

mode of spread and probable preventive measures will be investigated. Of course it should be stressed that "Sappe" is a farmer's term and perhaps be applied to a class of disease having similar symptoms rather than to denote any single ailment.

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GROWTH DYNAMICS AND DEVELOPMENTAL PATTERNS IN THE UNICELLULAR TRICHOMES OF ANGIOSPERMS

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ABSTRACT

Growth dynamics and developmental patterns of unicellular trichomes of angiosperms based upon calibration of specific growth components at critical stages of their ontogeny is presented. The stigmatic papillae of *Chrysanthemum carinatum* L., stigmatic hairs of sunflower (*Helianthus annuus* L.) and filament hairs of *Lagascea mollis* Cav. have been studied for the purpose. The trichomes bear a cuticular membrane right from the onset of ontogeny and their entire outer wall participates in differentiation rather than a predefined locus as in root hairs. Nuclear movement is independent of the elongation of the cytoplasm and of the cell wall, but markedly slows down in the last phase of trichome development, thus exercising its control on trichome growth, while being farther behind the trichome tip unlike in root hairs. The nucleus in its interphase is highly plastic, expanding or contracting according to the available space, but without detriment to its function. No inhibitory field effects of Bunning operate during the ontogeny of the trichomes, since they not only develop abutting over one another, but also simultaneously. As a part of cellular adjustment during growth, the lateral walls of trichomes which in their proximal region are organically connate with those of adjacent trichomes, show separation at their outward margin in *Lagascea mollis*. Depending on the trichome concerned, either the ontogeny involves both symplastic and apical intrusive growth or only the former. During development, trichome diameter and length show continuous increase; the nucleus also similarly shows increase, in its diameter. Four developmental patterns are so far recognisable in the unicellular trichomes of angiosperms including that of the root hairs.

INTRODUCTION

AMONG the unicellular trichomes of angiosperms, the root hairs^{1,4,5} and cotton hairs^{6,7} are the most extensively studied about growth and differentiation. But these investigations, however, did not identify specific growth components and

study them at appropriate ontogenetic stages, so that there is presently no precise information on the growth changes or dynamics of these trichomes. Understanding of the latter is valuable not only in relation to the trichomes themselves, but also regarding the general cellular growth patterns which is not feasible to follow in the usual plant tissues

due to the crowded nature of their component cells. This paper deals with the nature of growth dynamics and developmental patterns of the unicellular trichomes of angiosperms based on study of the ontogeny of the stigmatic hairs of the sunflower (*Helianthus annuus* L.), stigmatic papillae of *Chrysanthemum carinatum* L., and the filament hairs of *Lagascea mollis* Cav., with reference to specific growth components, viz., (1) T.L. (total length of the trichome); (2) L.C.W. (length of the maximal coalescent part of the lateral wall of the trichome); (3) L.F.W. (length of the free part of the lateral wall of the trichome); (4) D.N.B. (distance between the centre of the nucleus and trichome base actually found); (5) E.D.N.B. (expected distance between the centre of the nucleus and trichome base); (6) D.N.T. (distance between the centre of the nucleus and the trichome tip); (7) D.S.N. (diameter and shape of the nucleus) and (8) D.T. (diameter of the trichome—has been measured in the proximal part of the trichomes, as the latter attenuate towards the distal end (see Figs. 5, 17 and 18). Generally, nucleus of unicellular trichomes shows forward movement during ontogeny, but as will be shown here, since this is

synchronous with the elongation of the trichome, it was felt that the nuclear movement was possibly closely linked with the elongation of the trichome longitudinal wall and consequently determination of E.D.N.B. on the basis of the latter was regarded necessary for comparison with D.N.B. E.D.N.B. was calibrated according to the following:

$$E.D.N.B. = \frac{T.L._1 \times D.N.B.}{T.L._2}$$

where T.L.₁ = Trichome length of the present stage of development.

T.L.₂ = Trichome length of the preceding stage of development.

D.N.B. = Distance between the centre of the nucleus and trichome base of the preceding stage of development.

In order to measure the growth components, at different developmental stages, the latter were selected in relation to conspicuous changes in the trichome ontogeny (indicated in the explanation of Text-Figs.). The measurements of the growth components of each trichome, as given in Table I, are means of ten readings that were made on microtome sections of the materials. In the three

TABLE I

Measurements (in microns) of growth components of unicellular trichomes at different stages of their development

Stage	T.L.	L.C.W.	L.F.W.	D.N.B.	E.D.N.B.	D.N.T.	D.S.N.	D.T.
<i>Helianthus annuus</i> L.								
I	10.40	10.40	..	4.96	..	5.44	3.04 (spherical)	3.68
II	14.00	14.00	..	7.52	6.68	6.48	3.12 (elliptic to oblong)	4.88
III	22.08	17.84	4.24	10.64	11.86	11.44	3.28 (elliptic to elongate)	5.76
IV	35.12	19.69	15.36	14.72	16.92	20.00	3.60 (spherical)	8.96
<i>Chrysanthemum carinatum</i> L.								
I	15.68	15.68	..	7.45	..	7.72	2.72 (spherical)	3.47
II	21.07	21.07	..	10.12	10.01	10.40	3.20 (elliptic)	4.52
III	31.20	31.20	..	14.40	14.98	17.05	3.87 (elongate)	6.40
<i>Lagascea mollis</i> Cav.								
I	9.10	8.75	0.36	3.21	..	5.80	6.25 (spherical)	16.60
II	13.21	9.64	3.57	4.64	4.65	8.56	6.07 (spherical)	21.78
III	19.64	7.85	11.78	4.19	6.90	14.63	6.25 (spherical)	25.17
IV	44.19	8.57	35.52	8.03	10.17	37.84	8.57 (spherical)	39.38

Figures representing the respective stages of development are: *Helianthus annuus* L. stages I-IV correspond to Figs. 7-9 & 11. *Chrysanthemum carinatum* L. stages I-III correspond to Figs. 2, 3 & 5. *Lagascea mollis* Cav. stages I-IV correspond to Figs. 12-14 & 16.

species studied, the trichomes show maximal growth in the middle portions of the hairy region of the stigmas (in the case of sunflower and *Chrysanthemum carinatum*) and filaments (in *Lagascea mollis*), whereas they are reduced to mere papillae towards the end portions. Hence, the measurements were obviously confined to the trichomes of the middle portion so as to get a correct picture of the developmental changes.

OBSERVATIONS

Stigmatic hairs of the sunflower.—These occur adaxially on the stigmatic lobes, are laterally coalescent in the proximal region and have free tapering ends. The wall is thin and the nucleus is rounded and situated at about the middle of the proximal part of the trichome (Fig. 11). The precursors of the hair initials are square-like, densely cytoplasmic enclosing large rounded nuclei, and divide anticlinally, each giving rise to two initials (Figs. 6 and 7). The initials are mostly narrower and longer than the precursors and bear elongated nuclei. It is possible, however, that occasional precursors might not divide and develop as such into hairs; so also certain of the normal initials may divide again longitudinally before differentiating into hairs. Eventually, however, the trichome initials undergo simultaneous changes in the different growth components as shown by the measurements given in Table I and develop into mature trichomes.

These changes are as follows: The coalescent lateral walls progressively elongate through symplastic growth, while the trichome and the nucleus enlarge in diameter. The nucleus also elongates upto stage III, but becomes rounded in the last stage of the development (see Table I; Figs. 8–11). During these changes, the nucleus moves forward slightly at a rapid pace as compared to the elongation of the lateral wall, but finally slows down markedly. For example in stage II, it moves about a micron more than expected (see values of E.D.N.B. and D.N.B. at this stage in Table I), while in stages III and IV, the movement slows down by about 2μ (Table I). The apical intrusive growth is initiated at stage III, when the trichome had developed to nearly half its mature height (Table I; Fig. 9). The growth is hereafter vigorous particularly in the free portion of the trichome, due to apical intrusive growth, though this has no influence on the nuclear movement, since, as mentioned above, it is from this stage, that the nucleus starts retarding.

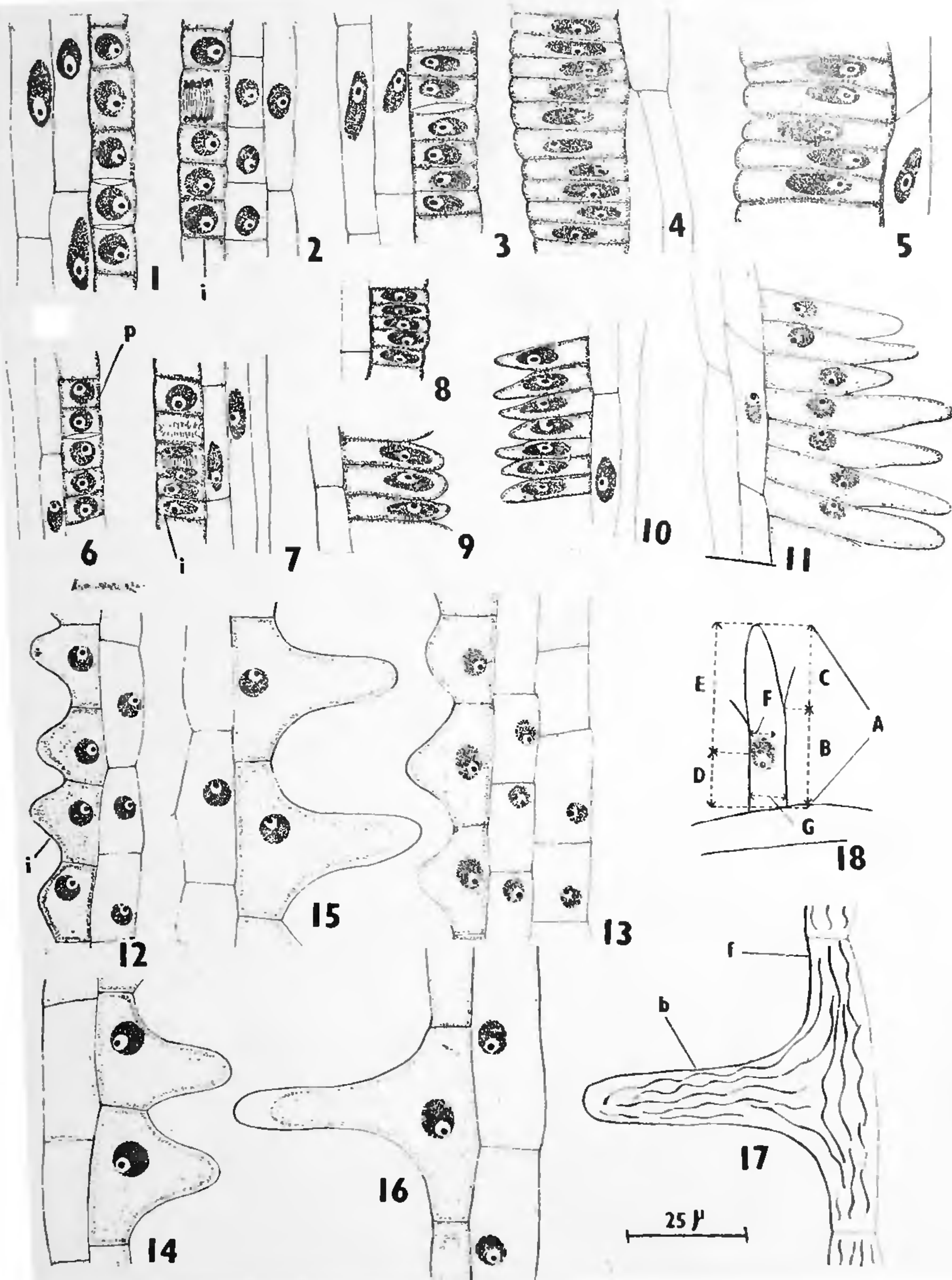
Stigmatic papillae of Chrysanthemum carinatum.—The papillae are borne on the adaxial surface of the two stigmatic lobes, and in longisections, appear

cylindrical, rounded at the tip, thin-walled and show elongated nuclei embedded in dense cytoplasm (Fig. 5). The trichomes are laterally completely coalescent with one another and appear like a palisade layer (Fig. 5). The precursors of the hair initials are rectangular to square in shape and possess a large rounded nucleus embedded in dense cytoplasm (Figs. 1 and 2). Each precursor divides anticlinally (Fig. 2), giving rise to two stigmatic hair initials (Fig. 3), which are longer than the precursors and also bear longer nuclei. Subsequent changes (see Table I) in the initials leading to the mature forms are in general comparable to those occurring in the sunflower, but for the following differences. The nucleus retards in the final stage of trichome development (Table I), increases in length and diameter upto the maturity (Figs. 4 and 5) and no apical intrusive growth occurs so that a free distal portion is not differentiated (Fig. 5).

Filament hairs of Lagascea mollis.—These are differentiated into an expanded foot and a tapering body (Fig. 17). The nucleus is rounded and situated nearly at the juncture of the foot and body. Cytoplasm is scanty and the wall is thin, covered with a striated cuticle. The initials of the trichome are nearly isodiametrical and somewhat curved at the outer end, while the nucleus is rounded and situated near the base (Fig. 12). Though further development involves changes similar to those observed in the sunflower (Figs. 13–16; Table I), there are differences characteristic of these trichomes. The initials expand at the base (tangentially to the filament axis) synchronous with the apical intrusive growth, thus leading to simultaneous differentiation of the foot and body. At the same time the coalescent part of the lateral walls also elongates through diffuse symplastic growth, but in the stage II, the wall shows about two microns reduction in the length (see Table I) indicating that the walls of adjacent trichomes at their outer end separate from one another (compare also Figs. 14 and 15). The nucleus is rounded and remains unchanged all through the ontogeny.

DISCUSSION

Regarding the angiosperm root hairs, which represent ontogenetically the most well-studied unicellular hairs by earlier workers^{1,3,4}, the following features have been established: (1) To begin with, the epidermal cells, in the root hair region, undergo tangential growth (parallel to the root axis) and also become externally deposited on the outer wall with calcium pectate; (2) the portion of the outer wall, which remains unpectinised, forms the focal point for lateral elongation of the root hair; (3) the elongation occurs primarily through growth



FIGS. 1-18. Figs. 1-5. From L.S. stigmatic lobes of *Chrysanthemum carinatum* L. Figs. 6-11. From L.S. stigmatic lobes of *Helianthus annuus* L. Figs. 12-17. *Lagascea mollis* Cav. Figs. 12-16. From L.S. filaments, Fig. 17. Surface view of filament hair. Fig. 18. Diagrammatic representation of a stigmatic hair of sunflower illustrating the different parts which were measured during ontogeny for obtaining values of various growth components, A - G: (A = T.L.; B = L.C.W.; C = L.F.W.; D = D.N.B.; E = D.N.T.; F = D.S.N.; Here this may be taken as meaning only the diameter of the nucleus; G = D.T.; b = body; f = foot; i = trichome initial; p = precursor of a trichome initial),

locus occurring at the tip of the hair where synthesis of new cellulose fibrils takes place; (4) along with this the nucleus also makes forward movement remaining close to the tip. In the trichomes presently studied these features are not confirmed. Initials of these trichomes at the outset either show direct axiate elongation (Figs. 3 and 7), or synchronous tangential end axiate elongation (Fig. 12), and the outer wall becomes progressively, but uniformly cuticularised rather than pectinised. Cuticle's presence at the early ontogeny of the trichomes was tested by first dissolving out the cellulose by 85% H_2SO_4 , followed by washing with water; later, the membrane left unaffected was stained with iodine solution which stained brown yellow indicating that it is cuticular⁵. Secondly, the entire outer wall participates in the elongation of the trichome (Figs. 12–16), rather than a pre-defined unpectinised locus as in the root hairs. Though the axiate elongation occurs through apical intrusive growth, in none of the trichomes studied a definitive thinner area of growth at the tip was detected, because prolonged immersion in distilled water of young hairs (or prolonged boiling in hot water and acidified water) did not bring forth bursting of the hair apex as reported in the case of root hairs¹. Lastly, the apical intrusive growth embraces only the cytoplasm and the cell wall and not the nucleus as the latter markedly slows its movement during this phase. Thus nuclear movement in the development of the trichomes studied indicates that it is independent of the growth changes in the cell wall and cytoplasm.

According to Haberlandt and others⁸, proximity of the nucleus is necessary for the growing point of the trichome to function. But in the trichomes studied here, specially in the stigmatic hairs of the sunflower and the filament hairs of *Lagascea mollis*, it is during the vigorous period of elongation which occurs through apical intrusive growth, that the nucleus slows its movement and remains further behind the tip, but without inhibiting the trichome growth.

In the trichomes studied, the observation of changing shape of the nucleus is interesting in that it reveals that the nucleus in its interphase is sufficiently plastic, to adapt itself to the space available without suffering any functional damage. For example, since the stigmatic papillae of *Chrysanthemum carinatum* are narrower, the nucleus remains elongated upto maturity (Figs. 3–5), whereas in the stigmatic hairs of the sunflower, it elongates when the hair initial is thinner, but regains its spherical form subsequently when the trichome

widens (Figs. 8–11). In *Lagascea mollis*, on the other hand, the nucleus remains in spherical form throughout ontogeny of the filament hair as the latter is sufficiently broader from the outset (Figs. 12–16).

The trichomes studied occur densely abutting one another and develop simultaneously in each of the species studied. This is important because it indicates that Bunning's² organogenetic inhibitory field effects considered responsible for spacing out of epidermal organelles from one another and for their asynchronous differentiation are absolutely absent in these instances.

A comparison of the development of the three trichome types studied suggests the following patterns of development in the unicellular trichomes of the angiosperms in relation to their major growth components:

- (1) Progressive elongation and broadening of the trichome through symplastic growth. Nucleus mobile in the axiate direction of the trichome, but retarding in the final stages of development, e.g., stigmatic papillae of *Chrysanthemum carinatum*.
- (2) In the beginning trichome develops as in the above, but in the later half of the ontogeny, is dominated by apical intrusive growth; nuclear movement as in the above, e.g., stigmatic hairs of the sunflower.
- (3) Trichome develops synchronously both at the base through symplastic growth and at the distal end through apical intrusive growth, the former giving rise to a flattened foot and the latter to a tapering body; nuclear movement as in the above, but considerably slower and reaching only the juncture of the foot and body, e.g., filament hairs of *Lagascea mollis*.

In the light of the data available regarding the root hair ontogeny^{1,3,4,8}, the following additional pattern is recognised.

- (4) Trichome develops through changes in the same growth components as in the above, but the symplastic growth at the base (in the tangential direction of the root) precedes the apical intrusive growth occurring: nuclear movement closely corresponding with the axiate elongation of the hair.

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THE GROWTH OF SILVER SULPHIDE CRYSTALS

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ABSTRACT

Crystals of Ag_2S were grown from the vapour phase reaction under H_2S - H_2 atmospheres. Morphological symmetry and X-ray rotation photographs showed that they are acanthite crystals which are formed under metastable conditions. This indicates that the phase transformation temperature of silver sulphide is dependent on the gaseous medium surrounding it and the stoichiometry.

INTRODUCTION

THERE are large discrepancies in literature on the equilibrium diagram of Ag-S system. Jeannot, Perrot and Tridot¹ reinvestigated this system in the temperature range of 170–800° C in H_2S - H_2 atmospheres. They reported the existence of the compound, Ag_4S , which they confirmed by thermoanalytical and electrical conductivity measurements. In the present investigation we tried to grow crystals of this metal-rich silver sulphide (Ag_4S) under the same set of conditions reported by the above authors. Ag_2S and Ag have been found to be the eventual products. However, Ag_2S grows into fine whiskers and quite often as well-grown tablets and larger needles with well-bounded faces exhibiting the monoclinic prismatic symmetry. In this report, we would like to communicate our observations on the crystal growth of Ag_2S in H_2S - H_2 atmospheres.

EXPERIMENTAL

Silver foil of high purity with 0.5 mm thickness was cut into 5 × 3 mm rectangles. A small amount of gold can be expected as impurity in this material. The metal was mixed with sublimed sulphur (Fluka, AG, 99.99 purity) such that the mole ratio was varied from Ag_4S to Ag_2S . The mixtures were taken in pyrex-glass ampoules and evacuated to 10⁻⁵ mm of Hg. The ampoules were subsequently filled with H_2S - H_2 gas mixtures which had a composition of 1 : 3 mole ratio. The total

pressure was adjusted such that at 450° C the internal pressure was 760 mm of Hg, as calculated from the measured volume of the ampoule. Each ampoule had a narrow tube portion fitted with a stopcock. After filling the gas mixture, the ampoule was isolated from the rest of the vacuum system by closing the stopcock. The ampoule was sealed at the narrow tube part, while cooled in liquid nitrogen. It was possible by this procedure to keep a constant H_2S : H_2 ratio at the time of filling. The ampoules were transferred to a horizontal tube furnace and slowly heated to 450° C. The furnace (50 cm long) had a constant temperature zone of about 10 cm in the middle, while about 5 cm on each side of this had a drop in temperature of about 5° C. The lengths of all ampoules were within 15 cm. The ampoules were kept at 450° C for 7 days and subsequently taken out. The growth of silver sulphide crystals as well as the growth of silver "hair" could be observed within a day, by illuminating from one end of the furnace through the loosely packed quartz-wool.

RESULTS

Irrespective of the nett composition of the initial charge with respect to silver and sulphur, the resulting products were Ag_2S crystals (whiskers, larger needles and tablets) and hair-like growth of silver. As the composition approached Ag_2S , the amount of silver separating as filaments was negligible. With slightly more sulphur than 2 : 1 ratio