

Anatomical studies of Oil Bearing Species

of Compositae: Vernonia galamensis (Cass.)

Less. and Guizotia abyssinica (L.f.) Cass.

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ABSTRACT

Anatomical features of stem internodes and the leaves of Vernonia galamensis (Cass) Less. and Guizotia abyssinica (L.f.) Cass. have been studied. Most of the anatomical characters of the two species are similar and hence are described together; the stems of both species possess uniseriate epidermis bearing uniseriate multicellular non-glandular hairs; phloem fibers develop in a discrete manner and do not form a continuous cylinder around the stem. At the mid rib region, mature leaves of both species contain three sets of vascular bundles. The thickening on the lateral vessel walls of both species is annular at an earlier ontogenetic stage, but scalariform and pitted vessel elements with simple perforation plates were observed at later stages of development.

Vessel dimensions and aggregation of vessels of both species, however, showed definite correlation with the habitat climatic condition that is prevalent in the natural area of distribution of the two species. In this respect G. abyssinica is characterized by wider and longer vessel elements as compared to V. galamensis which has shorter, narrower and denser vessel elements. Tangential longitudinal section through the vascular bundle of V. galamensis showed considerable development of vascular rays. Both uniseriate as well as multiseriate rays are observed.

Collenchyma develops in the stems of both species next to the epidermis. In V. galamensis there are 3-4 cell layers while in G. abyssinica there are only 2 layers of collenchyma. Considerable development of aerenchyma in the stem of G. abyssinica is observed indicating its usually moist natural habitat which probably induces development of lacunae. The pith of G. abyssinica starts to disintegrate at earlier stage during the development of the plant. Ecological significance of hollow pith as it occurs in G. abyssinica is discussed along with other anatomical characters.

1. Introduction

This study deals with the anatomy of two species within the family Compositae, namely Vernonia galamensis (Cass.) Less. and Guizotia abyssinica (L.f.) Cass. The work was started in July 1986 by raising specimens of the two species from seeds in glass houses in the Department of Biology, Addis Ababa University. The collection of specimens for anatomical studies lasted for about three months in G. abyssinica and for about ten months in V. galamensis. It was discontinued after the specimens produced fruits and started dying out.

Guizotia abyssinica (Noog in Amharic) is a very important oil crop in Ethiopia. According to Seegeler (1983) Ethiopia has the largest production of niger seed oil and exports the "seeds" of achenes more than any other country.

The genus Guizotia which is included in the tribe Heliantheae comprises of six species (Baagoe, 1974). They are G. abyssinica, G. scabra (Vis) Chiov., G. arborescens, I. Friis. G. villosa, Sch. Bip. G. zavattarii Cuf. and G. jacksonii. (S. Moore) J. Baagoe. G. villosa is endemic to Ethiopia while G. abyssinica and G. scabra subsp. Schimperi (Sch. Bip) J. Baagoe are native to Ethiopia. G. abyssinica is naturalized in Sudan, Tanzania, Uganda, Zaire, South Africa and India. G. Scabra subsp. Scabra is found in

Africa from Nigeria in West Africa to Ethiopia and as far south as Malawi, while G. jacksonii is confined to Kenya.

G. abyssinica is an annual herb which thrives well where the soil moisture is abundant. In glass houses it grew to a height of 1.2 m; its largest stem attained a diameter of 11 mm. In the field it grows to a height of about 90 cm. The stem is hollow and bears simple leaves with opposite arrangement. In Ethiopia it is grown at altitudes of 1500 - 2300 m (Baagoe, 1974). In the green house the plants started flowering when they were about 63 days old. The florets of the Capitulum terminating the stem, open first and subsequently the lateral branches elongate and produce flowering Capitula as the plants grow to maturity.

Vernonia galamensis is a herbaceous plant whose center of diversity is in East Africa (Gilbert, 1986). It attained a height of about 2.5 meters and produced considerable wood when grown in the glass house. It is known to grow only upto 75 cm in the wild state in Ethiopia. However, according to Perdue, Carlson, and Gilbert (1986) it is known to grow upto 5 meters. It started flowering at about 105 days after germination, at which time the first capitulum appeared at the apex of the stem. If continued moisture is available, V. galamensis can continue growing by elongation of the side branches. In this state the plant can continue growth for almost a year before it finally dies.

The sessile and alternate leaves have considerable amount of hair and waxy surface. In Ethiopia it grows wild in the southern, eastern and northern parts of the country; in Sidamo, Bale, Harrerghe and Eritrea. V. galamensis Var. ethiopica M.G. Gilbert is distributed between altitudes of 1250 and 2075 meters while V. galamensis Var petitiana (A. Rich) M.G. Gilbert is mostly found at lower elevations of 750-1500 meters where rainfall is scanty (Perdue et al 1986). In fact they reported the fatality of excessive soil moisture to V. galamensis at planting sites in Kenya.

Until recently V. galamensis had no agronomic or industrial value. But recently, its use as a potential source of epoxy oil has grown to the extent that at present it is cultivated in Kenya and South Africa (Perdue 1984) as an industrial plant whose oil is suitable for epoxy coatings (Perdue et al 1986)

Being a recently cultivated plant in some parts of Africa, not much is known about its anatomy. Thus the anatomical investigation of this plant together with that of G. abyssinica, a plant cultivated for a long time, is an attempt to add some information which may be utilized for taxonomic or agronomic purposes. More over, extensive anatomical investigations of dicots have proven to be significant in the systematic evaluation of many groups and have furnished documentations of structural specialization in plants which

aid in the establishment of relationships between plant groups (Chattaway, 1934; Recored, 1934). If the two genera are to be studied phylogenetically, there must also be much documented knowledge of the anatomy of their members before sound suggestions concerning relationships can be attempted. Accordingly this anatomical investigation was undertaken in an effort to contribute to such date. Above all, it was conducted in order to acquire knowledge on anatomical techniques and interpretation of data. The aims of this study then are (a) to provide an account of the stem and leaf anatomy of these two species with the view being to aid in future comparative studies of them with other related taxa in the family, (b) to determine the extent of structural differentiation in the stem and leaf with age of the plant, and, (c) to determine relationships between the structure of the plant and the environment.

These two species are especially interesting in the diversity of habitats which they occupy. G. abyssinica is cultivated in the relatively moist highlands of Ethiopia while V. galamensis naturally occupies the arid eastern, northern and southern parts of the country. Specialization of anatomical parts of these species seem to be closely related to the respective climatic situations. These variations in habitat are important in interpreting the variation patterns which occur in the anatomical structure of these plants.

2. Literature Review

Much information on the anatomy of Compositae is available, but it is largely scattered and more or less restricted in scope. In most respects the structure and organization of the wood in trees and shrubs of dicots is better known than other anatomical features (Randle and Clarke, 1934; Carlquist, 1957a 1958, 1960; Chalk and Chattaway, 1934). In the works of MetCalfe and Chalk (1950) who summarized the literature relating to the anatomical features of the Compositae, among others it was shown that emphasis has been given to the stem structure based exclusively upon studies of woody members. Most of the work done by Carlquist (1957a, 1958, 1960) on the anatomy of Compositae was undertaken to elucidate phyletic tendencies within the family. Carlquist (1957a) while working on the wood anatomy of Mutisieae tried to solve the question as to whether Compositae were ancestrally herbaceous, as postulated by Cronquist, or ancestrally woody. In some of his papers, Carlquist (1957a, 1958) arrived at conclusions by combining anatomical data with that of other disciplines. Eames (1957; cited in Carlquist, 1961) stated that "the study of morphology is above all the study of evolutionary modification of form ... morphology must go hand in hand with other fields in the establishment of phylogenetic relationship." Thus variation patterns in plants could be the result of

numerous factors, among which geographical and ecological factors are notable in bringing variability among closely related taxa. This variability originating from varied ecological and climatic factors can be so great as to negate the use of certain features for taxonomic purposes unless an anatomist can discriminate between heritable characters and those that are environmentally modified (Carlquist, 1958). Rendle and Clarke (1934a) also point out the type of variations that may occur in wood, like the vessel diameter as being influenced by local variations from pith to periphery. They further state that elements at successive annual rings are progressively larger until they reach the adult stage where the mean size remains approximately constant.

Difference in growth habits in compositae also presents contrasting features among members of related genera. Carlquist (1959c) compared the anatomical variations of the annual pacific coast Madinae with that of the Hawaiian Madinae Wilkesia and Argyroxiphium which were woody perennials and showed that the stem anatomy of these Compositae is naturally correlated with these differences in habit, He showed that the rosette stems of Raillardella scaposa (Gray) Gray, R. argentea (Gray) Gray, R. pringlei Greene and Madia bolanderi (Gray) Gray of the pacific coast and the Hawaiian species of Argyroxiphium all showed common features with regard to the possession of considerable

amount of parenchyma compared to the volume of the vascular cylinder, the presence of carbonized resin deposits in the large air spaces of the cortex and pith parenchyma and complete absence of sclerenchyma in pith, cortex and phloem except in Argyroxiphium. These features, however, are in sharp contrast with that of the large annual stems and fruticose perennial stems which are distinguished by a more limited quantity of cortical and pith parenchyma. These have prominent bundle cap fibers which do not form continuous cylinder around the stem. This type of construction with prominent bundle fibers that do not form a rigid complete cylinder allows for more secondary growth (Carlquist 1959b). On the other hand, cortical sclerification can proceed so far that the inner cortex, pith rays and even cambial region consists of sclerenchyma as shown by Calycadenia tenella Nutt. (Carlquist 1959b) in which little secondary growth takes place. This condition as well as the lack of it can be useful for systematic purposes. The list of families with this condition was given by MetCalfe and Chalk (1950). By considering the topography of fibers in these tarweed stems Carlquist (1959b) suggested the term "pericyclic fibers" to be used in relation to the fibrous cylinder occurring in these species. Thus anatomical data have proven useful on various occasions for use by systematists. McLaughlin's (1959) treatise on the Magnoliales in which he recommends, among other things, that Himantandraceae be transferred from that

order to the Anonales and Lactoridaceae to the piperales were presented in the hope that taxonomists would give them due considerations.

2.1 Xylem

The Xylem of flowering plants exhibits clear evolutionary trends in a given taxon (Carlquist, 1961), and discussion of the anatomical features of the Xylem cannot be alienated from discussion of the phylogenetic trends.

Though the abundance of woody species in the Compositae is remarkable, there is, however, a considerable scarcity of literature concerned with the wood anatomy of these plants. This discrepancy is given in a statement by Carlquist (1957a) and Gier and Burress (1942) as deriving partly from the limited commercial importance of Compositae timbers and partly from the unfamiliarity of botanists with tropical representatives of the family.

Thoday (1922) in his paper on the organization of growth and differentiation in the stem of the sunflower and Priestley and Scott (1936) in their paper on the Vascular anatomy of Helianthus annuus L. have described the main features of vascular differentiation. In a series of four papers, Carlquist (1957a, 1958, 1960a, 1960b) has presented a clear picture of the phylogenetic possibilities of the tribes Mutiseae, Heliantheae, Cichorieae and Astereae by considering 24, 54, 16 and 51 species of Mutiseae, Heliantheae,

Cichorieae and Astereae respectively.

Features of the Xylem which show "major trends" in evolution are based on the vessel element and its evolution (Carlquist 1961), Fahn (1974) noted that the arrangement of vessels in the secondary Xylem of dicotyledons presents a good characteristic feature that could be used for the identification of species, Esau (1977) also noted that the lines of specialization of the Xylem cells and tissues are better understood than other plant tissues.

"The vessel elements are phylogenetic derivatives of vertical series of tracheids in which the pit membranes have been lost" (Carlquist 1961). Thus characters of vessel elements that approximate that of a tracheid, like the possession of great length with comparatively narrow width, scalariform pitting and scalariform perforation plates were considered primitive (Carlquist 1958, 1960a, 1961). Angular vessels in transectional view were also considered primitive (Carlquist 1961). Scalariform lateral wall pitting, however, can be present in very advanced genera of Compositae like those of the Juan Fernandez Cichorieae and is interpreted as the protraction of metaxylem lateral wall pitting into secondary Xylem.

Some authors like Carlquist (1957a, 1958) have considered spiral sculpturing on Xylem elements an advanced phenomenon. Groupings of vessels are considered by many

authors to show advancement over solitary ones (Metcalf and Chalk, 1950; Carlquist 1957a). The various ways in which grouping can occur were given by a diagrammatic representation for many woods by Metcalfe and Chalk (1950). Cumbie (1960) and Stern and Greane (1958) present grouping of vessels as the average number of vessels that occur in a group. The angle the end wall makes with the vertical and the nature of perforation plates were used by anatomists to characterize woods of various origin. Adams (1949) used the number of bars in scalariform perforation plates to describe vessels in Cornaceae. Stebbins (1977) while discussing the developmental and comparative anatomy of the Compositae stated that "Wood anatomy shows trends of paedomorphosis plus specialization for Xeric habitats, and elongation of Xylem elements in more mesic habitats."

Several other works on the anatomy of Compositae include Diettert (1938) and Whittaker (1918) which showed several noteworthy features of the anatomy of Artemisia tridentata Nutt. and Solidago species respectively. Esau (1945) elucidated the course of differentiation of the first phloem and Xylem in the shoots of Helianthus annuus and Sambucus glauca Nutt and showed that the first sieve tubes of the apical portion of both shoots differentiate acropetally from the axis into the leaf in continuity with the sieve tubes of older traces and the earliest Xylem is initiated in the upper part of the shoot and differentiates upwards

towards the apices of the leaves and downwards into the axis.

Rendle and Clarke (1934b) described statistical treatment of vessel dimensions as being important in elucidating the variations that occur in vessels of different woods. Thus statistical terms like the mean, standard deviation were introduced. And in another paper, Rendle and Clarke (1934b) stressed on the importance of diagnostic features of tissues from comparative view point, like the number of vessels per unit area, groupings of vessels and the character of rays.

In his papers on the wood anatomy of Compositae, Carlquist (1957a, 1958, 1960a, 1960b) made use of quantitative characters by presenting the dimensions of average vessel element length, average diameter of vessel elements, the diameter of the widest vessel, average vessels per group, length of fibers, height of rays and maximum width of multi-seriate rays. He also used qualitative features like presence or absence of helical sculptures on vessel walls, storied elements and type of ray cells. But he also declared his skepticism concerning the values of statistical treatment of dimensions. This was particularly borne out in his investigation of Olearia argophylla F. Muell (Carlquist, 1960b) where the difference between two samples of the same species presented spectacular differences. Thus the measurement of dimension of vessel elements, while being a good comparative device for comparing different genera or species, is of little value to

segregate among plants that are closely related. But extreme differences in vessel dimensions are in all likelihood usable as specific criteria for comparing different species in a genus or family (Carlquist 1960b). The use of quantitative features, however, becomes necessary where no qualitative differences can separate any two plants.

Comparisons of species of Cichorieae (Carlquist 1960a) showed a number of qualitative differences. Carlquist (1958) noted that circular bordered pits with elliptical apertures alternately arranged are characteristic of vessel walls of Compositae. In his study of Heliantheae, Carlquist (1958) observed scalariform pitting of vessels in Coreopsis gigantea (Kell.) Hall, Espeletia incana Cuatr, E. pleiochasea Cuatr, E. hartwegii Cuatr, and Lecocarpus pinnatifidus Dec. These features were interpreted as being associated with the rosette tree habit of the species rather than indicating primitiveness. Carlquist's (1960b) work on Astereae, likewise is worthy of consideration for comparison of species. Here he made use of the differences in rays in Haplopappus parishii (Greene) Blake and H. pinifolius Gray which are distinctive in that they lack erect cells in rays. But the most outstanding differences among species in Haplopappus are offered by the degree and type of helical sculpturing in vessels and the relative degree of vessel aggregation. The importance of rays for comparative purposes is also seen from the works of Rendle and Clarke

(1934) and Stern and Greene (1958).

Leaf

The leaf, being anatomically the most varied organ of angiosperms, presents anatomical variations that concur closely with generic and specific lines. There is a large amount of literature on this aspect; some of these revealing pertinent characters of leaf histology. Thus the mesophyll could be bifacial or isolateral, and undifferentiated into palisade and spongy tissues (Metcalf and Chalk 1950). Mesophyll Cells could be converted into sclereids (Carlquist 1958), secretory canals or cavities could be present in leaves (Carlquist 1961), Vain sheaths may be present or absent (Metcalf and Chalk 1950), sclerenchyma could be present in bundle sheaths (Carlquist 1958b). Hydathodes also may be present in leaves (Lersten and Curtis 1985).

Carlquist (1957b) described the leaf structure and ontogeny of Argyroxiphium and Wilkesia. The leaf anatomy of Holocarpha, that of Calycadenia and the leaf anatomy of several pacific coast Madinae were dealt in Carlquist (1959b, 1959a, 1959c), respectively. The Studies on Argyroxiphium revealed some anomalous features, Argyroxiphium contains loosely arranged mesophyll parenchyma, the intercellular spaces of which are partly or completely filled with pectic compounds. A second anomaly is the presence and orientation of three sets of bundles in the leaf, the lower set of bundle being inverted in orientation while the other two sets are normal.

Comparison between the species A. caliginii Forbes and A. sandwichense Dc. also showed several anatomical differences. A. caliginii possesses paired secretory canals along the marginal veins whereas these are totally lacking in A. sandwichense. Other differences regarding trichomes and cuticle of these two species was also noted. The differences were attributed mainly to the differences in ecology and habitat climate.

In general, the leaves of some Compositae were shown to have great variations in structure between species and genera as well as within a single species. The lines of investigation were on differences between basal and upper leaves, presence of resinous secretory channels, arrangement of bundles and presence or absence of bundle sheath extension (Carlquist 1957b, 1959b, 1959c). Comparative leaf anatomy of Solidago and related Asteraceae was also done by Anderson and Creech (1970) in which they used the kinds of storage parenchyma, secretory cavities, mesophyll sheath extension and characters of the mid-vein as the major features of diagnostic value. Thus some Compositae could have longitudinally elongated areoles like Dubautia linearis (Gaud.) Keck (Carlquist 1959c) or Calycadenia multiglandulosa Dc (Carlquist 1958b) with lower leaves having bundles in a single plane or with arc of bundles recurved towards the lower surface of the leaf like Hemizonia pungens H & A (Carlquist 1959c) owing to a particular ontogenetic history.

This process of recurvature is found in the most advanced genera such as Blepharizonia and Calycadenia (Carlquist 1959a) and Holocarpha (Carlquist 1959b). Marginal strands of fibers are prominently represented in the basal leaves (Carlquist 1959b) and according to Carlquist (1956b) these bundle fibers, although some are associated with veins, appear to lack conducting tissues.

Apart from the gross histology of the leaves of Compositae, leaf surface features like the various induments were utilized for the characterization of taxa. Among Compositae, the sub-tribe Madinae are by far the most thoroughly studied regarding trichomes. From the study of Carlquist (1958b, 1959a, 1959b), some members of this taxon are shown to have more than one trichome types. In Madinae a uniseriate non-glandular and a biseriata glandular type have been basic to the development of all trichomes (Carlquist 1958b). Thus within each group trichomes can show phylogenetic trends. In Calycadenia (Carlquist 1959b) multiseriate capitate type trichomes have been derived from a single biseriata glandular trichome, these in turn have given rise to hollow stalked glands, "tack shaped" glands and sessile glands (Carlquist 1961). The term gland was used by the author when describing a glandular appendage, on account of the fact that tissues other than the epidermis are involved in mature glands and that these are not simple epidermal trichomes (Carlquist, 1959c, 1959a). The fact that

trichomes can sometimes be remarkably uniform in a given taxon and can be used for taxonomic purposes was revealed by some authors (Cutler, 1958; Esau, 1977, Fahn, 1974, Mesfin 1984). Metcalfe and Chalk (1950) also noted the importance of these appendages in the classification of genera and species.

In light of the various literature written on them, members of the family Compositae are notable on the whole for the possession of different kinds of appendages on their leaves. The ontogeny of some of these trichome types was investigated by Carlquist (1959b) as they occur on four species of Holocarpha. Several trichome types can occur on a single plant and some species show a change in indument from base to apex of a single leaf. This fact is exemplified by the leaves of Calycadenia (Carlquist, 1959a) in which large uniseriate trichomes are present near the base, especially along the margins and absent in distal portions. On the other hand, the "tack shaped" glands characteristic of the genus occur in distal portions of the leaf near the tip.

Other isolated anatomical details of compositae include the presence of hydathodes in the leaves (Lersten and Curtis, 1985). Carlquist (1957b) also reported massive hydathodes occurring along the leaf margins of Argyroxiphium caliginii but these are totally lacking in A. sandwichense. Intrusion of pectic materials into intercellular spaces are reported for the first time in Fitchia speciosa Cheeseman

and Wyethia ovata T. & G. (Carlquist 1956) and are found in petioles and absent from the leaf, while they are abundant in the leaves of Madinae (Carlquist 1959c).

3. Materials and Methods

G. abyssinica seeds were purchased at a local market in Addis Ababa and seeds of V. galamensis Subsp. galamensis Var petitiana were collected from Sidamo. Voucher specimens are kept at the ETH. herbarium (ie. collection Mesfin et al 3253). These were planted in glass houses on July 18, 1986. Beginning from the day after germination, specimens of leaves and stems were collected at intervals of three days. The materials were fixed in FAA. The specimens were dehydrated in a series of ethanol, cleared in chloroform and embedded in paraffin wax according to the technique described by Bass (1958). Sections were cut on an AQ "820" microtome, stained using safranin and fast green and affixed to slide using Canada balsam.

Xylem characters were analyzed following the outline of Carlquist (1957a, 1958a, 1960a 1960b). From the longitudinal sections of each specimen the length of about 25 vessel elements were measured according to the suggestions of Chalk and Chattaway (1934). Terminologies used in the paper are those proposed by the Committee on the Nomenclature of the International Association of Wood Anatomists (1957 and the illustrated glossary of Cutler (1978).

Because of the large amount of technical work involved in such a study, the materials investigated had to be restricted to those regarded as representatives for each

specimen. With this aim in view, special attention was given to the obtaining of more mature parts for every stem specimen taken. Thus collection of stem materials were made from the second internode from the base. Leaves that didn't show any sign of disease were chosen. The approach is to lay stress on the comparative relationship between the age of the plant parts and their structure. Attempts were made to survey the literature dealing with the anatomy of plants, especially those dealing with Compositae.

4. Results and Discussion

The following description of the anatomy of the stems and leaves of V. galamensis and G. abyssinica is based on studies of transverse and longitudinal sections of the stems and transverse sections of the leaves. Appendix 1, 2 and 3 provide summaries of some characters of the stem. Features which were observed in only one species or which are not suitable for summarization are described in the text.

The objective of this study and the nature of sampling demanded a consideration of the characters of both primary and secondary tissues. Except for secondary Xylem, no specific criteria or pattern of evaluation have been suggested in the limited literature on the anatomy of herbaceous plants. Furthermore, although various lists have been prepared as a guide to the important diagnostic features of the secondary xylem like those of Carlquist (1957a, 1958a, 1960) Chalk and Chattaway (1934) and Rendle and Clarke (1934), these are based largely upon the mature xylem of woody plants.

4.1 Stem

4.1.1 Epidermis

The epidermis in both species is uniseriate consisting of a single layer of cells. Multicellular hairs develop from the epidermis in both plants (fig. 1). In G. abyssinica

rectangular cells occur uniformly in longitudinal files with their longer sides perpendicular with the axis of the plant, while in V. galamensis the cells composing the epidermis are more or less isodiametric and of uniform shape (figs. 2 and 3).

4.1.2 Collenchyma

This tissue occurs in both species occupying the outer periphery of the cortical region just beneath the epidermal layer. In G. abyssinica, the collenchyma is two cell layers thick and is found next to the epidermis, though the cells composing the epidermis are not thick walled; two layers of collenchyma can readily be identified in all the specimens of G. abyssinica investigated as they stand out clearly in contrast to the larger and thin-walled cortical parenchyma cells. In the relatively younger sections of specimens of V. galamensis three layers of this tissue are observed while in the older ones, the layers increased to four. Figures 4 and 5 represent sections of V. galamensis at fifty five and seventy nine days after germination respectively.

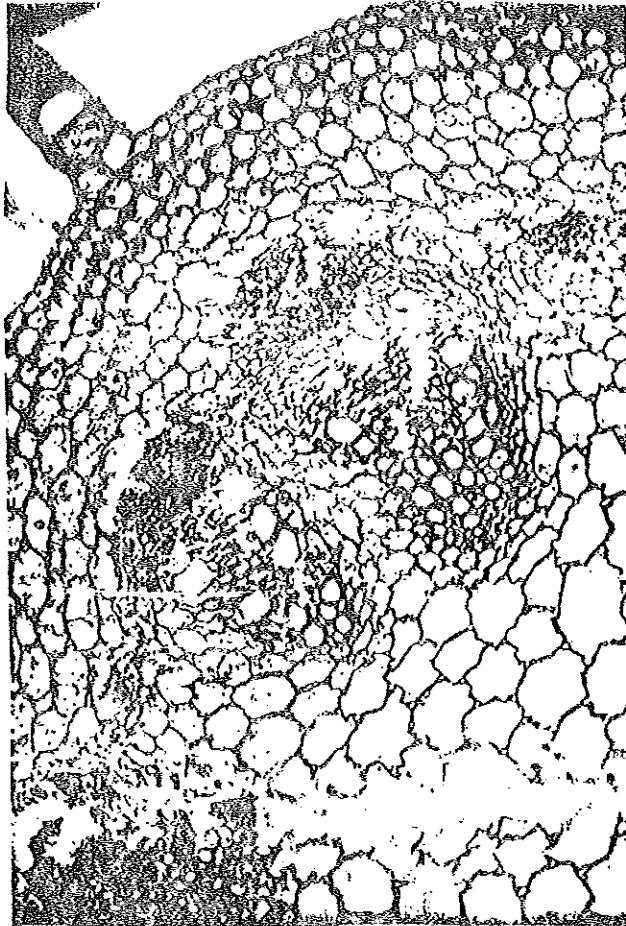


Fig. 1. Transverse section of part of the stem of Y. galamensis (X160) showing two layers of collenchyma and uniseriate multicellular hair.

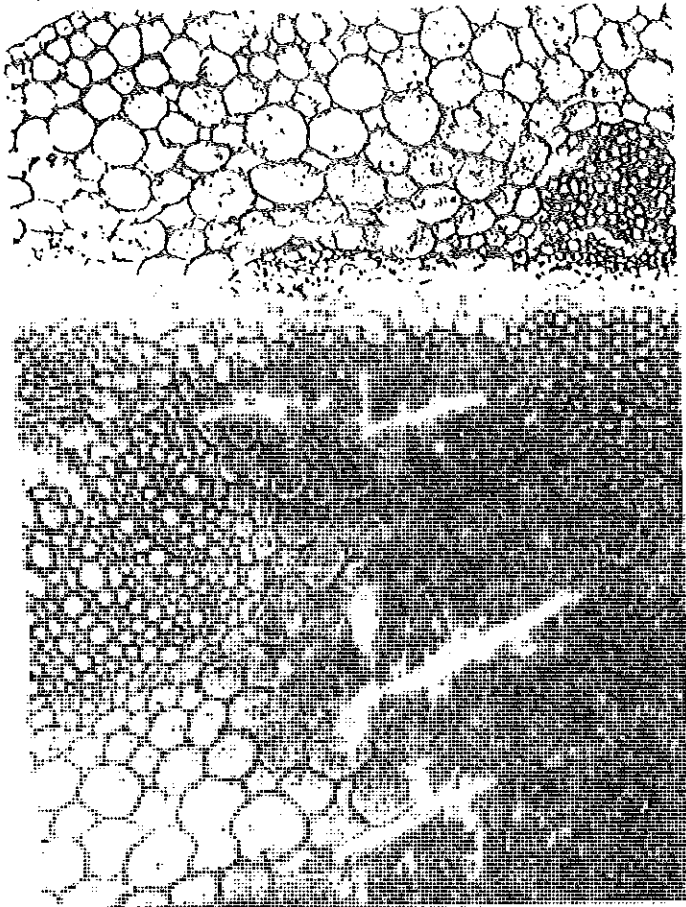


Fig. 2. Transection of stem of V. galamensis (X160) showing isodiametric epidermal cells and the first formed vessel elements in radial rows.

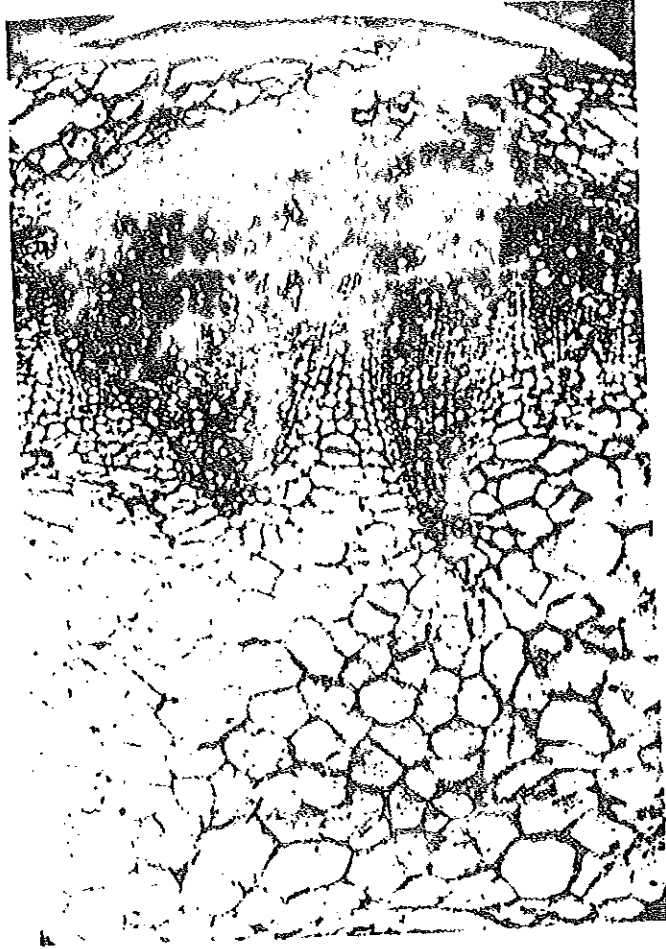
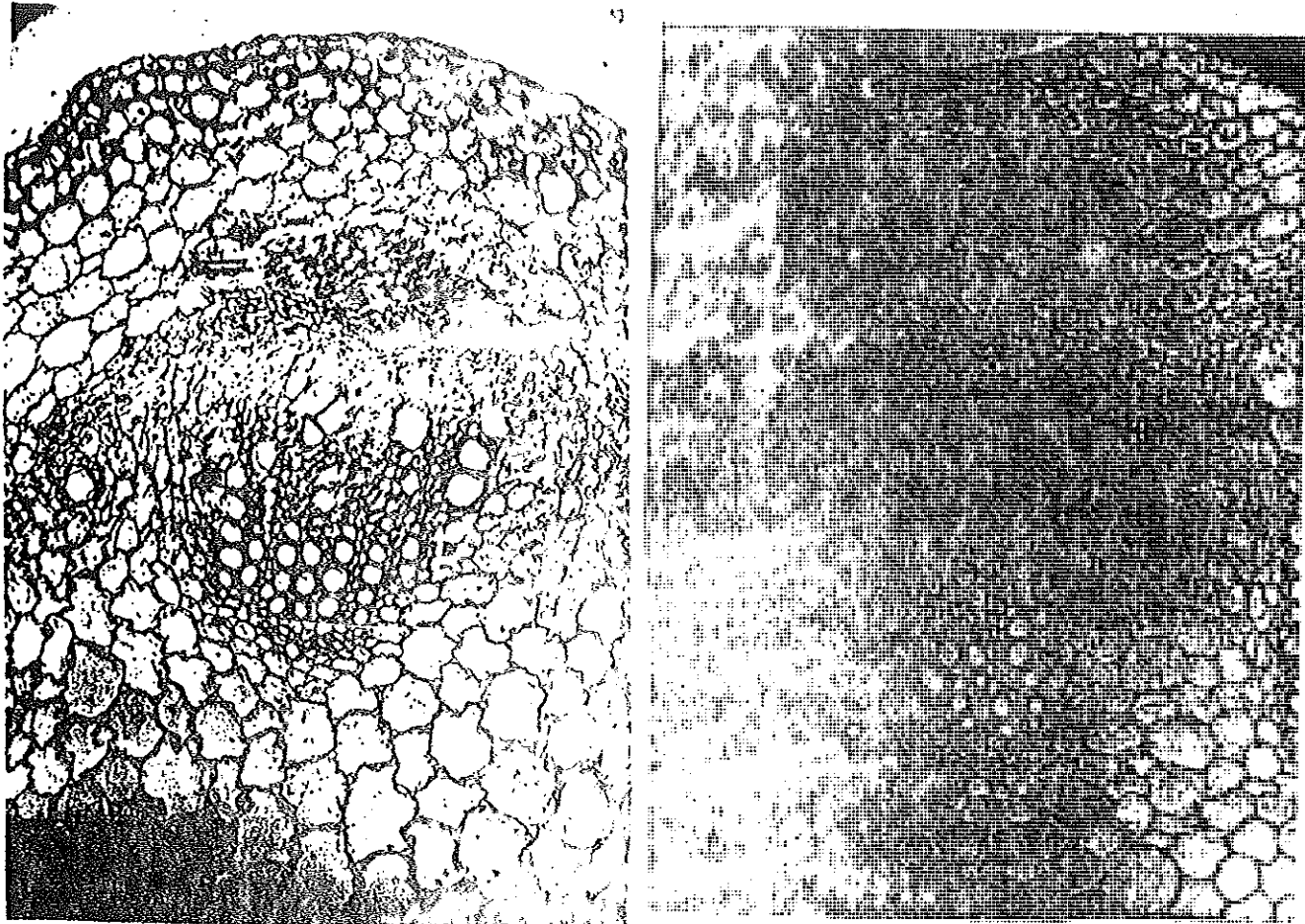


Fig. 3. Transsection of the stem of G. abyssinica ($\lambda 24$) showing epidermal cells that occur in longitudinal files and collenchyma layers.

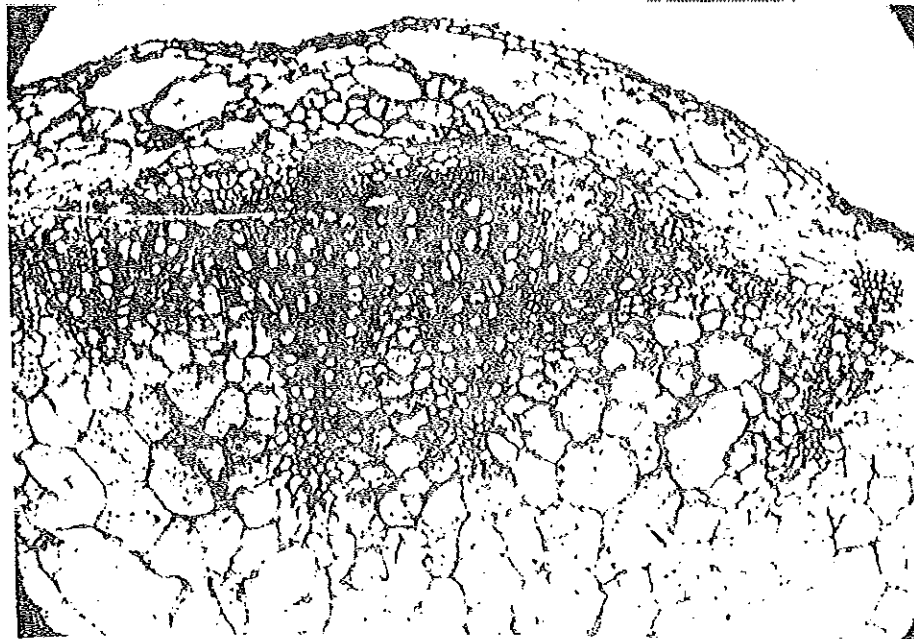
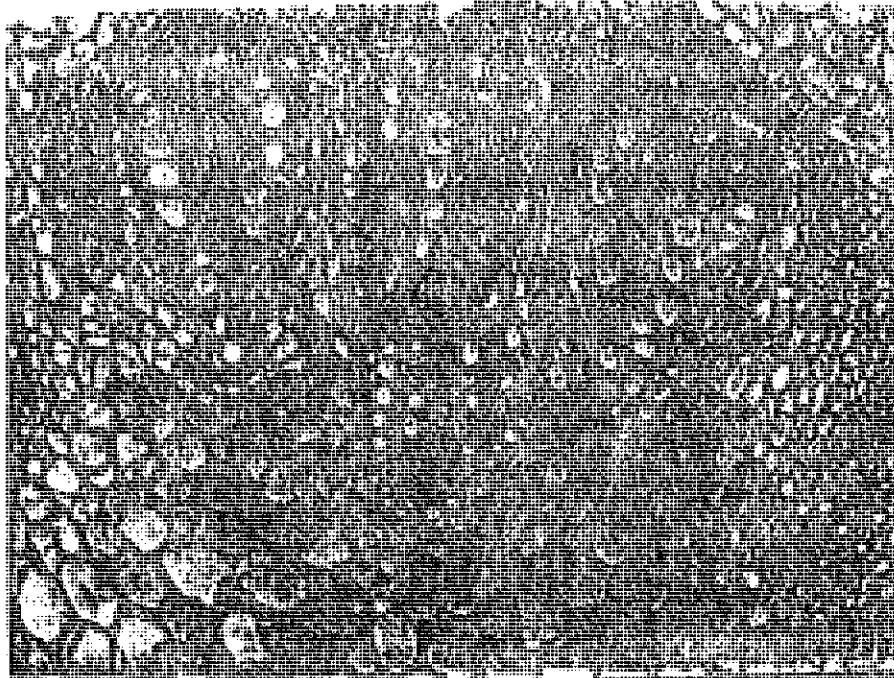


Figs. 4 and 5. Figures showing variation of collenchyma layers with age of the stem of V. galamensis, Fig. 4 55 days old stem of V. galamensis (X160) showing formation of three layers of collenchyma. Fig. 5 V. galamensis stem (X160) at 79 days after germination showing four layers of collenchyma.

4.1.3 Parenchyma

The cortical parenchyma is four cell layers thick in the relatively mature stems of both species. In the younger parts of both species, there are relatively more layers of cortical parenchyma and only one layer of collenchyma. Thus the one day old stem of G. abyssinica contains a layer of collenchyma and six layers thick cortical parenchyma. The parenchyma cells in older stems of G. abyssinica are larger than those in younger stems and is angular in outline (fig 7).

More or less round cells of uniform shape characterize the parenchyma of V. galamensis. These are depicted in Fig. 6. As indicated at appendix 3 and Fig. 8, at the initial stages of development of V. galamensis, the average diameter of the perenchyma cells is a little higher than at the mature condition. But as the plant advances in maturity the average diameter of these cells remains almost constant.



Figs. 6 and 7. Transsection of stems of V. galamensis and G. abyssinica showing relative parenchyma size and shape of the two plants at 70 days after germination. Fig. 6 - V. galamensis (X160) showing smaller and rounded parenchyma cells. Fig. 7 - G. abyssinica (X24) showing relatively larger and angular parenchyma cells.

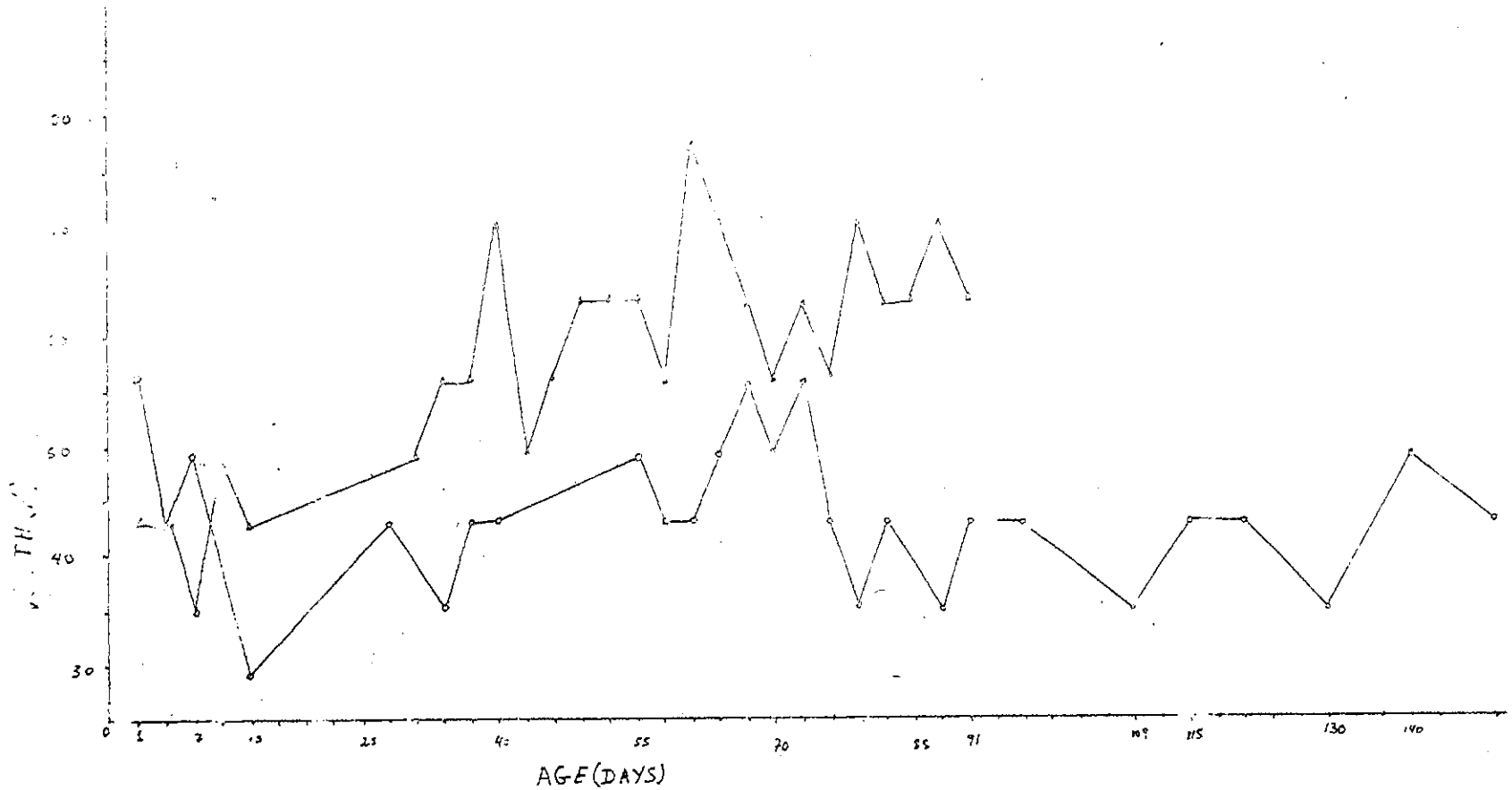


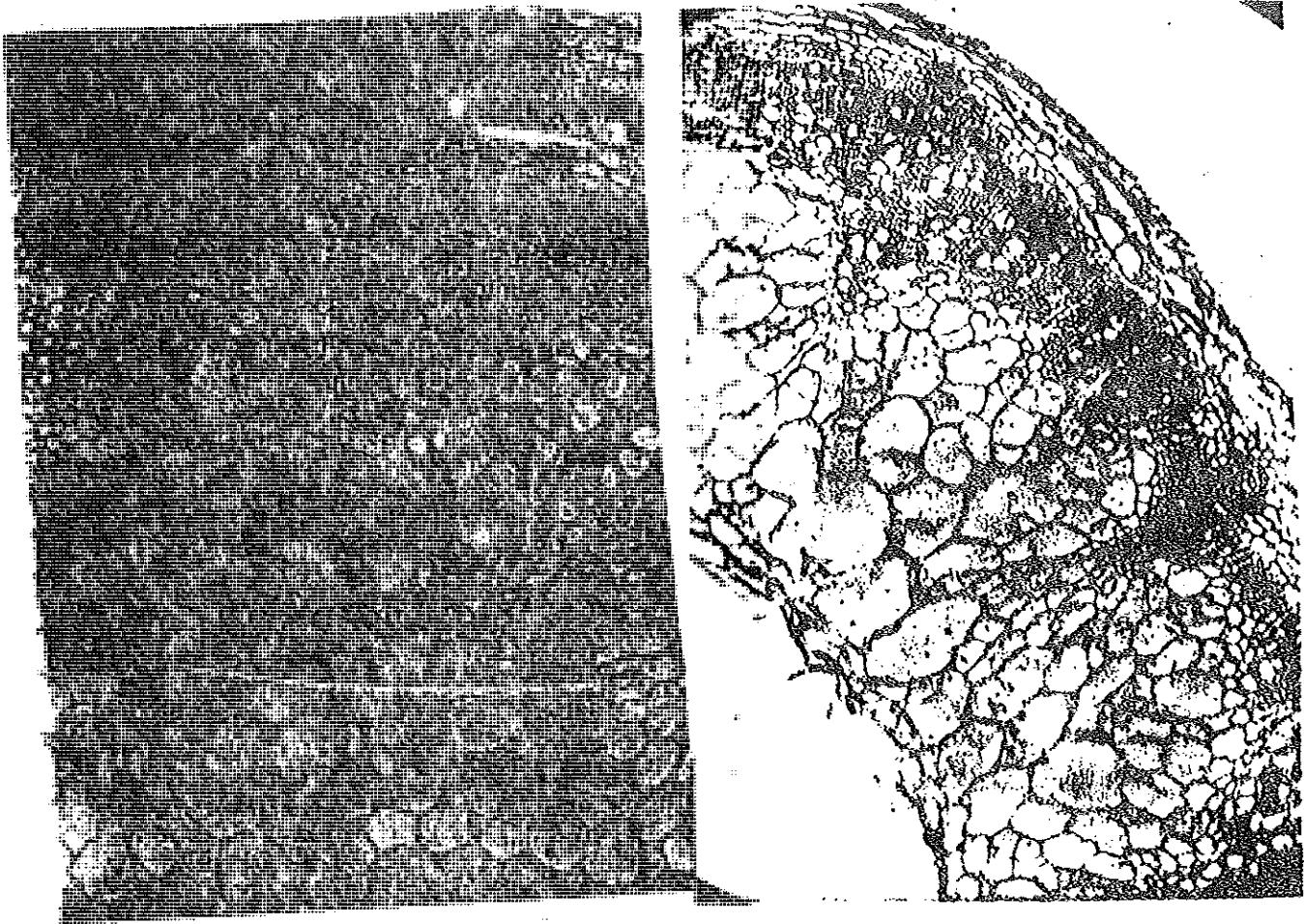
Fig. 8. Graph to illustrate relation of size of parenchyma with age of the plant for G. abyssinica and V. galamensis. The figures represent average diameter of ten cortical parenchyma measurements (O- V. galamensis, Δ -G. abyssinica)

The pith of both species comprises solely of parenchymatous cells. The pith cells in G. abyssinica is early maturing. This phenomenon is ascertained by the fact that the pith of G. abyssinica starts to disintegrate at a relatively young age ie beginning from day 37 hollow pith resulting from the disintegration of the central parenchyma cells is observed (fig. 10). This phenomenon of pith destruction as explained by Fahn (1974), Thoday (1922) and Hare (1941) as stemming from the ontogeny of pith cells. In herbaceous species like G. abyssinica the pith cells mature very early and stop growing while the surrounding tissues are still meristematic and enlarge longitudinally and in circumference thus tearing apart the pith cells. It will be seen from figure 10 that the cells surrounding the hollow pith in G. abyssinica are dead cells which were torn apart. Even in the earlier stages of growth of G. abyssinica, stem internodes which are far from the base have hollow pith while those near the base have intact pith. This is in agreement with Thoday (1922) who wrote that there is a diminution of tangential growth downwards in the lowest internode and that as the root is approached the pith suffers less and less strain which is an accomodation to the absence of pith in roots. In V. galamensis, the pith parenchyma is observed throughout keeping pace in development with the diameter of the stem. Figure 9 is a section of the stem of one of the

older specimens of V. galamensis which indicated the presence of intact and living pith cells. According to Hare (1941), great development and long persistence of a living pith provides the plant with good reserve of water storing tissues. In this respect it is interesting to note that the adaptability of V. galamensis in an arid or semi-arid habitat may in part be related to this condition of long persisting pith. Comparison of the amount of such water storing tissues to those engaged in conduction lends support to the contention that V. galamensis is suited to life in a moisture scarce environment. In figures 11-18 are depicted tissue maps representing stem cross sections of the two species at different stages of growth. Here increase in the age of the plant is associated with increase in circumference of the stem which in turn brings about the tearing apart of the pith cells the gradual development of rings of vascular tissues from vascular bundles, and the diminution of cortical parenchyma. As shown in figure 11 the disintegration of pith cells started at day 37 for G. abyssinica.

4.1.4. Sclerenchyma

Sclerenchyma occurs as Xylary and phloem fibers in the stems of both species. A well defined region of fibers is found in discrete bands peripheral to the phloem tissue (figs. 7 and 9). The bands of fiber represent the main strengthening tissue in the stems. Clear differen-



Figs. 9 and 10. Transsection of the stems of V. galamensis (X160) and G. abyssinica (X25) respectively showing ontogenetic variation in the development of pith cells. In fig. 9, V. galamensis stem is depicted with intact pith cells, while in fig. 10, is shown a section of G. abyssinica of the same age with collapsed cells surrounding the hollow pith.

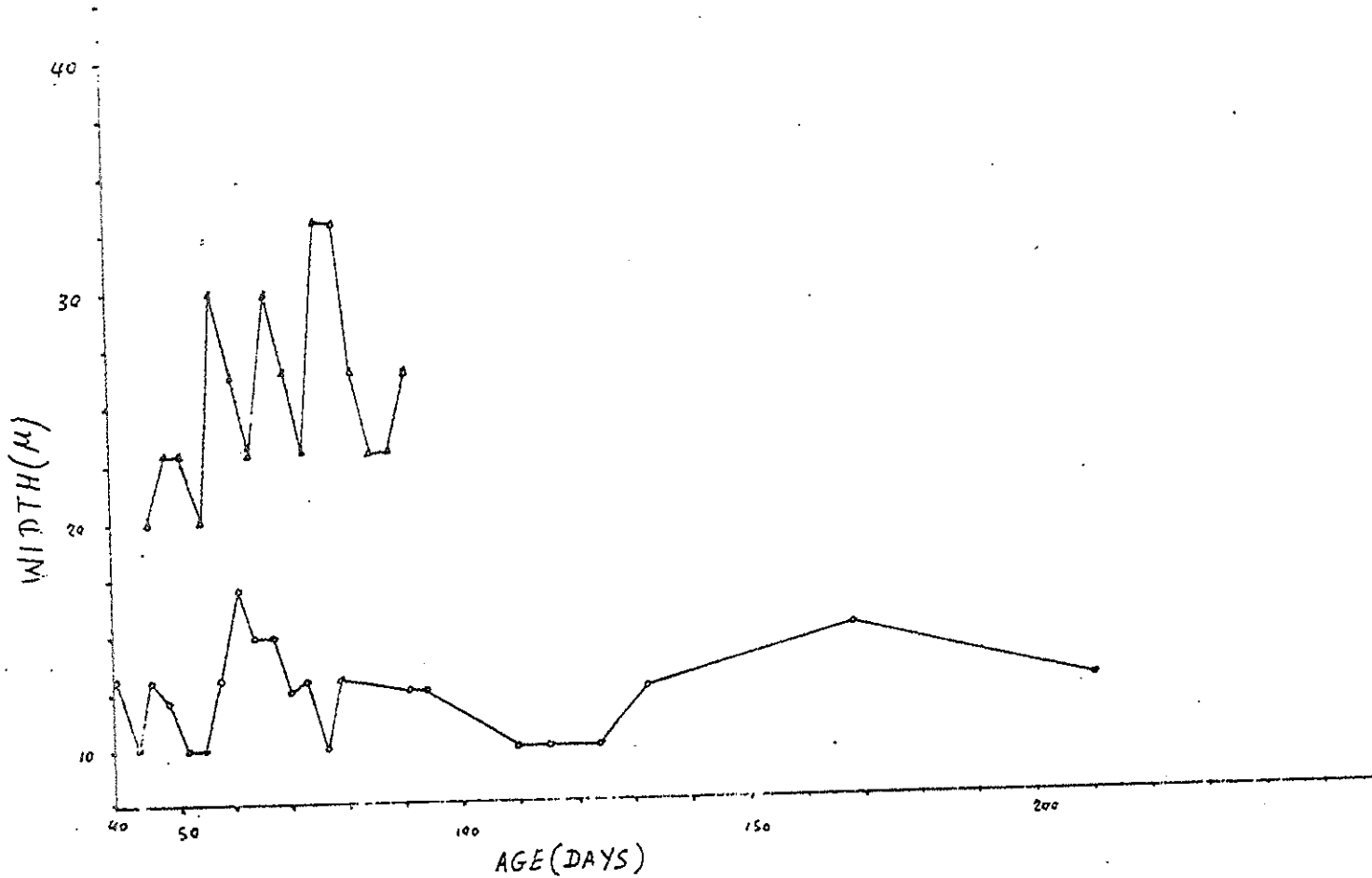


Fig. 19 Graph showing cross sectional diameter of phloem fibers of V. galamensis and G. abyssinica. The figures (O) for V. galamensis and (Δ) for G. abyssinica represent averages of ten measurements.

tiation of this tissue appeared at about forty days in V. galamensis and forty six days in G. abyssinica. This is depicted in the tissue maps shown in figures 11-18. As can be seen from figure 19, the width of the fibers in G. abyssinica varied from 20 to 33.3 microns and that of V. galamensis ranged from 10 to 13.3 microns (see also appendix 1). Unlike the vascular tissues that increase in volume along with the increasing age and circumference of the stem, the phloem fibers, however, show little or no increase in volume with increase in the girth of the stem. This can be compared from the figures between the younger and older specimens of both species relative to the volume of the vascular tissue with which they occur (figs. 20, 21, 22).

4.1.5. Aerenchyma

A highly lacunar tissue develops in the cortex of the stems of G. abyssinica. The parenchyma cells comprising the cortex remain thin walled, elongate and develop large intercellular spaces between them. These tissues are particularly well developed in the relatively older stems. They are observed to be quite common in specimens of G. abyssinica taken between sixty four and ninety one days after germination (figs. 7 and 23), but it appears to begin development after about a month. The development of this lacunar tissue is probably attributed to the climatic conditions prevalent in places where it is commonly cultivated. It is grown in the moist highlands of the country where rain-

fall is abundant. The fact that G. abyssinica plants require substantial quantity of moisture for growth was discerned when they were raised in glass houses. Reduced soil moisture in the glass house resulted in wilting of the plants. Thus G. abyssinica plants used for this study were watered daily.

Aerenchyma being a system through which diffusion of gasses occur, develops as an adaptive feature in plants that grow in an environment where aeration is poor (Esau, 1977). The presence of aerenchyma in the stem of G. abyssinica probably is related to the climatic condition that exists in its natural area of distribution that in turn affects the aeration in the soil. The distribution of this species in Ethiopia being in those areas where precipitation is high and evaporation is low compared to other areas of the country; destines the development of underground organs in a medium which is deficient in oxygen. This in turn would have made the evolution (development) of copious intercellular spaces inevitable to counteract the conditions of oxygen deficiency in the soil. Thus the development of aerenchyma in the stem of G. abyssinica is a notable feature indicating structural adaptation of the plant to its moist habitat. The production of aerenchyma in the stem of G. abyssinica thus could be attributed to the poor aeration condition of the soil to which the species was subjected for innumerable years in the

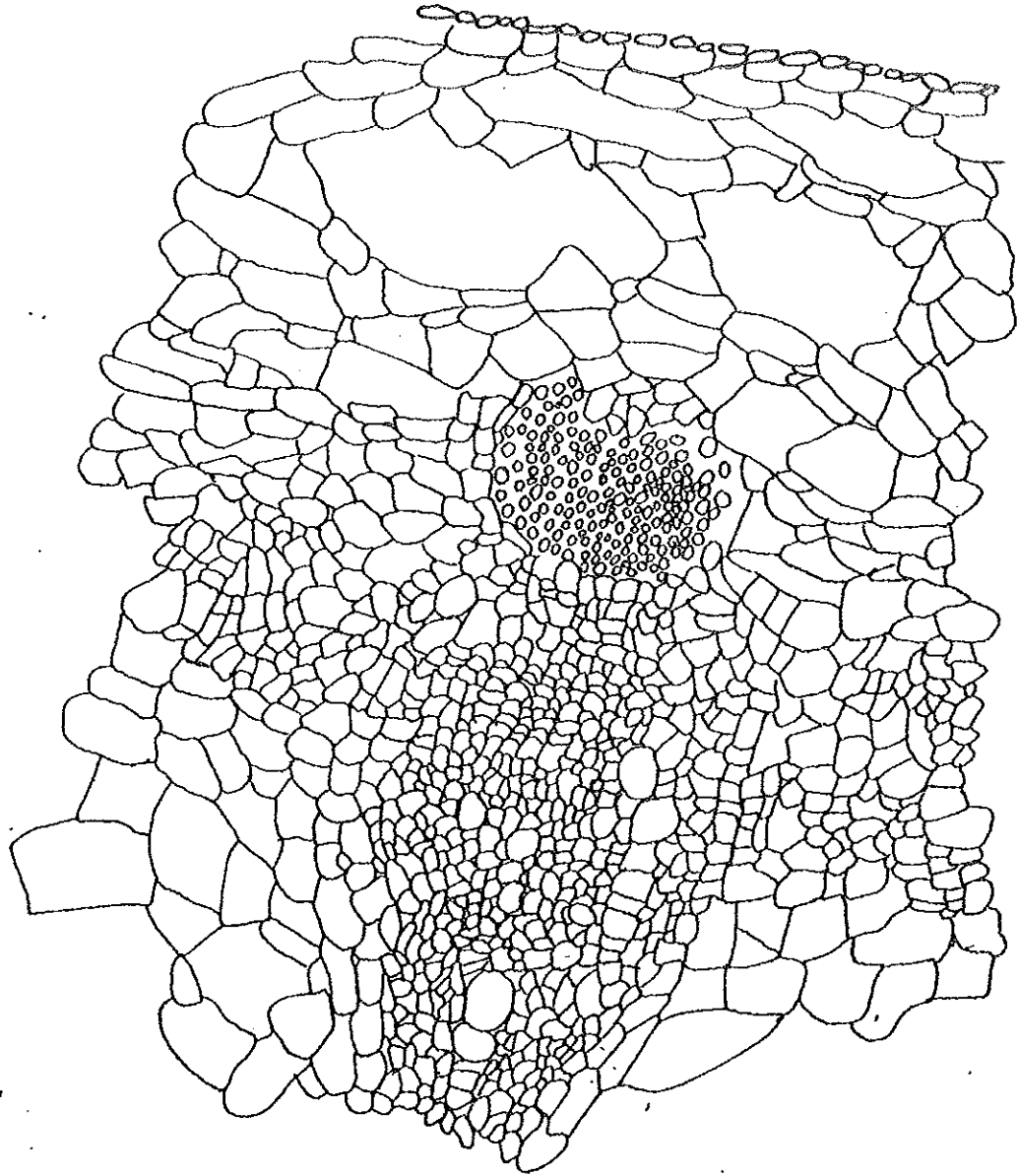


Fig. 23

Fig. 23 Camera Lucida drawing of stem cross section of *G. abyssinica* (X100) showing extensive development of aerenchyma in the cortex.

history of its evolution. However, whether the presence of this tissue is an anatomical feature inherent to all the species of Guizotia, or is a specific character confined only to G. abyssinica is worth investigating. Further studies concerning the anatomy of this species from representative specimen grown in the field is recommended.

4.1.6 Vascular Anatomy

4.1.6.1 Vessel size and shape

At the initial stages in their development the vascular tissues of both G. abyssinica and V. galamensis occur as separate bundles. The one day old stem of G. abyssinica has four conspicuous vascular bundles at four corners of the cylinder (fig. 11). These increase to eight after a week and to nineteen after thirteen days. The one day old stem of V. galamensis consists of five bundles initially but six and eight bundles at seven and thirteen days, respectively (fig. 16). The vascular bundles, as seen in figures 24 and 25, are fairly widely spaced and consist of radial rows of small vessels. With time, however, the number of vascular bundles and the total area covered by them increases along with complexities in the vascular tissue of both species. As the plants grow, cambial strips appear joining the vascular bundles. Complete interfascicular cambium is formed all around the axis of the plant around thirty four and forty days after germination

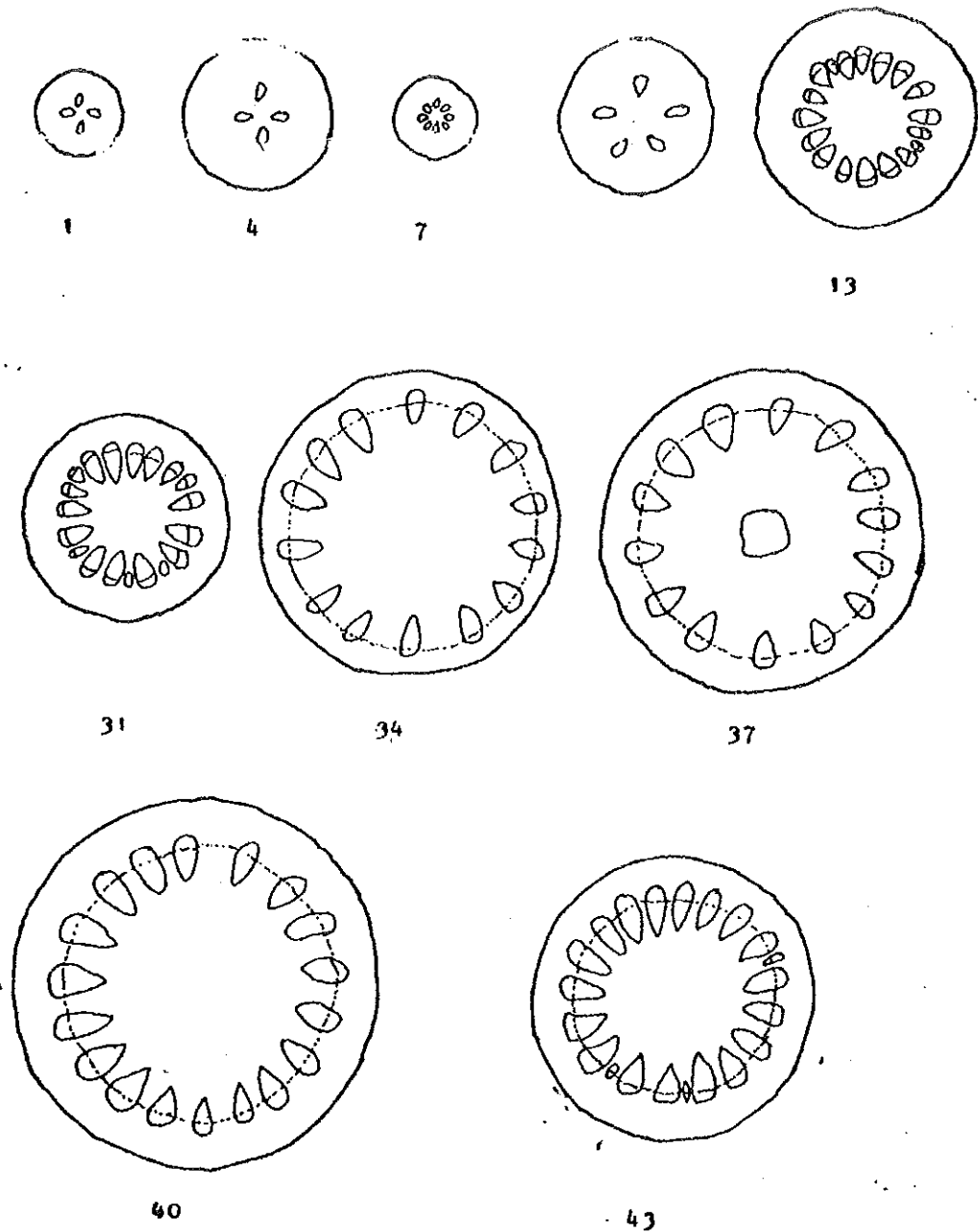
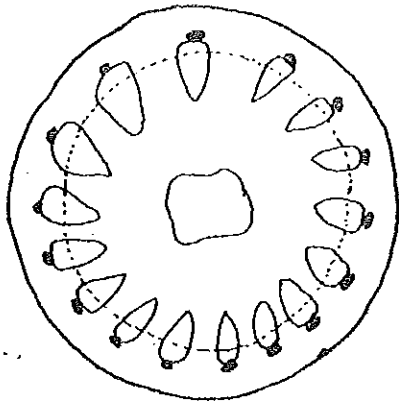
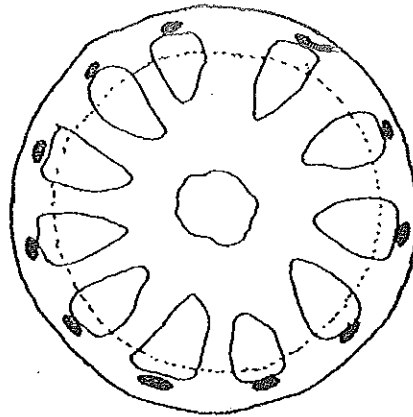


Fig. 11

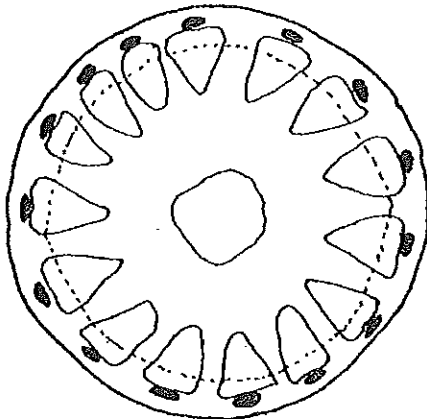
Fig. 11-14 Tissue maps of the stem (C.S.) of G. abyssinica at different stages of development. The gradual development of the cambium all around the stem, increase in the amount of vascular tissues with increasing age of the plant and the disintegration of pith cells are depicted. Figures represent days after germination.



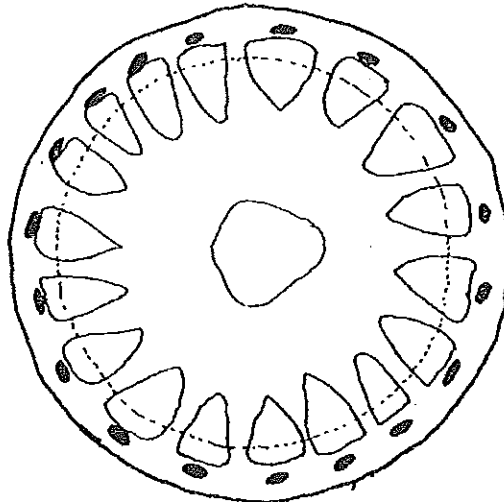
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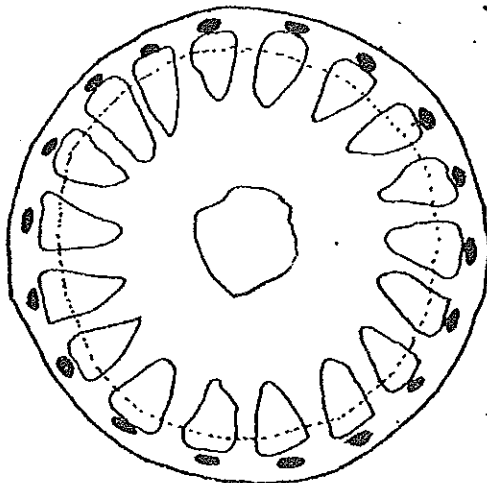
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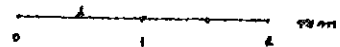
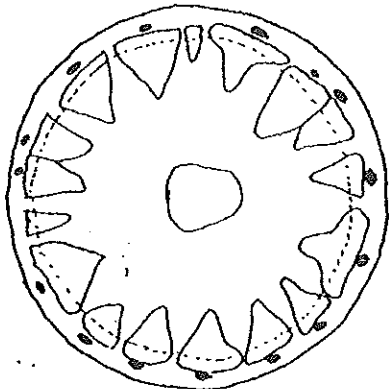
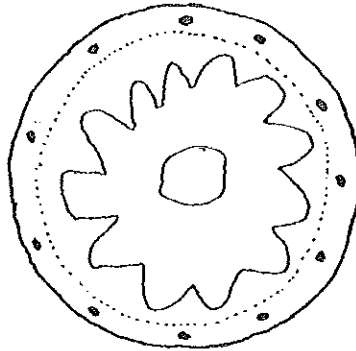


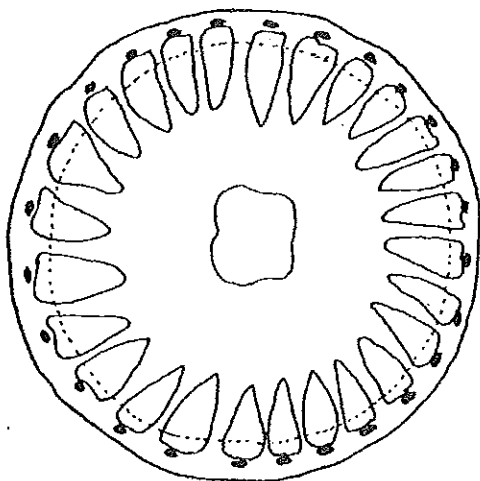
Fig. 12



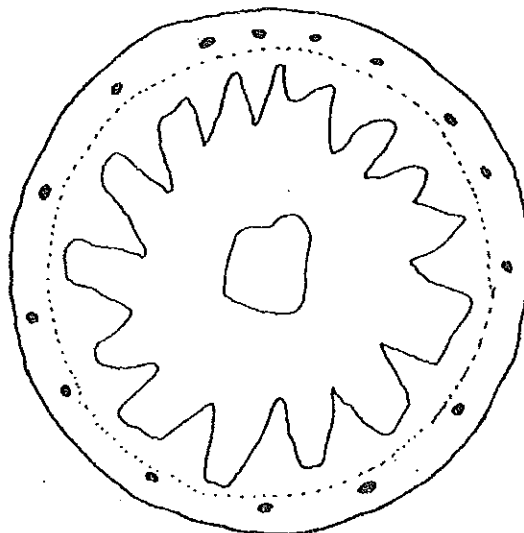
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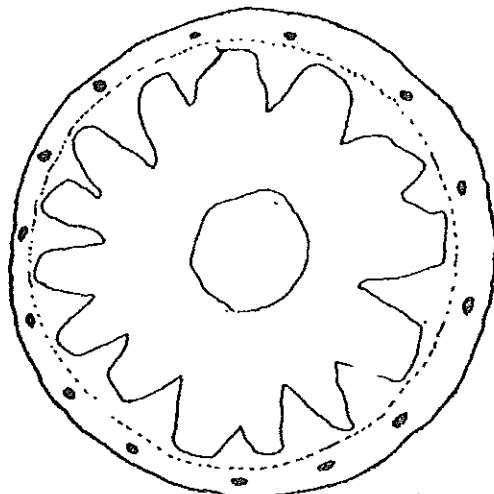
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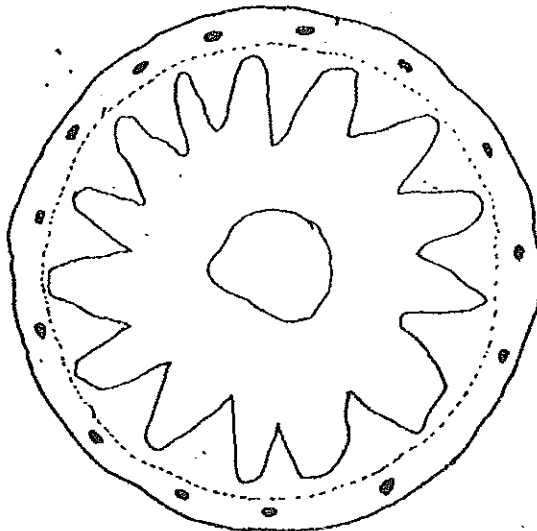
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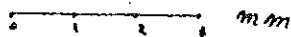


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Fig. 13



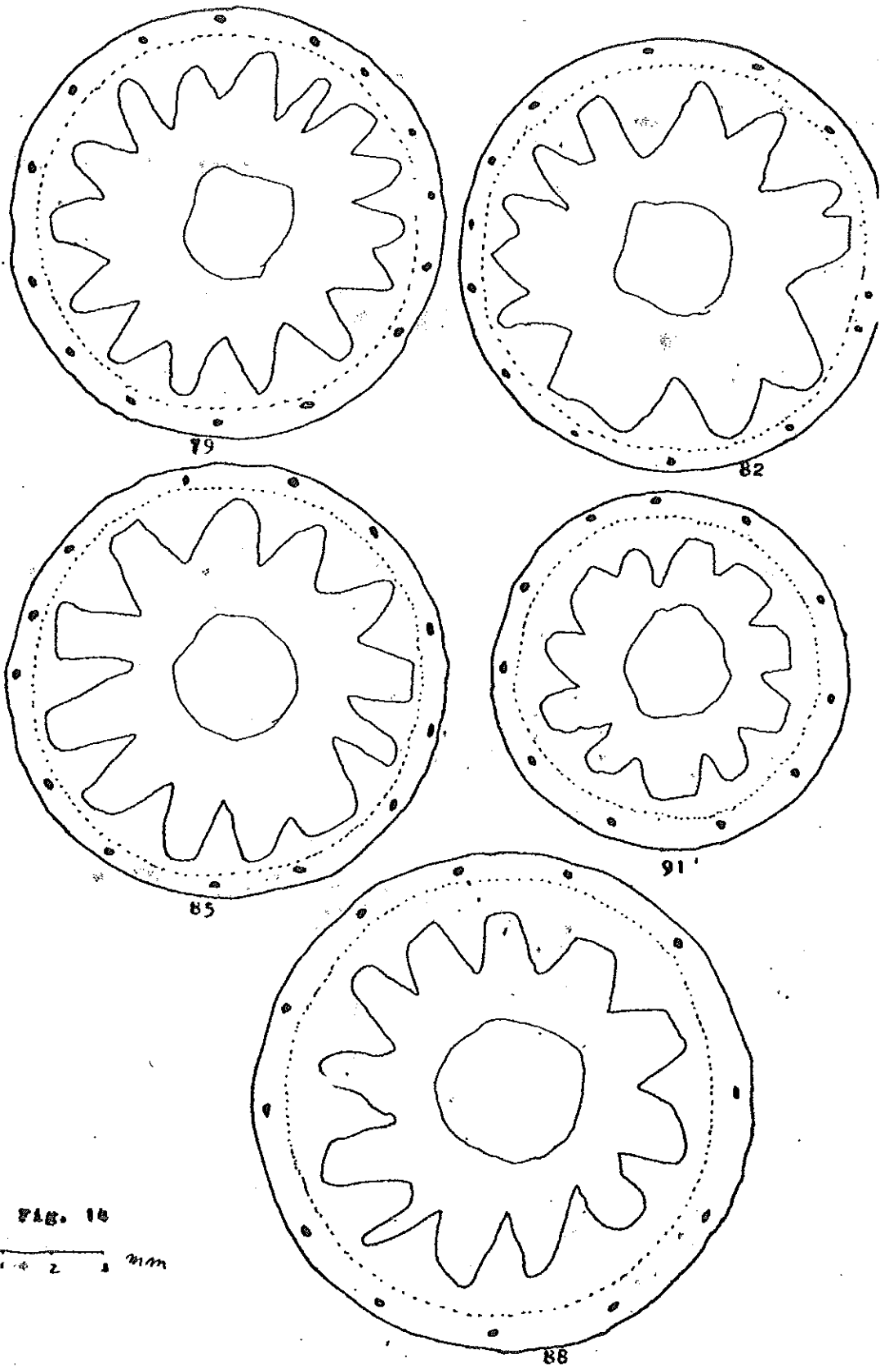


FIG. 14
0 1 2 3 mm

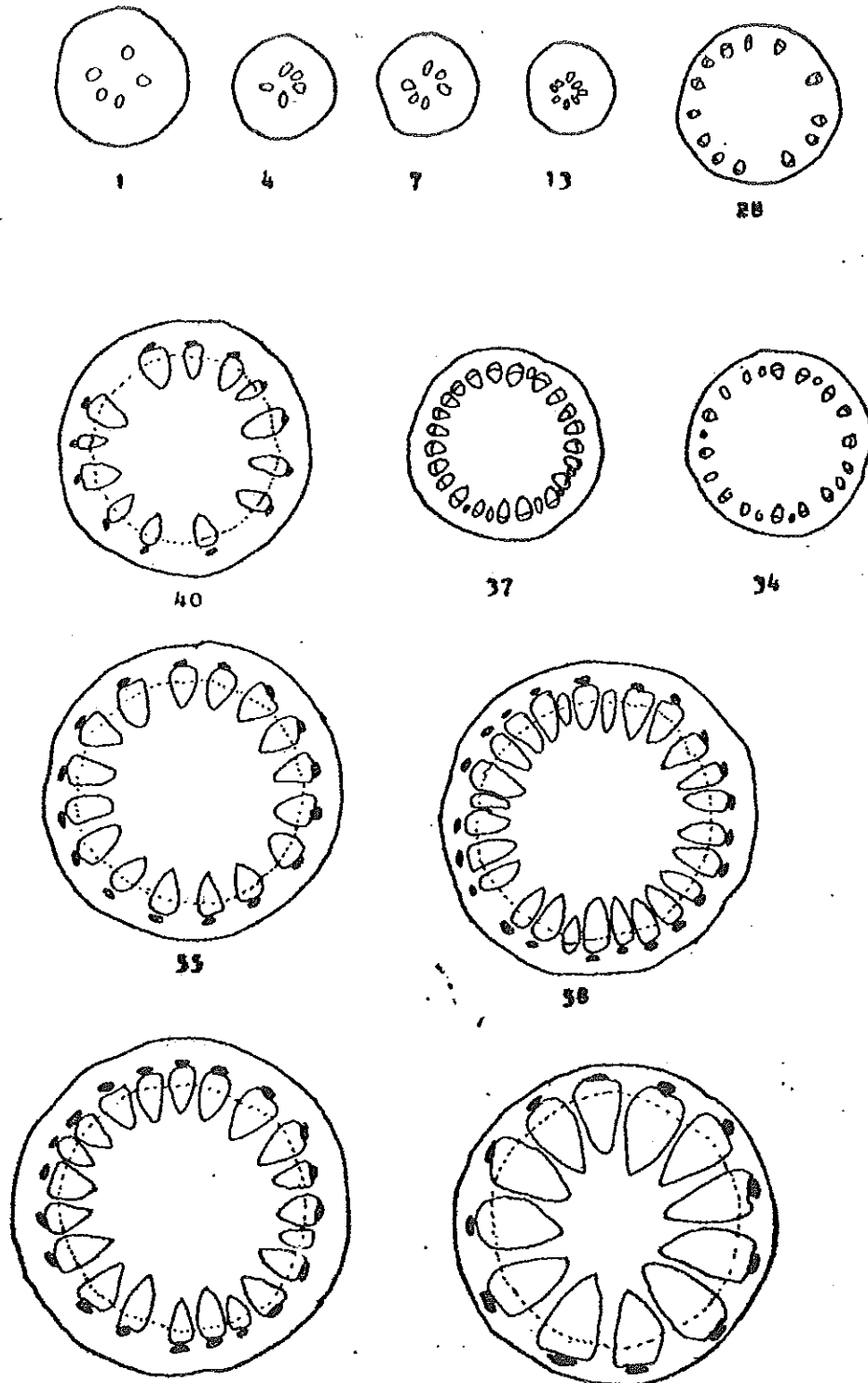


Fig. 15

61

1 mm

64

Fig. 15-18 Tissue maps of the stem (C.S) of V. galamensis at various stages of growth (Similar development as in G. abyssinica are depicted). Figures represent days after germination

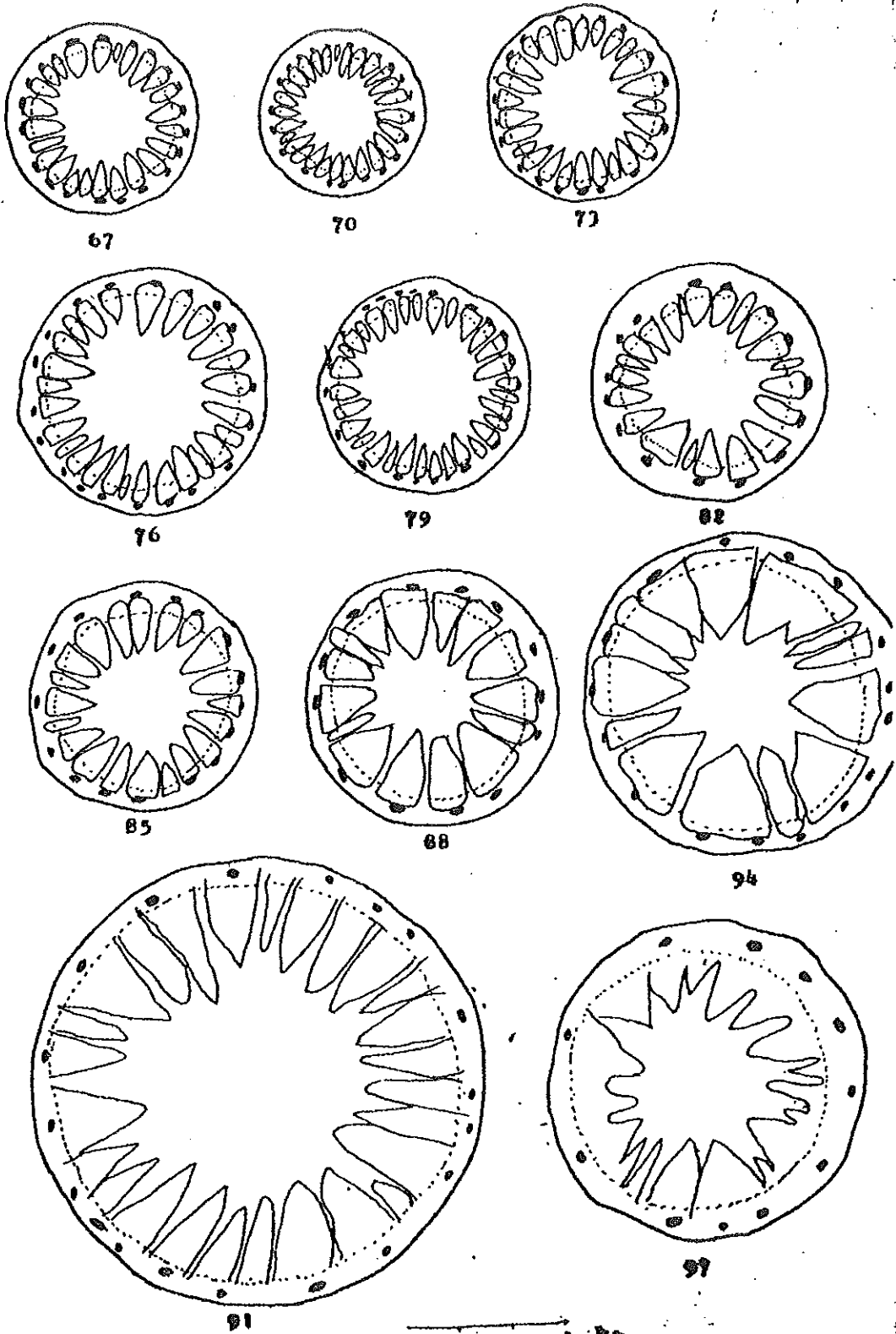
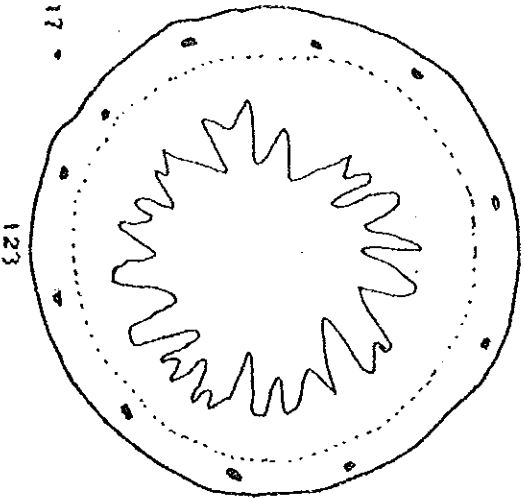


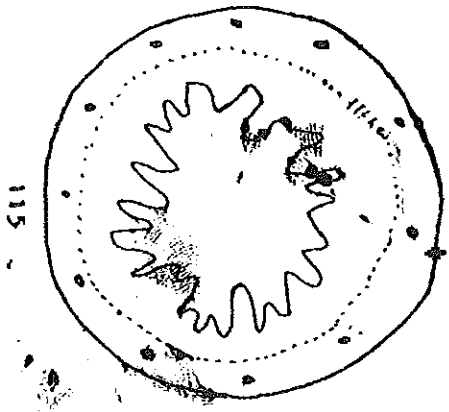
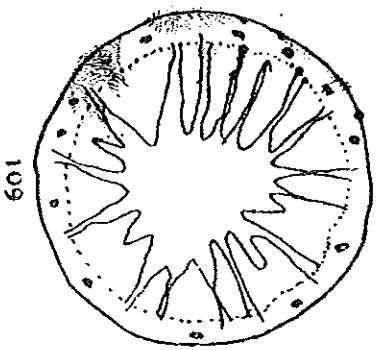
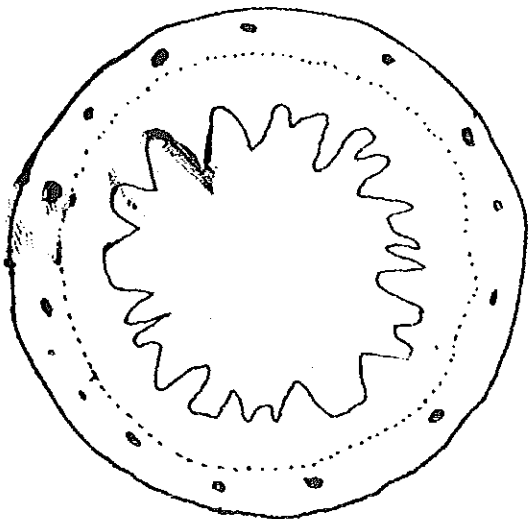
FIG. 16

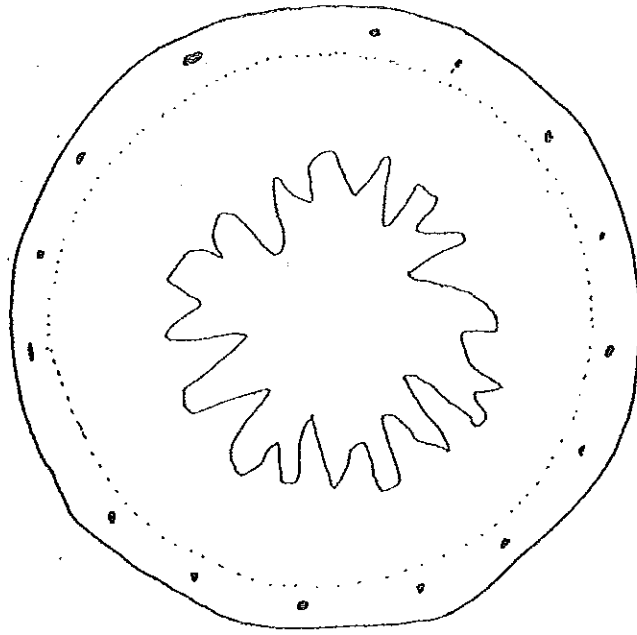
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FIG. 17

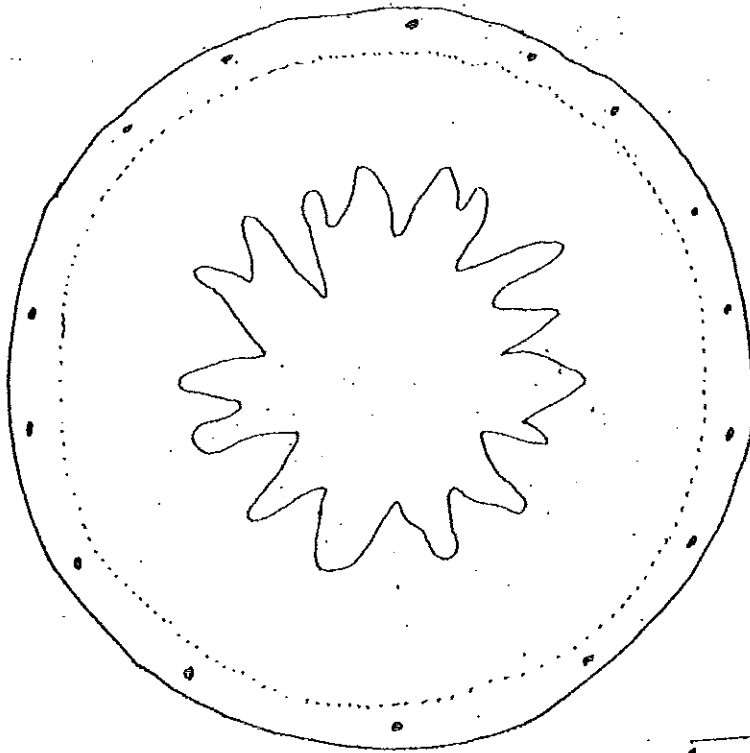


2 mm



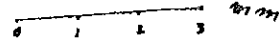


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210

Fig. 1B



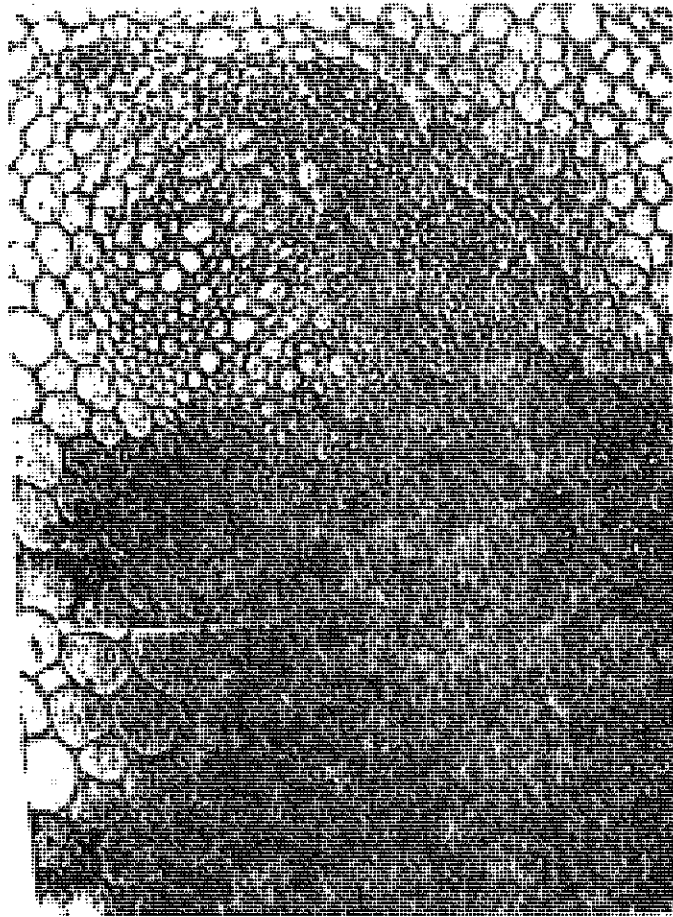
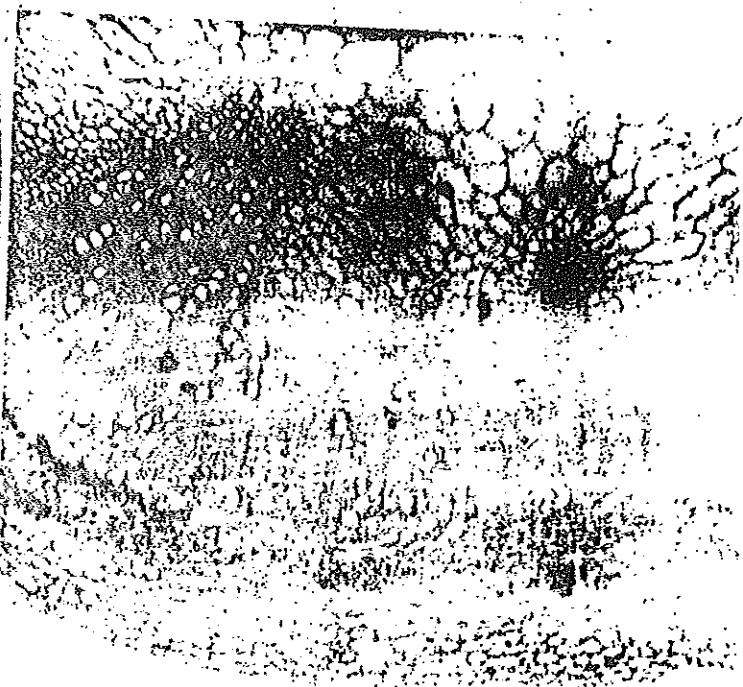
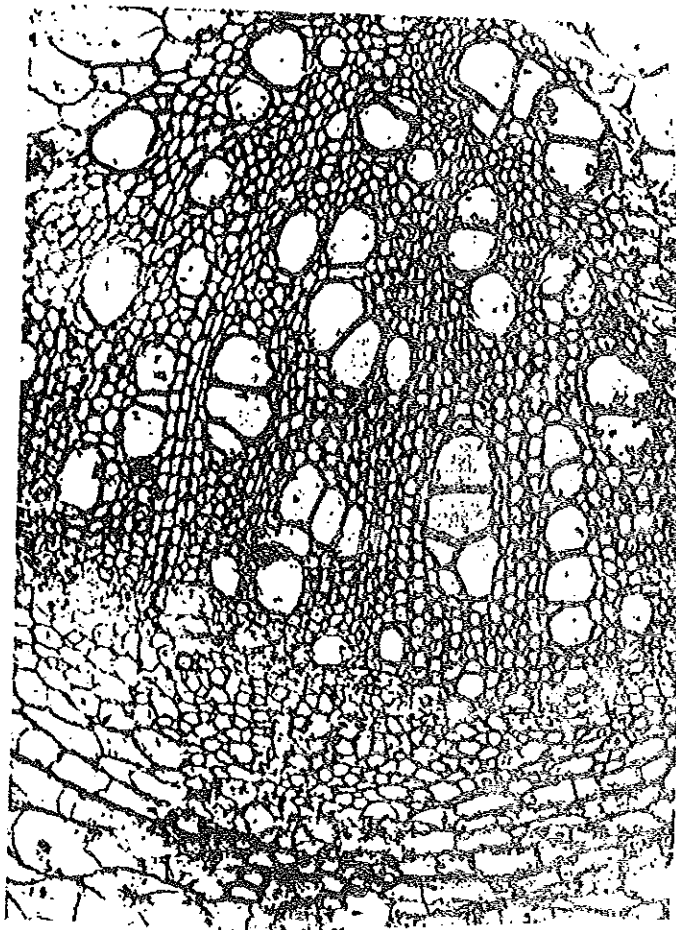
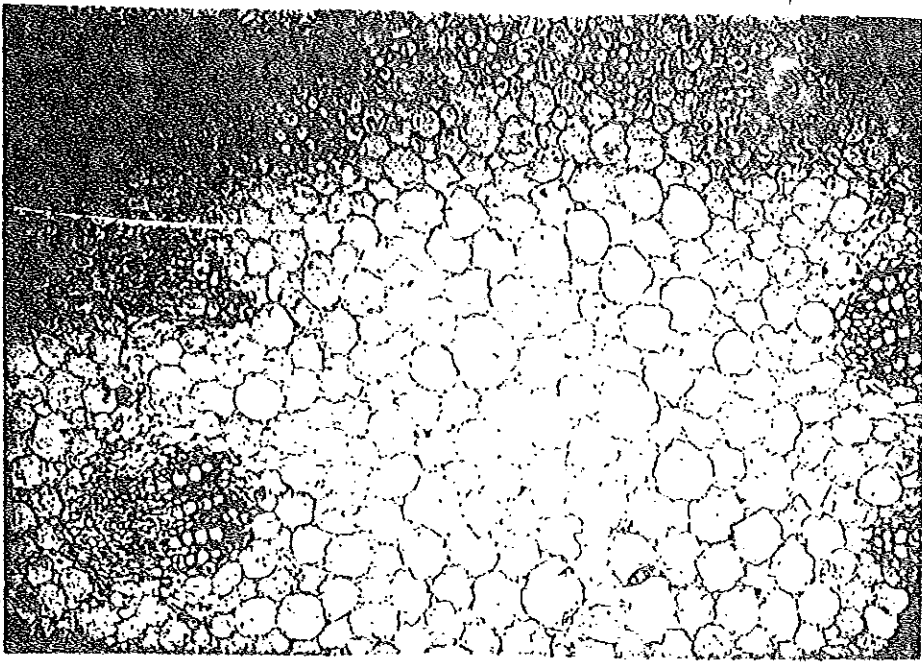
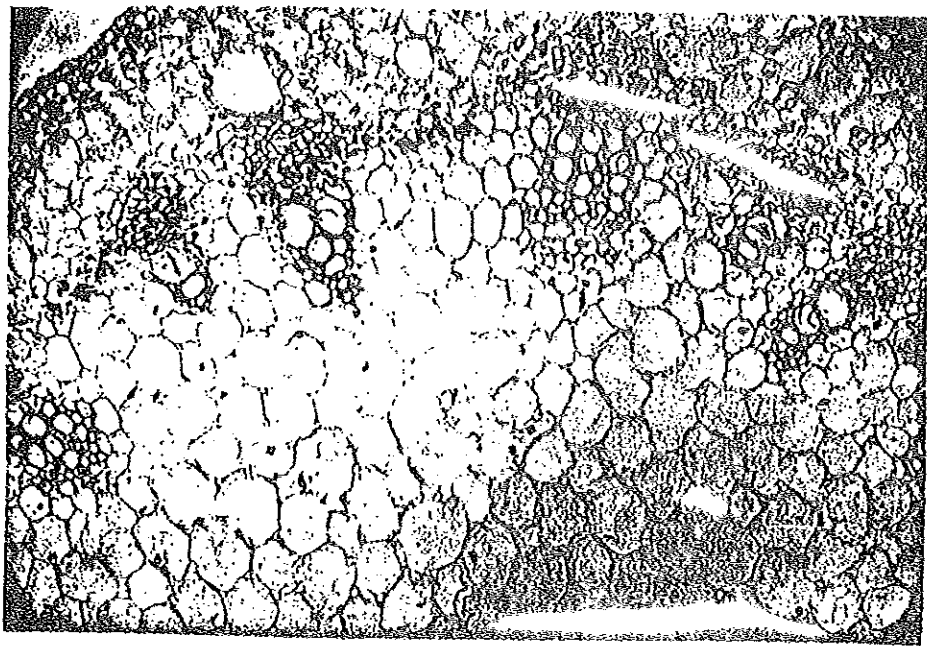


Fig. 20. Cross section of the stem of V. galunensis (X160) showing vascular tissues at an earlier stage of development. The vascular bundles occur in discrete bands. Earlier stages in the formation of new vascular bundles from dividing cambial cells are shown in the left hand corner.

The following description is based on the study of the
 material which was examined. The material was
 examined in the laboratory of the U.S. Department of
 Agriculture, Bureau of Plant Industry, Washington, D.C.
 The material was examined in the laboratory of the U.S.
 Department of Agriculture, Bureau of Plant Industry,
 Washington, D.C. The material was examined in the
 laboratory of the U.S. Department of Agriculture,
 Bureau of Plant Industry, Washington, D.C.

FIG. 21 and 22.





Figs 24 and 25. Transection of stems of *G. abyssinica*,
x24 (fig. 24) and *Y. galeensis*, x160
(fig. 25) showing distribution of vascular
bundles and differentiation of vascular
tissues from cambial cells. Darkly stained
areas between vascular bundles indicate
formation of interfascicular cambium.

in G. abyssinica and V. galamensis respectively. The phloem and Xylem tissues occur as discrete collateral bundles separated by the cambium (fig. 26). The Xylem consists of vessel elements ray parenchyma and fibers. The average vessel element length in G. abyssinica ranged from 252 to 343 microns and that in V. galamensis ranged from 224 to 287 microns (fig. 27) Carlquist (1957a) indicated that analysis of vessel element length for comparative purposes should be made after thorough consideration of the origin of the specimens, because the length of vessel elements varies greatly even within a single stem depending on the parts from which specimens are taken and their maturity. Thus younger plants of both species consist of long spirally or helically thickened vessel elements (fig. 28 and 29). On the basis of the formation of these helically thickened vessel elements, both species are considered to be advanced phylogenetically (Carlquist 1957a). Though Webber (1936; cited in Carlquist, 1957a) related the abundance of helical thickening to aridity in the dry country plants with which she worked, these sculpturing, however, are prominent features of the narrow vessels of both G. abyssinica and V. galamensis and cannot be correlated to aridity. However, since this study was carried out by taking specimens from comparable regions of the plants, the figures for the average length of vessel elements are assumed to aid in comparative studies of vessel element length with the age of the plants. Thus

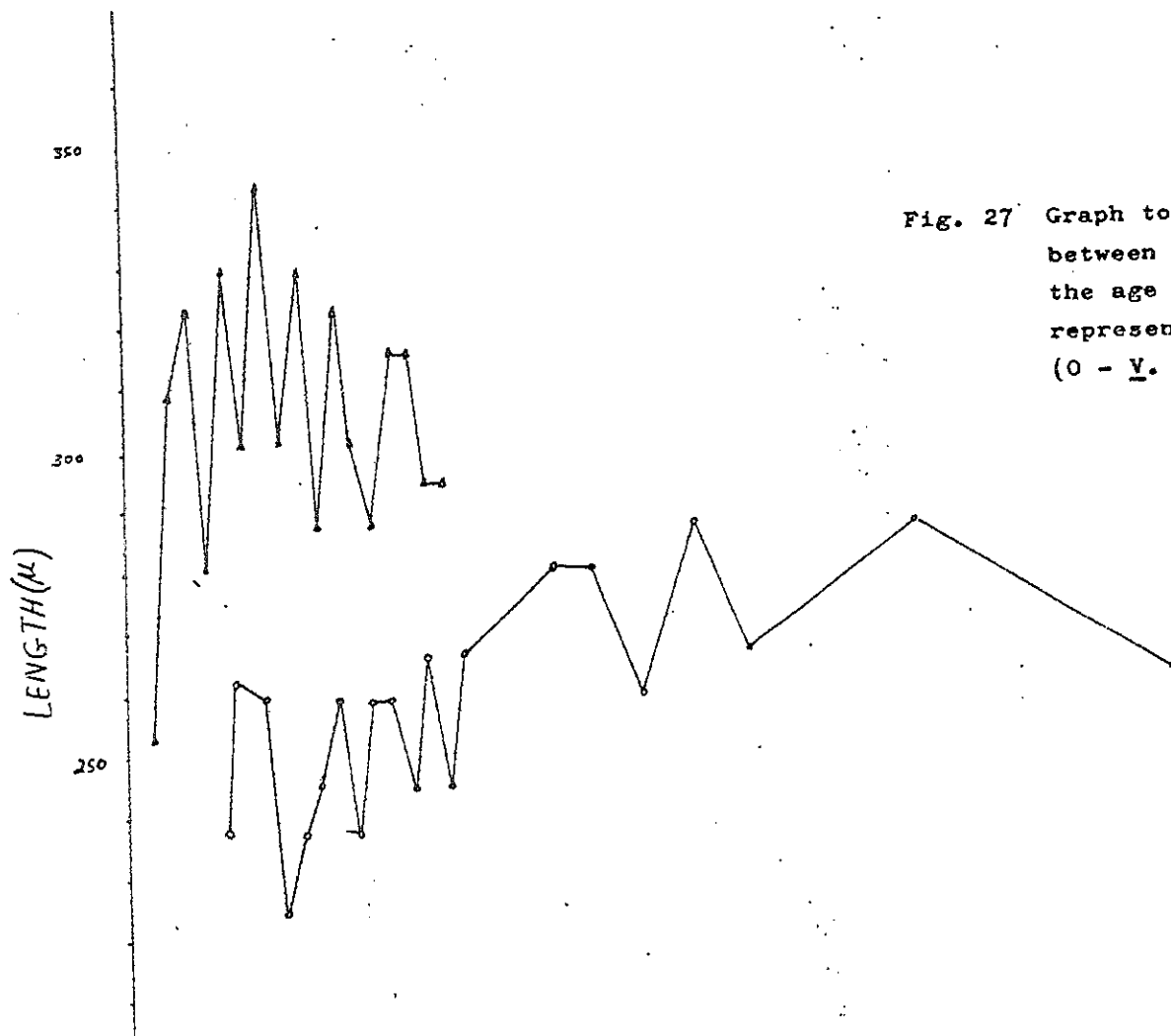


Fig. 27 Graph to illustrate the relationship between length of vessel elements and the age of specimens. The figures represent averages of 25 measurements (O - Y. galamensis, Δ - G. abyssinica)

the average length of vessel elements of both species show an increase with the maturity of the stems of the two plants. Many characteristics of the vessel element demand special considerations because of ontogenic variations. One feature, however, which according to Carlquist (1957a) seems to provide a significant figure is the diameter of the widest vessel observed in a species. Vessels are generally of smaller diameter in younger forms. It is to be noted here that even in mature stem of both plants the vessel elements near the pith are comparatively smaller than those located near the cambium (fig. 6 and 7). On the whole, vessel element diameter increases with age of the plant with the widest vessels occurring proximal to the cambium. Hence, the difference noted in this respect may only reflect the difference in the age of the material. Thus the largest figure for the most mature vessel element diameter of G. abyssinica is 93 microns and that of V. galamensis is 66 microns with averages of 61.7 and 41.2 microns respectively (fig. 30). The smallest diameter for G. abyssinica is 12.5 microns and the largest diameter which coincides with the vessel element from the oldest stem of G. abyssinica investigated is 93 microns. On the other hand, the diameter of the widest vessel of V. galamensis is only 66 microns. Here it is interesting to note that narrowness of vessel elements is correlated with aridity for some desert shrubs and Compositae as indicated by Webber (1936, cited in Carlquist 1958a).

WIDTH (μ)

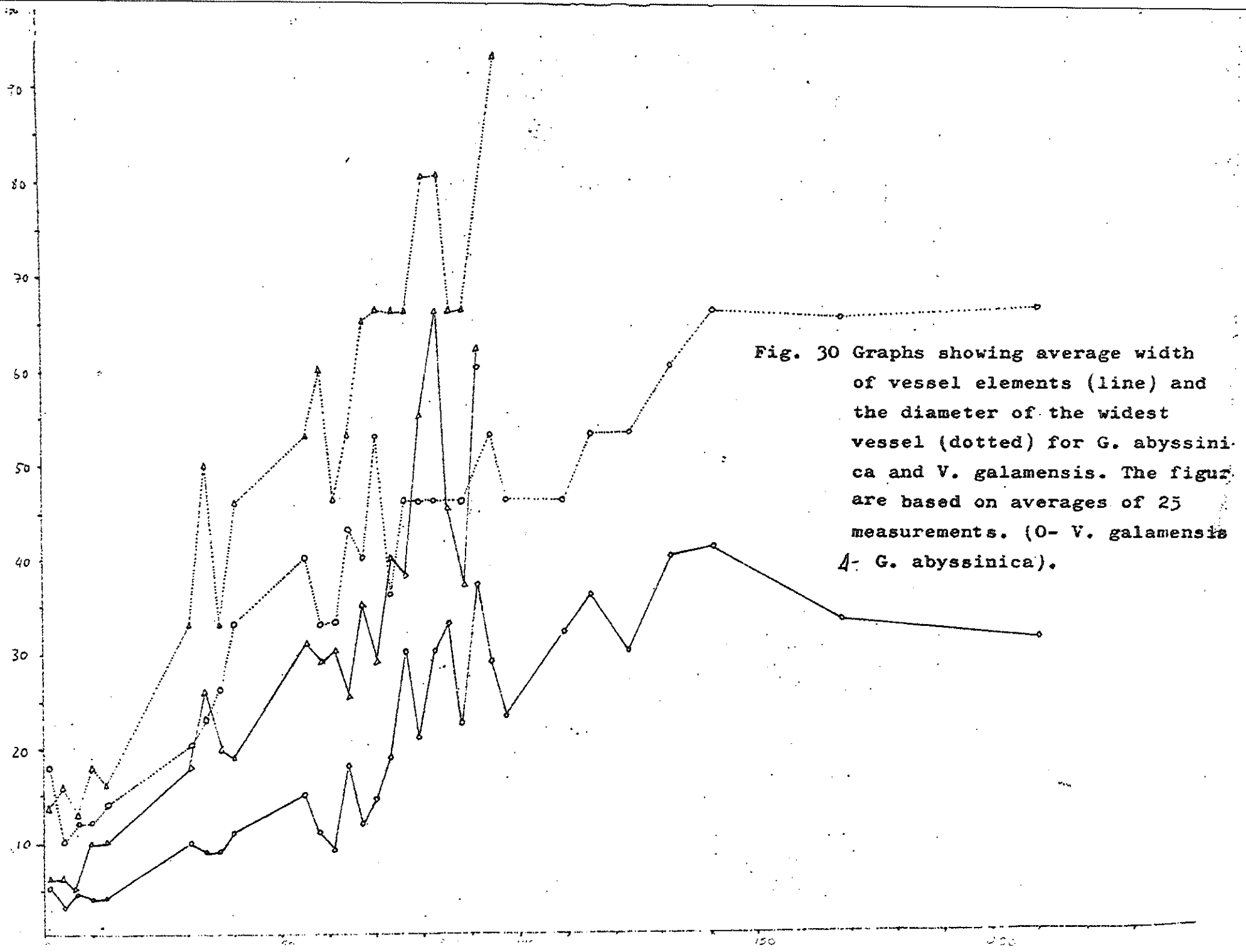


Fig. 30 Graphs showing average width of vessel elements (line) and the diameter of the widest vessel (dotted) for *G. abyssinica* and *V. galamensis*. The figures are based on averages of 25 measurements. (O- *V. galamensis* Δ- *G. abyssinica*).

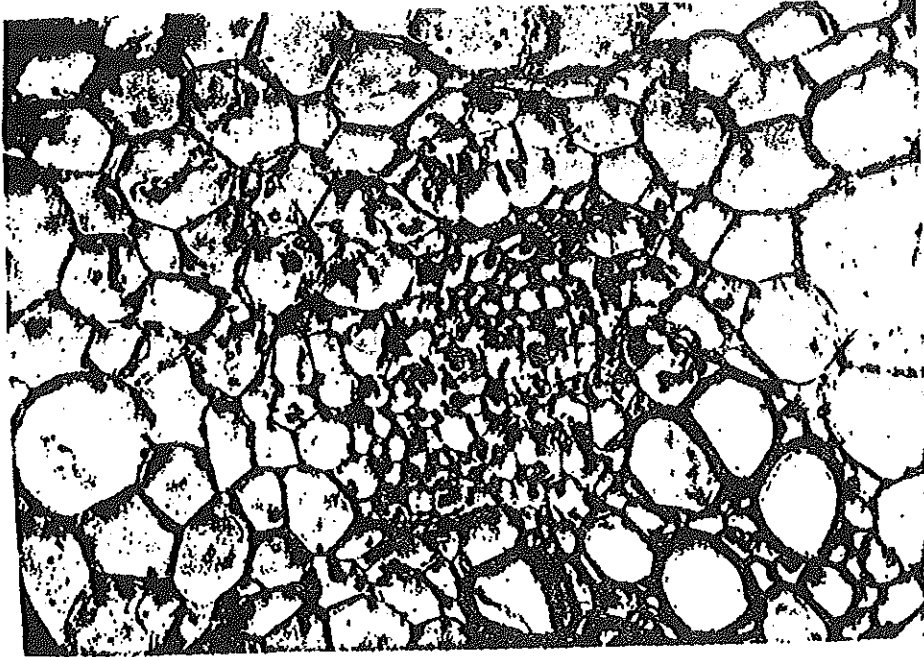


Fig. 26. Transsection of 37 days old stem of Q. abyssinica (X400) showing collateral vascular bundle surrounded by parenchymatous cells.

4.1.6.2 Vessel Arrangement

In all the young stems of V. galamensis and G. abyssinica investigated, the first formed vessel elements occur in solitary radial rows (figs. 24 and 25). But with increased age and development, solitary as well as aggregates of two or three vessel elements occur dispersed throughout the vascular bundles. The orientation of these being radial to oblique radial chains of two or three vessels (figs. 31 and 32). In both species the vessels are commonly polygonal when viewed in transection (fig. 33). As shown in figure 34 and appendix 2, the average figure for vessels per group of V. galamensis ranged between 2.80 and 3.50 and that of G. abyssinica ranged from, 2.00 to 3.00. Thus the larger vessels of both G. abyssinica and V. galamensis usually appear solitary although they are in contact with numerous narrow vessels so that the true figure for the vessels per group would be high. High figures for vessels per group in V. galamensis is probably associated with its naturally dry habitat which induces greater aggregation of vessels (fig. 35, 36).

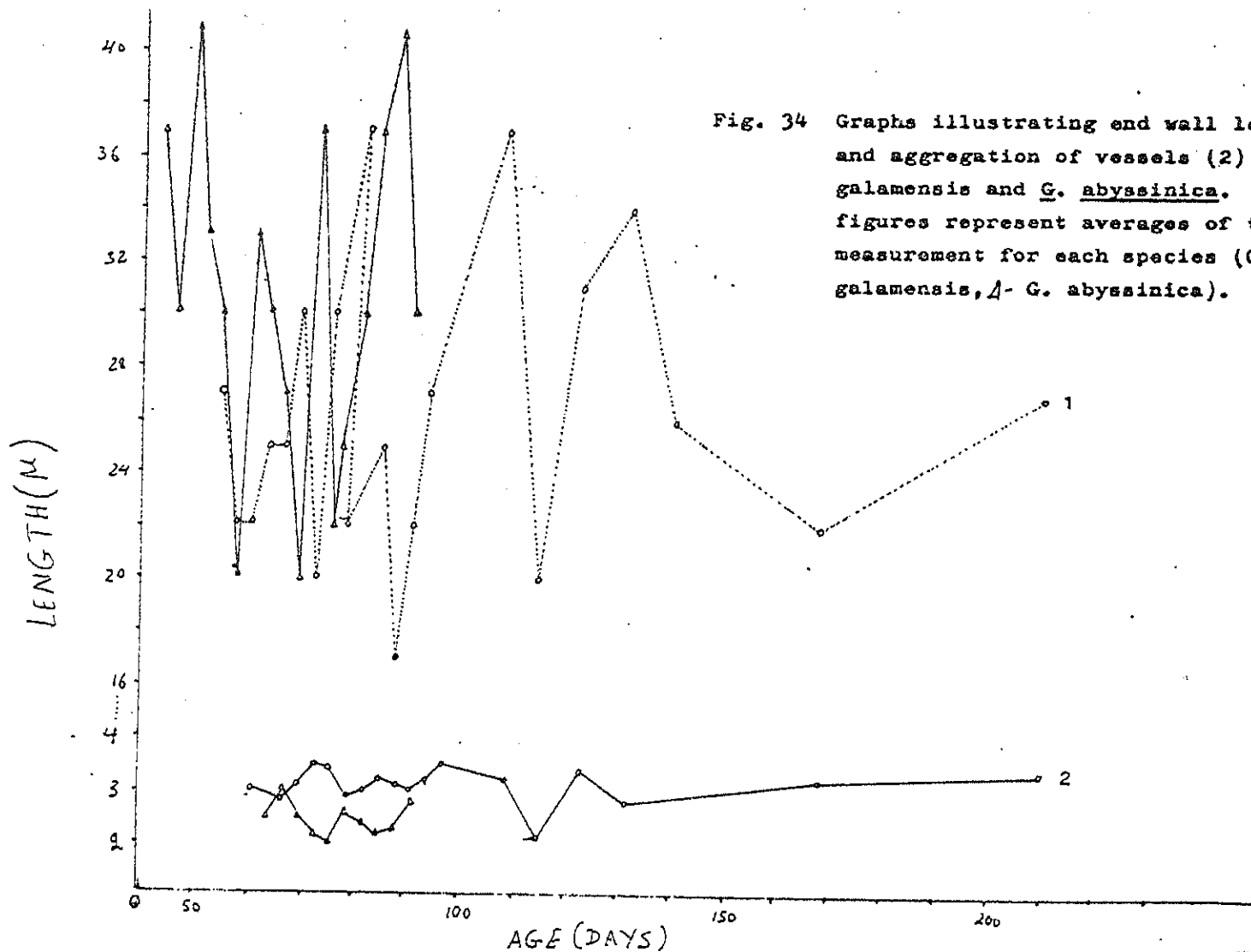
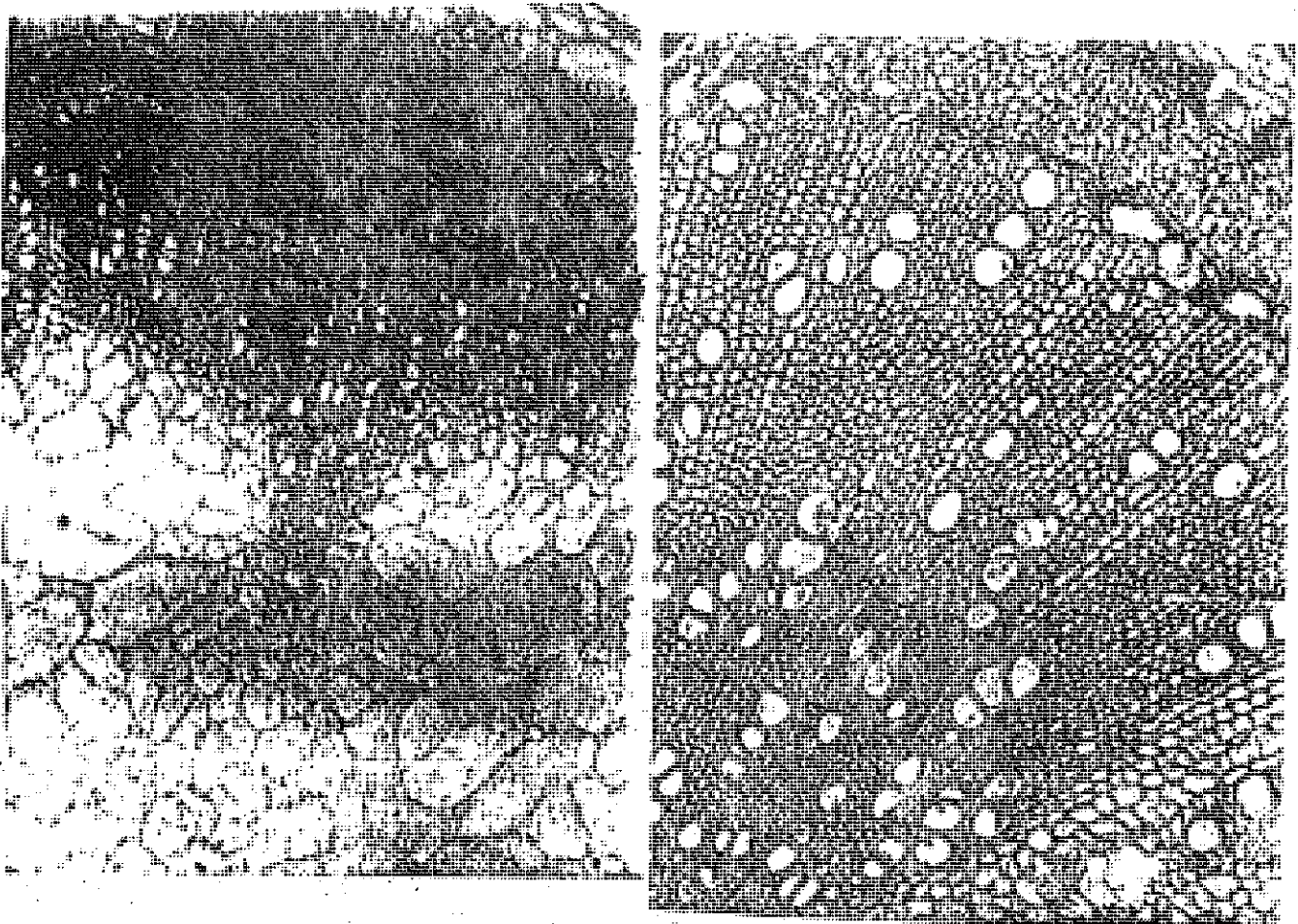


Fig. 34 Graphs illustrating end wall length (1) and aggregation of vessels (2) for V. galamensis and G. abyssinica. The figures represent averages of ten measurement for each species (O - V. galamensis, Δ - G. abyssinica).



Figs. 31 and 32 Transsections of stem of G. abyssinica,
x300 (fig. 31) and V. galamensis, x100
(fig. 32) showing oblique radial orientation
of vessel elements.

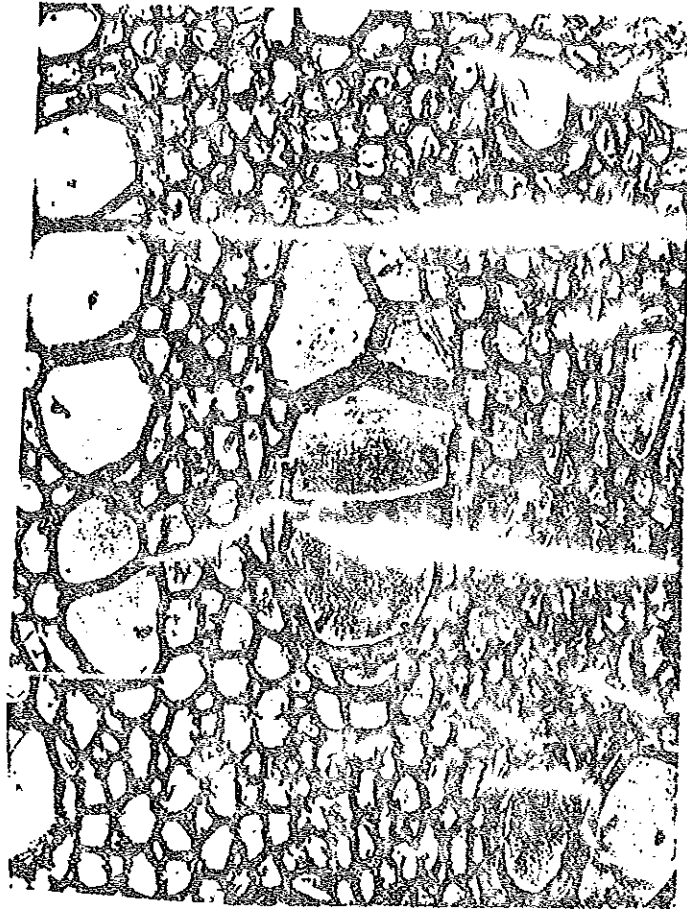
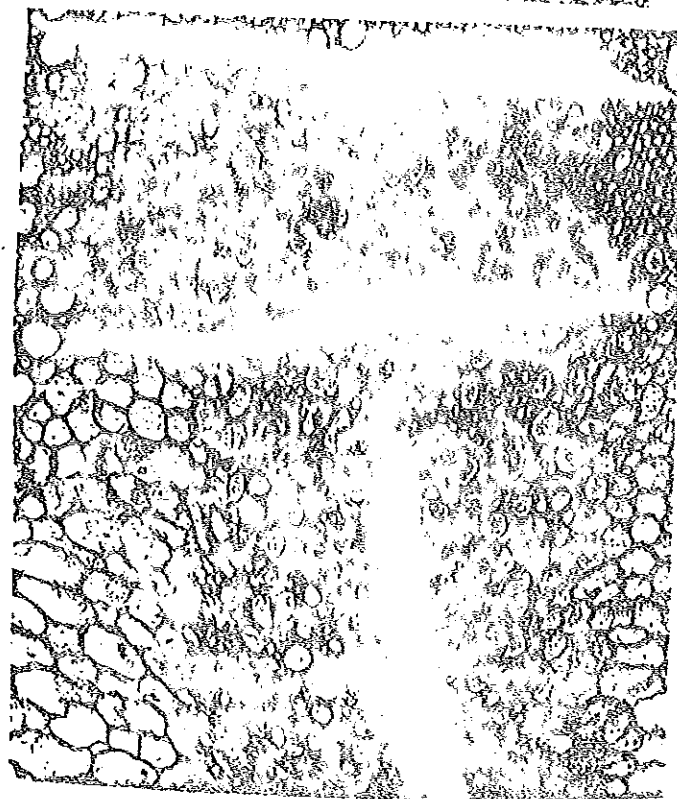
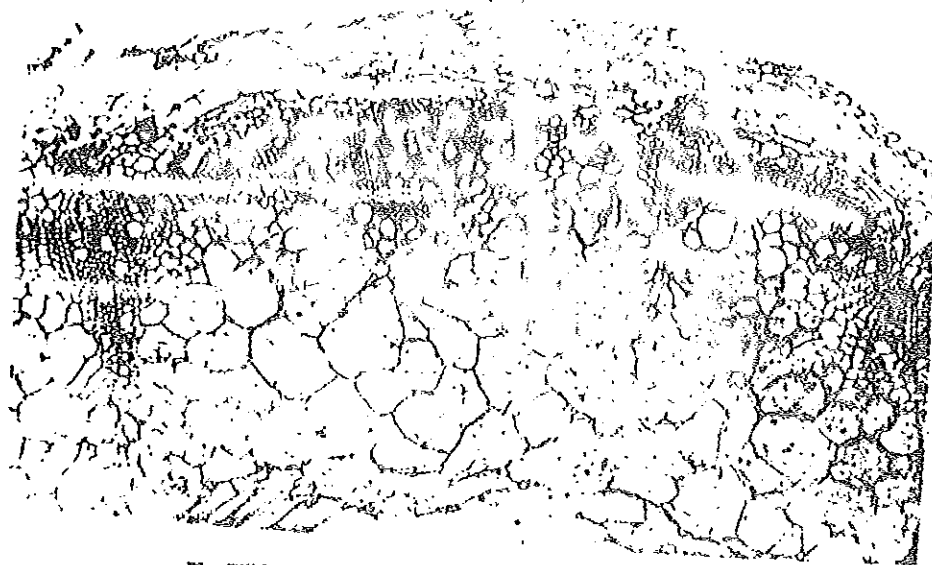


Fig. 33. Transsection through the vascular bundle of G. abyssinica (x400) showing prominent vessel elements which are angular in outline.



Figs. 35 and 36. Transsection of stems of U. abyssinica X25 (Fig. 35) and V. lamonsis, X100 (Fig. 36) showing relative density of vessel elements in the vascular tissues. U. abyssinica possesses solitary as well as aggregates of two or three vessels that are sparsely distributed in the vascular tissue, while denser aggregations of vessels in the vascular tissue are found in V. lamonsis.

4.1.6.3 Lateral vessel walls
and perforation plate

The lateral vessel walls of both species exhibit similar characteristics. In the longitudinal sections of the vascular bundles of both species depicted in figures 28 and 29, the thickening on the walls of the first formed vessel elements of both species is annular and spiral or helical. Figures 37 and 38 are longitudinal sections of the stems of the two species which show vessel elements formed at a later ontogenetic stage. From these sections it can be observed that the lateral vessel walls of the secondary Xylem of both species are pitted. Only simple perforation plates which were round in outline were encountered in both species (figs 28 and 39). The vessel elements of both species have comparable end wall length.

4.1.6.4 Rays

V. galamensis showed a more pronounced secondary growth in the stem. This is confirmed when one compares the extent of complexity in the vascular tissues of this plant. The vascular tissue of V. galamensis showed both the vertical and horizontal systems in its organization. The wood of V. galamensis produced uniseriate as well as multiseriate rays. The uniseriate rays consist of 2-7 cells while multiseriate rays are variable in their width. In most of the specimens encountered, the multiseriate



Fig. 28. Radial longitudinal section of stem of G. abyssinica (X160) showing types of lateral wall thickening of vessel elements. Note at the far right hand side (a) vessel elements with helical thickening. The larger vessel element next to these (b) have scalariform lateral wall thickening. The others that come next (c) are all pitted.

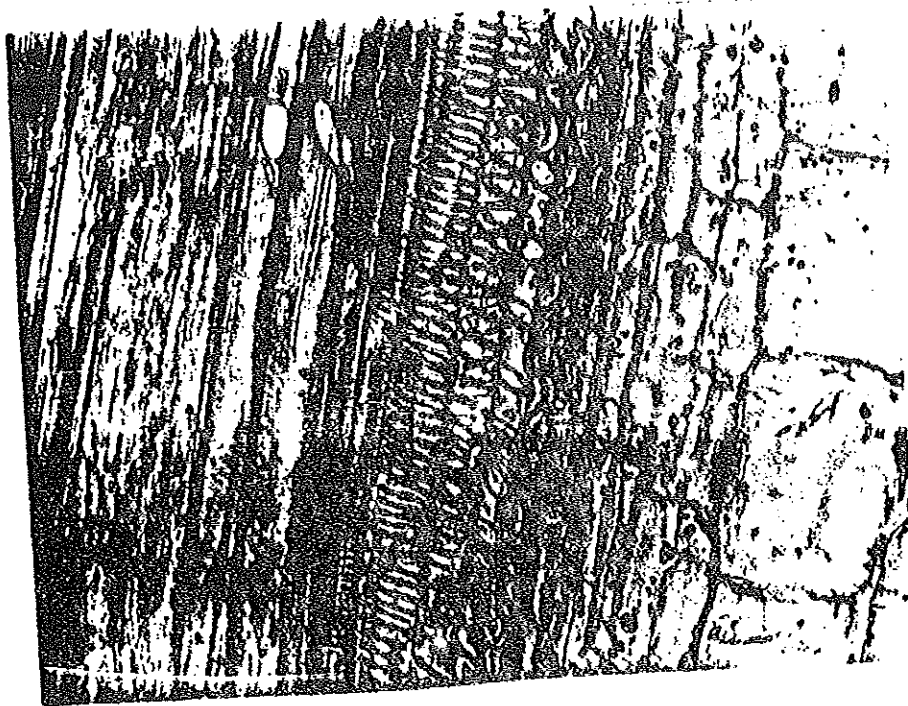
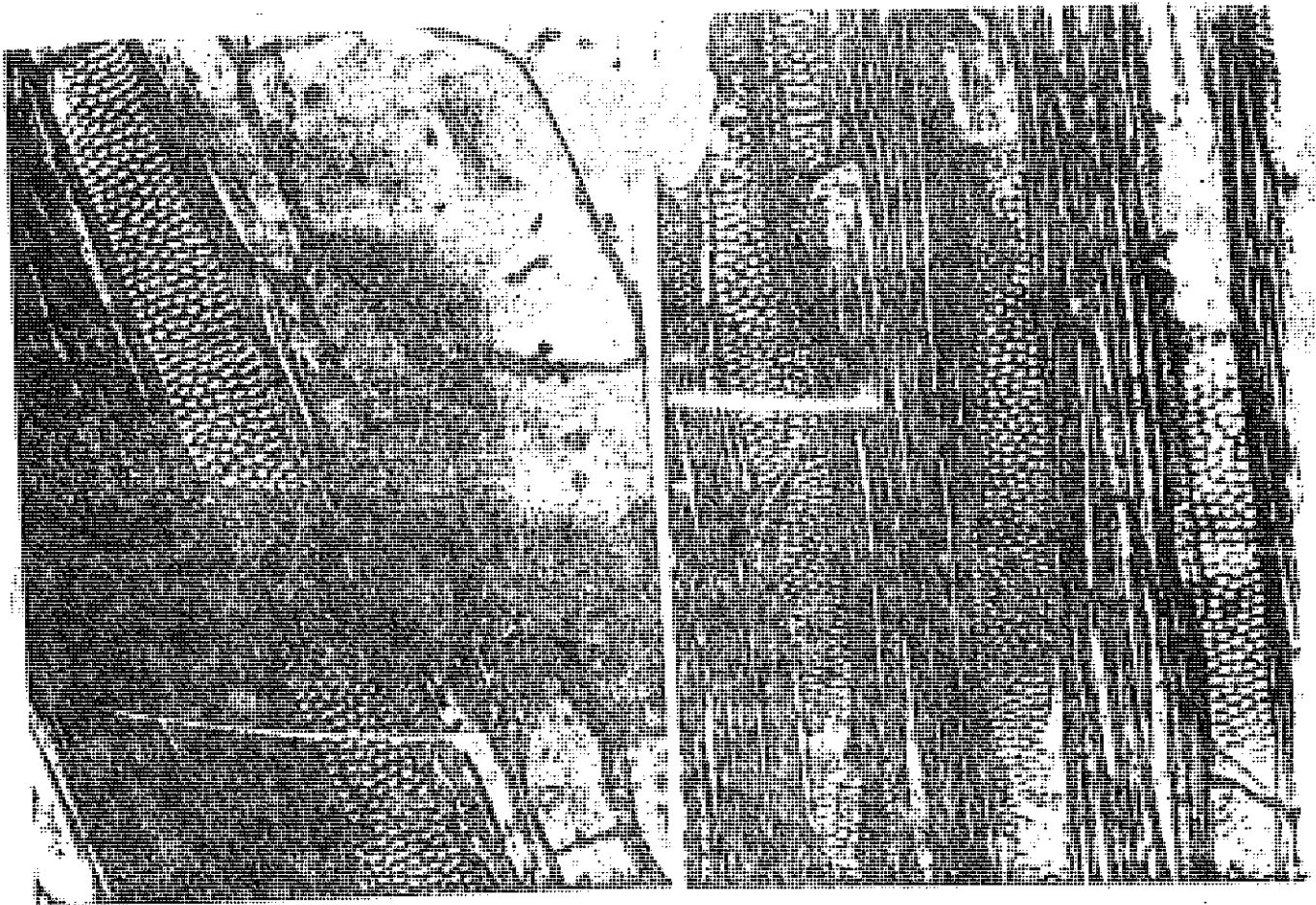


Fig. 29. Radial longitudinal section of stem of V. palamensis (x400) showing different types of lateral vessel wall sculpturing and simple perforation plates. The vessels at far right (a) have annular thickening, and those next (b) have spiral vessel wall thickening.



FIGS. 37 and 38. radial longitudinal section of stems of G. abyssinica, $\times 400$ (fig. 37) and G. galamensis, $\times 1160$ (fig. 38) showing pitted vessel elements formed at later stages of their development.

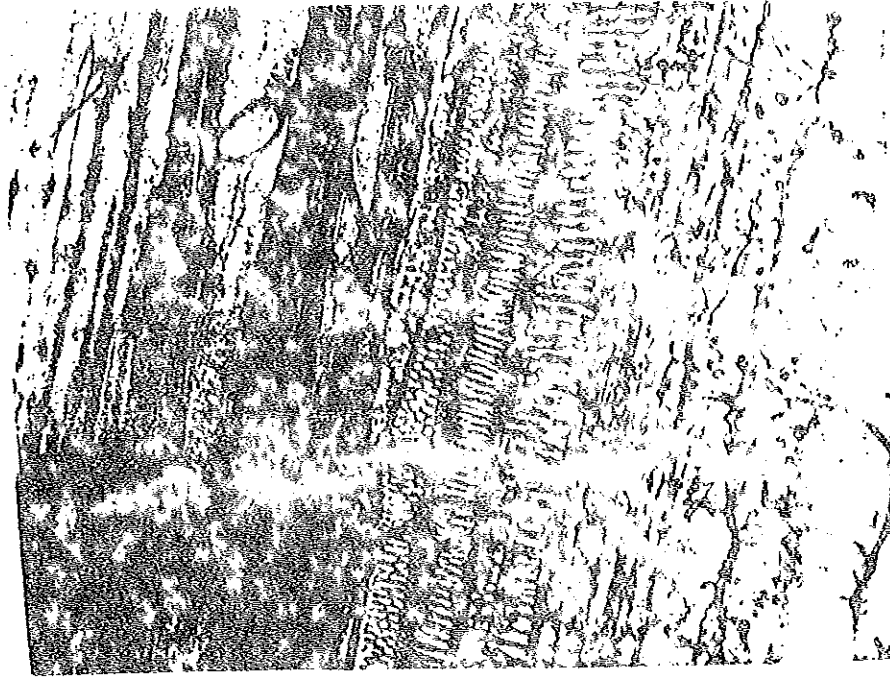
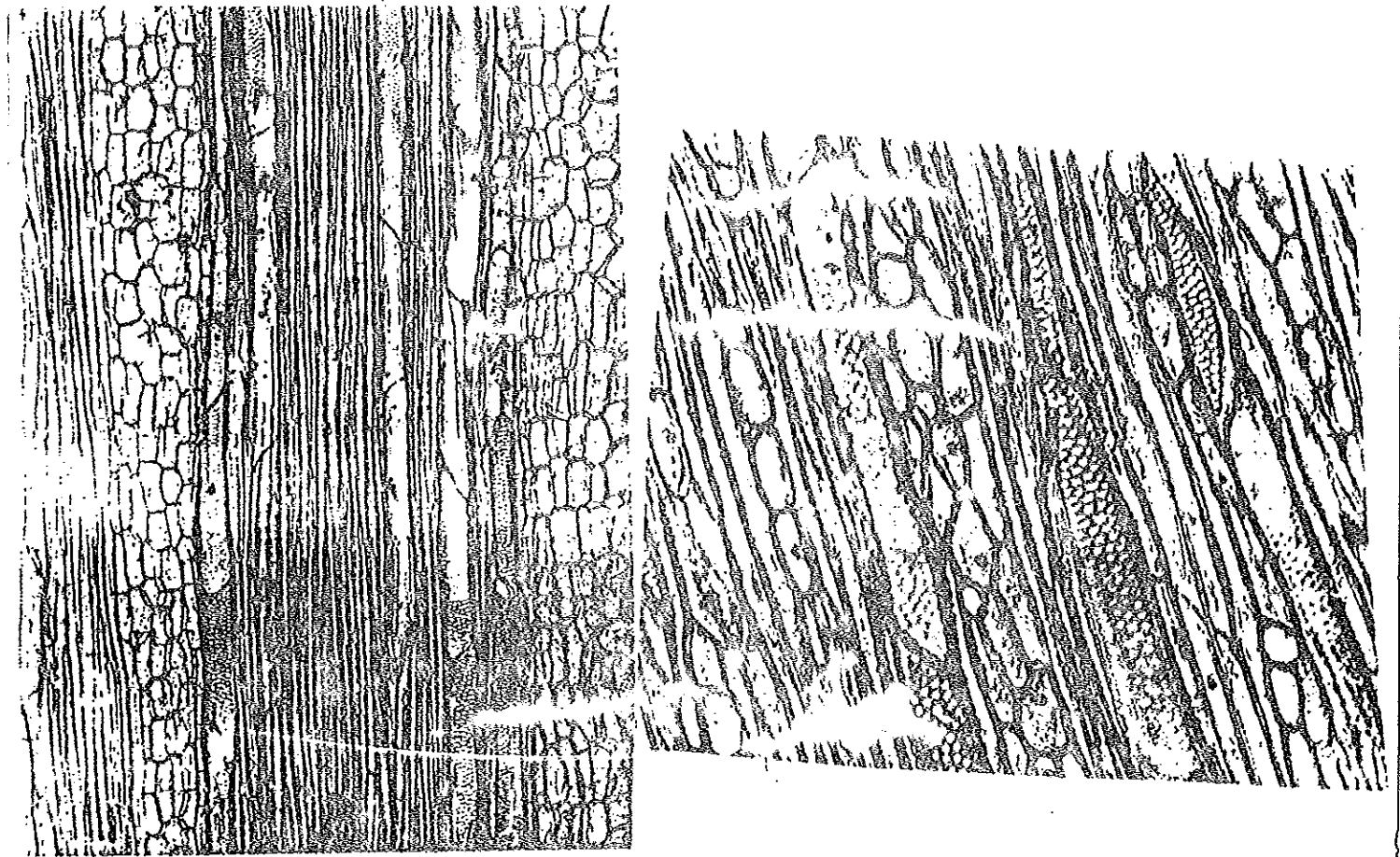


Fig. 59. Radial longitudinal section of stem of V.
galamensis (X400) showing a perforation
plate (arrow) characteristic of the species.



Figs. 40 and 41. Tangential longitudinal sections of stem of Y. galamensis showing development of vascular rays. Fig. 40 (X160), Fig. 41 (X400)

rays are made up of 2-4 cells along their maximum width (fig. 40) while others may possess much more than these (fig. 41). Square and upright cells compose these rays.

4.2 Anatomy of the Leaf

the epidermal cells of the leaves of both G. abyssinica and V. galamensis are arranged with the long axis of the cells parallel to the long axis of the lamina. In V. galamensis these cells measure 17 microns on the average and those of G. abyssinica measured 12 microns. The outer surface of these cells are thick because of Cuticular deposition of their walls. Both species possess uniseriate, multicellular non glandular hairs. The dense coating of hair and the conspicuous cuticle in V. galamensis may be correlated with the sunny dry natural habitat in which the species occurs (Perdue et al 1984). Generally, concerning the epidermis of both species, there is not much difference in structure and distribution of cells in the adaxial and abaxial parts of the mesophyll of the two sides of the lamina, except that the adaxial cells are much thickened compared to the abaxial cells in both species.

The leaves of both V. galamensis and G. abyssinica are both bifacial having distinct palisade and spongy tissues in their mesophyll. The leaves of both species have only one layer of palisade tissue and no hypodermis; the loosely arranged cells of the spongy tissue are similar

morphologically. These have diverse shapes, some being circular while others are lobed. The spongy tissues occupy, the greater part in the leaves of both species.

St the mid rib region the vascular tissue of both species consist of three sets of collateral vascular bundles with abaxial xylem. The vascular tissue lacks bundle sheath of any kind. In the mid rib region larger parenchyma cells fill the area outside the vascular tissues in both species while a one layer of cellencyma are localized just immediately below the epidermis in both cases. Unlike the anatomy of the stem, fibers were not observed in the leaves of both species.

Note on phylogenetic relationship

The anatomical features of G. abyssinica and V. galamensis have been discussed separately because the two species occupy different positions in the evolutionary outline laid down by Mabry and Bohlmann (1977). Here the tribe Heliantheae to which G. abyssinica belongs is depicted as the ancestral stock from which other tribes within compositae have evolved. The tribe Vernoniae, however, is placed at a higher phyletic position within the family.

The purpose of this research was not to compare the anatomical features of these taxa but rather to suggest the type of variation pattern that is found in these plants with development and also to assess the systematic value of

some of the anatomical features. The following notes concerning the evolutionary relationship of these two taxa are given here with the view to contribute to the established phyletic relationships between the taxa to which the two species belong.

The ensuing generalizations follow the fundamental logic which have been applied by Fahn (1974) and Carlquist (1961) which presumes vessels to be phylogenetic derivatives of tracheids and that tracheidlike features in vessel elements like great length with comparatively narrow width, long end walls that form small angles with the vertical and angular vessels in transectional view were considered primitive.

The fact that V. galamensis is phylogenetically advanced over G. abyssinica can clearly be seen from the evidence of the length of vessel elements, diameter of vessel elements, aggregation of vessel elements and the thickness of vessel walls. In all these aspects G. abyssinica is less advanced when compared to V. galamensis in possessing longer vessel elements with comparatively thinner walls that are sparsely distributed throughout the vascular tissue. Though the vessel elements of both species are angular in transectional view, the above characters show a strong correlation with each other and lend support to the assumption of Mabry and Bohemann (1977) that the tribe Vernonieae is phylogenetically advanced over Heliantheae.

Appendix 1: Summary of average length of vessel elements, diameter of phloem fibers and end wall length (in microns) The Figures represent average measurement of 25 vessel elements, while the figures for the diameter of sclerenchyma and end wall length represents averages of 10 measurements each.

Age days	Average length of Vessels in Microns		Diameter of Sclerenchyma		End wall length of Vessel elements	
	V. galamensis	G. abyssinica	V. galamensis	G. abyssinica	V. galamensis	G. abyssinica
40	-	-	13.3	-	-	-
43	-	252	10.0	-	-	36.70
46	-	308	13.3	20.0		30.00
49	-	322	12.5	23.2		41.70
52	-	280	10.0	23.2		33.30
55	238	329	10.0	20.0	26.60	30.00
58	280	301	13.3	30.0	21.67	20.00
61	266	343	16.7	26.7	21.67	33.30
64	224	301	15.0	23.2	25.00	30.00
67	238	329	15.0	30.0	25.00	26.70
70	245	287	12.5	26.7	30.00	20.00
73	250	322	13.3	23.2	20.00	36.70

Age days	Average length of Vessels		Diameter of Sclerenchyma		End wall length of Vessel elements	
	V. galamensis	G. abyssinica	V. galamensis	G. abyssinica	V. galamensis	G. abyssinica
76	238	301	10.0	33.3	30.00	21.67
79	259	287	13.3	33.3	21.67	25.00
82	259	326	-	26.7	36.60	30.00
85	249	315	-	23.2	25.00	36.00
88	266	294	-	23.3	16.60	41.70
91	245	294	12.5	26.7	21.70	30.00
94	266	-	12.5	-	26.60	-
109	280	-	10.0	-	36.60	-
115	280	-	10.0	-	20.00	-
123	259	-	10.0	-	30.00	-
132	287	-	12.5	-	33.60	-
141	266	-	13.3	-	25.00	-
168	287	-	15.0	-	21.67	-
210	252	-	12.5	-	26.60	-
300	259	-	13.5	-	25.00	-

Appendix 2: Table showing measurement of widest vessel, average width of vessels and aggregation of vessels (in microns). Figures for width are averages of 25 measurements of vessel elements and average number of vessels in counts of ten vessel groups.

Age	V. galamensis			G. abyssinica		
	Widest Vessel (microns)	Average Width	Vessels Group	Widest Vessel (microns)	Average Width	Vessels Group
1	18.3	5.2	-	13.0	5.7	-
4	10.0	3.1	-	16.0	6.1	-
7	11.7	4.8	-	12.5	4.9	-
10	11.8	3.9	-	18.0	9.8	-
13	13.5	4.3	-	16.4	10.0	-
31	20.0	9.8	-	33.0	18.2	-
34	23.0	8.3	-	50.0	26.0	-
37	26.0	9.2	-	33.0	20.0	-
40	33.3	11.5	-	46.0	18.0	-
55	40.0	15.0	-	53.0	31.2	-
58	33.0	10.9	-	60.0	28.5	-
61	33.0	8.6	-	46.0	30.0	-
64	43.0	17.6	3.00	53.0	25.0	2.50
67	40.0	12.0	2.80	60.0	35.0	3.00
70	53.0	13.6	3.15	66.0	29.0	2.50

Age	V. galamensis			G. abyssinica		
	Widest Vessels (Microns)	Average Width	Vessels Group	Widest Vessel (Microns)	Average Width	Vessels Group
73	36.0	18.7	3.50	66.0	40.0	2.15
76	46.0	30.0	3.42	66.0	38.0	2.00
7	46.0	21.2	2.90	80.0	55.0	2.60
82	46.0	29.6	3.00	80.0	66.2	2.40
85	46.0	33.3	3.20	66.0	45.0	2.18
88	46.0	25.0	3.10	66.0	37.0	2.30
91	60.0	37.4	3.00	93.0	61.7	2.80
94	53.0	29.3	3.22	-	-	-
97	46.0	23.0	3.50	-	-	-
109	46.0	31.8	3.16	-	-	-
115	53.0	35.5	2.09	-	-	-
123	53.0	27.7	3.41	-	-	-
132	60.0	38.9	2.80	-	-	-
141	66.0	41.2	2.90	-	-	-
168	65.0	33.0	3.15	-	-	-
210	66.0	30.8	3.45	-	-	-
300	65.0	31.5	3.25	-	-	-

Appendix 3: Table showing average diameter of cortical parenchyma of G. abyssinica and V. galamensis (figures represent averages of 10 parenchyma counted)

Age	G. abyssinica Diameter (Microns)	Age	V. galamensis Diameter (microns)
1E	43	1	56
4E	43	4	43
7E	35	7	49
10E	49	13	28
13E	43	28	43
37E	49	34	35
34E	56	37	43
37E	56	40	43
40E	70	55	49
43E	49	58	43
46E	56	61	43
49E	63	64	49
52E	63	67	56
55E	63	70	49
58E	56	73	56
61E	77	76	43
64E	70	79	35
67E	63	82	43
70E	56	88	35

Age	G. abyssinica Diameter (Microns)	Age	V. galamensis Diameter (Microns)
73	63	91	43
76	70	97	43
79	56	109	35
82	70	115	43
85	63	123	43
88	70	132	35
91	63	141	49

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