and anther filaments. In his treatment of the *Centaurean*-group, Jeffrey (1968) constructed a key that shows the genera which have good grounds for separate recognition apart form *Centaurea* based on pollen morphology, phyllary characteristics, pappus structure and pubescence on style arms and anther filaments. He recognized 20 genera including *Plectocephalus* within the group as being distinct.

The pollen of the tribe Cynareae was intensively investigated by Wagenitz (1955, cited in Heywood et al. 1977) based primarily on the genus *Centaurea*. He established phyletic trends within the tribe starting with the most primitive *Anthemoid* pattern to the most advanced *Helianthoid* pattern which comprises pollen having great reduction or absence of the inner columellae layer. Studies on *Compositae* pollen by Skvarla & Turner (1966) revealed four types of pollen based on the exine patterns at ultra-structural level - i.e. *Helianthoid*, *Senecionoid*, *Arctotoid* and *Anthemoid* patterns. The *Anthemoid* pollen pattern, earlier recognized in the *Anthemideae*, which is also common within the tribe *Cynareae*, is characteristic of non-caveate exines. Essentially it consists of thick, long series of basal columellae which support shorter levels of columellae alternating with internal tecta. Noteworthy in the reports of Wagenitz (1956), Duigan (1961) and van der Spoel-Walvius and De Vries (1964), (all cited in Heywood et al. 1977) is that the pollen morphology of those taxa which seem *Compositae*-like, are all related to one *Compositae* morphologic pattern, the *Anthemoid* pattern. These studies suggest that the *Anthemoid* pattern is ancestral to the family.

Based on pappus and pollen structure Jeffrey (1968), described *Plectocephalus* as having homogenous pappus with spiny, thick-walled pollen of *Serratula*- type; whereas most species of clearly - differentiated relatively broader and shorter scales, and the pollen varies from being slightly spiny to strongly spiny and thin - walled. However, according to Jeffrey (1968), some few species of *Centaurea* have homogeneous pappus and smooth pollen which is either thin or thick - walled.

As far as the tribe *Cynareae* is concerned, Jeffrey (1968) has tried to delimit the genera within the tribe by studying the floral characters. In the above cited work he stated that ...."these studies have revealed a remarkable uniformity within the tribe, and I have been unable to divide it satisfactorily even into series....." Based on the above reasons, studies on the much disputed genera *Plectocephalus* and *Centaurea* n other disciplines such as anatomy, palynology and morphology in addition to floral characters is warranted. Also the uniqueness of the disjunct distribution of *Plectocephalus* i.e. that one species is confined to Ethiopia, one to Mexico and some few others to the temperate regions of south America can arouse a lot of interest to phytogeographers (Jeffrey 1968).

3. MATERIALS AND METHODS

3.1. Materials

Most of the specimens used in this study were obtained from the National Herbarium-Addis Ababa, Ethiopia (ETH), where the main part of the work was performed. Specimens kept in the East African Herbarium (EA) were also studied. Specimens of *Plectocephalus* and *Centaurea* commonly found in Ethiopia were studied thoroughly. Some two species of *Centaurea* from Kuwait were also examined to understand the differentiating generic characters. The material for the Latin American species of *Plectocephalus* and *Centaurea* including type specimens was obtained on loan from the Herbarium of the Royal Botanic Gardens at Kew, England (K). The abbreviations of the respective herbaria are in accordance with Holmgren,Keuken and Schofield (1981).

Field trips were made between October and November in various administrative regions of Ethiopia, particularly Shoa, Kaffa, Bale, Arssi and Sidamo. The plants were studied in the field and representative samples collected. These were carefully dried and are deposited in the National Herbarium, Ethiopia (ETH) and Dar-es Salaam University Herbarium (DSM) respectively.

Light microscope (LM) studies were made using an Olympus BH Binocular Microscope. The structures studied include epidermal peel (to study the stomata), pollen grains (to assess viability) and transverse sections of leaf blades, stems and petioles.

Light microscope photographs were taken at the traditional Medicine Unit of the Ministry of Health, Addis Ababa, Ethiopia, using Zeiss Axiophot photomicroscope with a magnification range of up to x 250.

3.2. Gross Morphology

Specimens used for studying vegetative and reproductive structures were carefully sorted out from the available herbarium specimens and from the field collections. Mature, intact, floral and vegetative parts in more or less the same stage of development were selected for this purpose. Features of larger parts of the plant such as sizes of leaves, capitula, peduncle and phyllaries were measured directly from the herbarium sheets using a hand ruler calibrated in millimetres. In the measurement of phyllaries the first, third fifth and seventh series were considered. The first series (outermost phyllaries) closely resemble the second series, likewise the third series (middle phyllaries) resemble the fourth series. Stem diameters were taken from dried herbarium specimens (Appendix 1). Measurements of smaller parts of the plant such as anthers, style arms, filaments etc. were made under a Bausch and Lomb dissecting microscope equiped with a finely scaled x 10 ocular with a magnification of up to x 30.

Dried flowers were measured usually after softening in boiling water for about 5 minutes. A minimum of three measurements were made for the ray and disc florets in each capitulum, but as for the leaves up to 5 measurements were made.

3.3. Palynology

Plectocephalus varians is widely distributed in Ethiopia, and occupies diversified habitats. The morphological data alone could not explain whether populational differences exist, and therefore, these had to be supplemented with palynological data. Preliminary study on the shape of the pollen grains, surface ornamentation and thickness of various layers of specimens was made using an Olympus BH Binocular Microscope with a magnification of up to x 1000. Pollen acetolysis was done following Erdtman's (1969) procedure. The acetolysed pollen was mounted in Kaiser's glycerol gelatin and sealed with wax. A minimum of 18 measurements were made per slide to determine the polar axis length and the equatorial diameter, and 15 measurements were made per slide to find out the thickness of the nexine and sexine layers, spine base width and the length of the spines. The terminology used to describe the pollen grains is in accordance with Erdtman (1969) and Skvarla et al. (1966).The voucher slides are kept at the National Herbarium, Ethiopia (ETH).The non-acetolysed pollen grains were critically point-dried using liquid carbon dioxide, mounted directly on brass stubs with a double sided adhesive tape, gold -coated using a Jeol- fine coat ion sputter- JFC- 1100, and scanned using a JEOL- T 100 scanning electron microscope operated at 15 kV and a working distance of 20 mm in the SEM Laboratory of the East African Herbarium (EA).

3.4. Anatomy

Only fresh material collected from the field was used in the anatomical studies.Cross-sections were made from the materials, which had been preserved in Formaldehyde-Acetic acid- Ethyl alcohol (FAA) mixture (Cutter 1979) for at least a fortnight. The material was dehydrated in a graded series of ethanol, embedded in a parrafin with a melting point of 60°C, and casted into blocks according to procedures outlined by Sass (1958), Gray (1958) and Cutler (1978). Parrafin sections of 10 - 18 microns thickness were cut in an Optical "A 820" microtome, attached to clean slides using Haupt's adhesive and flooded with 4 % formalin. Safranin - fast green differential staining method was used to stain the tissues. The sections were subjected to a treatment of 30 - 45 minutes in safranin as opposed to 24 hours suggested in Sass (1958), and from 30 seconds to 1 minute in fast green. Trichomes were studied from the sectioned parts after staining using an Olympus BH Binocular Microscope at a magnification of x 1000.

3.5. Micromorphology

Only achene and leaf surfaces were studied using SEM. The achenial features studied under SEM included surface sculpturing and pubescence of the fruits of both Centaurea and Plectocephalus. The leaves were compared in terms of pubescence, stomata distribution on both abaxial and adaxial surfaces and presence or absence of glands.

4. RESULTS AND DISCUSSION

The outcome of the studies on *P. varians* and related taxa are provided below. For the sake of clarity the results and discussion are provided under separate headings.

4.1. Gross Morphology

4.1.1. Habit and life form

Plectocephalus varians (A. Rich) C. Jeffrey ex Cufodontis is a perennial herb which is known only to occur in Ethiopia (Jeffrey, 1968). The plant survives for most of the year as an under-ground rhizome; all the above ground parts wither. The stem is decumbent, prostrate to semi prostrate or erect, measuring 18 to 150 cm high, and usually unbranched below (Fig. 1A, B). The rootstock is woody. Populations growing in well developed soils under shade such as in forests tend to attain a maximum height of up to 150 cm (Fig.2, Appendix 1) whereas those found in open areas with poorly developed soils are short. The stem is more or less terete, striate-sulcate with non-glandular, uniseriate hairs. The stem diameter is between 1.5 mm and 6.0 mm. The internode ranges in length from 6 mm to 54 mm, with individuals from forests and forest edges having the longest internodes.(cf. Appendix 1).

4.1.2. Leaves

The terminology used to describe the leaf architecture and particularly leaf venation incorporates modifications of the earlier classification of von Ettingshausen (1861, cited in Radford et al. 1974; Hickey 1973). Hickey (1973), points out that ..." leaves are generally a neglected organ in taxonomic and comparative morphologic studies due in large part to the lack of unified, unambiguous and detailed classification of their features...." Generally the leaves in *P. varians* are simple, and measure 3.2-19.6 x 0.6-5.9 cm. They are distichous, rarely alternate, sessile, decurrent, and follow the ommon trend in Compositae of increasing in size basipetally (Fig. 3). Leaves riginating from near the base are petiolate. The lamina is ovate, lanceolate, to blanceolate or spathulate (Fig. 4 A-D). The young leaves tend to be lanceolate or vate. In petiolate leaves, the petioles are winged and they measure between 0.6 and .9 cm. The base is cuneate, sometimes attenuate or decurrent. The margins are ommonly dentate, widely dentate, ocassionally entire with long-stiff white hairs. The pex is usually acute, sometimes mucronate, obtuse or rarely acuminate.

n most leaves, the venation is campylodromous-brochidodromous, and by this it is meant that the secondary veins are not terminating at the margins and are joined together in a series of prominent arches. This is observed in populations from higher altitudes and from forests (Fig. 4 B-C). In some leaves the venation is hyphodromous where all the veins are missing except the primary vein or are rudimentary or concealed within the coriaceous mesophyll (Fig. 4 D). This is a common feature in grassland populations. The primary vein is straight, unbranched and relatively massive as calculated from the relation VW/LW x 100% (Hickey, in Radford et al. 1974), where VW is the vein width and LW represents the leaf width. In secondary veins, the angle of divergence from the primary vein is moderately acute and is nearly uniform in leaves with brochidodromous venation. The veins are thick and proportionately wider relative to the tertiary orders. The secondary veins are sinuous, joining the super adjacent secondary veins at an obtuse angle. Intramarginal veins or the veins closely paralleling the leaf margins and into which the secondary veins are fused are common in all populations. The angle of anastomosing of the tertiary veins with the secondary veins is variable. In most cases the angle is obtuse or rarely acute.

According to Van Cotthem (1970, cited in Radford et al. 1974), the stomata type in *Plectocephalus varians* is anomocytic, that is, the stomata is surrounded by 4 to 5 cells that are distinguishable in size and shape from the other epidermal cells. The distribution is amphistomatic occuring on both adaxial and abaxial surfaces of the aves with slightly assymetrical guard cells. Generally the adaxial surface has a lower nsity of stomata compared to the abaxial surface, except for some populations om the Harenna forest in Bale in which the upper surface is devoid of stomata (Fig. 5). The grassland populations seem to have comparable number of stomata on both urfaces, and are many compared to forest populations (Table 1).

.1.3. Indumentum

he degree of hairiness in populations of *P. varians* seems to correlate with the cological niche in which the plants are found. Populations differ in the density of the ndumentum and are either tomentose, pubescent or glabrous. Glabrousness is a ondition common to forest populations only (Fig. 5 A) whereas hairiness is observed nostly in grassland populations. (Fig. 5 E-F). Only one type of hair is prevalent among he populations, making it less useful for taxonomic purposes. The hairs are simple, unbranched and are made up of nucleated, uniseriate, lignified cells. The number of cells ranges from 4 to 20 per hair (Fig. 6 A-B). Rarely, a pair of basal cells is found in some hairs.

4.1.4. Capitulum

The inflorescence is solitary terminating the main stem and /or branches. The capitula are radiant with hermaphroditic disc florets (Fig. 7 A,B) and neuter marginal ray florets. At anthesis it measures 1.6 - 2.7 x 4.4 - 10.0 cm. It was found that the size of the capitulum is correlated with the ecological niche of the different populations. The forest populations tend to have wider capitula than the grassland populations(Fig.1 A,B; Fig. 2; Appendix 2). In grassland populations the widths of the capitula range from 3.5 cm to 6.7 cm, whereas those derived from forests measure between 5.5 cm and 10.0 cm. The involucre is ovoid, subglobose, nearly cylindrical or oblong.

.5. Phyllaries

thin the tribe Cardueae (Syn.Cynareae), the shape of the appendages of the yllaries is an important character for identification and characterization, in mbination with other characters. According to Wagenitz (cited in Davis 1975), this aracter shows great variability even in one capitulum, and more so between dividuals and populations, particularly the length of the spines. In all materials udied, the phyllaries are 5- to 7- seriate depending on the level of development of e involucre, and increase in size from the outermost to the innermost. They are bricate. The colour is variable, i.e. they may be brownish-yellow, greenish-yellow, een or light brown. They are also variable in shape (Fig. 8). There are no significant fferences in shape and ornamentation of the phyllary appendages between some ries within a capitulum.

he outermost phyllaries are the shortest and measure 4.0 - 11.0 x 1.5 - 3.0 mm, and re either ovate or lanceolate in shape (Fig. 8 A,E). In most cases, this series is omentose or pubescent. In other series only the exposed parts of the phyllaries are omentose or pubescent. The middle phyllaries show variations in shape and size ithin a capitulum. They are lanceolate to oblanceolate, ovate to narrowly obovate or near lanceolate (Fig. 8 B,C,F). They measure 8.0 - 21 x 2 - 5 mm. The appendages re ornamented with reflexed, spine-like structures, and are normally few in number compared to those of the outermost series. The innermost series measure 17 - 21 x .0 - 2.5 mm, and are more or less linear lanceolate (Fig. 8 D,G). The reflexed spine-ike structures on the phyllary appendages are fewer in this series compared to any other series, and, in addition, they are either ciliated or glabrous. In *P.varians* only the nner series of phyllaries are nerved.

he phyllaries of *P.varians* were compared with those of *P. americanus*, *P. chilensis*, nd closely related *Centaurea* spp. from Latin America such as *C. tweediei*; *C. occosa*, *C. bulbosa*, *C. atacamensis*, *C.rothrockii* and *C.cachinalensis*. In the aterials from Latin American species, all the phyllaries are nerved as compared to *.varians*, and the nervation extends even into the spines (Fig. 9 C, D-I,Fig. 10 D-F). he Latin American species have strikingly variable phyllary morphology in terms of hape, size and nature of the appendages. Their innermost series of phyllaries easure between 30 mm and 39 mm in length, whereas in *P. varians*, the same series easure between 17 mm and 21 mm. They are lanceolate, oblanceolate, ovate, linear r linear lanceolate and, as in *P.varians*, are 5- to 7-seriate (Fig. 9 C-I, 10 D-F). The ppendages are commonly ornamented with rigid spines or reflexed spine-like tructures of different sizes, but in some cases they are membranous. In *P.varians* nly the reflexed spine-like processes are present (Fig. 8 A,G).

4.1.6. Florets

The florets are made up of marginal ray florets and disc florets.

Marginal florets: The ray florets are neuter with sterile exaristate ovary. The corolla lobes are glabrous, purple, yellow or rarely white, 4-5 fid at apex. They measure between (24-) 28 - 61 x 0.5 - 1.0 mm. The measurements for different populations are given in appendix 1.

Disc florets: The disc florets are hermaphroditic and measure 11 - 36 x 0.75 - 1.5 mm (appendix 2). The corolla is 5 -lobed, tubular and glabrous, and strongly zygomorphic. The partition of the lobes and the tube coincides with the place of insertion of the stamens in most Compositae, nervation of the florets is uniform, and the 5 -longitudinal own nerves diverge at each sinus and follow the margins to the apices of the lobes. e style is usually exserted at anthesis, and slightly thickened below the point of urcation, and ranges in length between 10.5 mm and 35 mm. It is usually minutely ubescent. The stigmatic branches are 0.5 mm to 1.0 mm long and are papillate on e underside. As in all Compositae, the 5 -anthers are fused. They vary in length from mm to 6.5 mm, and are brown or rarely black in colour. They dehisce introrsely. The ases are tailed or sagittate. The filaments are band-like, hairy or papillose and easure between 6 mm and 13 mm long.

.1.7. Achenes

P. *varians* the achenes are ellipsoid, cylindrical or subglobose, narrowly ovate to bovate, and measure between 2 mm to 5 mm. They are usually brown to dark brown r grey, rarely black, but more or less yellow at the articulation point. They are labrescent when ripe and compressed laterally or flattened at the sides. Under SEM ome few scattered, long, simple hairs on the surfaces are evident (Fig. 11 A).

The achenes are crested with three conspicuous ridges on the articulating side. The idges terminate somewhere above the point of articulation. The articulation type in P. *arians* is basal - lateral (Fig. 12 D).As shown in Figure 12, the type of articulation observed in P. *varians* is somewhat similar to those seen in P. *americanus*, (Fig. 12 A) and P. *tweediei* (Fig. 12 B). In *Centaurea melitensis* (Fig. 12 C) the articulation is lateral and there are no ridges. The pappus is inserted apically and consists of bristles of equal form and length. It is between 2 mm and 10 mm long and is barbellate or plumose, setaceous with silky-white hairs and caducous.

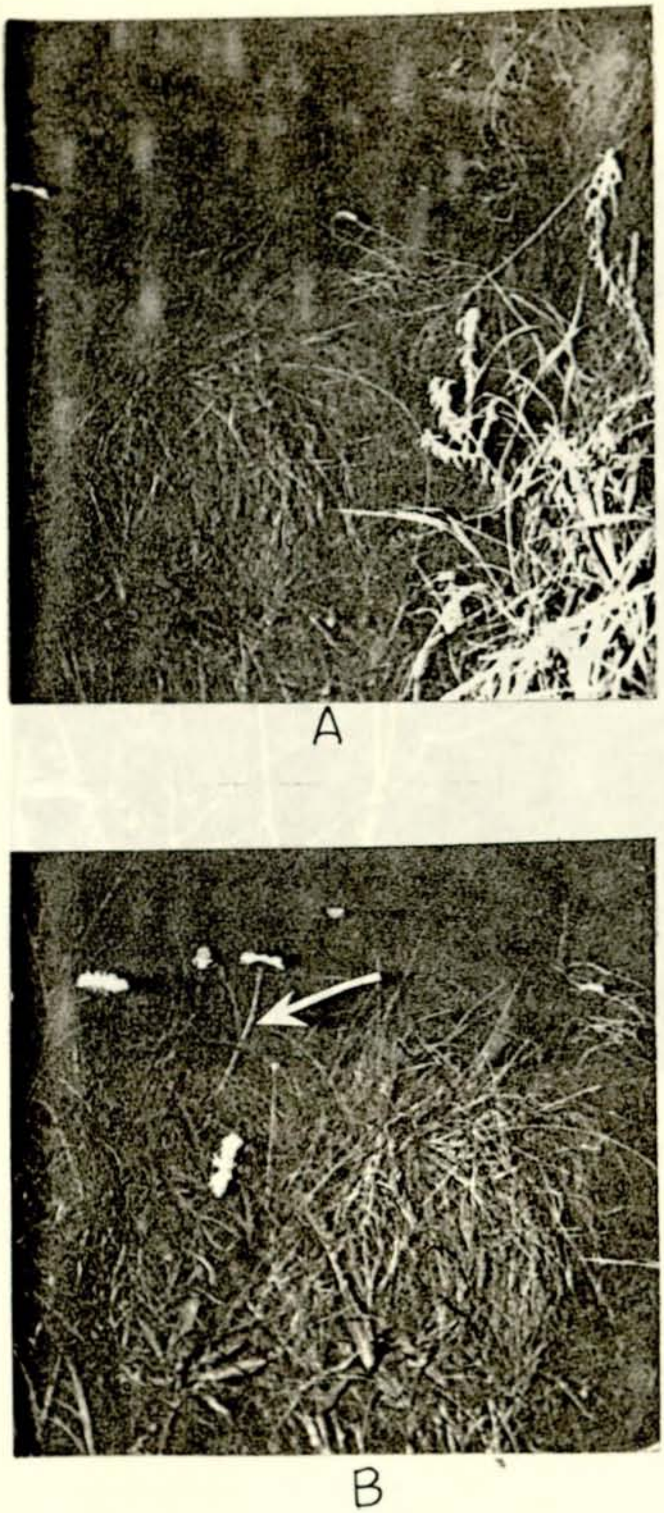


Fig.1 - Habit and life form in *Plectocephalus varians* (arrows). (Photo: Lyaruu H., Nov. 1990).

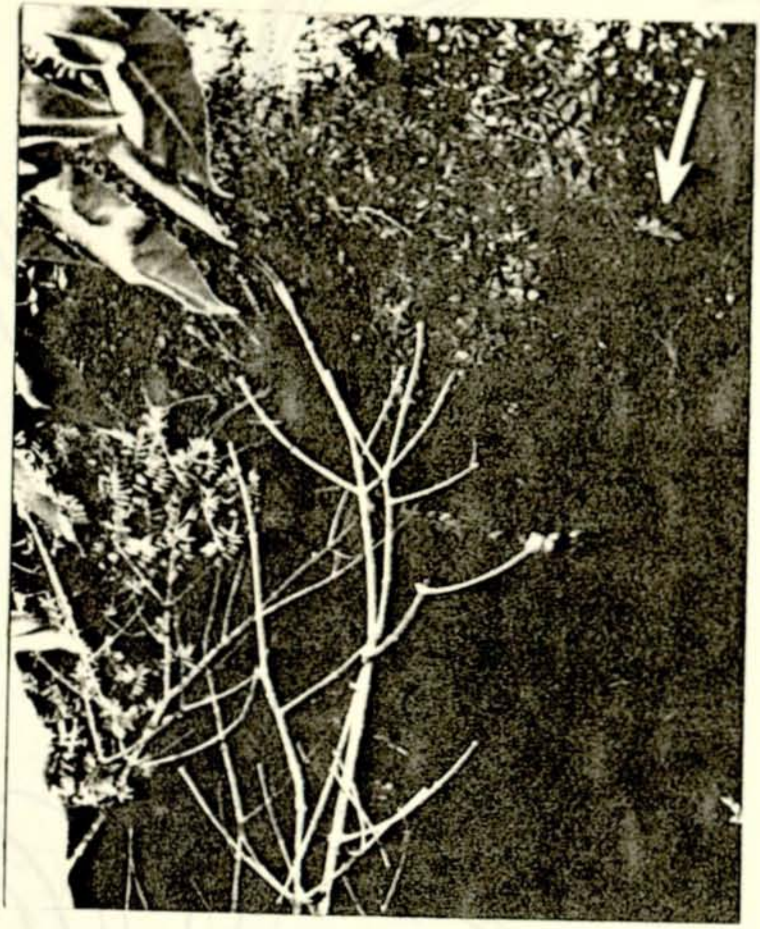
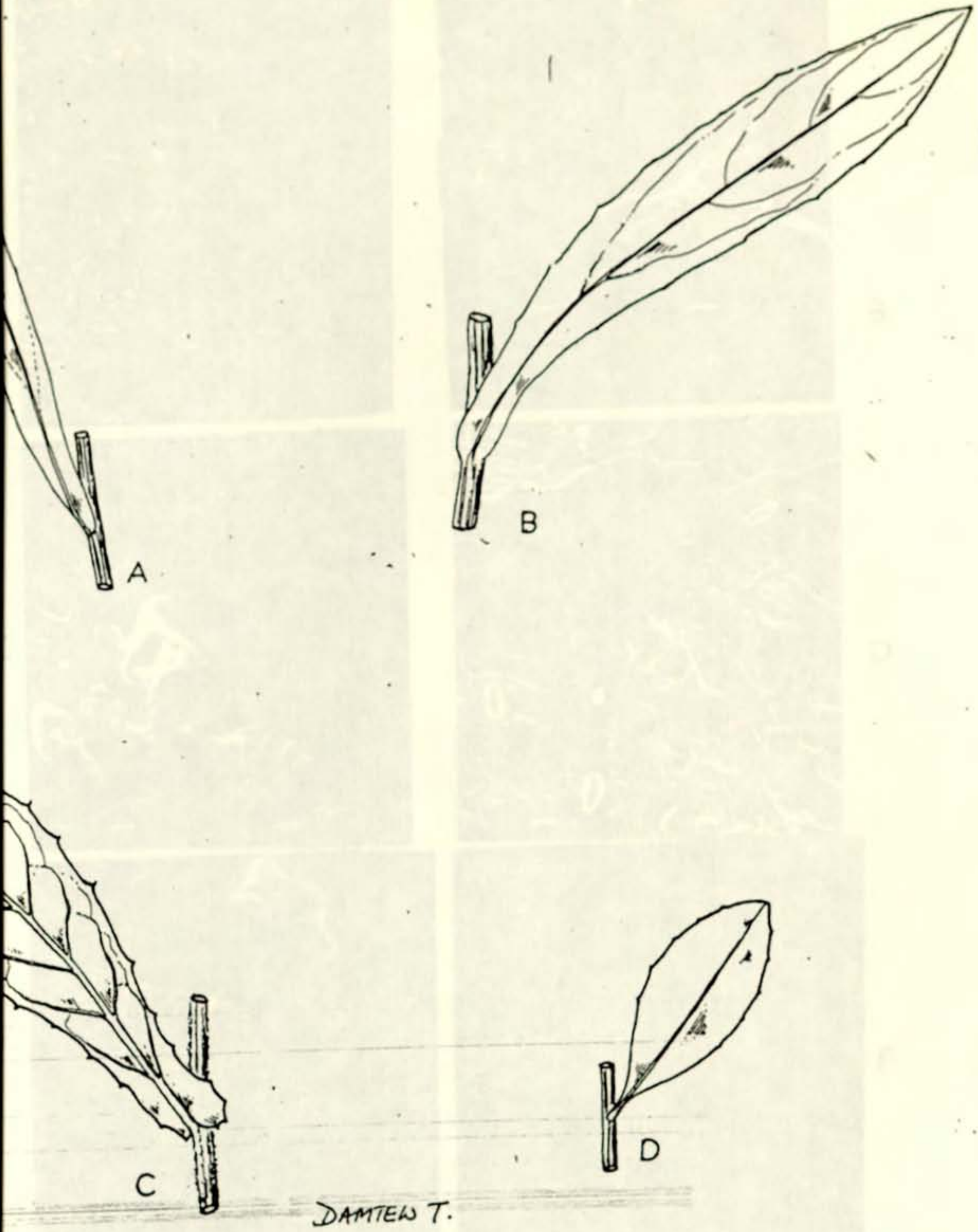


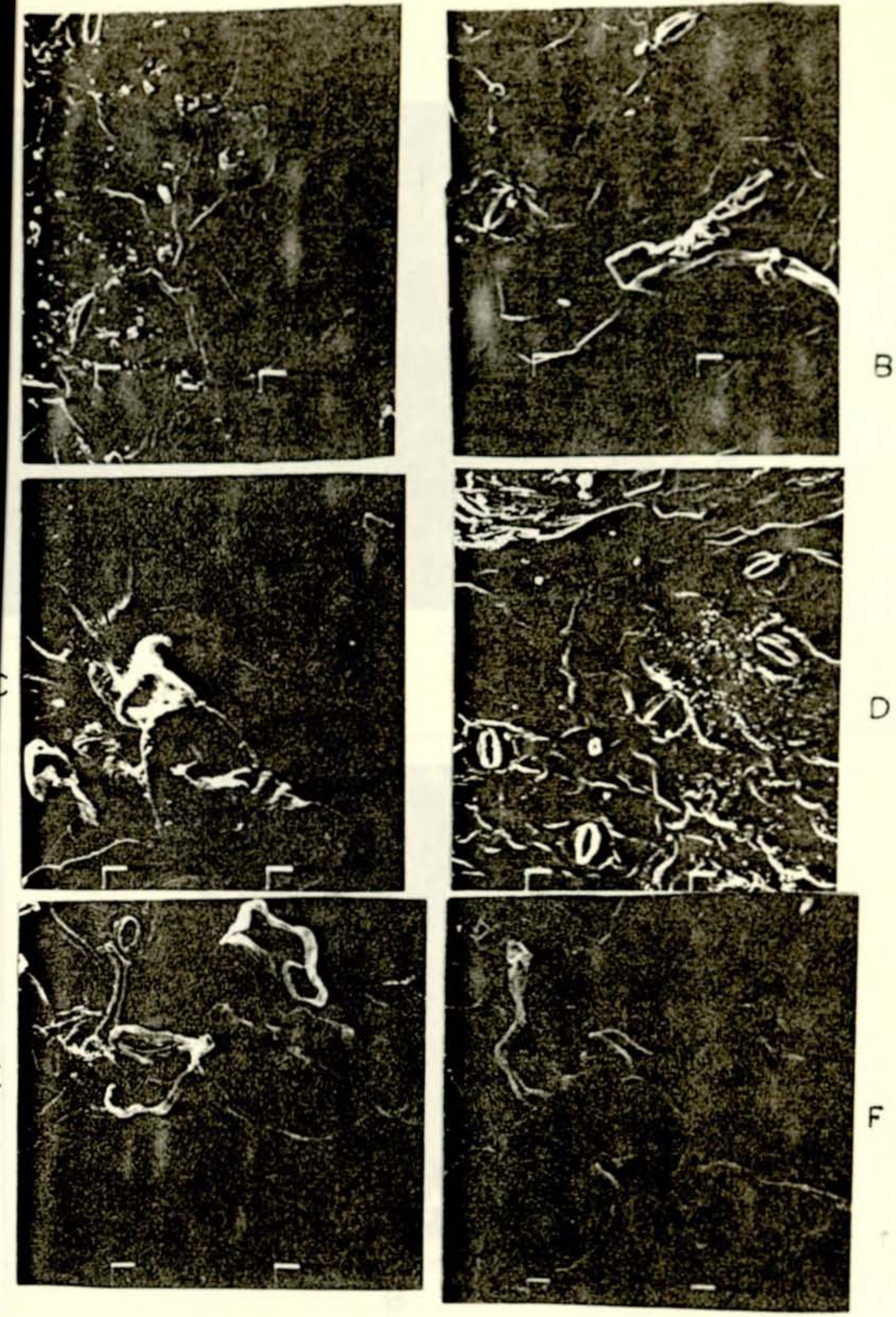
Fig.2 - *P. varians* growing under shade (arrow). Note the height of the plant compared to Figs.

1A, B.

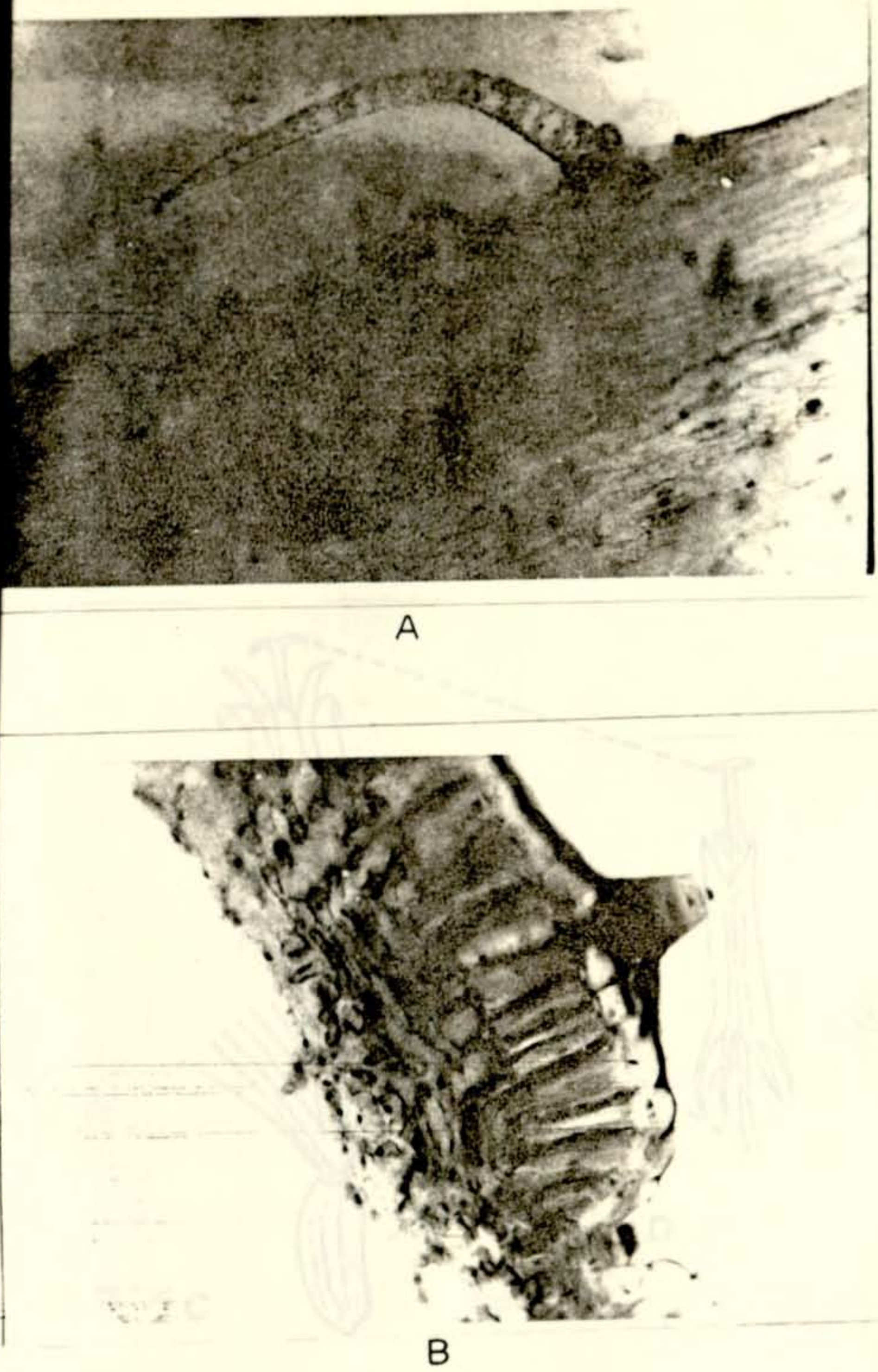
3 - P. varians - Habit showing upper part of the plant, from M.G.Gilbert et al. 465 (x 0.65).



g.4 - Variation in leaf shape and venation in *P.varians*. A: linear lanceolate with faint secondary veins (from Puff et al. 82092-2/13), B: Spathulate with brochidodromous venation from (Evans et al. 385), C: Oval spathulate with brochidodromous venation (from De Wilde 8547), D: Ovate with hyphodromous venation (from Lyaruu H 43). All x 1.



.5 - Distribution of stomata and degree of pubescence on leaf surfaces in *P. varians*. A:adaxial B: abaxial surfaces (both from Lyaruu H 21), C: adaxial D:abaxial surfaces (both from Lyaruu H 52), E: adaxial F: abaxial surfaces (both from Lyaruu H 43). All x 260.



- Trichome in *P. varians*.A: Epidermal peel x 25 (from Lyaruu H17), B: TS leaf surface to show trichome x 50 (from Lyaruu H 52).

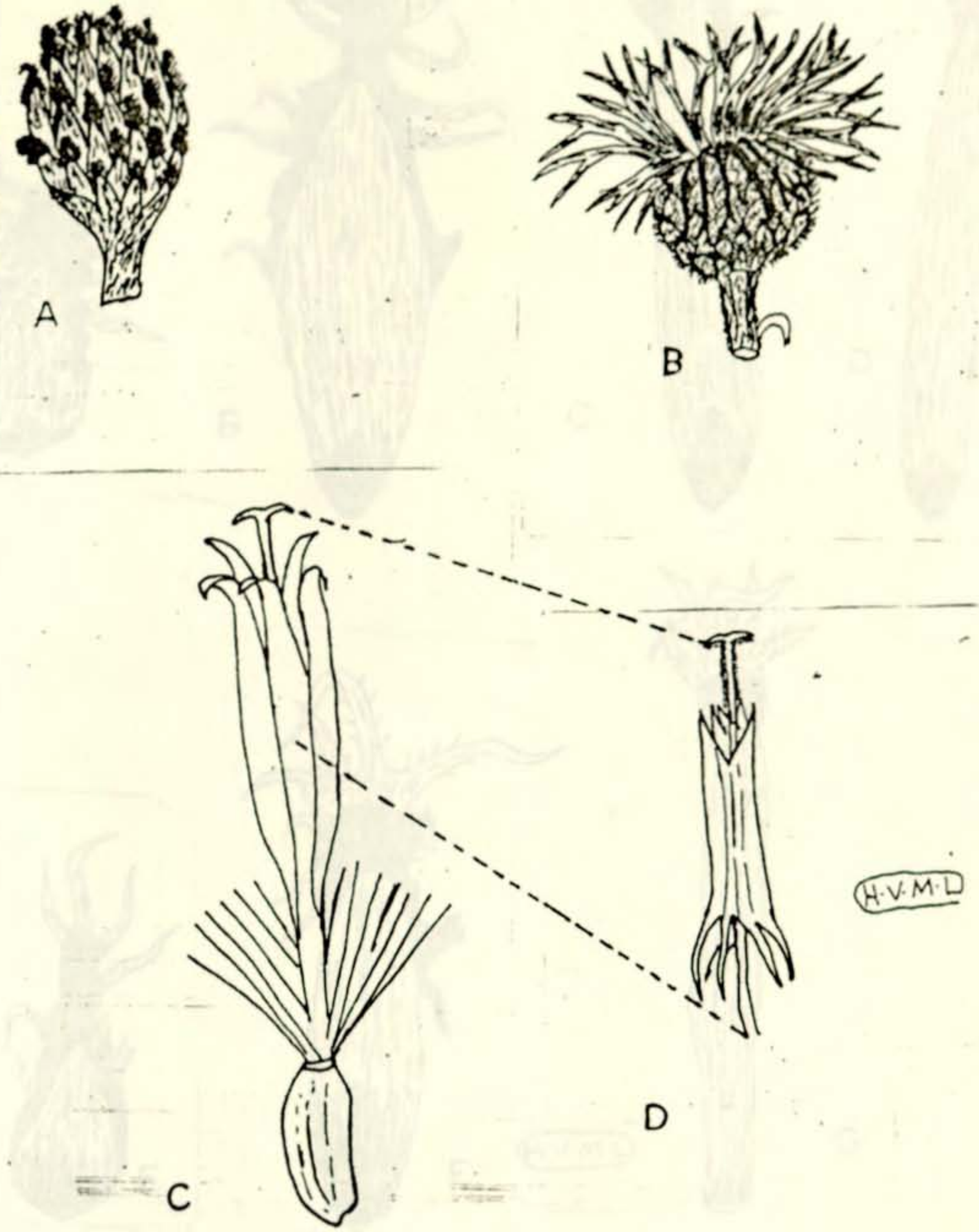
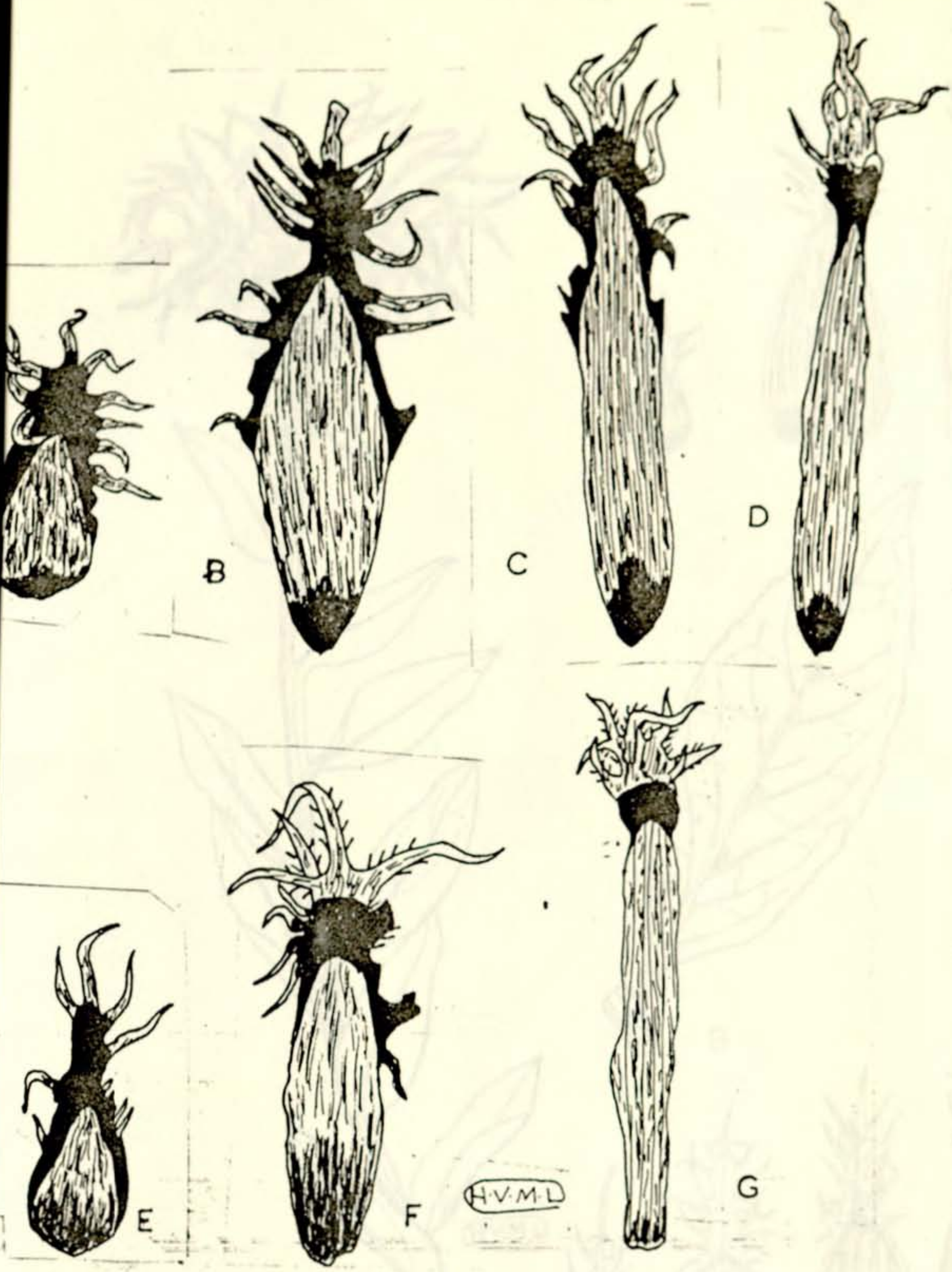
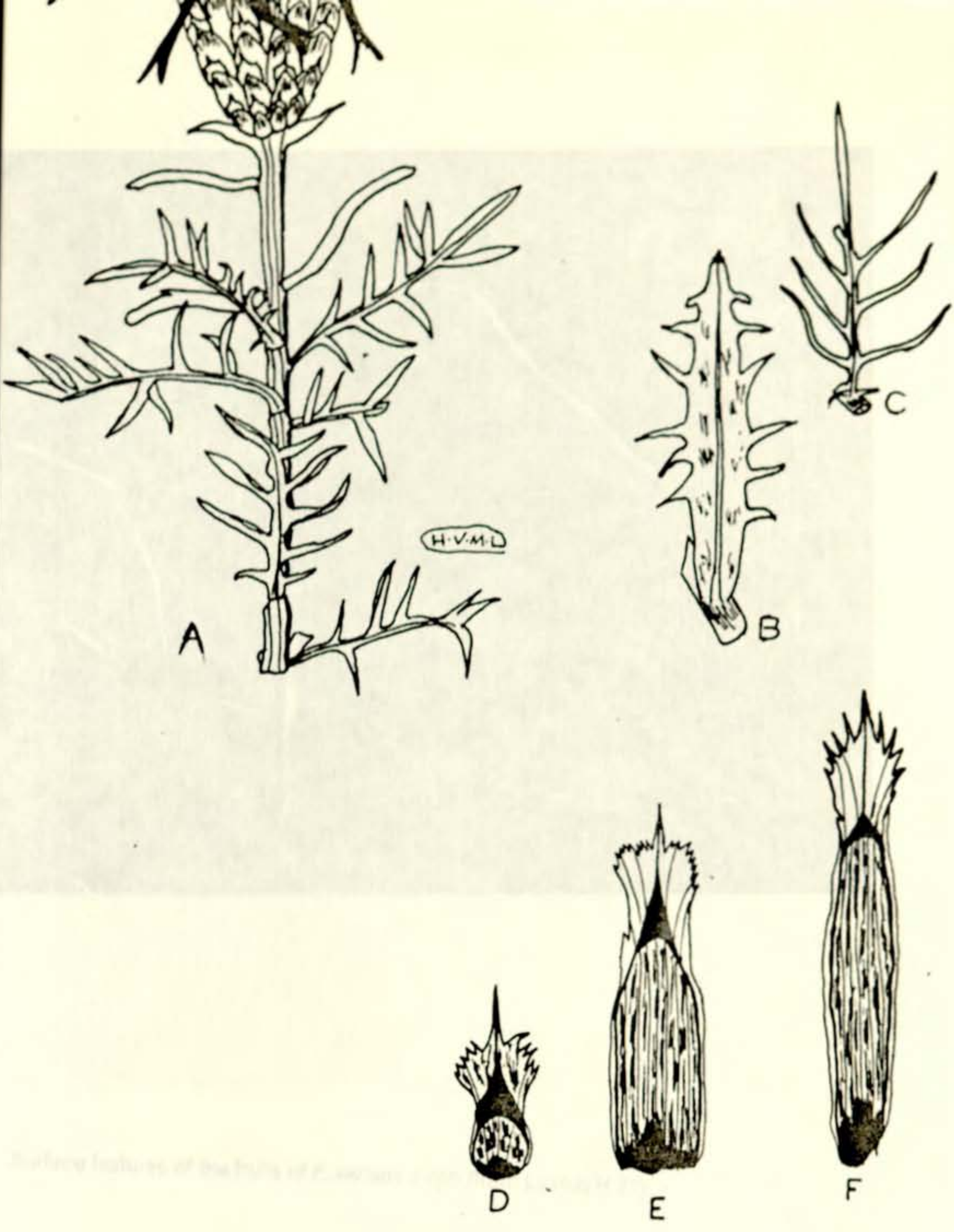


Fig.7 - Details of the capitula in *P.varians*. A: Capitula at bud stage x1 (from Lyaruu H21). B:Capitulum at anthesis x1 (from Thulin & Gilbert 465). C: Disc floret . D:Apical part of the pistil and syngenecious stamens with tailed anthers x 10 (both from Thulin & Gilbert 465).

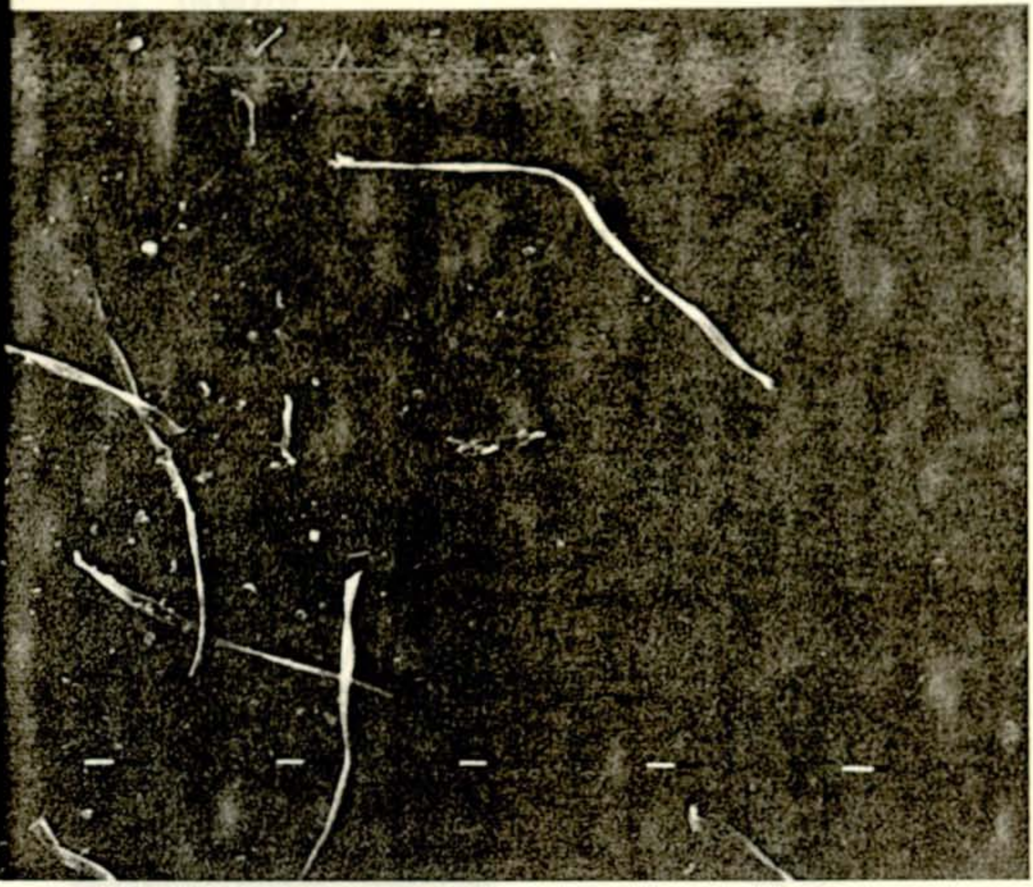


g.8 - Variation in shape of the phyllaries in *P. varians*. A-D: Outermost, two middle and innermost series x 10 (from S.B.Gilbert 1641), E-G: outermost, middle and innermost series x 8 (from Evans and Flenyl 385).

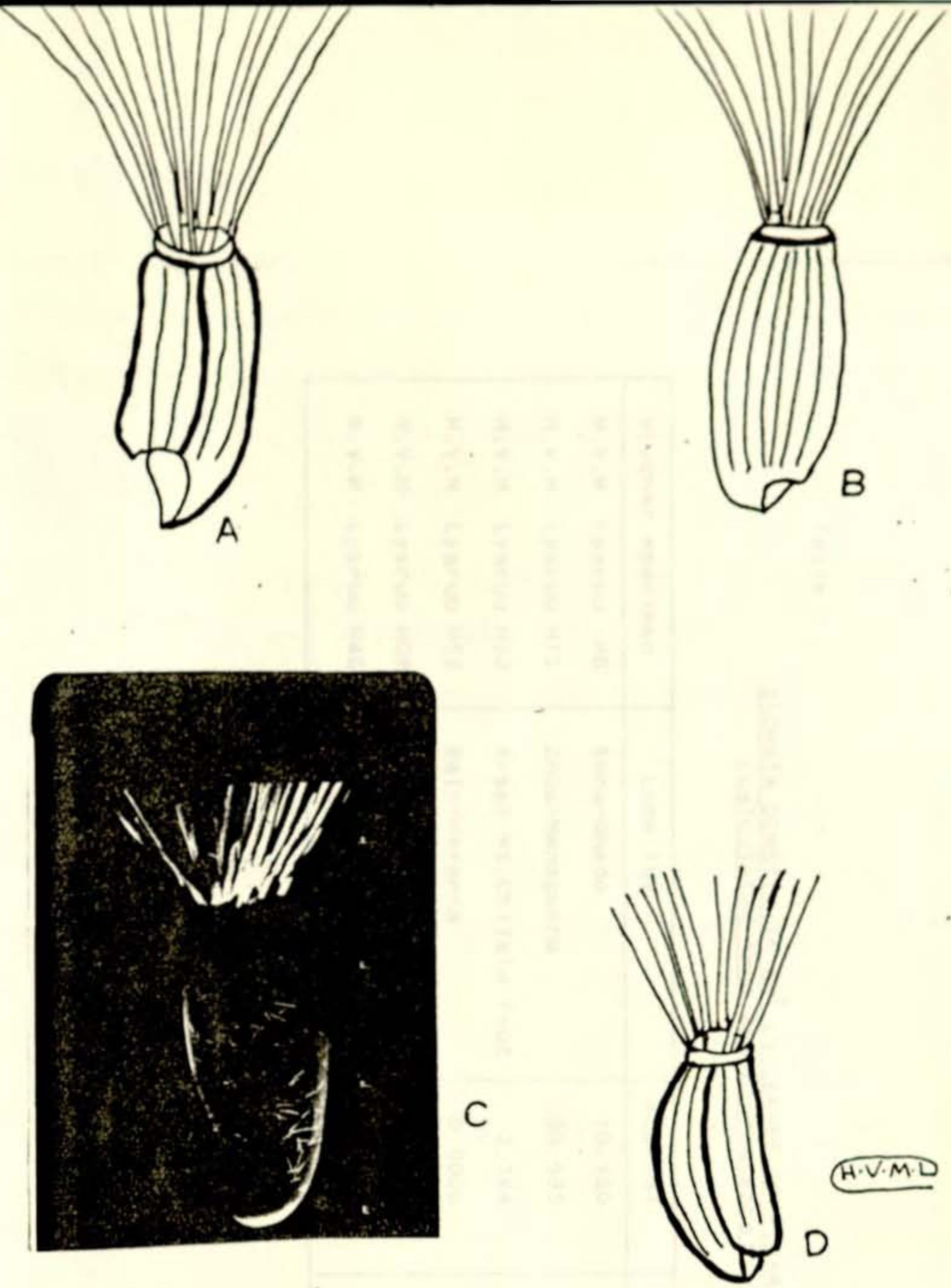
9 - *Plectocephalus americanus* - A: Upper part of the plant x 0.5, B: Petiolate leaf from the lower part of the plant, x 1, C-E: Phyllaries from the outermost (C) to innermost (E), x 3. (A-E from Darlington



0 - *Plectocephalus chilensis* A:Upper part of the plant x 0.5 (from J.L.Morrison 16871), B-C: Variation in leaf forms (B from Werdeman 267), (C from I.M.Johnston 4795) - both x 1. D-F: Phyllaries from the outermost (D) to innermost (F) x 3 (from J.L.Morrison 16871).



- Surface features of the fruits of *P. varians* x 260 (from Lyaruu H 21).



- Achene surfaces and types of articulation in *Plectocephalus* and *Centaurea* - A: *P. americanus* with three prominent ridges (from McVaugh 13267), B: *P. tweediei* with several faint ridges (from Morel 588), C: *C. melitensis* without ridges (from Mesfin & Kagnew 1615), D: *P. varians* with three prominent ridges (from Lyaruu H 21).

Table 1

STOMATA DENSITY IN mm^2 IN LEAVES OF P.VARIANS
(calculated from SEM micrographs)

Voucher specimen	Locality	Adaxial	Abaxial	Habitat
H.V.M. Lyaruu H8	Shoa-Ghedo	10.150	27.068	Grassland
H.V.M. Lyaruu H12	Shoa-Menagesha	23.685	40.602	Forest
H.V.M Lyaruu H33	Arssi-Mt Chilalo foot	3.384	87.972	Scrubland
H.V.M Lyaruu H52	Bale-Harenna	0.0000	128.574	Forest
H.V.M Lyaruu H08	Shoa-Wolmera	71.00	87.972	Grassland
H.V.M Lyaruu H45	Sidamo-Near Megada Forest	33.835	74.437	Grassland

4.2 Pollen Morphology

The exomorphology of pollen walls in Compositae have been studied by several workers at the light microscopic level. Pollen wall interpretations were started by Fischer (1890; cited in Skvarla et al. 1977) and this was followed by the classic works of Wodehouse (1935), culminating with a family conspectus by Stix (1960; cited in Skvarla et.al. 1977).

Initial studies to elucidate the internal features of the pollen wall were conducted by Stix (1960; cited in Skvarla et.al. 1977) using ultra violet microscope on sectioned pollen. She described species representing all 13 tribes of Compositae where she recognized 42 "distinct pollen types." The pollen of the tribe Cardueae (syn. Cynareae) was intensively investigated by Wagenitz (1955; cited in Skvarla et.al. 1977) primarily on the genus *Centaurea*. Wagenitz established phyletic trends starting with an Anthemoid pattern pollen and ending in a pollen having a great reduction or absence of the inner columellae layer, resembling the more advanced Helianthoid pattern.

Jeffrey (1968) studied the pollen morphology of *Plectocephalus varians* and indicated that it is of *Serratula* type in that it had spiny thick walls. In the present work the external morphology of P.*varians* was studied using both light and scanning electron microscopes . The results are summarized in Table 2.

4.2.1. Size

In *Plectocephalus varians* the pollen grains are highly variable. The length of the polar axis ranges from 33 microns to 56 microns, while the equatorial diameters range from 33 microns to 54 microns (Table 2). There are variations in size within individuals. The largest pollen grains were measured from forest populations where the length of the polar axis is 42 microns to 56 microns and the equatorial diameter is 44 microns to 55 microns. However, some materials from grassland and forest edges showed consistency in their pollen grain sizes in terms of variations. For example the following specimens showed very slight variation in pollen sizes: T.Kebede 8,_ the length of polar axis (P) was from 40-46 microns and equatorial diameter (E) 38-46 microns; in Lyaruu H43, P= 40-48 microns, and E=42-50 microns; and in Lyaruu H33, P=40-48, and E=38-48 microns.

Large variation was found in Anderberg 1639 where P=39-53 microns and E=41-51 microns and in Burger 1011, where P=42-56 microns and E=44-55 microns (Table 2).

4.2.2. Shape and apertures

As in most Compositae, the pollen grains in P. *varians* are isopolar, radially symmetrical, spheroidal or circular and rarely also sub-prolate (Fig. 13 A-B, Fig.14 C, Table 2). The ratio of polar axis (P) to equatorial diameter (E) is (0.869-) 0.909-1.17 (Table 2). The grains are echinolophate, 3-colporate, and the colpi are short and narrow with lalongate ora. In this study measurements of colpi and ora sizes could not be made as their boundaries were not clearly visible. In most cases, the colpi are not well developed and they converge at some distance midway from the poles.

The tectum is microperforate, continuous or sometimes discontinuous and ornamented with spines or spinules (Fig. 13 C, Fig.14 B).

4.2.3. Spines

In all studied material of P.*varians*, the grains are ornamented with pointed processes, and these processes fall under two categories: spines whose length exceed 3.0 microns and spinules whose lengths are less than 3.0 microns (Erdtman, 1969).

In all cases the spines are conical, broadened at the base with sharp apices, and vary in length from 1.5 microns to 5.0 microns. The width of the spine bases vary from 5 microns to 9 microns, and there is a correlation between the spine length and the width of the spine base (Fig. 15 A,B). Among the forest populations the spines are very short and never exceed a length of 3.0 microns. Generally forest species tend to have very short spines compared to grassland species (Table 2). Tecta with and without perforations were encountered (Fig. 13 C-D). Sub-apical pores which are rare in Compositae (Mesfin, 1984) were evident only in a single specimen of *P. varians* from Menagesha state forest (Lyaruu H21, Fig. 16). In a pollen grain, the tectum can exhibit both continuous (imperforate) and discontinuous (perforate) characters . The same case was observed in other studies (Wattimah 1990, Skvarla and Turner 1966). This consistent morphological feature negates tectum unity or disunity as a taxonomic marker. There is not much variation in the size of the micropunctae in an individual pollen grain but are unevenly distributed around the spines and along the ridges (Fig. 13 C, Fig.14 B).

The presence or absence of sub-apical holes in spines which have been referred to by several authors under different names such as "lacunae", "hohlraum", (= empty space), "cavity", "sub-apical holes", has been a centre of controversy among palynologists and paleoecologists (Bolick et al. 1984). Some authors have found sub-apical hole to be good taxonomic characters. Stix (1971; both cited in Bolick et al. 1984) employed it to separate a number of closely related Inuleae taxa and Praglowski and Grafstrom (1980; cited in Bolick et al. 1984), have shown that *Calendula maritima* can be distinguished from five other species in the genus using this character. Skvarla et al. (1977), disqualify the presence or absence of sub-apical holes as a good taxonomic marker as it shows inconsistency within species and populations. The conclusion by Skvarla et al. (1977), finds support in this study as has also been done in the revisionary work of the genus *Bidens* (Mesfin, 1984). Ruffin

(1977; cited in Bolick et al. 1984), advocates a more thorough survey of the size, number and arrangement of sub-apical pores to evaluate their utility as characters for Compositae pollen.

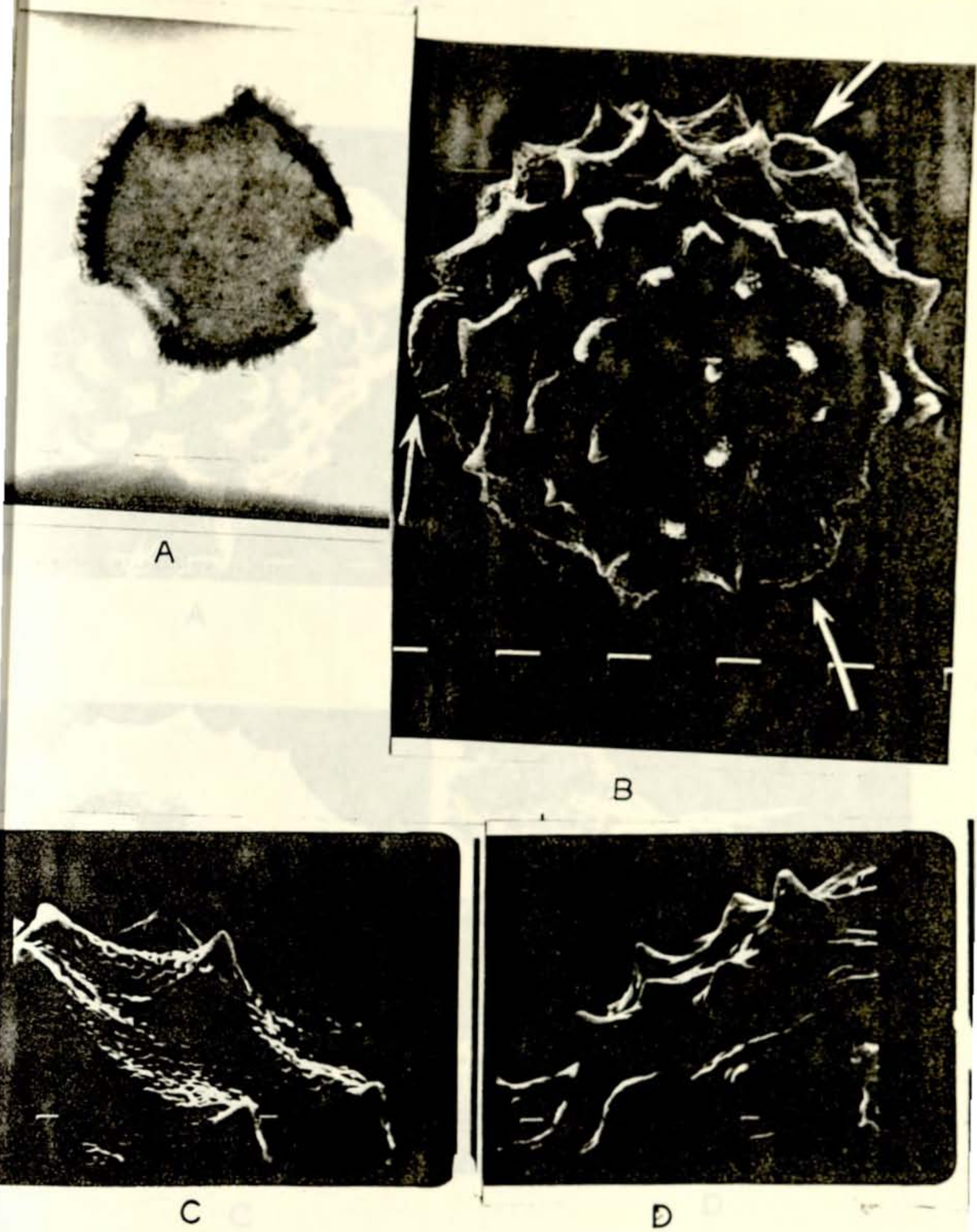
4.2.4. Endomorphology of the pollen wall

The internal morphology of the pollen wall was studied from acetolysed pollen grains using transmitted light. Since the intine layer disintergates on treatment with acetolysing chemicals, only the exine (sexine and nexine) was studied. The sexine layer is baculate and ranges from 3.0 microns to 5.0 microns, whereas the nexine layer is 2.0 microns to 5.0 microns thick. The two layers differ considerably in architecture. The nexine layer is more or less uniform in thickness, whereas the sexine layer is irregular and is much more thickened just below the spine bases. The surface morphology of the exine in *P. varians* shows the pattern most commonly found in the tribe Vernonieae (Type A, Keeley and Jones 1979: Type IV, Kingham 1976: Type I, Bolick 1978b: all cited in Bolick 1983).

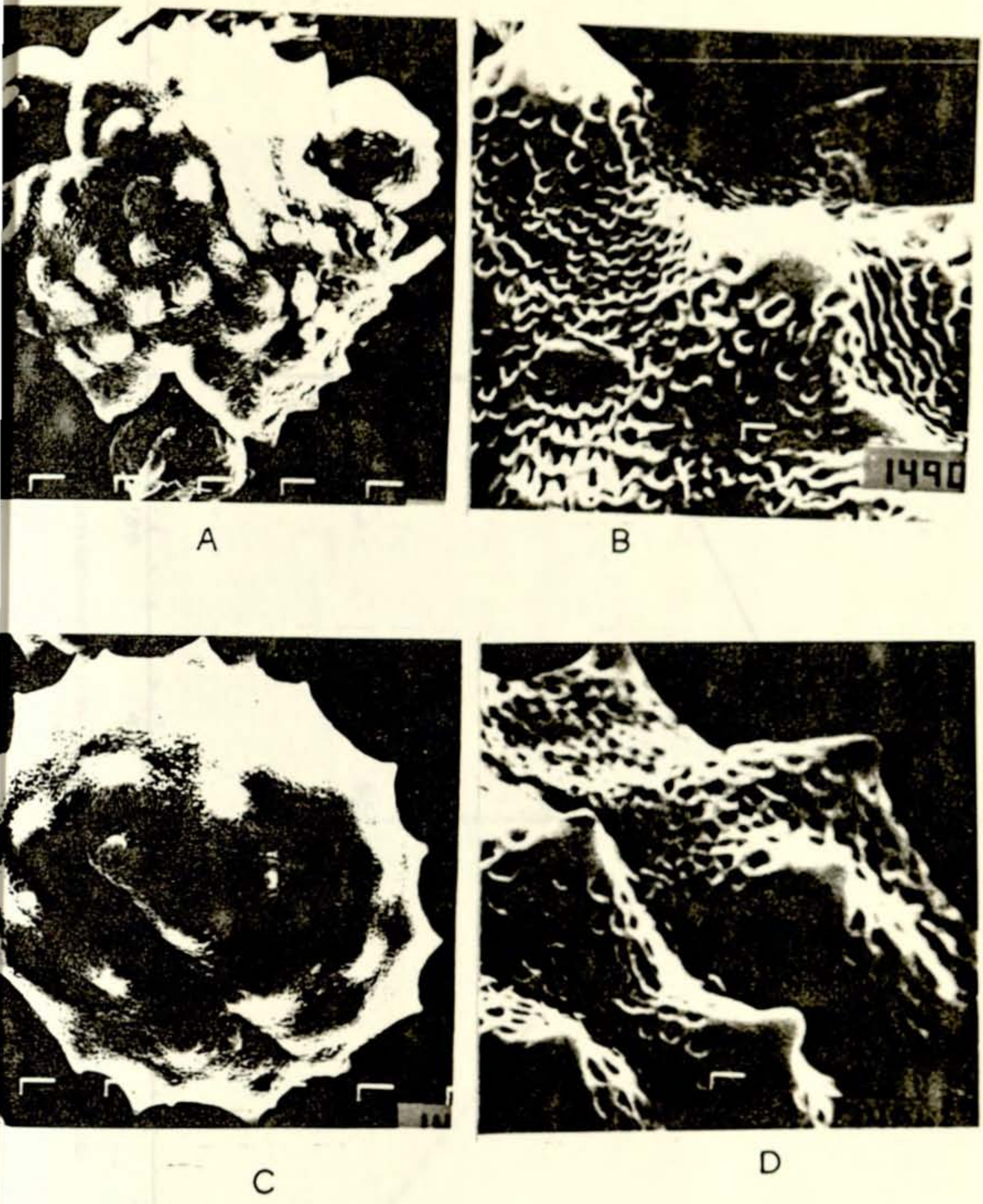
These are considered to be the most primitive of the pollen types in *Vernonia* (Wattimah, 1990) and therefore their presence in *Plectocephalus* indicated a degree of primitiveness among the taxa. In this study a more or less linear relationship was found to exist between the exine thickness, the spine base width and the spine length (Fig. 15 B). Based on this observation, the pollen grains examined fall under two categories: those derived from grassland populations and those from forest populations. The pollen from grassland populations tend to have a much thicker exine layer with much more elongated spines and broadened spine bases compared to those derived from forest populations (Table 2, Appendix 4).

4.2.5. Pollen viability

The pollen fertility status ranges from 73.1 - 90 % (Table3). The high percentage viability is a clear indication that *Plectocephalus varians* is a homogeneous taxon regardless of the geographical division from where the populations are derived, that is whether from the north, south , east, west or central Ethiopia, they show very slight variations in their pollen fertility levels. Similarly the demarcation between the grassland and forest populations is not clear when compared in terms of pollen viability, just like the case when morphology is considered. In this aspect it can be argued that populations of *Plectocephalus varians* irrespective of where they are derived from are essentially the same genetically and therefore constitute a single taxon.



g.13 - Light (A) and scanning micrographs of pollen grains in *P. varians*. A:Polar view x 250 (from Lyaruu H08), B: With germinal furrows (arrows) x 1900 (from Lyaruu H 21), C: Perforate tectum x 3800 (from Anderberg 1639), D: Imperforate tectum x 3800 (from Lyaruu H 8).



14 - Scanning electron micrographs of *P. americanus* (A,B) and *P. chilensis* (C,D). A: polar view x 1900, B: Tectum ornamentation x 6900 (both from McVaugh 13267). C: Colpus area x 1900, D: Tectum ornamentation x 6900 (both from Werdeman 267).

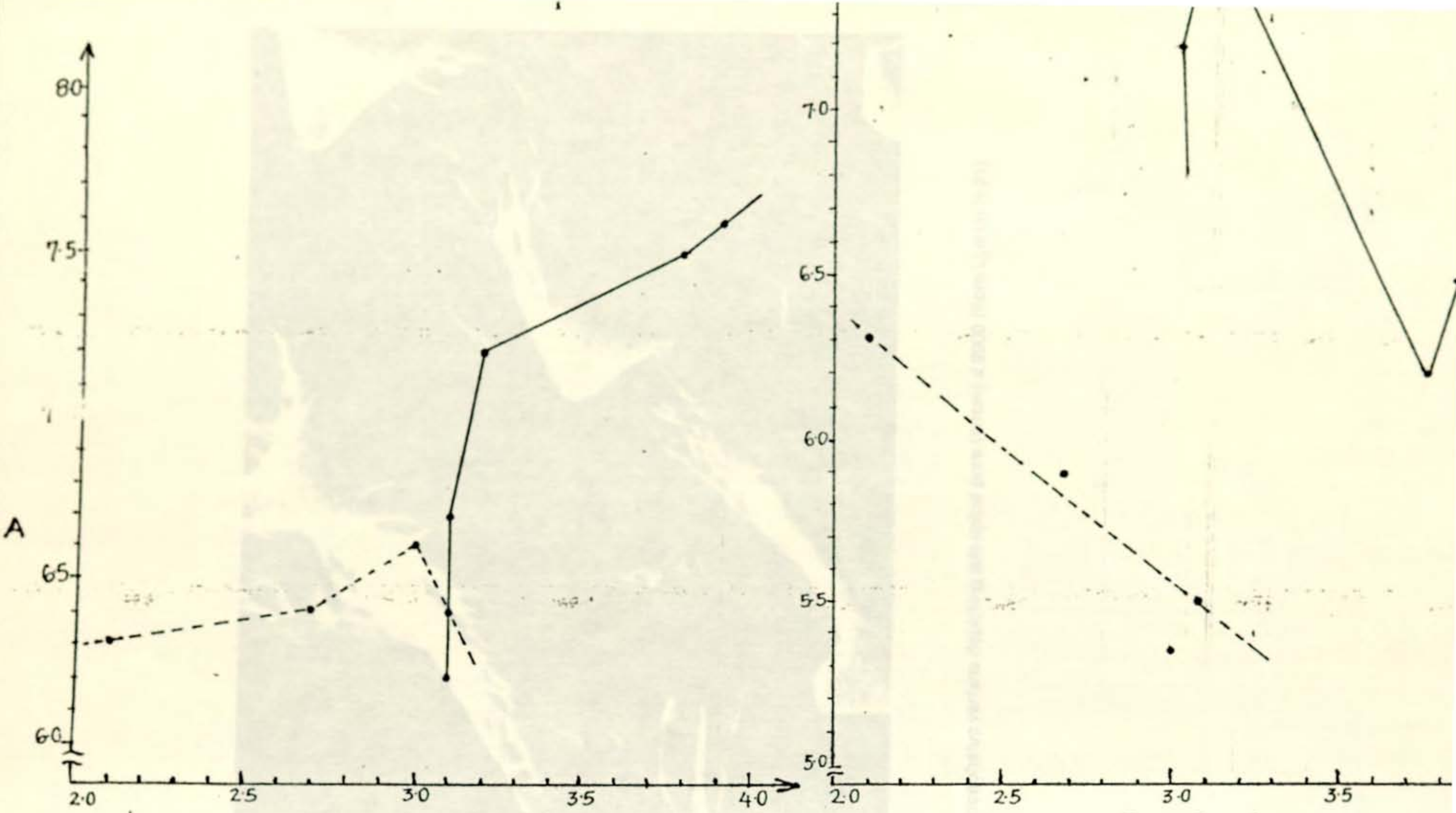
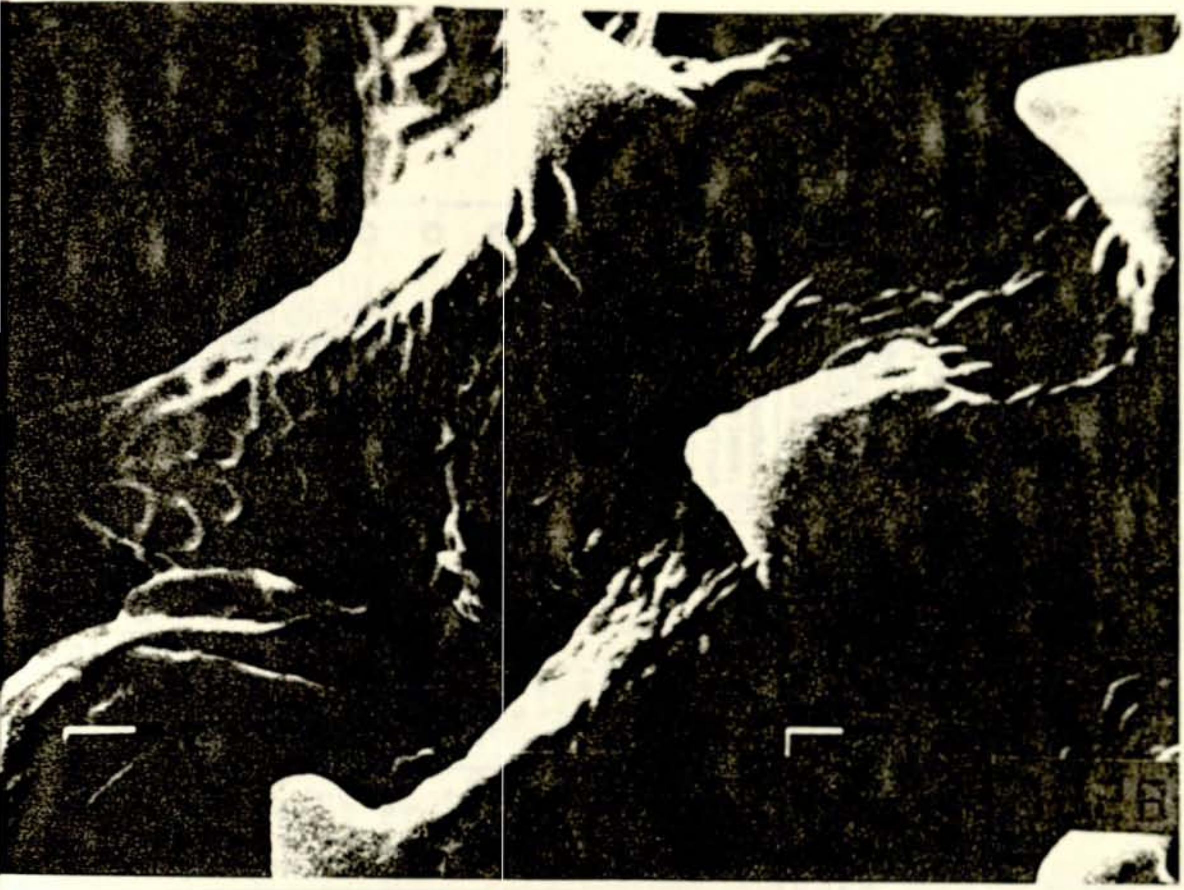


Fig.15 - Graphs showing the relation between the spine length (horizontal axis) and exine thickness (vertical axis)in pollen grains of *P. varians* (A)and the relation between the spine length



Ig.16 - *Plectocephalus varians* depicting sub-apical pore (arrow) x 9900 (from Lyaruu H 21).

Table 2

POLLEN MEASUREMENTS IN MICRONS FROM ACETOLYSED POLLEN OF P.VARIANS. THE DATA IN PARENTHESES IS THE MODE FOR 18 MEASUREMENTS PER VOUCHER SPECIMEN.

Voucher specimen, Province	Spine Length	sexine	nexine	Spine base width	Polar diameter (P)	Equator. diameter (E)	P/E
A.Anderberg 1639 (WG)	2.0-4.0 (3.0)	3.0-5.0 (3.5)	2.0-4.0 (2.0)	5.0-8.0 (6.0)	41.0-51.0 (45.0)	41.0-50.0 (47.0)	0.9111-1.119 (0.9574)
Lyaruu H52 (BA)	2.0-5.0 (3.0)	3.0-5.0 (4.0)	2.0-3.5 (3.0)	5.0-6.0 (5.0)	39.0-48.0 (44.0)	40.0-46.0 (44.0)	0.9302-1.0667 (1.0000)
Lyaruu H21 (SU)	2.0-4.0 (3.0)	3.0-5.0 (4.0)	2.0-3.5 (2.5)	5.0-7.0 (6.0)	40.0-49.0 (40.0)	40.0-49.0 (48.0)	0.9090-1.0952 (1.000)
Lyaruu H08 (SU)	3.5-4.5 (3.5)	4.0-5.0 (5.0)	2.0-3.5 (3.0)	5.0-7.0 (6.0)	40.0-49.0 (42.0)	38.0-50.0 (45.0)	0.8695-1.0454 (1.0000)
Lyaruu H43 (SD)	3.0-4.5 (4.0)	4.0-5.0 (4.5)	2.5-3.5 (3.0)	6.0-7.0 (7.0)	42.0-49.0 (37.0)	42.0-50.0 (36.0)	0.9130-1.1627 (1.0000)
Lyaruu H8 (SU)	2.5-4.0 (3.0)	3.5-5.0 (4.5)	2.0-5.0 (3.0)	7.0-9.0 (7.0)	33.0-44.0 (37.0)	33.0-47.0 (36.0)	0.9285-1.1578 (1.0000)
W.Burger 1011(HG)	1.5-3.0 (2.0)	3.5-4.5 (4.0)	2.0-3.0 (2.0)	5.0-8.0 (5.0)	42.0-56.0 (56.0)	44.0-54.0 (54.0)	0.9215-1.0370 (1.0000)
Lyaruu H33 (AR)	3.0-3.5 (3.0)	3.0-5.0 (4.0)	2.0-3.0 (2.5)	5.0-6.5 (5.0)	40.0-48.0 (45.0)	38.0-48.0 (45.0)	0.8695-1.1707 (1.0000)
T.Kebede 8 (GD)	2.5-3.5 (3.0)	4.0-5.0 (4.0)	2.0-5.0 (2.0)	6.0-8.0 (7.0)	40.0-46.0 (40.0)	38.0-46.0 (44.0)	0.9090-1.1052 (1.0000)

Abbreviations for the provinces:- WG = Wellega, BA = Bale, SU = Shoa
SD = Sidamo, HG = Hararge, AR = Arsi,
GD = Gonder

Table 3

POLLEN VIABILITY COUNT IN MEMBERS OF PLECTOCEPHALUS VARIANS (A.RICH) C.JEFFREY Ex cuf.

Voucher specimen	Province	Habitat	Total No. of grains Counted	Total No. fertile gr.counted	% Viability
Tenagne Kebede 8	Gonder	Waterlogged area	563	458	85.9
Arne Anderberg 1639	Wellega	Waterlogged area	377	318	84.4
W. Burger 1011	Hararge	Forest	406	355	87.4
Evans & Flenyl 385	Gojjam	Scrubland	521	469	90.0
Friis et al. 476	Keffa	Grassland	444	370	83.3
Mesfin et al 3386	Sidamo	Forest edge	442	375	84.8
H.F Mooney 7262	Bale	Scrubland	396	342	86.3
Lyaruu H.24	Arssi	Thicket	417	321	77.0
Lyaruu H.56	Bale	Forest	562	434	77.2
Lyaruu H.40	Sidamo	Forest edge	462	371	80.3
Lemma G.Sellasie 506	Shoa	Forest	451	372	82.5
Brehme s.n. (23/11/61)	Shoa	Forest	388	344	88.7
Lyaruu H.06	Shoa	Grassland	580	424	73.1
Lyaruu H.008	Shoa	forest	516	384	74.4

4.3 Anatomy

4.3.1. Petiole

The petioles in most populations of P. *varians* are winged. They are smooth and rarely ornamented on the surface with uniseriate, lignified trichomes. Only populations from Arssi had hairs on the margins. In transverse section, only two forms of petiole can be recognized- a most common triangular type and the semi-circular type. Both are with a moderately thin layer of cuticle that is up to 3 microns thick; the thickness being much more pronounced at the midrib section and towards the petiole margins. The cuticle in most cases is smooth or serrulate. The epidermis is uniseriate, with nucleated cells of varying sizes. The cells are more or less isodiametric to transversely elongated (Fig. 17 A, B Table 4). The outer periclinal walls are curved or convex in outline and their wall thickness varies from thin to moderately thickened. The walls on the adaxial side are much more thickened than those on the abaxial surface. The anticlinal walls are however slightly thickened with straight walls (Fig. 17 A,B).

Just below the epidermal layer is the collenchyma. Depending on the nature of the petiole, the collenchyma layer can be one or two layers thick, continuous or discontinuous. Where it is discontinuous, it is confined to the midrib section of the petiole (Fig.17 A,B). In some cases the collenchyma layer is totally missing in the adaxial surface and only prominent in the midrib abaxially . The collenchyma, being a supporting tissue in the petiole, comprises of hexagonal to more or less rectangular, heavily lignified cells with angular thickening, and are much more elongated compared to other epidermal cells, but slightly smaller than the parenchyma cells (Fig.17 A,B). The collenchyma cells on the abaxial surface are much bigger and much more thickened compared to those of the adaxial surface. In some petioles, the collenchyma cells found just below the epidermis in the adaxial surface are more or less sub- palisade like and include chloroplasts.

The parenchyma tissue comprises of very thin walled isodiametric cells and more or less polygonal cells of differing size, and is located just below the collenchyma. The cells are enucleated and devoid of chloroplasts and hence could be assumed to lack both meristematic and photosynthetic activities. Those away from the midrib towards the margins and around the vascular bundles are heavily packed with chloroplasts, with the density of the chloroplasts per cell increasing towards the petiole margin. The chloroplasts are centrifugally positioned in the cells, and are ovoid to elliptic in structure, sometimes joined together to form a more or less ring-like structure.

In all studied materials, the vascular bundles are found in odd numbers and are either 5, 7 or 9. The vascular bundle in the midrib is the largest (Fig.17 A). The remaining vascular bundles tend to become progressively smaller towards the petiole margins. The number of vascular bundles in the petiole can vary in the same individual depending on the position where the sectioning was done . If the sectioning was done close to the base, then it is likely to have maximum number of vascular bundles. For example sections from different areas of the petiole from Arssi (Lyaruu H33) had either 5 or 7 vascular bundles. The same observation was made among the members of *Polygonum* s.l. by Haraldson (1978).

In all petioles, the xylem pole is directed towards the adaxial side, with the phloem tissue pointing to the abaxial surface (Fig.17 A,B). Around the vascular bundles, the thin walled parenchyma cells are crushed to form cavities (Fig.17 A,B). According to Dittrich (in Heywood et al. 1977), these cavities are supposed to be secretory in function. Bundle sheaths are prominent around the vascular bundles and are normally two layered: a continuous outer bundle sheath (sometimes referred to as endodermoid layer) with sclerified thick walled, hexagonal, elongated cells, 1 to 2 cell layers thick and slightly smaller than the normal parenchyma cells. A discontinuous inner bundle sheath which is confined to the caps of both the xylem and phloem tissue as small hexagonal sclerified cells, usually in 2 to 3 layers (Fig.17 B).

4.3.2. Leaf Anatomy

The cuticle is fairly thick, and it is about 3.75 to 5.30 microns, and slightly thicker at the margins and on the midrib with fair periclinal striations. The epidermis is uniseriate, with thin cell walls except for the outer walls (=periclinal walls) and outer ends of the anticlinal walls which are thick and cutinized (Fig.18 A,B).

The epidermal cells are transversely elongated or rectangular in outline, sometimes isodiametric, in most cases the adaxial surface cells being much larger than abaxial cells (Fig. 18 A & B). Whereas the adaxial epidermis measures between 17.5 and 52.5 microns thick, the abaxial epidermis ranges between 12.5 and 37.5 microns (Table 5). The leaf is bifacial and the mesophyll can be described as "loose mesophyll" (Radford et al. 1977) due to the presence of air lacunae (Fig. 6 B). Around the mid-rib, the pallisade layer and the spongy mesophyll are indistinguishable as all the cells are more or less isodiametric (Fig. 18 A). The pallisade is one to two cell-layers thick, and measures between 60 and 220 microns. This layer is composed of elongated rectangular cells, densely rich in peripheral chloroplasts (Fig. 6 B). Where the pallisade layer is two cell-layers thick, the innermost layer comprises of shorter cells than those of the outer layer, and this layer is continuously interrupted by secondary veins. In some cases, the secondary veins appear between the spongy mesophyll and the pallisade layer occupying the lacunae. The spongy mesophyll is two to three cell-layers thick, thin-walled, with more or less polygonal to isodiametric cells. The layer is 58 - 180 microns thick and consists of chloroplasts. The size of the pallisade and mesophyll cells decreases towards the leaf margins and the layers become quite distinct. The collenchyma layer is only one cell-layer thick, discontinuous and is confined to the midrib portion of the leaf. The cells are hexagonal, angularly thickened or lignified. The number of vascular bundles differs in different populations and is either one, three or five. The vascular bundles are collateral and semicircular in outline with a large median vascular bundle, and the rest diminishing in size towards the leaf margins. Cavities are also common around the vascular bundles as secretory bundles. As in petioles, the xylem tissue is formed towards the adaxial side of the leaf and the vessels are axially arranged (Figs 17 B & 18 B). In rare cases, the fibres form a continuous layer around the vascular bundles but commonly these are found laterally occupying peripheral positions and in cross-section they appear as caps on top of xylem and phloem tissues. The xylem vessel diameter ranges between 10 and 27.5 microns (Table 5). The parenchyma cells surrounding the vascular bundles are very thin-walled, isodiametric to polygonal in outline, and nucleated, devoid of chloroplasts and, therefore, of no significance as a meristematic or photosynthetic tissue.

4.3.3. Nodal Anatomy

A study of nodes from free-hand sections and anatomical sections revealed the presence of a single gap, one median leaf trace with four small rib traces, two on each side (Fig. 19 A). The vascular bundles are collateral and semi-circular in outline. The nodal pattern in *Plectocephalus varians* is, therefore, unilacunar.

The evolutionary status of different nodal types in angiosperms has been the subject of considerable interest. Following an extensive survey of angiosperm taxa, Sehgal and Paliwal (1973) concluded that the tri-lacunar node is the most primitive node organization and that reductions and amplifications of this basic condition resulted in uni-lacunar and multi-lacunar conditions. Therefore, *P. varians* with its uni-lacunar node appears to be amongst the advanced members of the angiosperms.

4.3.4. Stem Anatomy

4.3.4.1. Epidermis

In *Plectocephalus varians* the epidermal layer is entirely uniseriate measuring between 17.5 and 26.25 microns and comprises of irregularly shaped cells of varying sizes. The cells are isodiametric, rectangular or transversely elongated in outline, and are more or less one and a half times as wide as long (Fig. 19 B). Bullate cells are also common in some cross sections. The outer periclinal walls are curved or undulate, heavily thickened, measuring up to 3.75 microns thick. The anticlinal walls are straight or sinuous and they are much more elongated when compared to the periclinal walls and are about 2.5 microns thick (Fig. 19 B). In most stems, multicellular, non-glandular, uniseriate trichomes are evident.

4.3.4.2. Collenchyma

The collenchyma tissue is located directly beneath the epidermis and comprises of 2-4 layers of cells, and is 25-45 microns thick. Frequently it forms a continuous layer around the circumference of the axis. According to Esau (1977), the peripheral position of collenchyma in stems is highly characteristic. The collenchyma tissue consists of thick-walled cells and is regarded as a supporting tissue in young stems. However, in some cross-sections the collenchyma layer is discontinuous and is confined to only some portions of the stem (see C in Fig. 19 B). Where the layer is discontinuous, there are chlorenchyma cells just below the epidermis (see CH in Fig. 19 B). Generally in most cross-sections the collenchyma cells are pentagonal or hexagonal with angular thickening. Size-wise the collenchyma cells are the smallest compared to other cortical cells (Fig. 19 B). In some cases, inter-cellular spaces are also common between the chlorenchyma cells.

4.3.4.3. Cortical Parenchyma

The cortical parenchyma comprises of more or less isodiametric thin-walled cells and is 4-7 cell-layers thick. The cells vary in diameter from 20-57.5 microns (see CP in Fig. 19 B). In most cases the increase in size towards the pith except those cells surrounding the vascular tissue which have been referred to as collenchymatous-parenchyma by Esau (1977). Depending on the level of development of the plant, the cortex may be fully or partially photosynthetic. In young stems, the entire cortex was found to be photosynthetic, but in older stems the cortical parenchyma were enucleated, devoid of chloroplasts and therefore non-functional.

4.3.4.4. Pith Parenchyma

The pith parenchyma are 8 - 12 cell-layers thick, isodiametric or spherical in outline and increase in size towards the pith centre. The cells are characteristically thin-walled, devoid of nuclei and chloroplasts with inter-cellular spaces and measure between 36.25 and 117.5 microns in diameter. In some transverse sections, the pith cells were crushed to form a hollow-cylinder, whereas in others the pith cells were intact (Fig. 19 D). Since the anatomy was done on materials in which the maturity status could not be ascertained, then it would be quite wrong to draw any conclusions on the above findings as regards the condition of the pith. However, according to Yohannes (1988), the intactness of the pith cells has an ecological significance where there is water stress and, therefore, it serves as a mechanism for water storage. Sections from populations from Arssi represented by the collection Lyaruu H33 which is derived from a more or less dry scrubland vegetation , had intact pith cells (Fig. 20 B). Populations from Menagesha Forest, represented by the collection Lyaruu H21 and where there is a lot of precipitation, had disintegrated pith cells (Fig. 16 D).

4.3.4.5. Vascular Tissue

The vascular bundles are collateral, semi-circular in transverse section with the phloem formed abaxial to the xylem. Both pericyclic and xylary fibres are common forming the bundle caps (see F in Fig. 19 C). The pericyclic fibres form a crescent-shaped cap on the pericyclic regions of the vascular bundles. This is a distinctive character among the Compositae according to Metcalfe and Chalk (1950). The pericyclic layer measures between 90 and 112.5 microns thick, while the xylary fibre layer is only 60-72.5 microns. In well-matured stems, the pericyclic fibres tend to form a continuous layer around the circumference of the axis (Figs. 16 C & 17 C). The fibres are scelenchymatous with hexagonal cells, secondarily thickened and generally the caps around the vascular bundles are well developed in mature stems than in young stems (Fig. 17 B & C). Esau (1977) observed that the role of collenchyma as a supporting tissue in stems becomes less important because of the development of sclerenchyma in the deeper parts of the stem or petiole. Moreover, in stems with secondary thickening, the xylem becomes the chief supporting tissue because of the predominance of cells with lignified secondary walls. The xylem vessels are axially arranged in rows, sometimes bordering each other in an oblique manner or stacked on top of each other (Fig. 20 A). The vessels are more or less isodiametric or pentagonal to hexagonal with lignified secondary walls and measure between 12.5 and 27.5 microns in diameter. The parenchyma cells separate the vascular bundles and consist of 4-6 layers of ellipsoid or transversely elongated cells (Figs. 19 C & 20 C). Some of the cells have chloroplasts and are generally thin-walled with length almost twice that of the width. The cells increase in size towards the pith and measure between 25 and 48.75 microns in diameter.

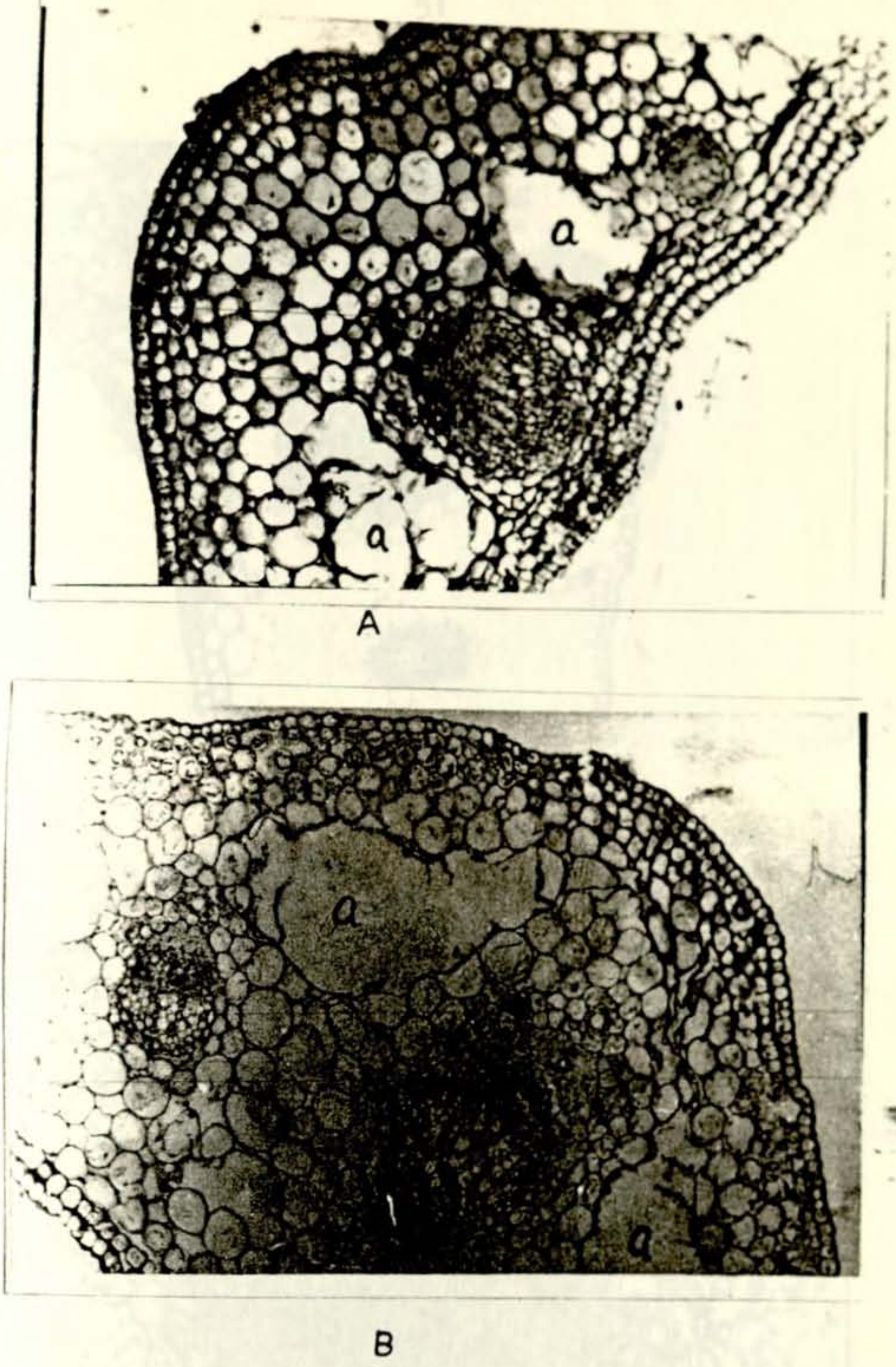
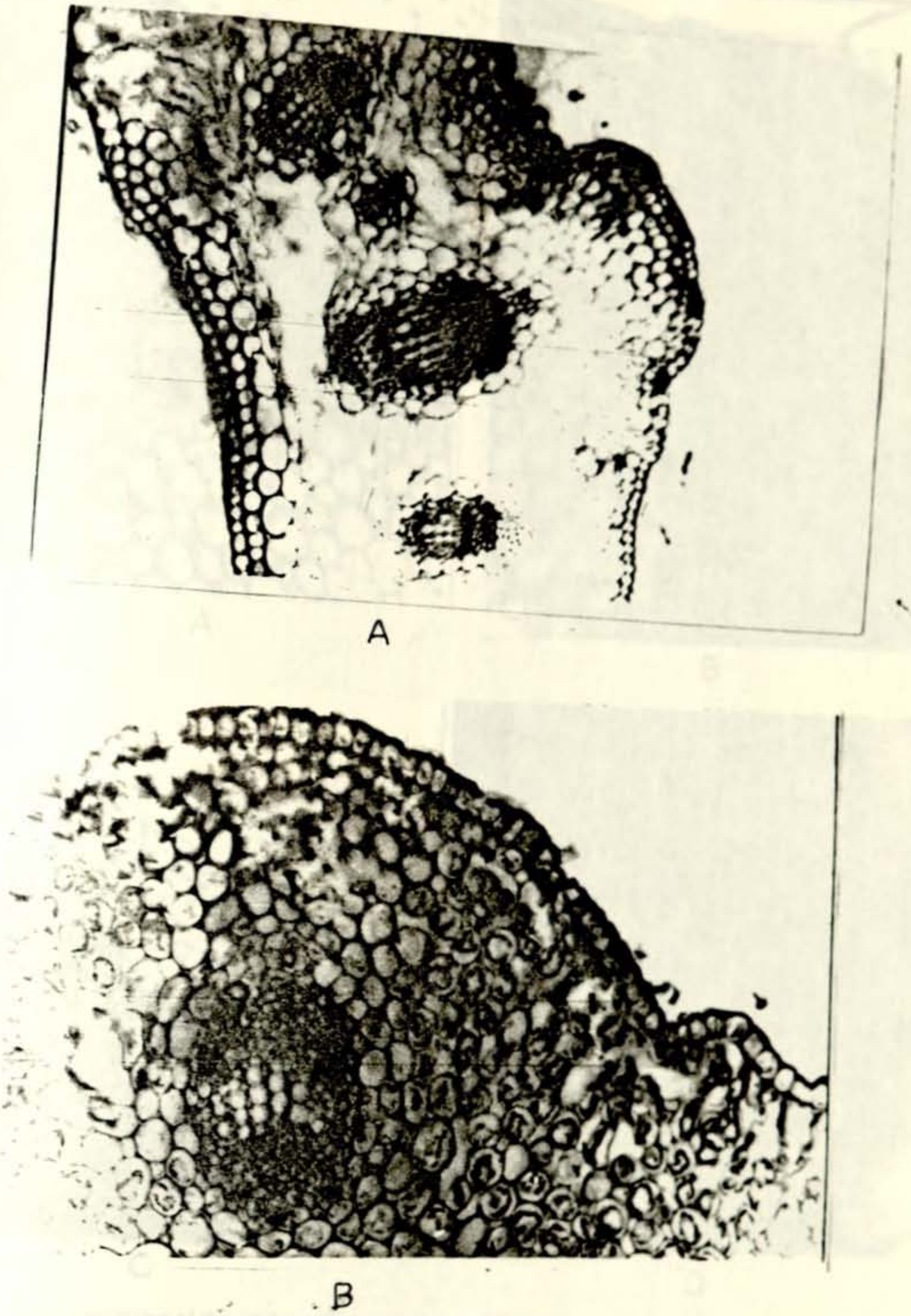


Fig.17 - Cross-sections of petioles in *P. varians* showing the midrib region with secretory canals (a), collenchyma layer (b), phloem tissue (p), xylem tissue (x) and sclerenchymatous tissue (s). A from Lyaruu H 12, x 25. B from Lyaruu H 33 x 25.



18 - Transverse sections of leaves of *P. varians* depicting uniseriate epidermis (A) and differential thickening of collenchyma tissue (B). A from Lyaruu H 09 x 25. B from Lyaruu H 21 x 25.

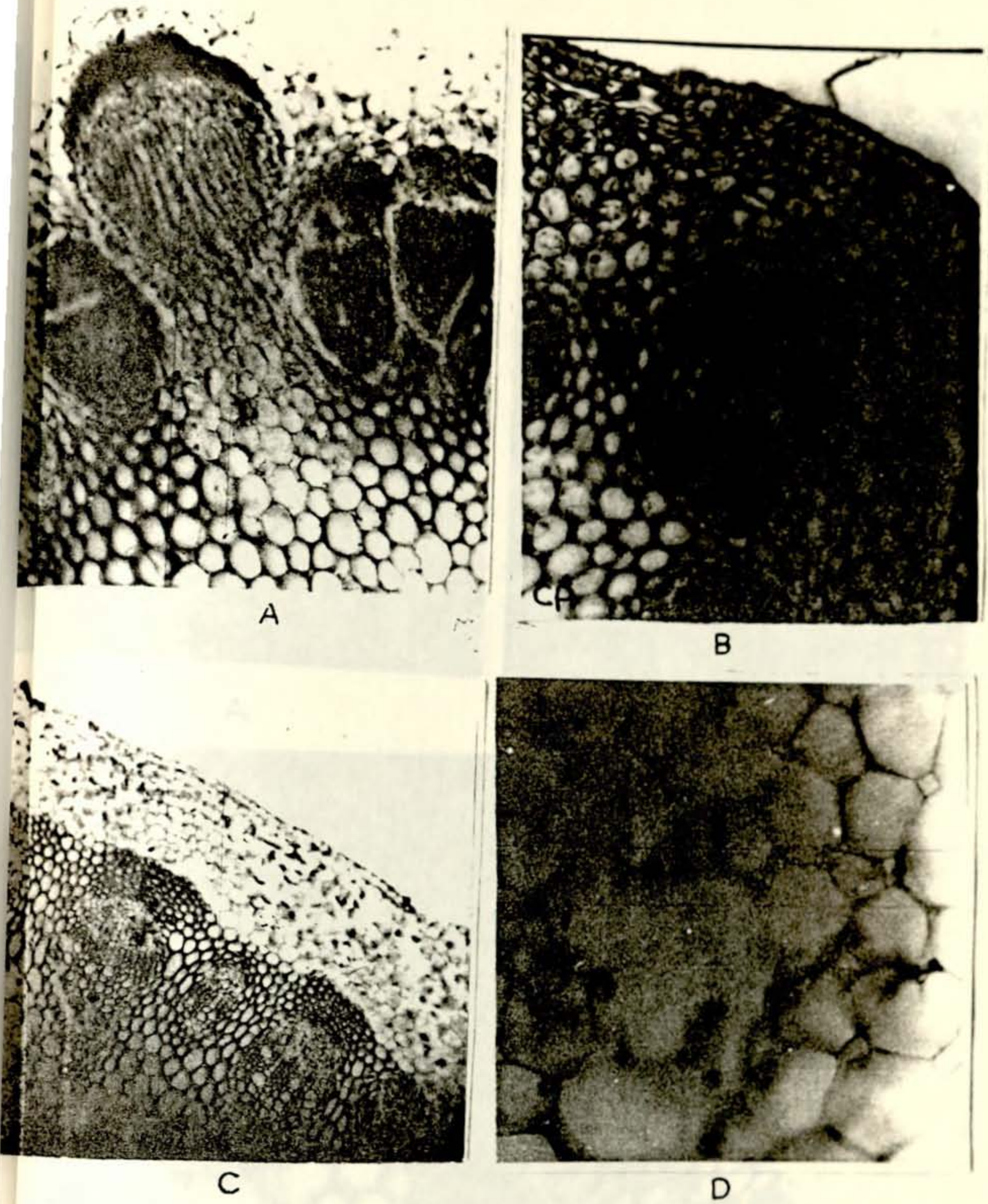
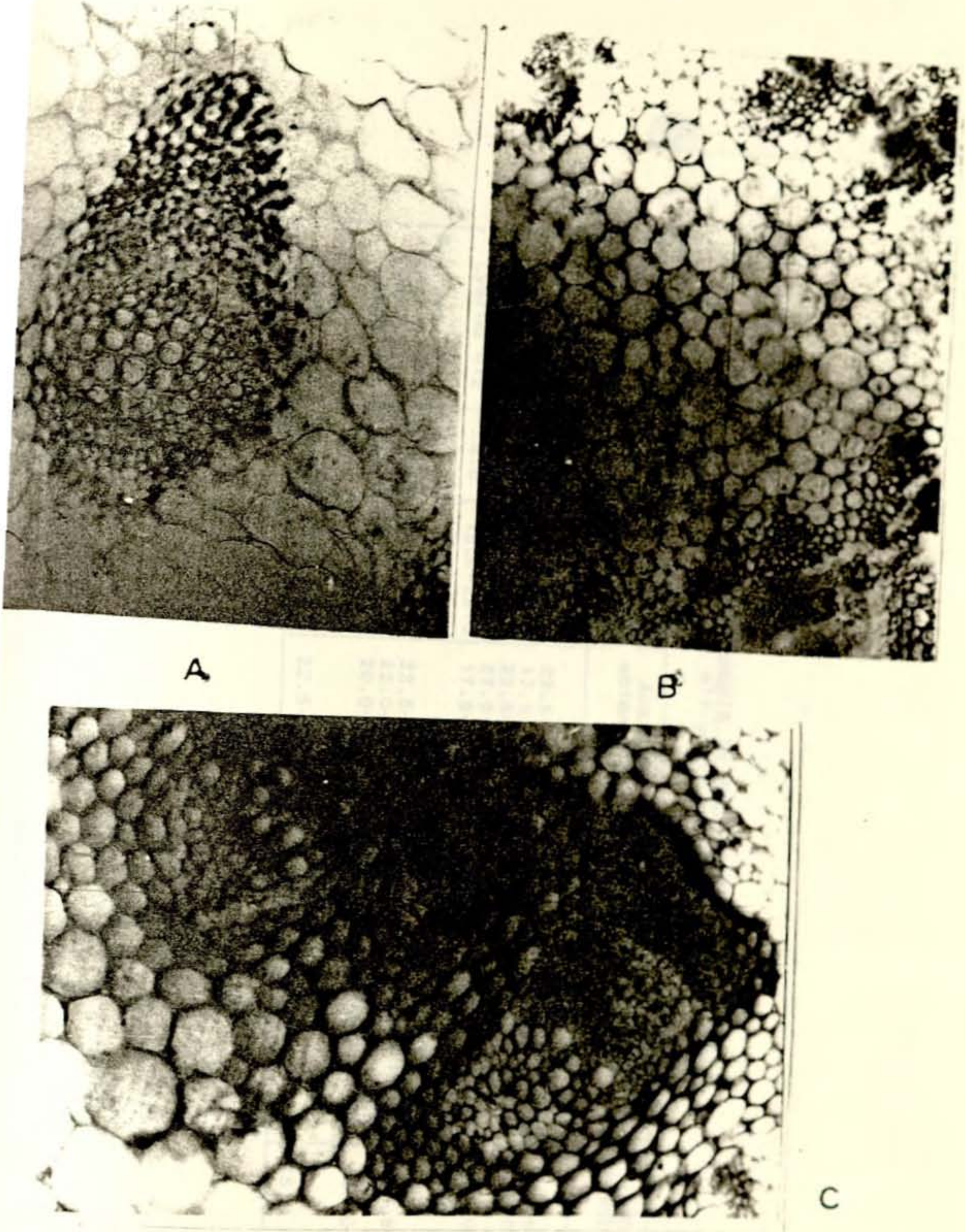


Fig.19 - Cross-sections of the nodal region and stems of *P. varians* A: A section of a node depicting a median and four lateral bundles x 25 (from Lyaruu H 21), B-C: Stem sections - note the arrangement of parenchyma cells around the vascular bundles and the chlorenchyma cells (ch) x 25 (from Lyaruu H 12), D Pith parenchyma x 50 (from Lyaruu H 21).



ig.20 - Cross-sections of stems of *P. varians*. A:A vascular bundle with axially arranged vessels (from Lyaruu H 52). B: Intact pith parenchyma (from Lyaruu H 33). All x 50. C: Elongated parenchyma cells around the vascular bundles x 50 (from Lyaruu H 21).

Table 4

LEAF MEASUREMENTS IN PLECTOCEPHALUS VARIANS
(all units in microns)

Province & Voucher specimen	Midrib	Xylem Vessel diameter	Adaxial epidermis	Abaxial epidermis	Palisade layer	Spongy mesophyll
1. Shoa						
Lyaruu H12	830	10.0-20.0	22.5-40.0	22.5-30.0	175.0-197.5	150.0-170.0
Lyaruu H12	890	12.5-17.5	17.5-35.0	20.0-27.5	117.5-120.0	142.0-150.0
Lyaruu H09	850	20.0-25.0	22.5-27.5	15.0-27.5	-	-
Lyaruu H21	1310	12.5-20.0	27.5-35.5	12.5-37.5	180.0-220.0	167.0-180.0
Lyaruu H12	810	15.0-22.5	17.5-27.5	15.0-22.5	100.0-122.5	60.0 - 75.0
2. Arssi						
Lyaruu H33	1120	15.0-22.5	22.5-40.0	15.0-27.5	157.5-192.5	112.5-122.5
Lyaruu H36	760	10.0-17.5	22.0-38.0	15.0-22.5	60.0 - 72.0	58.0 - 67.5
Lyaruu H36	950	17.5-27.5	20.0-52.5	22.5-37.5	150.0-237.5	135.0-180.0
3. Bale						
Lyaruu H52	740	10.0-20.0	22.5-27.5	12.5-20.0	85.0 -112.5	75.0 - 87.5

Table 5

Mesurements (in microns) of anatomical features in petioles of P.varians

Locality, Specimen code	Adaxial epidermis	Abaxial epidermis	Diameter collenchyma	Diameter parenchyma	Xylem vessels
a) Arssi					
Petiole (1)	15.0-25.0	15.0-20.0	45.0-50.0	35.062.50	8.75-12.50
Petiole (2)	15.0-20.0	11.25-13.75	16.25-22.50	32.50-67.50	20.0-28.75
Petiole (4)	22.5-32.50	23.75-37.50	-	25.0-52.50	22.50-31.25
b) Shoa					
Petiole (3)	20.0-33.75	15.0-20.0	23.75-28.75	45.0-65.0	17.5-22.50
Petiole (5)	20.0-57.50	25.0-47.50	25.0-37.50	35.0-70.0	15.0-22.50
Petiole (6)	30.0-37.50	17.5-25.0	27.50-57.50	47.50-81.25	12.50-17.50

4.4. PHYTOGEOGRAPHY

Plectocephalus is a genus with four species and is known to have disjunct distribution. One species, *P. chilensis* is known only to occur in Chile, whereas *P americanus* is found in Mexico, and in some parts in southern USA and Chile. *P. tweediei* is known to occur in Argentina. *Plectocephalus varians* is an endemic plant, found in the Ethiopian highlands (Jeffrey 1968). The Ethiopian highlands make up part of the Afromontane archipelago-like regional centre of endemism (White 1983). Friis (1983), mapped local centres of endemism in the Ethiopian highlands. These are:

1) A southwestern centre of endemism where the phytochorion is mainly characterized by forest species.

2) A central plateau centre of endemism, which can be regarded as a transitional zone in the sense of White (1983).

3) An eastern escarpment, southeastern slope and Somalian mountain centre of endemism.

4) A high mountain centre of endemism.

The Afromontane region is the most important centre of endemism for many plants such as *Helichrysum*, *Euryops* (Hedberg 1957), *Bidens* (Mesfin 1984), *Echinops* (Mesfin 1990), *Maytenus* (Sebsebe 1985) and *Justicia* sect. *Ansellia* (Ensermu 1990). It is also an important centre for *Justicia* sect. *Harnieria* (Hedren 1989).

P. varians is found in the central, southern and southwestern Ethiopian highlands and in the high altitudes on the Simien mountains - northern Ethiopia. Also it is common in south eastern Ethiopia. It is found at high altitudes on relatively shallow soils, mostly overlying limestone, in east Hararge, where the soils are deep and very poor in nutrients, and in Harenna forest in Bale. The plant is also common in the dry *Juniperus* forests of Sidamo which occur at altitudes between 1500 m and 2000 m with an average rainfall of 400 mm to 700 mm distributed bimodally (Mesfin Wolde Mariam 1970). The plant has both wide altitudinal and latitudinal distribution. It is found between 1900 m and 3600 m, and between 5° 33'N - 13° 15 'N and 36° 37' E - 42° 20' E.

4.5 TAXONOMY

4.5.1. PLECTOCEPHALUS versus CENTAUREA - a comparison

A synopsis between *Plectocephalus* and *Centaurea* could not be provided as there is a great overlap in the range of variation of characters and character states. Therefore the following comparison is made between them, using characters derived from representative samples and the literature in order to portray the similarities and differences.

Centaurea and *Plectocephalus* are taxa that have many unifying characters. Hence it is difficult to have a straightforward key that would enable the separation of the two taxa. The north east tropical Africa taxa can easily be separated based on the involucral bract appendages and the marginal florets. The gross morphology and the involucral bracts among the studied Latin American species of *Centaurea* and *Plectocephalus* are essentially the same. However, most members of *Centaurea* are shrubby or suffrutescent whereas in *Plectocephalus* the herbaceous condition is dominant. Some few characters can be employed to separate the two taxa - i.e. the achenial features, phyllaries and the pollen morphology. In both taxa the pappus is pluriseriate. In *Centaurea* the pappus is heterogeneous and the series tend to become progressively longer towards the centre whereas in *Plectocephalus* the series are homogeneous. The pappus is shorter than or at most equalling the achene in *Centaurea* and is sometimes quickly caducous or may be entirely absent. In *Plectocephalus* the achenes are smaller with a smooth surface sculpture and few scattered hairs (Fig. 12 C). In *Plectocephalus* the surface is crested with some few scattered hairs and in all studied taxa the surface is ribbed (Fig. 12A, B, D). Among the *Plectocephalus* species studied, the pollen is spiny and thick-walled i.e. *Serratula*-

type whereas in *Centaurea* the pollen is spiny to slightly spiny - i.e. *Centaurium*- type, *Jacea*- type, or *Scabiosa*- type and in rare cases the pollen grains are smooth and thick - walled, i.e. *Dealbata*-type as described by Jeffrey (1968). In *Plectocephalus* the mode of articulation in the fruits is entirely basal- lateral (Fig. 12 A, B, D) but in *Centaurea* the articulation is both lateral and basal - lateral (Fig. 12 C; Wagenitz in Davis 1975).

In this study *Centaurea tweediei* is tentatively treated as *Plectocephalus tweediei*. The taxon is found to share most of its morphologic characters with *Plectocephalus*. Moreover, in the herbarium sheets it has been transferred from *Centaurea* to *Plectocephalus*. From recent communication with Jeffrey (in litt.), *Centaurea tweediei* H. & Arn.is considered to belong to *Cheirolophus* Cass. and not to *Plectocephalus*. But as only a segment of the population has been studied and the author has no knowledge of *Cheirolophus*, the issue in question cannot be solved here.

4.5.2. PLECTOCEPHALUS *D. DON* (1830)

Annual or perennial herb, rarely small shrub, with or without woody rootstock, sometimes tap root common, often tomentose, scabrous to hirsute, with non-glandular uniseriate hairs, rarely glabrous. Stem terete to striate-sulcate, usually variously branched. Leaves simple, scabrous rarely glabrous, alternate or distichous, sometimes all radical, petiolate or sessile, pinnatifid or pinnatipartite simple to deeply and irregularly 3-7 pinnatisect; margins of various forms - entire, dentate to widely dentate, serrate or variously incised, lamina or segments ovate , lanceolate, spathulate to oval - spathulate or oblanceolate; apex acute, obtuse rarely mucronate. Capitula erect at anthesis, heterogamous, single-headed, radiant; peduncle tomentose or pubescent, rarely glabrous, terete to striate - sulcate. Phyllaries 5 - 7 seriate, imbricate, rigid. ovate lanceolate, linear-lanceolate; appendages, scarious, coriaceous or chartaceous, variable in form, 3-11 -striated; apex ending with rigid or reflexed spine- like structures, ciliated or glabrous, sometimes spines absent. Ray florets neuter, commonly purple, rarely mauve or yellow, funnel-shaped; nervation usually 5; lobes irregularly incised; apex acute. Disc florets hermaphrodite, yellow or purple ,rarely white; corolla 5-lobed, campanulate or bell-shaped, glabrous and 5-nerved. Anthers brown to black ,dehiscing introrsely; base sagittate; apex ovate - triangular. Style swollen at the base, bifurcate at the apex, slightly swollen below the point of bifurcation, pilose ,arms usually exserted at anthesis. Achenes black, rarely brown or grey; laterally compressed; glabrescent ,rarely pubescent; articulation basal or laterally at the base. Pappus silvery white, apically inserted, pluriseriate, homogeneously elongated, setaceous with or without hairs, caducous or rarely persistent.

The genus *Plectocephalus* consists of four species which are disjunctly distributed. One species is endemic to the Ethiopian highlands and the remaining three species occur in Latin America, Mexico and southern USA (Jeffrey, 1968).

A key to distinguish the Latin American species of *Plectocephalus* from the Ethiopian species is provided in Appendix 3.

4.5.3. PLECTOCEPHALUS VARIANS (A. Rich) C. Jeffrey ex Cufodontis

Plectocephalus varians (A. Rich.) C. Jeffrey ex Cuf. in Senck. Biol. 47: (1966); Cufodontis, Enum; Pl. Aeth. 1177(1967). Types: Ethiopia Quartin - Dillon & A. Petit (P. syntypes, n.v.).

Perennial herb with erect, decumbent, prostrate or semi-prostrate stem; stem (18-) 20 - 100 - (-150) cm high, 1.5-6.0 cm in diameter, terete to striate - sulcate rarely branching from the base, with a woody rootstock. The indumentum is variable, i.e. from woolly-white or brownish-grey tomentum to glabrous; hairs non-glandular and uniseriate. Leaves simple, alternate or distichous, sessile, only those originating from the rootstock petiolate, sub-amplexicaule, auriculate or exauriculate; lamina 3.2 -19.3 x 0.6-5.9 cm, old leaves ovate- oblanceolate, spathulate or oval-spathulate, young leaves entire; lanceolate, scabrid especially on the adaxial surface, pubescent, tomentose, rarely glabrous; margins entire, dentate to widely dentate, less commonly serrate; apex acute, acuminate or mucronate; base sessile, attenuate or decurrent. Capitula erect at anthesis, heterogamous 1.6 - 3.1 x 3.5 - 10.0 cm; involucre cylindric or radiant, campanulate or turbinate. Peduncle and receptacle base tomentose or pubescent, terete to striate - sulcate, peduncle (7.0-)11 - 296 mm long. Phyllaries 5-7-seriate, yellowish-brown, greenish-yellow or green, imbricate, 3-to 7-nerved, appendages with reflexed yellowish spine-like structures, coriaceous or chartaceous, outer surface densely tomentose, inner surface glabrous. Outermost series ovate to lanceolate, 4.0 - 11.0 x 1.5 - 3.0 mm., greenish yellow. Middle phyllaries 8.0 - 21.0 x 2.0 - 5.0 mm., lanceolate to oblanceolate, ovate to narrowly obovate, or linear lanceolate, appendages fewer than in the outermost series. Innermost series 17.0 - 21.0 x 1.0 - 2.5 mm., more or less linear to linear lanceolate, reflexed, spine - like structures ciliated, sometimes glabrous. Ray florets neuter, campanulate, purple, rarely mauve, 25 - 58 mm long: apex 5 (-4) -fid, acute; glabrous, 5 -nerved, lobes deeply incised. Disc florets tubular, campanulate: yellowish or purple, less commonly white, (11.0-) 15 - 35 x (0.75-) 1.0 - 1.5 mm, hermaphroditic; corolla 5-lobed, glabrous, 5-nerved, apex acute or triangular ovate; style bulbous (10.5-) 14.5 - 29.5 mm, bifid at the apex, arms of more or less equal length, rarely more than 0.5 mm long; style swollen below the point of bifurcation, pilose, arms usually exserted at anthesis. Anthers 5, (3.0-) 4.0 - 6.5 mm long; brown or black, less commonly yellow; base sagittate, tailed, syngenesious and dehisce introrsely. Filaments 6.0 -12 (-13.0) mm long. puberulent. Achenes black, sometimes brown or grey, ,2 - 4 mm. long, elliptic-oblong, laterally compressed, glabrescent, rarely pubescent, crested, 3 main ridges (ribs) prominent in the articulation side, articulation zone rib free, yellowish, articulation type basal- lateral (Fig. 12 D).

Pappus 2 - 10 mm long, pluriseriate, silvery - white, setaceous, barbellate, apically inserted (=comose), homogeneously elongated, caducous, rarely persistent.

Pollen grains radially symmetrical, isopolar or spherical, (33-) 38 - 50 (-54) microns, echinolophate, tricolporate, with lalongate ora; tectum ornamented with regular or irregular micro -punctae. Fig.1 A, B; Fig. 2; Fig. 8 ; Fig 4 A-D; Fig. 8 A-G; Appendices 1,2; Fig. 21; Fig. 22; Fig. 23.

4.5.4. Variations in P. VARIANS

Due to the diversified habitats occupied by *P. varians*, a number of vegetative and floral differences that enable the categorization of the species into two distinct populations exist. The observed phenotypic variations are correlated with environmental and ecological parameters. The two categories are forest populations with certain plants occurring at high elevations and grassland populations with some plants occurring in lowlands. Although *P. varians* is widely distributed in Ethiopia, the taxon is found to constitute a single taxonomic species . (Figs. 23 & 24), hence authenticating the previously established synonymy by Cufodontis (1966) and Jeffrey (1968). The continuous variation observed in the length of the disc florets and leaf length to width ratio among the specimens studied (Fig. 25) substantiates further the existence of a single taxonomic species within *Plectocephalus varians*.

Forest populations are taller than grassland populations. Whereas the forest populations can attain a maximum height of 1.5 m, the grassland plants can only attain a height of 0.6 m. The height difference among the two populations could be attributed to light being limiting and therefore increased internode lengths in forest populations compared to grassland populations.

Forest populations have very broad, large, dark green -coloured leaves with prominent brochidodromous venation pattern. Grassland populations in most cases have light green small leaves, and venation is not conspicuous except in the older leaves. In addition among the forest populations, leaves are auriculate tending towards petiolate condition which is not the case for grassland populations. The indumentum for grassland populations is densely tomentose compared to forest populations. A dense hair cover may therefore, be ecologically significant. Hedberg (1964), points out that the pubescent leaves of several afroalpine and paramo species have usually been interpreted as xerophytic adaptations as observed in Giant *Senecios*. Xerophytes are, according to Warming (1909:101; cited in Hedberg 1964),"... those plants that are adapted to meet the conditions of strongest transpiration and most precarious water supply.... " Such structures which appear to enable plants to restrict transpiration are commonly called xeromorphic characters, e.g. small, leathery leaves, with much sclerenchyma, a thick cuticle, small and numerous stomata. Therefore a high degree of hairiness reflects xeromorphic condition where water is a limiting factor as opposed to forest areas where mesic conditions prevail throughout the year. A thick indumentum may evidently serve not only to reduce transpiration but also to protect the plant tissues against strong insolation (Hedberg 1964).

The variation in the number of stomata per unit area, in this case being higher among grassland populations (Table 1), is a morphological adaption to cope with xeromorphic conditions. The implications that forest populations have bigger and very dark green leaves is that, since under shade or in forests light is the limiting factor, the leaves must have high concentration of chlorophyll, the green colouring matter, to enhance maximum harvest of light, which is primary in photosynthesis. For the grassland populations, smaller and shiny leaves are equally efficient as dense pubescence in reflecting much of the incident radiation (Hedberg 1964).

The size of the capitula is biggest and well developed in those plants found in forests or under shade as compared to grassland populations. The colour of the ray florets in grassland and open area populations is always purple, whereas among the forest species, the ligulate flowers are yellow or mauve. The significance of this observation is not clear. The two population groups exhibit striking differences in their pollen morphology. The grassland populations tend to have pollen grains with much longer spines compared to forest populations (Table 2). The exine layer is also thicker in the pollen grains derived from grassland populations as compared to those from the forest. Some forest plants (represented by W. Burger 1011) have very small spines. These are correctly referred to as spinules as they do not exceed 3.0 microns in length (Erdtman 1969). However , even plants found growing in the same ecological niche have some variations. This is substantiated by the fact that plants collected in Entoto mountains in *Eucalyptus* plantations showed extreme differences in height and capitula sizes. The plants observed in well developed, humic, black soils in gorges attained a height of 1.2 whereas those found in undeveloped red soils in rocky outcrops rarely exceeded 0.4 m. The difference in size could be attributed to the soil type and moisture gradients where the plants were growing.

4.5.5. Distribution of P. VARIANS

Plectocephalus varians is endemic to Ethiopia (Jeffrey 1968), occupying mainly the highlands and the central plateau. Its distribution is widespread being common in 10 out of 16 administrative regions.

The plant is common within latitude 5° 33' N - 13° 15' N and longitudes 36° 37' E - 42° 20' E. Its distribution in Ethiopia is as follows: Arssi (Chilalo Awraja): Wellega (Amarti Valley); Keffa (Mt. Maigudo), Gamu-Gofa(Ghuge Highlands); Gojjam (Choke Mts.; Debra Markos); Sidamo (Arero Awraja - Megada forest); Hararge (Gara Mulata Mt.; Kondudo Mts.); Gonder (Simien Awraja); Bale (Harenna forest, Genale Awraja, Mendoyu Awraja); Shoa (Menagesha Awraja - forest; Jibat Mecha Awraja, Mt. Wuchacha, Gafaresa, Bole valley, Mt. Zuqualla, Solulta village, Wolmera Woreda (Fig. 21).

4.5.6. Ecology of P. VARIANS

P. varians occupies diversified habitats - open grasslands, dry evergreen forests, dry scrubland, gorges and roadside thickets, well drained hillsides, cloudy mosit forests, cultivated land, riverine, water logged areas, remnant montane forest, and long forest margins. In different habitats, the plant is found growing in association with *Pennisetum glabrum* Hochst. ex Steudel; *Heteromorpha trifoliata* (Wendl). Eclk. & Zeyh.; *Ekebergia capensis* (Fres.) A.Rich., *Olea* spp.; *Croton macrostachyus* Hochst. ex A. Rich. *Erica arborea*. L.; *Hypericum revolutum* (Forsk.) Vahl.; *Discopodium penninervum* Hochst.; *Myrisine africana* L.; *Jasminum stans* Pax; *Rosa abyssinica* Lindley; *Rubus* spp.;*Maytenus putterlickioides* (Loes.) Exell & Mendonca; *Carissa edulis* (Forsk.) Vahl.; *Eucalyptus globulus* Labill.; *Myrica salicifolia* Hochst. ex A. Rich. and *Maesa lanceolata* Forsk.

In water logged areas the plant is found growing in association with sedges, whereas in cultivated areas commonly *Trifolium* spp. form the cushion. There is no pronounced trend in soil preference for the plant. The plant is found growing in deep well developed humic soil, vertisols, red altisols, to weakly developed soils in a basement rock which is very poor in nutrients. The plant is also common in leached water logged soils in lowlands. The altitudinal range is 1900-3600 m.

4.5.7. Synonymy of P. VARIANS

As I was not able to obtain all the type specimens, the following list of synonymy is based on the works of Jeffrey (1968), Cufodontis (1967) and Mesfin (Unpublished Flora Manuscript).

- *Centaurea varians* A. Rich. Tent. Fl. Abyss. 1: 453 (1848); Vatke in Linnaea 39: 512 (1875); Oliv. & Hiern in Oliv. Fl. Trop. Afr. 3:436 (1877); Engl. Hochgebirgsfl. Trop. Afr.: 451 (1892).Type: Ethiopia, Ouadjerata, Quartin-Dillon et Petit s.n.(P,lectotypes, K,isolectotype, n.v.).

- *Plectocephalus abyssinicus* Boiss., Diagn., Ser. 2, 3:61(1856). Type: Ethiopia , Schimper (G. Holotype n.v.).

- *Plectocephalus cyanoides* Boiss., Diagn., Ser. 2,3 : 62 (1856). Type: Ethiopia, Schimper 519 (G. holotype n.v.).

- *Centaurea varians* A.Rich. var *macrocephala* Vatke in Linnaea 39 : 512 (1875). Type: Ethiopia, Schimper (G. holotype n.v.).

- *Centaurea abyssinica* (Boiss.) Sch. Bip. ex Oliv. & Hiern in Oliv. Fl. Trop. Afr. 3: 436 (1877); Engl. Hochgebirgsfl. Trop. Afr. : 451 (1892). Type: Ethiopia, Schimper (G. holotype n.v.).

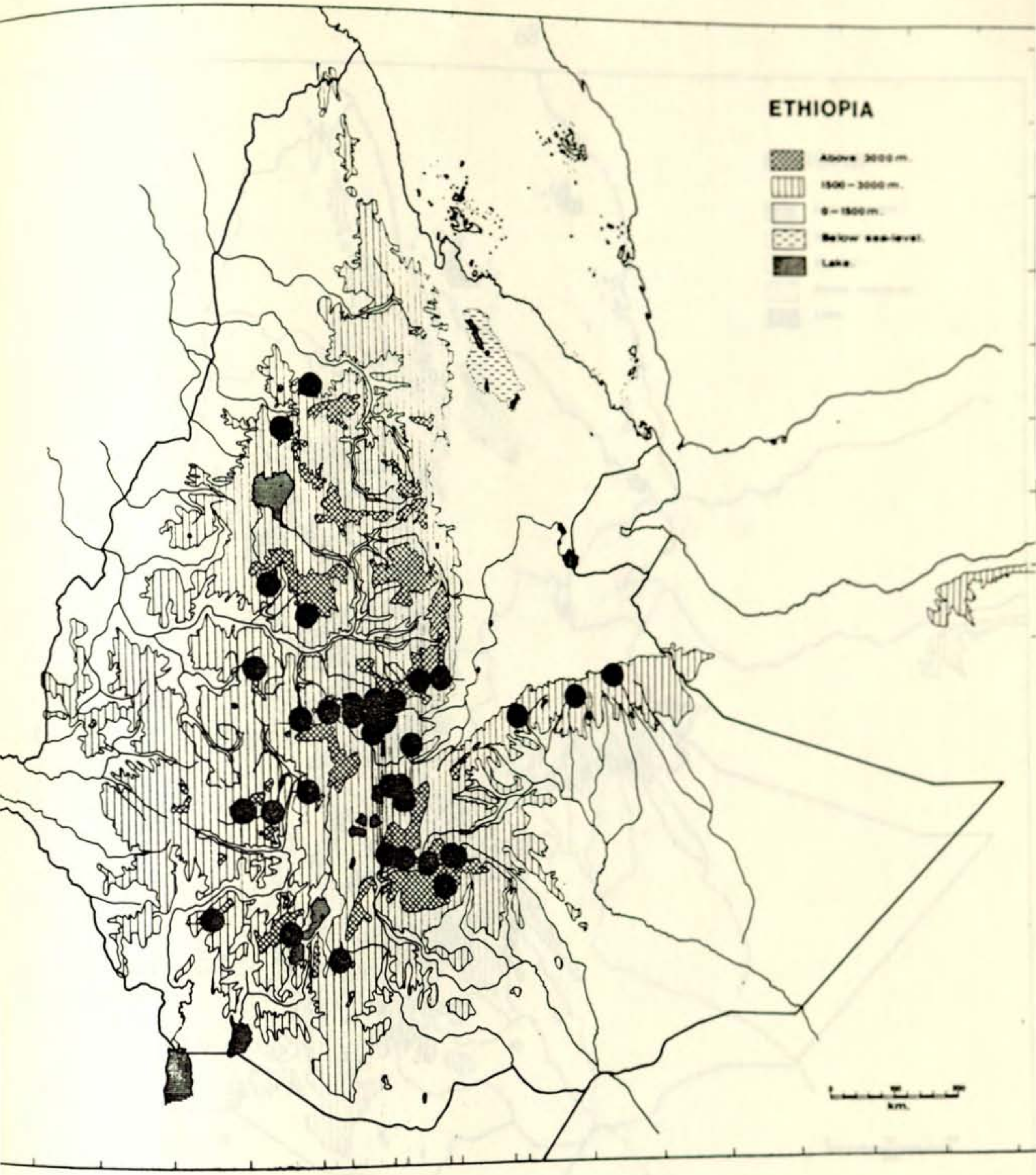


Fig.21 - Map to show the distribution of *P. varians* in Ethiopia.

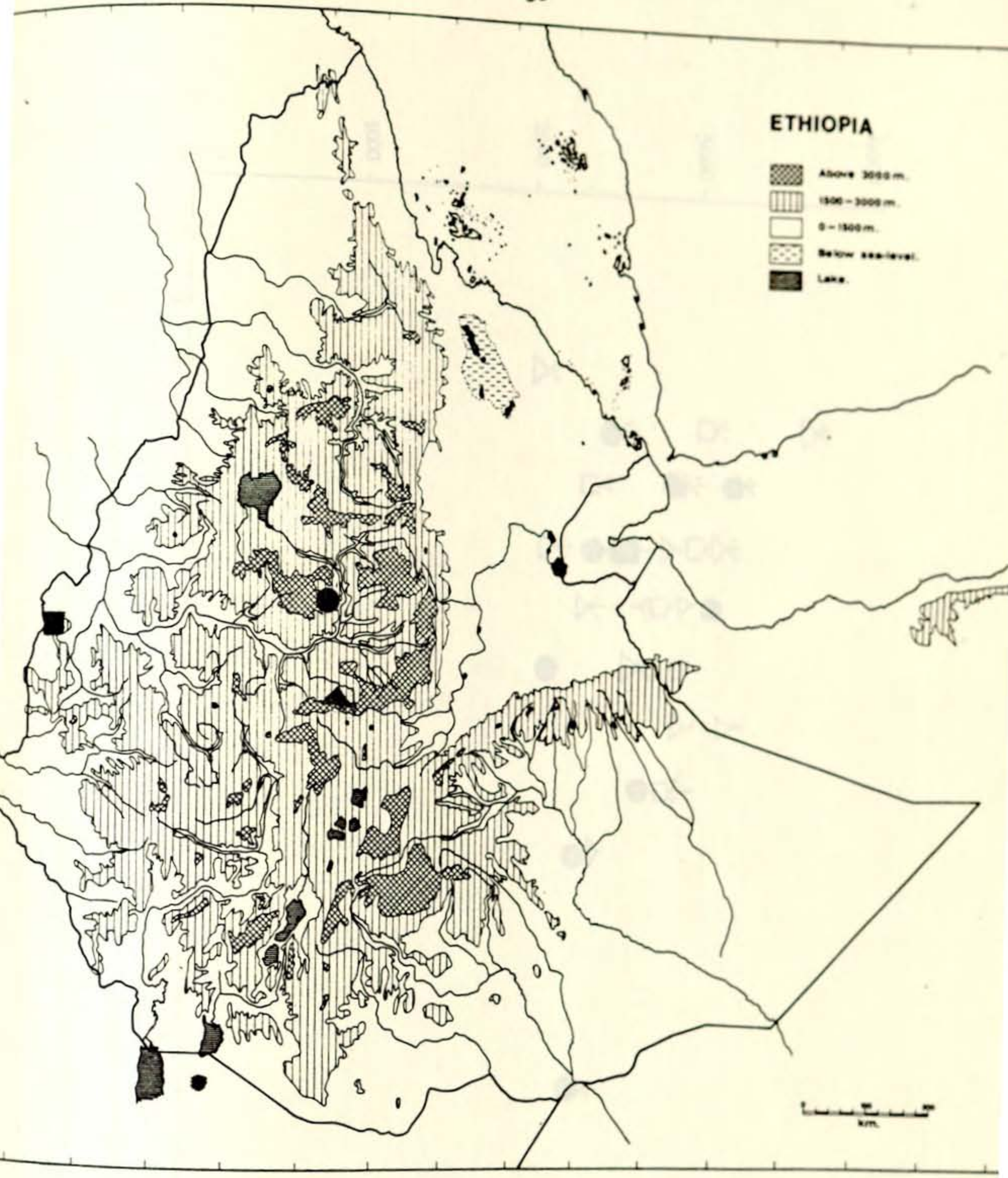


Fig.22 - Map to show the distribution of *Centaurea* in Ethiopia. *C. melitensis* is represented by ●, *C. praecox* by ■ and *C.solstitialis* by ▲.

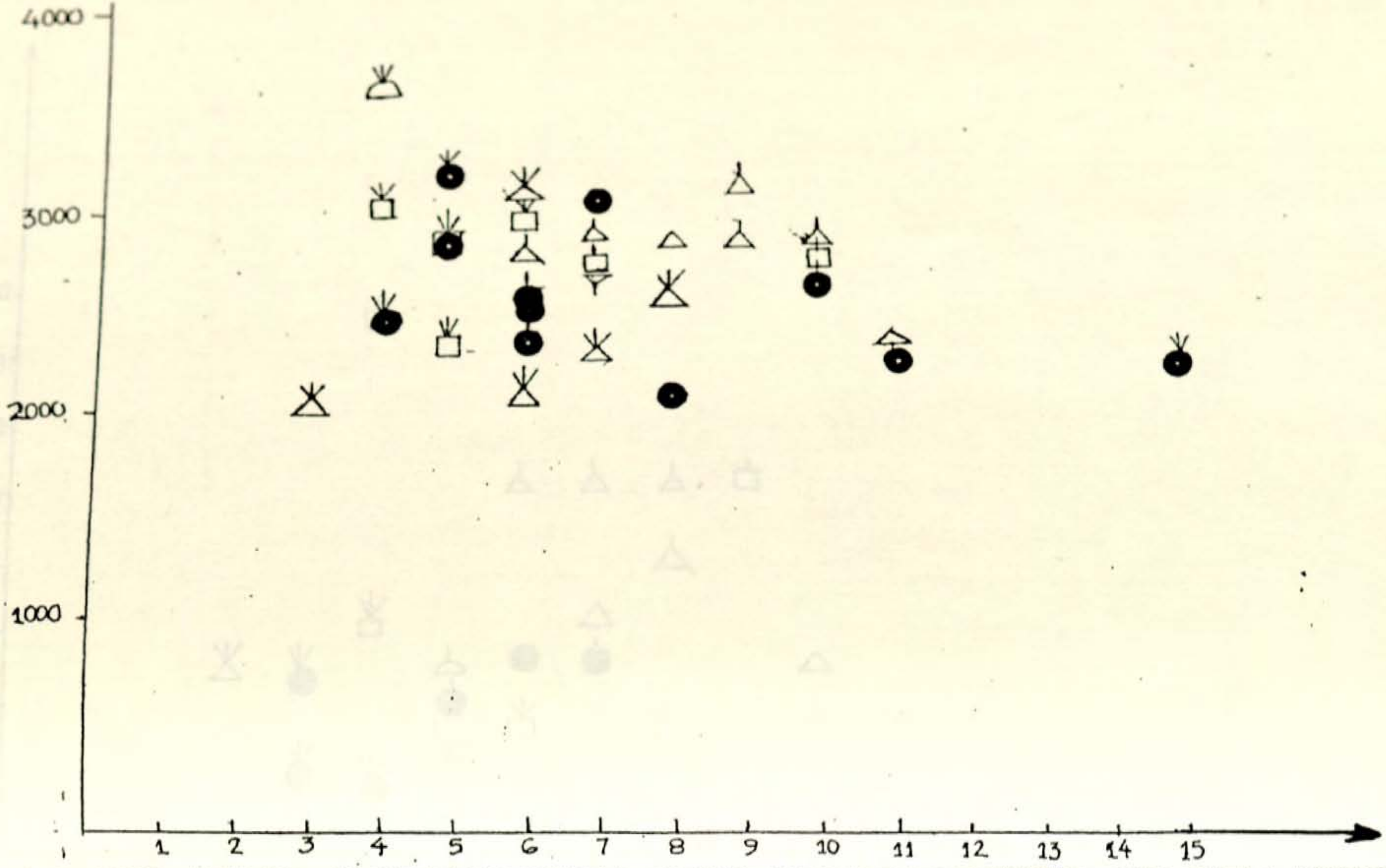


Fig. 23 - Scatter diagrams for *P. varians* - leaf length to width ratio (horizontal axis) and altitude in metres (vertical axis). For figs.23 & 24 stands for ● grassland, △forest, □scrubland and ⌓ riverine populations. Tomentoseness is indicated by three radiating lines, pubescent by 1 and

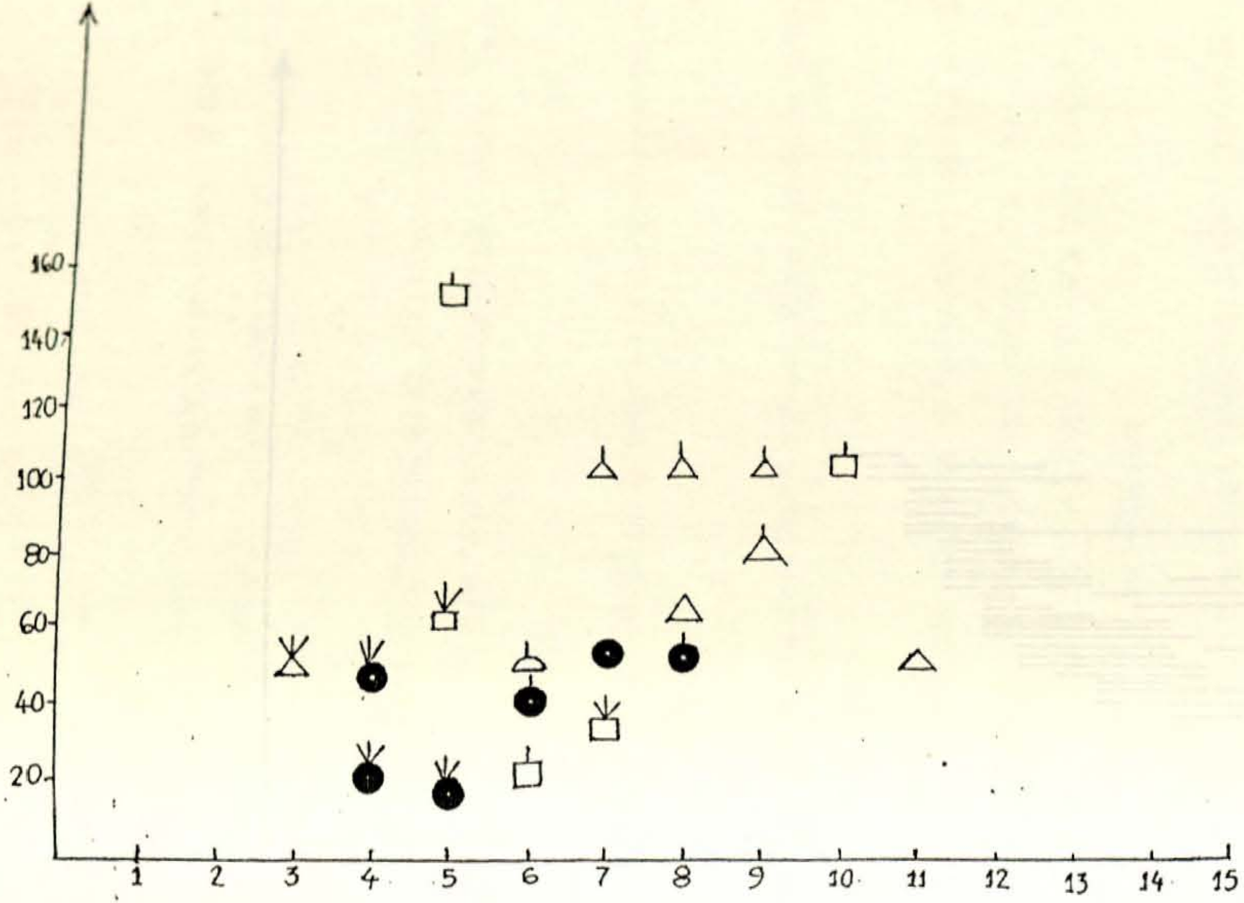


Fig.24 - Scatter diagram for *P. varians* - leaf length to width ratio (horizontal axis) and height in cm (vertical

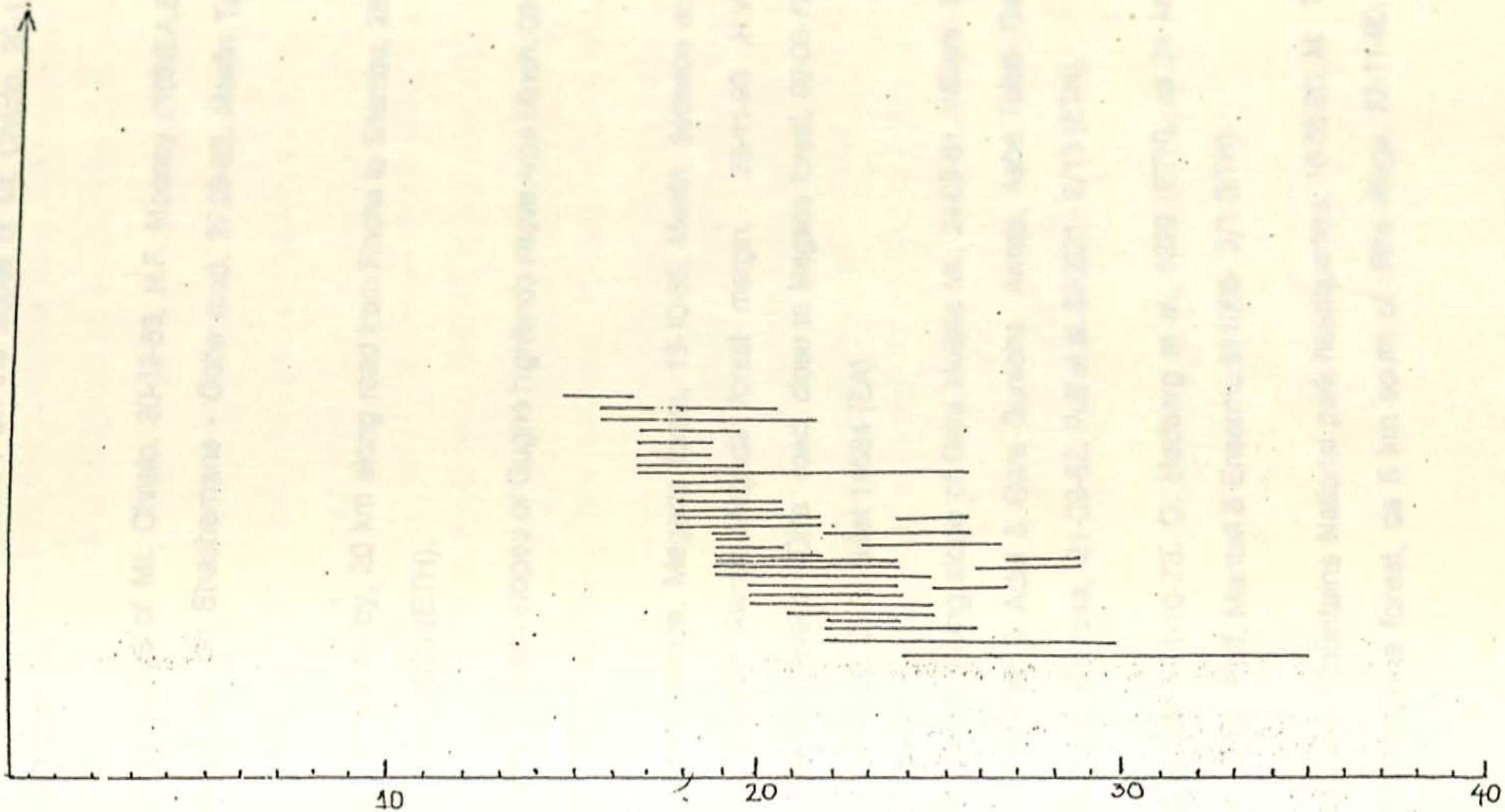


Fig. 25 - Overall variation in length of disc florets in *P. varians*. (units in mm)

SPECIMENS STUDIED

1. P. varians (A. Rich.) C. Jeffrey ex Cuf.

ARSSI : Lower Slopes of Mt. Chilalo, near Swedish mission, 9: 9.65, W.J.J.O. de Wilde et al.8004 (ETH); ASSELA : On the slopes of Mt. Chilalo, 20-11-90, H.V.M. Lyaruu H25 (ETH);

ASSELA : On slopes of Mt. Chilalo, 20-12-53, H.F. Mooney 5159(EA,ETH); Chilalo Awraja, ca 41 km on Shashemane - Goba road, 27.09-83, Mesfin Tadesse 3038 (ETH).

WELLEGA: Amarti valley, 20 km along road from Fincha to Shambu, 28-10-82, Arne Anderberg et al., 1639 (ETH).

GAMU GOFA: Eastern slopes of Gughe highlands above Arba Minch, 03-09-75 ,M.G. Gilbert et al. 465(ETH).

SIDAMO: Arero Awraja, Megada forest, 13-10-85, Mesfin, Sebsebe and Ensermu, 3586 (ETH); Arero Awraja-Megada forest margin, 23-11-90 ,H.V.M. Lyaruu H43(ETH); 90 km Yavello - Dilla road, close to Megada forest, 02-09-72, G. Aweke 547 (ETH); 03-12-52, J. B. Gillet 14584 (EA).

HARARGE: South facing slope of Gara Mullata Mt., 24-09-61, William Burger 1210 (EA,ETH); Chercher & Adal & Gara Guracha Awraja, Asbe Teferi- Gelemso road between Kuni and Bedesa, 21-09-82, Puff et al. 820921 - 2/13 (ETH).

GONDER: Simien, 14-10-73. O. Hedberg et al., 5329 (ETH); ca 24 km north of Gonder, 05-10-81, Puff, Mantell & Ensermu 811005- 3/1 (ETH).

BALE: Near Bale Mountains National park headquarters, 19-05-80, M. Thulin et al., 3844 (ETH); Harenna forest, ca 5 km south of Rira village, 22-11-90, Lyaruu H

55(ETH); Goba- Bale, 21-04-58, H.F. Mooney 7262(ETH); River Danka, Bale, 01-10-71, Tewolde 288 (ETH); Near Batu - west of Goba, 31-10-70.,M.G. & S.B. Gilbert 1939 (EA, ETH); ca 20 km. Genale Awraja- west of Dinshu, 20-11-90, H.V.M. Lyaruu H 61 (ETH); Mendoyu Awraja, 3 km south of Rira, 10-08-86, Mesfin T. 5116 (ETH).

SHOA: Menagesha Awraja, Wolmera Woreda along Addis - Ambo road 04-12-71, Sebsebe D. 118 (ETH); Solulta village ca 15 km North of Addis Ababa, 14-09-73, J.W.Ash 2078 (EA,ETH); Mt. Zuqualla, near Addis Ababa, 05-10-61. Dr. Brehme s.n. (ETH); Jibat & Mecha Awraja, West of Ghedo, 29-10-85, Sebsebe & Ensermu 1651 (ETH); Menagesha Awraja - forest 24-11-61, Dr. Brehme s.n. (ETH) ; ca 3 km from Solulta village along Gojjam road, 09-11-90. H.V.M. Lyaruu H 21 (ETH); ca 6 km North of Addis Ababa- Entoto, 09-11-90, H.V.M. Lyaruu H 008 (ETH); Menagesha State Forest, western slope of Mt. Wuchacha, 19-11-72. Ib Friis et al., 1256 (ETH); ca 3 km from Solulta village along Gojjam road, 09-11-90, H.V.M. Lyaruu H 006 (ETH); ca 8 km north of Addis Ababa along Blue Nile road, 11-10-65, W.J.J.de Wilde et al., 8226 ETH), Menagesha Awraja, Holetta Research Station, 01-10-79, Kassahun Zewdie s.n. (ETH); Gafaresa, 18 km west of Addis Ababa, 13-11-64, Lema G. Sellasie 506 (ETH); Menagesha Awraja - Bole valley, 50 km North of Addis Ababa, 25-10-81, Mesfin et al. 1531 (ETH); Gafaresa reservoir, 17 km west of Addis Ababa, 24-08-69, S.B. Gilbert 1641 (EA, ETH); Jibat & Mecha Awraja, 15 km west of Ghedo, 04-11-90. H.V.M. Lyaruu H 8 (ETH); Mr. Zuqualla, ca 60 km South of Addis Ababa, 30-10-65, W.J.J.de Wilde et al. 8547 (ETH); 27-10-65, De Wilde 8482 (EA); 10-11-67, P.R.O. Bally 13088 (EA); Menagesha Awraja, 21-11-54 Mooney 6351(EA).

ERITREA: 02-10-69, S.A. Robertson 1182b (EA); 29-10-1902, A. Pappi, 2216 (EA).

(2) Centaurea *L.*

(a) Centaurea melitensis *L.*

GOJJAM; Debre Markos Awraja, 14 km North of Dejen, 29-10-81, Mesfin & Kagnew 1615(ETH)

KENYA:K4 Machakos, 10-05-64, Mwangangi 890 (EA); K3, 27-08-64,A. Bogdan 5117(EA); Feb. 1952, Someren s.n..(EA); 29-01-52, A.O. 793 (EA); 02-01-47, B.B.Fraser H2/47 (EA); Feb.1942,R.M.Nattrass 303 (EA); March 1933, Harvey 218 (EA); 24-09-29, J.Mc Donald 1220(EA).

SOUTH AFRICA: 31-10-65, A.J.Guillarmod 5042 (EA).

(b) Centaurea praecox *Oliv. & Hiern.*

WELLEGA: 10 miles north of Asosa, 12-02-59, Mooney 7740 (EA,ETH).

TANZANIA: T4, 29-09-77, Leedal 4624(EA); T4 Mahale, August1975, Nishida 257 (EA); T7 Paget-Wilkes 142 (EA); T4,15-07-60, Verdcourt 2830 (EA); T7, 27-08-58, Gaetan 59(EA).

KENYA: K3, 19-12-85, D.B.Ekkens 314(E.A); Trans-Nzoia, 27-01-67, Njoroge 143 (EA); Kitale, May 1954, Someren s.n., (EA); 04-04-59, Symes 523 (EA); Kitale, 15-02-57. P.H. Irusin 316 (EA); August 1931,. Hill 282 (EA).

BURUNDI: 12-10-78, Reekmans 7216 (EA); 25-09-74, Reekmans 3635 (EA).

UGANDA: April 1960, J. Wilson 1014 (EA).

ZAMBIA:27-09-47, Greenway & Brenan 8111 (EA).

(c) **Centaurea solstitialis** *L.*

ETHIOPIA

SHOA: Menagesha Awraja, Holetta Research Station, 06-05-59, Mooney 7900 (ETH).

TURKEY: 25-05-62, Duddley 34988 (EA).

(d) **Centaurea pseudosinaica** *Czerep.*

KUWAIT: 21-04-83. A. Rawi & Students AR 2273 (ETH).

(e) **Centaurea bruguierana** *(D.C.) Hand-Mazz.*

KUWAIT: May 1962, A. Macksaad et al. 142 (ETH).

(f) **Centaurea pallesceus** *Del.*

SAUDI ARABIA: 27-04-44, A. Khatab 8 (EA); 13-04-45, A. Khatab 7 (EA).

(g) **Centaurea dhofarica** *Bak.*

OMAN: Sharjah, April 1952: Oldfield. FNLO 154, (EA); Jebel, Feb 1952, Oldfield-FNLO 45 (EA).

(h) **Centaurea sinaica** *DC.*

SAUDI ARABIA: 27-02-52, Gilliland 4208 (EA); 11-06-1950, K.Grichom 341 (EA).

(i) **Centaurea salmantica** *L.*

SOUTH AFRICA: 17-10-69. J.P.H. Acocks 24270 (EA).

(j) **Centaurea diffusa** *Lamm.*

TURKEY: 09-06-62, Duddley 35547 (EA).

(k) **Centaurea virgata** *Lam.*

IRAN: 05-11-77, T. F. Hewer 3994 (EA).

(l) **Centaurea** sp.

KENYA: 22-09-50, R.M. Nathan 682 (EA).

(m) **Centaurea aegyptiaca** *L.*

ISRAEL: 14-04-54 ,Negev Revivim 583 (EA).

(n) **Centaurea alexandrina** *Del.*

EGYPT: 16-04-67, Tackholm et al. s.n. (EA).

(o) **Centaurea behen** *L.*

ISRAEL: 25-06-70, D. Peri s.n. (EA).

(p) **Centaurea calcitrapa** *L.*

EGYPT: 21-05-67, Tackholm et al. s.n. (EA).

(q) **Centaurea glomerata** *Vahl.*

EGYPT: 07-04-67, Tackholm et al. s.n.(EA).

SPECIMENS STUDIED FROM LATIN AMERICA

(1) **Centaurea atacamensis** *(Reiche) Johnston.*

CHILE: Antofagasta Prov., 12-10-1938, J.L.Morrison et al. 15784(K); Antofagasta prov., 25-11-1925, I.M. Johnston 5111(K); 15-01-1939 J.L. Morrison 17101(K).

(2) **Centaurea cachinalensis** *Phil.*

CHILE: Antofagasta Prov., 14-12-1925, I.M. Johnston 5720(K); 16-12-1925, I.M. Johnston 5749(K).

(3) **Centaurea bulbosa** *H. & Arn.*

CHILE: Jan. 1930; C. Elliott 604(K); Prope, Valparaiso,1831, H. Cumming 396(K); Prope Valparaiso,1832, Bridges 119(K).

(4) **Centaurea rothrockii** *Greenm.*

MEXICO:- Chihuahua State, 18-08-1898, E.W. Nelson 4774(K): Mexico State, 04-09-1958, J. W. Hawkes et al. 1394(K); Chihuahua State, 25-08-1899, E.W. Nelson 6175(K).

(5) **Centaurea floccosa** *H. & Arn.*

CHILE: 1864, M. Cl. Gay s.n.(K); Bridges 1400/1398(K); Cruinckshanks 5 (K); H. Cumming 171(K); Bridges 117(K).

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APPENDIX 1

MEASUREMENTS IN SOME GROSS MORPHOLOGICAL CHARACTERS OF P. VARIANS

Voucher Specimen, habitat	Stem height (cm)	Stem Internode (mm)	Stem diameter (mm)	Capitulum l x w (cm)	Phyllaries (mm)	Ray florets l x w (mm)
SCRUBLAND						
Mooney 7262	20-30	18.2	3.0	2.3 x 8.6	5-17	46-49 x 0.5-1.0
Mooney 5159	30.5	27.0	2.0	2.3 x 5.2	7-20	
Lyaruu H25	100	30.0	4.0	2.5 X 10	-	40-42 X 0.5
Evans et al. 385	-	37.0	2.0	2.5 x 6.4	6-18	37-41 x 0.75-1.0
De Wilde 8547	50	8.8	3.0	2.5 x 6.4	6-21	53-58 x 0.5
Lyaruu H43	50	18	1.5	2.9 x 6.1	5-15	29-33 x 0.5
GRASSLAND						
G. Aweke 547	50	25.0	4.0	2.9 x 5.2	5-18	37-42 x 0.5
Mesfin 3038	50	35.0	2.5	2.2 x 6.1	45-18	38-39 x 0.5-1.0
De Wilde 8004	40	29.6	2.5	1.0 x 3.5	6-15	28-30 x 0.75-1.0
Lyaruu H8	60	18.3	2.0	2.3 x 4.4	-	26-28 x 1.0

Friis et al 476	-	26.0	2.0	2.6 x 3.5	4-14	30-35 x 05
Mesfin et al. 1531	40	38.6	3.0	3.4 x 5.5	7-20	32-34 x 1.0
Gilbert 1641	-	18.6	2.5	2.9 x 6.3	5-18	34-35 x 1.0
Kassahun S.N.	-	30.6	3.0	2.4 x 6.5	6-18	28-36 x 0.5
Lemma 506	-	34.0	2.5	2.5 x 6.6	6-19	37-43 x 0.5
M.G. Gilbert 1939	-	18.5	3.0	2.7 x 9.2	9-17	47-61 x 0.5-1.0
J.W. Ash 2078	-	24.4	3.0	3.1 x 6.4	7-20	40-43 x 0.5
RIVERINE						
Sebsebe 118	40	36.6	2.5	2.7 x 6.0	6-17	36-37 x 0.5
Anderberg et al. 1639	40	22.0	3.0	2.7 x 8.6	5-18	39-45 x 0.5
Tewolde 228	20	7.0	2.0	2.3 x 6.4	4.5-15	46-61 x 0.5
FOREST						
Mesfin et al. 3586	-	33.0	3.0	2.6 x 7.4	5-15	39-44 x 0.5
Lyaruu H55	150	46.0	5.0	2.4 x 7.2	6-18	40-42 x 0.5
Gilbert et al. 465	-	38.0	3.5	2.7 x 5.6	6-15	31-42 x 0.5-1.0
Lyaruu H61	100	23.0	3.0	3.0 x 10.0	-	54-55 x 0.5
Lyaruu H21	60	49.5	3.0	2.8 x 6.2	6-17	37-39 x 0.75-1.0
[illegible]	100	43.0	3.0	2.6 x 6.8	5-17	32-35 x 0.5-0.75

Burger 1011	-	40.0	3.5	2.3 x 6.8	10.5-17	44-54 x 0.5-1.0
Puff et al. 820921-2/13	-	35.0	2.0	2.4 x 6.9	6-21	31-34 x 0.5-1.0
Burger 1210	-	37.0	4.0	2.3 x 6.9	6-18	45-46 x 0.5-0.75
Thulin et al. 3833	-	30.0	1.5	1.6 x 6.4	6-14	28-42 x 0.5
Mesfin 5116	75	25.7	2.0	1.8 x 5.9	5-16	25-28 x 0.5-1.0
De Wilde 8226	-	31.8	3.5	2.8 x 8.1	6-19	34-39 x 1.0
Friis et al. 1256	-	29.8	2.0	2.6 x 6.5	6-13	27-37 x 0.5-0.75
Lyaruu H008	40	25.0	2.0	3.2 x 5.5	-	32-33 x 0.75-1.0
Dr. Brehme(a)	-	27.4	2.0	1.8 x 5.9	6-16	25-28 x 0.5-1.0
Dr. Brehme(b)	-	28.1	2.5	2.2 x 8.1	7-17	46-54 x 0.5-0.75
Lyaruu H006	100	19.5	3.5	2.5 x 8.6	5-16	40-42 x 0.75-1.0

Apendix 2: MORPHOLOGICAL CHARACTERS OF P.VARIANS (A.RICH.) C.JEFFREY EX CUFODONTIS
(All measurements in milimetres except those of the leaves).

Voucher specimen	LEAF		DISC FLORETS			Achene length
	Length	Width	Length	Style len.	Filament len.	
Friis et al. 1256	6.0-12.4	0.9-1.8	17.0-20.0	16.5-17.5	10.0-11.0	1.0-3.0
Lyaruu H008	4.9-9.8	0.8-1.6	20.0-24.0	21.5-26.0	8.5 -10.0	-
Hedberg et al. 5329	5.0-8.5	1.2-1.5	24.0-26.0	25.7-28.5	6.0 - 7.0	3.0-4.0
Puff et al. 811005-$^{3/1}$	5.1-7.0	1.0-1.5	27.0-29.0	27.5-28.5	6.0 - 7.0	4.0-4.5
Burger 1011	5.1-7.0	1.0-1.5	21.0-23.0	21.5-22.5	12.0-13.0	2.5-3.0
Puff et al. 820921-$^{2/13}$	11.1-14.4	0.7-0.9	22.0-24.0	20.5-23.5	6.5 - 7.0	3.5-4.0
Burger 1210	7.2-15.6	0.9-2.5	20.0-22.0	21.5-23.0	9.0-10.0	2.5-3.0
Friis et al.476	5.2-17.0	0.8-1.3	19.0-24.0	20.5-23.5	8.0-9.0	3.5
Anderberg et al. 1639	-	-	19.0-20.0	18.5-20.5	9.0-10.0	2.0
Evans et al.385	9.0-16.6	1.7-2.2	23.0-27.0	23.5-28.0	6.0-7.0	3.0-4.0
M.G. & S.B. Gilbert 1933	6.0-12.3	0.4-1.2	21.0-26.0	22.0-23.0	6.5-8.0	1.5-2.0
Thulin et al. 3844	-	-	11.0	10.5-11.0	7.0-8.0	2.0-2.5
Mesfin 5116	10.4-18.2	1.0-2.1	19.0-22.0	17.5-21.0	7.0-8.0	1.5-2.5
Mooney 7262	4.4-8.7	0.8-1.4	19.0-23.0	18.5-20.0	7.0-8.0	1.5-2.5
G.Aweke 547	5.6-9.2	1.2-2.2	21.5-25.5	22.5-27.0	7.0	3.0-3.5
Mesfin et al. 3586	4.2-17.0	0.6-2.4	26.0-29.0	25.5-29.5	11.0-12.0	3.0-4.5
Mooney 5159	4.0-6.3	0.5-0.9	18	17.5-19.5	7.0-8.0	1.5-2.0

Voucher specimen	LEAF		DISC FLORETS			Achene length
	Length	Width	Length	Style len.	Filament len.	
Masfin 3038	4.2 - 7.0	0.6-0.9	18.0-20.0	19.5-20.5	9.0 -11.0	3.0
De Wilde 8004	8.6 -14.0	1.2-1.5	18.0-20.0	18.5-21.5	9.0 - 3.0	2.5-3.0
Lyaruu H55	12.8-14.4	1.9-2.9	15.0-17.0	15.5-18.0	8.0 - 9.0	-
Lyaruu H25	14.2-18.3	1.3-2.3	17.0-20.0	18.5-19.5	7.0 - 8.0	-
Tewolde 228	2.0 - 4.1	0.5-1.2	19.0-20.0	19.5-20.5	6.0 - 7.5	2.0
M.Gilbert et al. 465	10.8-17.5	1.6-2.5	18.0-19.0	20.5-22.0	6.5 - 7.0	2.0-2.5
Lyaruu H61	16.4-23.9	1.8-2.4	19.0-24.0	20.5-25.5	8.0 - 9.0	-
Lyaruu H43	3.9 - 4.4	1.1-1.5	25.0-27.0	26.5-27.5	10.0-11.0	-

APPENDIX 3: KEY TO THE SPECIES OF PLECTOCEPHALUS

1. Ascending perennial herb, stem usually unbranched, rootstock woody. *P. varians*

- Annual, perennial or suffrutescent woody herb, stem muchbranched, root stock not woody. 2

2. Leaves pinnatifid to pinnatipartite, 4-6-partite, whorled, radical or conglomerate lower down the stem, glabrous, linear or linear-lanceolate, only primary vein prominent, the ratio of phyllary to appendage more or less 1:1, long medium spine present 0.4-0.5 cm long, hyaline appendage around phyllary margin present. *P. chilensis*

- Leaves simple, alternate, sessile or petiolate, lanceolate, oval-spathulate, scabrous, venation brochidodromous sometimes eucamptodromous, the ratio of phyllary to appendage almost 2:1, longer median spine in the appendages lacking, hyaline appendage around phyllary margin absent. 3

3. Phyllaries always linear lanceolate, golden yellow, reflexed spine-like structures, 4-11-nerved, glabrous, spines not prickly; pappus of achene commonly persistent. *P. tweediei*

- Phyllaries ovate, lanceolate to linear lanceolate, yellowish, puberulent, 5-8-nerved, straight, rigid, prickly spines present; pappus of achene caducous. *P. americanus*

C. TWEEDIEI *H.& A.**

Prostrate annual herb, 0.15-1.1 m high; root system taproot, stem much-branched in upper parts. Stem dark green to yellowish-green, terete to striate-sulcate, more or less glabrescent with sparse white tomentum on the sulcations, the density getting higher towards the receptacle; ridges with small, white, rigid spines which give the stem a scabrid texture. Internode (1.6-)2.2-4.2(-4.6) cm long. Leaves simple, linear ,lanceolate, oblanceolate to spathulate; alternate or distichous, sessile, sub-amplexicaule, scabrous, indumentum lanate, margins serrate, apex acute, base decurrent or attenuate, venation pattern brochidodromous.

Phyllaries 5-seriate, linear -lanceolate in all series, 0.45-2.4(2.6) cm, imbricate, greenish or brownish yellow, progressively increasing in size towards the innermost series, exposed surfaces and spines pubescent, inner surfaces glabrous. Phyllaries bicolourous, -lower part greenish-yellow, appendages purple or lilac, golden yellow reflexed spine-like structures, less prickly than in *P. americanus*, nervation common in all series, 4-11 striae, extending to the spines. Capitulum heterogamous, 2.7-3.5 cm at anthesis. Achenes black, yellowish at articulation point, obovate or elliptic, 0.5-0.6 cm long, glabrous rarely pubescent, crested with three prominent ridges (ribs). Pappus of achene pluriseriate, apically inserted, 0.65-1.1 cm long, white, barbellate, persistent rarely caducous.

Pollen grains medium sized, isopolar, radially symmetrical or spherical: P = 32-34(-39) microns, E = 34-38 microns. Spinules much more elongated with more or less blunt apices.

* This species should rather belong to *Plectocephalus* but as A. Susanna who currently seem to be working on the genus has not done the proper combination and since I can not do it here, the previous name is used here.

Specimens studied

ARGENTINA - Formosa, 14/10/1945, I. Morel 588 (K); Puerto Rico, 24/10/1947, E. Schwindt 481 (K); Puerto Rico, 12/11/1948, J.E. Montes 3351 (K).

P. AMERICANUS *Nutt.*

Erect annual herb to c. 1.0 m high, root system taproot , stem green to dark green, terete to striate-sulcate, scabrous. Internode (1.8-)2-3.3(-3.9) cm long. Leaves simple, lanceolate to narrowly elliptic, 7.3-9.9(-33.4) x 1.8-2.6(-9.0) cm, alternate, sessile or petiolate, petioles winged 0.7-1.5(10.8) cm long, margins serrate to doubly serrate or irregularly dentate. Apex apiculate, acute, acuminate or mucronate. Indumentum scabrid with greyish or woolly white tomentum, glabrescent or scabrid on the ridges, sulcations more or less glabrous. Venation brochidodromous, rarely eucamptodromous, base sessile, decurrent, attenuate, in some leaves oblique. Phyllaries 5- to 7-seriate, imbricate, lanceolate to linear-lanceolate, (0.4-)0.6-2.9(-3.9) cm, bicolourous -phyllaries green chartaceous on the margin, phyllary appendages yellow; prickly, puberulent, straight spines present; nervation common in all phyllary series and extend to cover the spines, 5-8 brownish striae which become more conspicuous towards the inner series. Capitulum heterogamous, turbinate or cylindric 3.1-4.0 cm at anthesis, ray florets purple and neuter, disc florets hermaphroditic, fertile, receptacle with woolly white tomentum.

Achenes glabrous, bicolourous, black on the upper part, yellow at the articulation zone, laterally compressed, obovate, 0.5-0.6 cm long; crested with 3 prominent ridges, articulation zone rib free, and basal-lateral articulation type. Pappus of achene pluriseriate, 0.5-0.9 cm long, white, barbellate, setaceous and caducous.

Specimens studied

MEXICO - Coahuila, 17/6/1936, Lyle Wynd et al. 149 (K); Chihuahua, 16/10/1887, C.G. Pringle s.n. (K); Chihuahua State, 9/8/1899, Townsend et al. 247 (K); near Guadalajara, 20/9/1897, J.N. Rose 3033 (K); Guadalupe, J.Arsine s.n. (K); Mexico, 1848-1849, Dr. J. Gregg 307 (K); Coahuila State, Feb.-Oct. 1880, Dr. E. Palmer 766 (K); Coahuila State, 1898, Dr. E. Palmer 294 (K); Southwestern Chihuahua, 29/8/1830, Dr. E. Palmer 415 (K); New Mexico, 16/7/1880, E.L. Greene s.n. (K); Chihuahua, 18/9/1891, C.V. Hartmann 781 (K); Mexico, 15/11/1907, Ekrenberg 1537 (K).

KEW CULTIVATED - 13/11/80 Acc. number 446-79-04458 (K).

CHILE - San Ignacio, 30/9/1952, R. McVaugh 13267 (K).

U.S.A. - Flora of North America, Toor & Gray s.n. (K); Houston, Texas, July 1843, Lindheimer 114 (K); Oklahoma, 26/6/1913, G.Stevens 1343 (K); Dallas, Texas, May 1880, J. Reverchon 560 (K); Kerrville, Texas, May 14-21, 1894, Heller 1774 (K); Texas, 1843, Lindheimer 114 (K); New Brannfels, Texas, May 1849, Lindheimer 892 (K); Arizona, 17/10/1906. J.C. Blumer 1480 (K); Asa Gray Herbarium, 1845, A.G. s.n. (K); Dallas, Texas, 1872, Elihu Hall 373 s.n. (K).

P. CHILENSIS *Hook. & Arn.*

A much-branched erect, suffrutescent, fructicose or woody herb, 0.3-1.2 m high, stem terete to striate-sulcate, especially the upper part, glabrous, sometimes pubescent with white or greyish hairs, branchlets common at each leaf node, Stem greenish fading to brown. Leaves alternate high up the stem, whorled or radical or conglomerate at the branching point, glabrous, sessile, pinnatifid to pinnatipartite, 4-6 partite, acicular or linear in outline, incision on the pinnatifid leaves much pronounced closely approaching the primary vein; margins ciliate, apex acute, base cuneate or decurrent, indumentum glabrous. Phyllaries 5-seriate, outermost series (0.3-) 0.5-1.0 x 0.2-0.4 cm, innermost series (1.6-)1.9-2.7 x 0.15-0.3 cm, shape various- ovate, lanceolate, with innermost series tending to become linear to linear lanceolate, bicolourous - appendages yellow, main phyllary greenish yellow, the ratio of appendage to phyllary almost 1:1, cartilaginous, chartaceous or coriaceous, hyaline appendage extended to cover the phyllary margins, median spine common 0.4-0.5 cm long, prickly yellowish and straight, striations common directed towards the median spine. Capitulum at anthesis 2.4-3.9 x 5.9-7.2 cm, heterogamous, rays with deeply incised lobes, peduncle 0.3-3.9 cm long, receptacle base whitish pubescent. Pappus of achene 0.9 cm long, white, glabrous.

Pollen grains with very short spines, spherical, radially symmetrical large grains. P = 50-53 microns, E = 53-54 microns.

Specimens studied

CHILE: Aconcagua Province, 14/12/1938, J.L.Morrison 16871 (K); Atacama Province, Jan. 1924, Werdemann 267 (K); Prope Valparaiso, 1825, Macrae s.n. (K); Atacama Province, 20/10/1938, Morrison 16145 (K); Atacama Province, 07/01/1926, I.M.Johnston 5999 (K); Royal Botanic Gardens Kew, 10:09:1930, T.Hay 576-30 (K); Cumbre Andium Claustrum, 1825, Lord Colchester s.n. (K); Chile, Cruickshanks 6 (K); Mendoza, June 1876, Moseley 1396 (K); Santiago, Gay s.n. (K); Coquimbo, October 1929, C.Elliot 530 (K); Aconcagua valley, October 1939, Saudeman 269 (K); Mendoza, December 1873, Bridges 118 (K); Prope Valparaiso, 1831, H.Cumming 580 (K); Coquimbo, October 1929, C.Elliot 529 (K); Coquimbo, September 1927, C.Elliot 33 (K); Aconcagua, 09/12/1951, Hutchinson 126 (K); Andacolla valley, October 1927, C.Elliot 89 (K); Coquimbo, July 1856, W.H.Harvey s.n. (K); Coquimbo, 20/09/1957, A.L. Cabrera 12698 (K); Santiago, R.A. Philippi s.n. (K).

APPENDIX 4

MEASUREMENTS OF POLLEN GRAINS IN MICRONS

Voucher speciman: Arne Aderberg et al. 1639
Locality : WELLEGA

S.No	Spine length	Sexine	Nexine	Polar axis	Equatorial diameter	Spine base width	Exine	P/E
1	3.5	3.0	4.0	44.00	45.00	8.0	7.0	0.97777
2	3.0	3.5	2.0	51.00	50.00	7.0	5.5	1.0200
3	3.0	4.0	2.0	46.00	45.00	5.0	6.0	1.0222
4	3.0	4.5	2.5	39.00	37.00	6.0	7.0	1.05405
5	2.5	4.0	3.0	45.00	44.00	6.0	7.0	1.02272
6	2.5	4.0	3.0	47.00	42.00	5.0	7.0	1.11904
7	2.0	4.0	2.0	43.00	47.00	6.0	6.0	0.91489
8	2.5	4.0	2.5	42.00	46.00	7.0	6.5	0.91304
9	3.0	5.0	2.5	46.00	47.00	7.0	7.5	0.97872
10	3.5	3.5	3.0	41.00	45.00	5.0	6.5	0.91111
11	4.0	3.0	2.0	45.00	41.00	8.0	5.0	1.09756
12	3.5	3.0	2.0	44.00	41.00	6.0	5.0	1.07317
13	3.5	3.5	2.0	47.00	46.00	6.0	5.5	1.02173
14	4.0	3.5	2.0	42.00	45.00	5.0	5.5	0.93333
15	3.0	3.5	3.0	49.00	47.00	5.0	6.6	1.04255
16				53.00	51.00			1.03921
17				45.00	47.00			1.93744
18				43.00	43.00			1.00000

Voucher specimen : Lyaruu H33
Locality : ARSSI - Mt. Chilalo

1	3.5	3.0	2.5	45.00	45.00	5.0	5.5	1.0000
2	3.0	3.5	2.5	40.00	46.00	5.0	6.0	0.86956
3	3.5	5.0	3.0	48.00	41.00	5.0	8.0	1.17073
4	3.0	4.0	2.5	45.00	48.00	5.5	6.5	0.93750
5	3.0	4.0	2.5	40.00	38.00	5.0	6.5	1.05263
6	3.0	4.0	2.0	45.00	39.00	6.0	6.0	1.15384
7	3.5	3.0	2.0	48.00	42.00	6.0	5.0	1.14285
8	3.0	3.5	3.0	48.00	45.00	6.0	6.5	1.06667
9	3.0	4.0	3.0	46.00	44.00	5.5	7.0	1.04545
10	2.5	4.0	2.5	45.00	44.00	5.0	6.5	1.02272
11	3.0	3.5	2.5	44.00	43.00	6.0	7.0	1.02325
12	3.0	4.0	2.0	47.00	44.00	6.5	6.0	1.06818
13	3.5	4.0	2.0	43.00	43.00	6.0	6.0	1.0000
14	3.0	3.5	2.5	47.00	48.00	5.0	7.0	0.97916
15	3.0	4.0	2.0	44.00	39.00	5.0	6.0	1.128205
16				44.00	43.00			1.02325
17				40.00	42.00			0.95238
18				42.00	45.00			0.93333

Voucher specimen : Tenagne Kebede 8
Locality : GONDER

1	3.0	4.0	3.0	40.00	44.00	8.0	7.0	0.90909
2	3.0	5.0	3.0	42.00	38.00	6.0	8.0	1.10526
3	3.0	5.0	2.5	40.00	44.00	7.0	7.5	0.90909
4	3.5	4.0	2.5	40.00	43.00	6.0	6.5	0.93023
5	3.5	4.0	3.0	45.00	45.00	8.0	7.0	1.0000
6	2.5	4.0	2.5	44.00	44.00	8.0	7.0	1.0000
7	3.0	4.0	2.0	42.00	45.00	7.0	6.0	0.93333
8	3.5	4.5	2.0	42.00	42.00	7.0	6.5	1.0000
9	3.0	4.0	2.0	41.00	44.00	7.0	6.0	0.93181
10	3.0	4.0	2.0	44.00	45.00	8.0	6.0	0.97777
11	3.5	4.5	2.5	40.00	43.00	8.0	7.0	0.93023
12	3.0	4.5	2.5	41.00	40.00	7.0	6.5	1.0250
13	3.0	5.0	2.0	46.00	46.00	7.0	7.0	1.0000
14	3.5	4.0	2.0	41.00	42.00	8.0	6.0	0.97610
15	3.0	5.0	2.0	45.00	41.00	6.0	7.0	1.09756
16				40.00	43.00			0.93023
17				43.00	40.00			1.0750
18				44.00	43.00			1.0750

Voucher specimen : Lyaruu [illegible]
Locality : [illegible] Ghedo

1	3.0	4.0	5.0	40.00	42.00	7.0	9.0	0.93020
2	3.5	4.0	3.0	45.00	47.00	7.0	7.0	0.95740
3	3.5	3.5	2.0	37.00	38.00	8.0	5.5	0.97360
4	3.0	4.5	2.0	46.00	47.00	7.0	6.0	0.97870
5	3.0	3.5	3.0	44.00	38.00	7.0	6.5	1.1578
6	4.0	5.0	2.5	45.00	41.00	7.0	7.5	1.0975
7	3.0	5.0	3.0	49.00	44.00	8.0	7.5	1.1136
8	3.0	4.5	2.0	33.00	33.00	7.5	6.5	1.0000
9	4.0	4.0	3.0	38.00	37.00	9.0	7.0	1.02702
10	3.0	4.0	2.5	37.00	36.00	9.0	6.5	1.02777
11	3.5	4.0	4.5	36.00	36.00	7.0	8.5	1.0000
12	3.0	5.0	3.0	46.00	45.00	8.0	8.0	1.02222
13	2.5	4.5	3.0	39.00	35.00	7.0	7.5	1.11428
14	3.0	4.5	2.0	40.00	40.00	8.0	6.5	1.0000
15	2.5	4.5	3.5	36.00	36.00	7.0	8.0	1.0000
16				39.00	42.00			0.92857
17				44.00	46.00			0.95652
18				41.00	40.00			1.0250

Voucher specimen : Lyaruu H43
Locality : SIDAMO - Megada Forest

1	4.0	5.0	3.0	43.00	45.00	7.0	8.0	0.95555
2	4.0	4.5	2.5	42.00	45.00	7.0	7.0	0.93333
3	3.5	4.5	3.0	45.00	45.00	7.0	7.5	1.00000
4	3.5	4.5	3.0	48.00	42.00	6.5	7.5	1.14280
5	3.5	4.5	3.0	42.00	46.00	6.0	7.5	0.91304
6	4.0	4.5	3.0	45.00	45.00	6.0	7.5	1.00000
7	3.5	5.0	2.5	47.00	43.00	6.0	7.5	1.09302
8	3.0	4.5	3.5	48.00	43.00	6.0	8.0	1.11627
9	4.0	5.0	3.0	44.00	48.00	6.0	8.0	0.91666
10	4.0	4.5	3.0	46.00	44.00	6.0	7.5	1.04545
11	4.0	4.0	2.5	48.00	43.00	6.0	6.5	1.11627
12	3.5	4.5	3.0	45.00	45.00	6.0	7.5	1.00000
13	3.5	4.5	3.5	40.00	42.00	6.0	8.0	0.95238
14	4.0	4.5	3.0	46.00	46.00	6.0	7.5	1.02083
15	4.5	4.5	3.0	46.00	46.00	6.0	7.5	1.00000
16				47.00	43.00			1.09302
17				45.00	47.00			1.95744
18				49.00	50.00			1.98000

Voucher specimen : Lyaruu H08
Locality : SHOA - Wolmera - Woreda

1	3.5	5.0	2.0	42.00	48.00	7.0	7.0	0.8750
2	4.0	4.5	2.0	42.00	49.00	7.0	6.5	0.85714
3	3.5	5.0	2.5	46.00	44.0	6.0	7.5	1.04545
4	4.5	4.0	3.0	50.00	50.00	7.0	7.0	1.00000
5	4.5	5.0	3.0	43.00	44.00	6.0	8.0	0.97727
6	3.5	5.0	3.0	41.00	46.00	6.0	8.0	0.89130
7	3.5	5.0	3.0	40.00	41.00	6.0	8.0	0.97560
8	3.5	4.5	3.0	41.00	45.00	6.0	7.5	0.91111
9	4.0	4.5	3.0	44.00	44.00	6.0	7.5	1.00000
10	3.5	5.0	3.5	49.00	50.00	7.0	8.5	0.89000
11	3.5	4.5	3.5	45.00	47.00	7.0	8.0	0.95744
12	4.5	5.0	3.5	42.00	45.00	7.0	8.5	0.93333
13	4.0	5.0	3.0	42.00	46.00	6.0	8.0	0.91304
14	4.0	4.5	2.5	44.00	45.00	6.0	7.0	0.97777
15	4.0	4.5	2.5	41.00	47.00	7.0	7.0	0.87234
16				41.00	43.00			0.95348
17				41.00	42.00			0.97619
18				42.00	38.00			1.10526

Voucher specimen : W. Burger 1011

Locality : HARARGE

1	2.0	4.0	2.0	55.00	54.00	8.0	6.0	1.0185
2	2.0	4.0	2.0	56.00	54.00	8.0	6.0	1.03703
3	2.5	4.0	2.0	52.00	49.00	7.0	6.0	1.06120
4	3.0	3.5	2.0	54.00	54.00	8.0	5.5	1.0000
5	2.0	3.5	3.0	53.00	52.00	8.0	6.5	1.01923
6	1.5	4.0	3.0	44.00	44.00	5.0	7.0	1.0000
7	2.0	4.0	2.5	50.00	48.00	5.0	6.5	1.04166
8	2.0	4.5	2.0	47.00	51.00	5.0	6.5	0.92156
9	2.0	3.5	3.0	54.00	54.00	6.0	6.5	1.0000
10	2.0	3.5	2.0	56.00	55.00	7.0	5.5	1.01818
11	2.0	4.0	3.0	44.00	44.00	7.0	7.0	1.0000
12	2.0	4.0	2.5	42.00	45.00	5.0	6.5	0.9333
13	3.0	4.5	2.5	48.00	51.00	5.0	7.0	0.94117
14	2.0	4.0	2.0	50.00	49.00	5.0	6.0	1.02040
15	2.0	4.0	2.0	51.00	52.00	6.0	6.0	0.98076
16				55.00	48.00			
17				52.00	52.00			
18				56.00	55.00			

Voucher specimen : Lyaruu H21
Locality : SHOA - Menagesha forest

1	4.0	4.5	3.5	43.00	43.00	7.0	8.0	1.0000
2	2.0	4.0	3.0	46.0	47.00	7.0	7.0	0.9787
3	2.5	4.5	2.5	45.00	47.00	6.0	7.0	0.9574
4	2.0	4.0	3.0	40.00	44.00	6.0	7.0	0.90909
5	2.0	4.0	2.5	46.00	42.00	6.0	6.5	1.09523
6	2.5	3.5	2.5	42.00	43.00	6.0	6.0	0.97674
7	3.0	4.0	2.0	40.00	40.00	5.0	6.5	1.0000
8	3.0	4.0	2.0	47.00	48.00	6.0	6.0	0.97916
9	2.5	3.5	2.0	46.00	44.00	6.0	5.5	1.04545
10	3.0	4.0	2.5	42.00	42.00	6.0	6.5	1.0000
11	3.0	4.5	2.0	45.00	47.00	6.0	6.5	0.95744
12	2.5	3.5	2.0	46.00	48.00	5.0	5.5	0.95833
13	2.5	3.0	3.0	49.00	50.00	6.0	6.0	0.98000
14	3.0	4.0	2.5	45.00	48.00	6.0	6.5	0.93750
15	3.0	4.0	2.0	44.00	46.00	5.0	6.0	0.95652
16				40.00	44.00			0.90909
17				40.00	42.00			0.95238
18				48.00	48.00			1.0000

Voucher specimen : Lyaruu H08
Locality : SHOA - Wolmera - Woreda

1	3.5	5.0	2.0	42.00	48.00	7.0	7.0	0.8750
2	4.0	4.5	2.0	42.00	49.00	7.0	6.5	0.85714
3	3.5	5.0	2.5	46.00	44.0	6.0	7.5	1.04545
4	4.5	4.0	3.0	50.00	50.00	7.0	7.0	1.00000
5	4.5	5.0	3.0	43.00	44.00	6.0	8.0	0.97727
6	3.5	5.0	3.0	41.00	46.00	6.0	8.0	0.89130
7	3.5	5.0	3.0	40.00	41.00	6.0	8.0	0.97560
8	3.5	4.5	3.0	41.00	45.00	6.0	7.5	0.91111
9	4.0	4.5	3.0	44.00	44.00	6.0	7.5	1.00000
10	3.5	5.0	3.5	49.00	50.00	7.0	8.5	0.89000
11	3.5	4.5	3.5	45.00	47.00	7.0	8.0	0.95744
12	4.5	5.0	3.5	42.00	45.00	7.0	8.5	0.93333
13	4.0	5.0	3.0	42.00	46.00	6.0	8.0	0.91304
14	4.0	4.5	2.5	44.00	45.00	6.0	7.0	0.97777
15	4.0	4.5	2.5	41.00	47.00	7.0	7.0	0.87234
16				41.00	43.00			0.95348
17				41.00	42.00			0.97619
18				42.00	38.00			1.10526

Appendix 5: SEM magnification calculation chart

Obtaining the magnification:

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

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

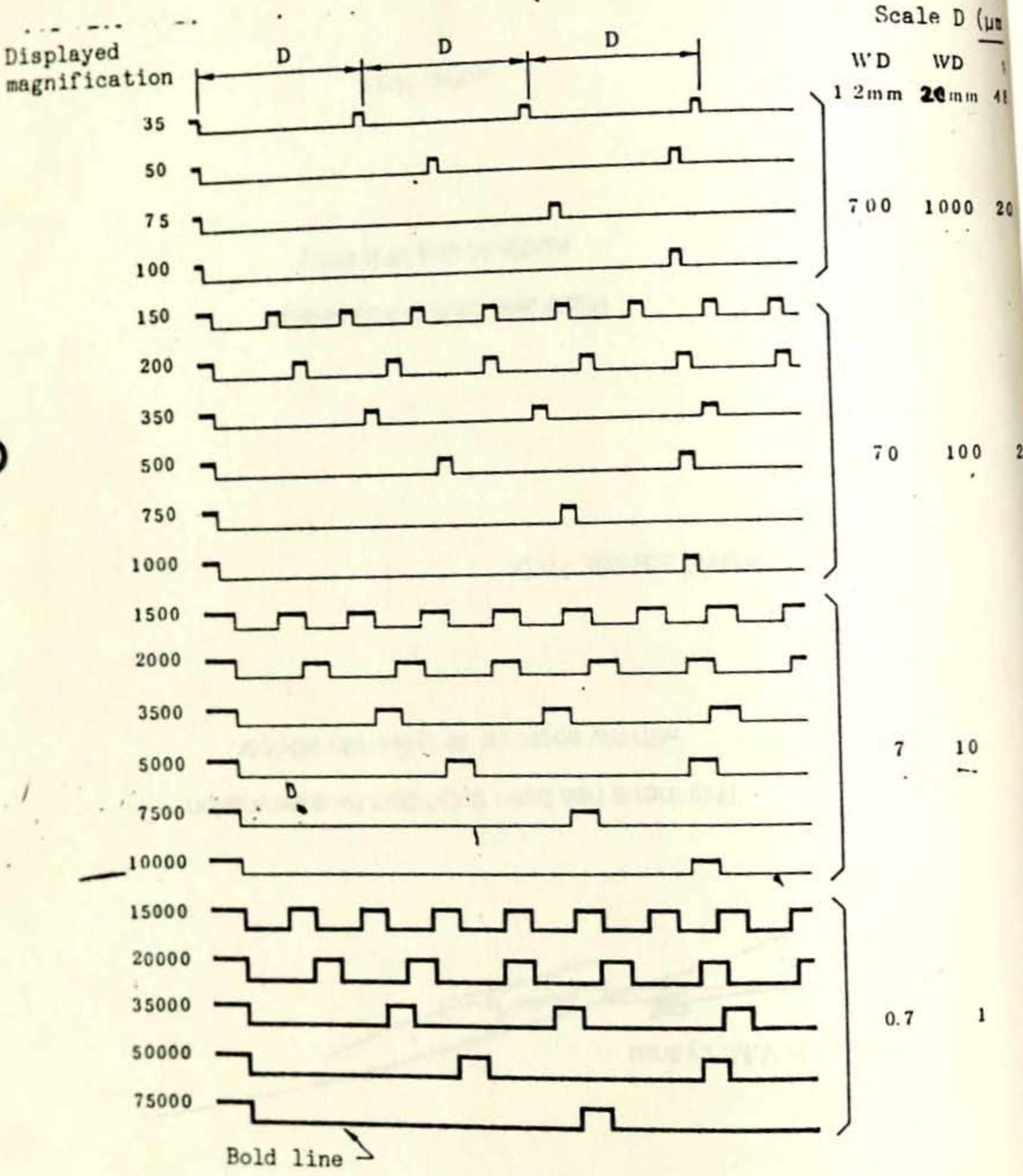

Fig. 4.8 Magnification mark and scale

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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: H.V.M. Lyaruu

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, 1991