OBSERVATIONS ON PECULIAR AIR PASSAGES IN THE STEMS OF *GLORIOSA SUPERBA* L. AND *IPHIGENIA INDICA* KUNTH

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ABSTRACT

Every basal internode of *Gloriosa superba* possesses a highly specialized air passage which connects the underground rhizome to the aerial atmosphere. This air passage can be as long as 80 cm and is completely surrounded by an epidermis which has stomata. The air passage opens to the atmosphere in the axil of the first aerial leaf, and the passage appears to arise due to ontogenetic fusion between the first leaf and the basal internode. We have designated it as *Gloriosa*-type air passage and its epidermis and stomata as 'included epidermis' and 'included stomata'. *Iphigenia indica*, another liliaceous plant, also possesses such air passages. These air passages probably are of adaptive significance in supplying O_2 to underground storage organs for respiratory energy as ATP which is required to reconvert sugar to starch. CO_2 released in the process may be recaptured through the included stomata.

INTRODUCTION

The basal internodes of *Gloriosa superba* and *Iphigenia* possess internal air passages providing an uninterrupted connection between the underground storage organs and the aerial atmosphere. Internal air cavities and passages are common in stems, leaves and roots of many plants, particularly those growing in marshy and aquatic habitats and requiring adequate aeration[1]. In all these plants the air passages develop either schizogenously or lysigneously[2] by separation or dissolution of cells internal to the epidermal system.

The air passages described here in *G. superba* and *I. indica* are unique since they appear to develop through ontogenetic fusion of the first aerial leaf with the basal internode. These air passages are bound by their own epidermal system provided with stomata. Thus, in a cross-section, the basal internode presents an unusual feature: an internal air cavity bound by epidermis in the peripheral region of ground tissue and with no apparent relation to the usual epidermis located as the outermost layer (figure 2). This is a preliminary report on the structure and probable physiological significance of these air passages. We propose to describe these as "Gloriosa-type air passages" and the epidermis and stomata that surround these cavities as "Included epidermis" and "Included stomata" (see below).

MATERIALS AND METHODS

The presence of an included epidermis was first observed in November 1984 in a cross-section of a basal internode of a young plant of *Gloriosa superba* L collected from the Madras Christian College Campus, Tambaram, Tamil Nadu. The section was stained with iodine potassium iodide (I_2KI) for the localization of starch as part of a study surveying the presence of starch statoliths in plants that respond to gravity. An examination of a pair of cells stained by I_2KI in the 'cortical' region revealed the presence of guard cells, and a cavity surrounded by epidermis with well-developed cuticle. Further observations were made on specimens collected from other parts of the campus, from around Tambaram, and other sites in Chingleput district. Collections were also made from Sendurai near Ariyalur in Tiruchi district, and Andipatti in Madurai district. In several cases the entire underground rhizome system was dug up to study the connections between storage organs and aerial shoots.

Plants of *Iphigenia indica* Kunth were collected from the Madras Christian College Campus. Cultivated specimens of *Gladiolus sp*, *Freesia sp*, and *Montbretia sp*, all cormous plants, were obtained from the Government Botanical Gardens, Ootacamund, Tamil Nadu.

Serial free-hand sections of the entire basal internodes, nodes, upper internodes as well as portions of the rhizomes of *G. superba* and corms of *I. indica* and other genera were stained with I_2KI, safranin or toluidine blue O. Sections were examined with a Nikon 'Labophot' microscope equipped with a Nikon camera and automatic exposure system.

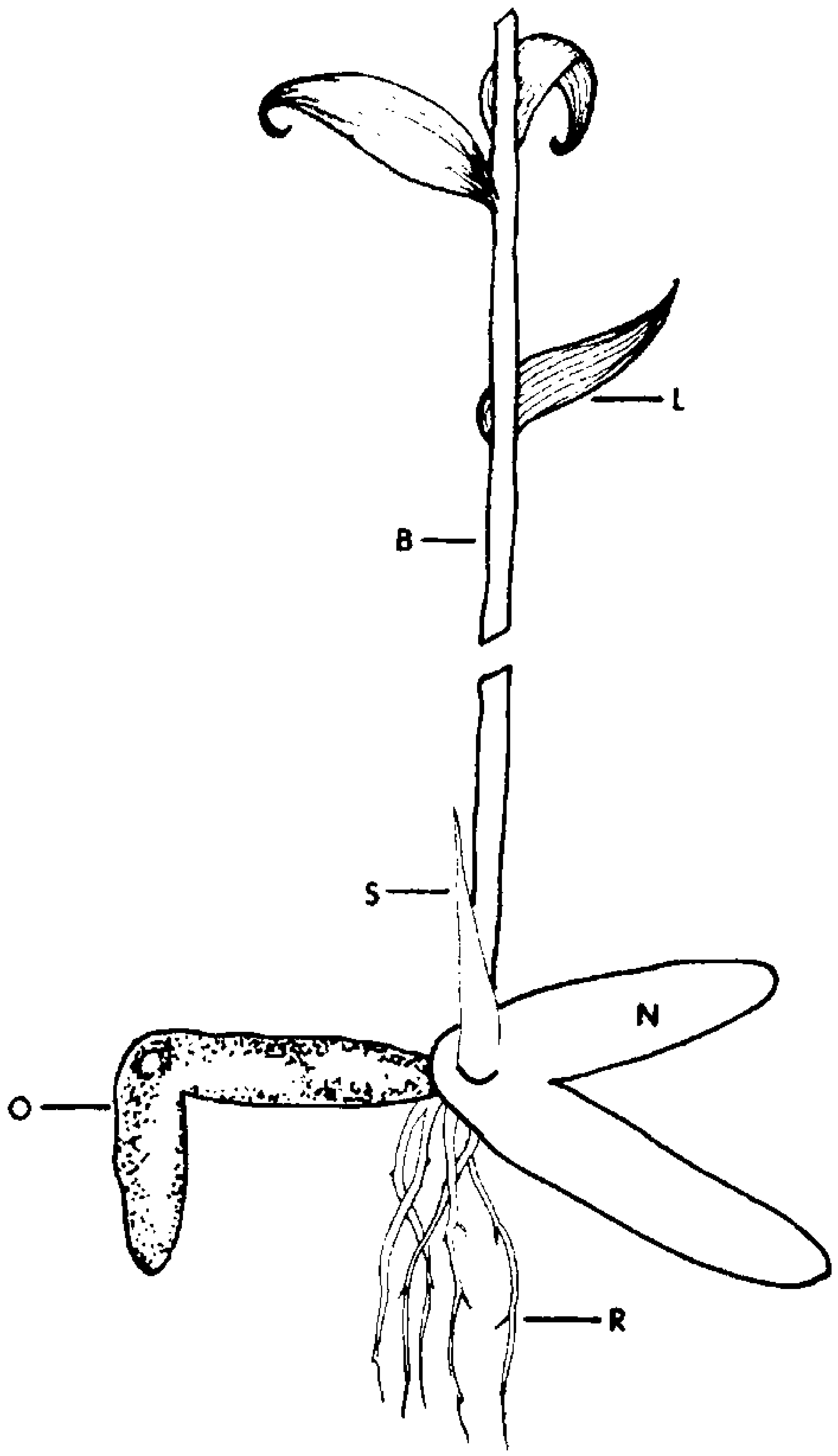

Figure 1. Diagram of old (O) and new (N) rhizomes and portion of an aerial shoot. B—basal internode; L—first aerial leaf; R—roots; S—scale leaf.

RESULTS AND DISCUSSION

The occurrence of Gloriosa-type air passages first noted in *G. superba* has now been confirmed as a regular feature in every one of the more than 100 specimens observed from different locations. These air passages are confined to the basal internodes which arise from the apex of the underground rhizomes. Generally a single arc-shaped cavity is observed in cross-sections of the basal internodes (figure 2); occasionally two such cavities are present. The cavity is located about one third the distance from the epidermis to the central pith region. Serial hand-sections reveal that each air passage is unbranched, and offers continuous contact between the rhizome and the axil of the first aerial leaf where the air passage opens to the external atmosphere. The length of this passage, which depends on the length of the basal internode, varies in our obsertation from a few centimeters to a maximum of 80 cm. Estimation based on cross-sectional area and length of internode suggests that in a 70–80 cm basal internode the air passage occupies an approximate volume of 1 ml.

It appears that adnation of the first leaf to the basal internode and the pronounced intercalary growth of this internode results in the presence of the air passage surrounded by epidermis. Thus, the epidermis of the air passage towards the centre of the internode is homologous with the epidermis of the internode above, while the epidermis of the air cavity towards the periphery is homologous with the adaxial epidermis of the first leaf. The presence of stomata only on the side of the epidermis towards the pith region is consistent with this interpretation since internodal epidermis possesses stomata while adaxial leaf epidermis lacks stomata. We have counted about 1,400 stomata distributed in two rows in the air passage of a 70 cm long basal internode. The guard cells are of the same dimensions as those found on the external epidermis and likewise accumulate starch (figure 2). The presence of substomatal cavities (outlined in 2 G) and starch-accumulating chlorenchyma in this region would suggest that the included stomata are functional. As in the external sub epidermis, some of the sub-epidermal cells of the air passage accumulate a red pigment, possibly anthocyanin. Also, the epidermis of the air passage has a thick cuticle (figure 2) similar to that found on the external epidermis. Based on the interpretation presented here the epidermis and stomata around the internal air passage in *G. superba* could be described as 'included epidermis' and 'included stomata'. Since this interesting structural feature was first observed in *G. superba* it may be called 'Gloriosa-type air passage'.

Surprisingly, a survey of other rhizomatous or cormous monocots revealed that the basal internodes of the corm-producing *Iphigenia indica*, another member of the Liliaceae, also possesses gloriosa-type air passages with included epidermis and stomata (figure 2). Such cavities however, are lacking in *Montbretia*, *Freesia*, *Gladiolus*, *Curcuma*, *Asparagus*, *Dioscorea*, *Habenaria* and *Zingiber*. Although *Gloriosa* is a rhizomatous plant and *Iphigenia* a cormous one, they share the common feature of seasonal production of new aerial shoots associated with new storage

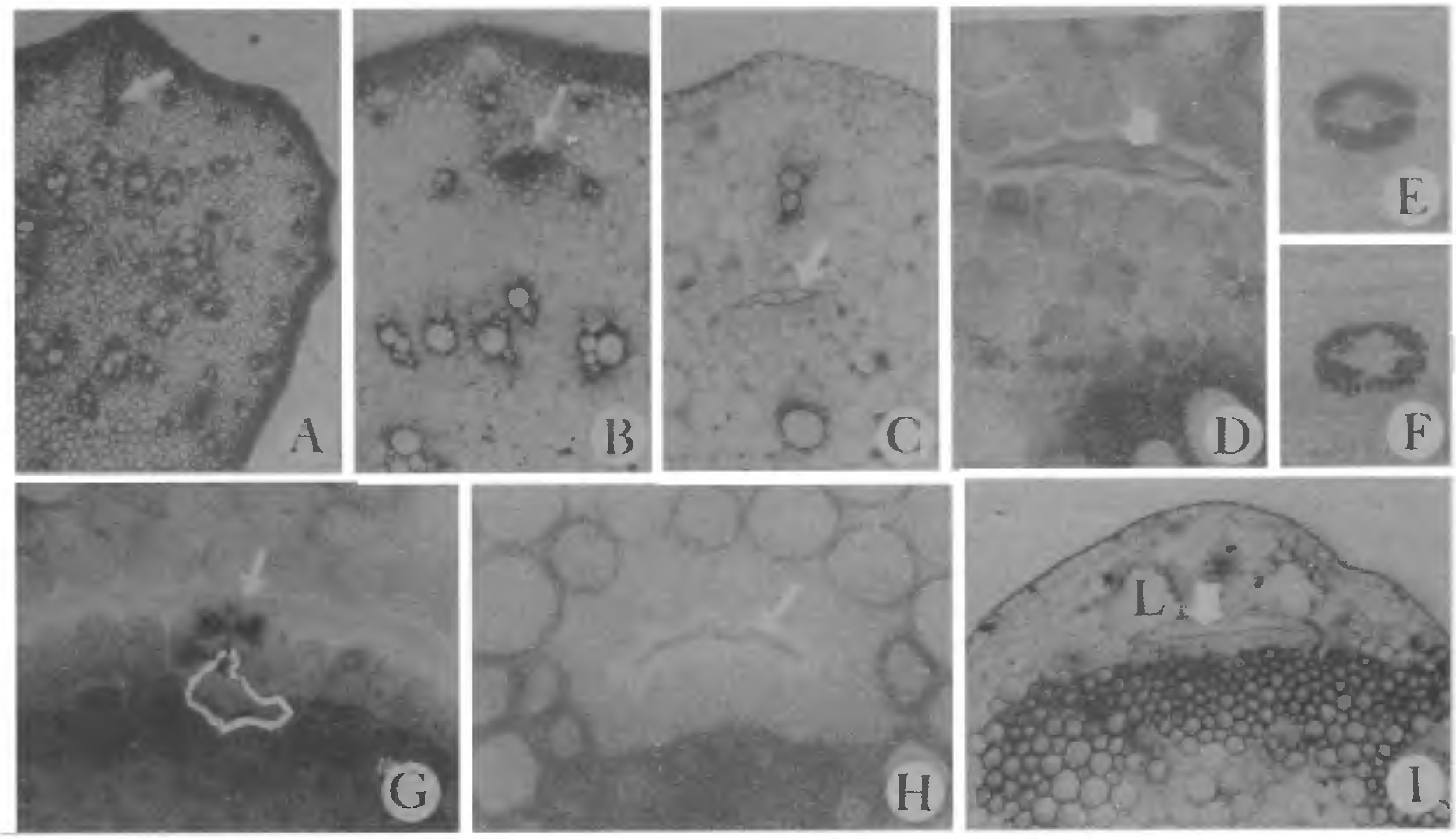

Figure 2. A–H. *Gloriosa superba*. Arrows indicate the location of gloriosa-type air passages—A–D, G, H. Transections of basal internode. A, B. Location of air passages in peripheral ground tissue in mature internode. (A—X 17.5; B—X 35). C. Air passage in young internode immediately above the level of rhizome (× 85). D, G, H. Air passages possess thickened tangential walls towards the cavity. A pair of guard cells with starch is seen in G (arrow), and a corrugated cuticle is prominent in H. (all × 350). E, F. Paradermal views of stomata stained for starch from peels obtained from external and included epidermis (both × 350). I. Transection of basal internode of *Iphigenia indica*. Adjacent to the gloriosa—type air passage (arrow) are two lysigenous air cavitieis (L). Cuticle of the included epidermis is poorly developed in the side towards these lysigenous cavities (× 85).

organs, and the channelling of reserve food from the rhizome or corm of the previous season to those of the current season. It is very likely that other species of *Gloriosa* and *Iphigenia*, and other members of the Liliaceae that are closely allied to these plants, such as *Sandersonia* and *Littonia*, also possess gloriosa-type air passages.

The gloriosa-type air passage might be a structural adaptation for the special physiological requirements of these plants which store starch during the flowering season, perennate during the drier periods and mobilise the reserve material to the new storage organs that develop during the next season. *Gloriosa* for instance, possess underground Y-shaped rhizomes (figure 1) whose growth pattern seems to follow the hexagonal grid pattern described by Bell and Tomlinson[3] for *Alpinia* and other rhizomatous plants. The tip of each arm of the fork possesses an apical meristem which develops into the aerial leafy shoot which may subsequently bear flowers. It is the basal internode of this aerial shoot which possesses the internal air passage. As the aerial shoot is developing, the tip of each rhizome produces two new arms of a rhizome (that of the current season) which develop as axillary branches. Simultaneously, roots are also produced at the lower surface in this region. As the arms of the new rhizome grow the old arms slowly degenerate.

The gloriosa-type air passage might play an important role in the supply of O_2 to the juncture where a new shoot is developing at the location where the old rhizome, the current season's rhizome, and the roots meet. Mobilisation of food from the old rhizome to the new one would involve: (1) breakdown of starch to sucrose or other transportable sugars, (2) transport to the new rhizome, and (3) redeposition of starch as amylose and amylopectin. Since starch is considered to be synthesized primarily by starch synthase which uses ADP-glucose as the preferential substrate[4], there is a requirement for large amounts of ATP, and hence respiration in the developing rhizomes. This requirement for O_2 would still persist in later stages when sucrose derived from photosynthesis of the aerial shoot would reach the rhizome. Thus, the gloriosa-type air passage might be an adaptation for the supply of O_2 from the aerial atmosphere. The stomata present in the air passage could recapture the CO_2 released by the developing rhizome during respiration. Interestingly, both *Gloriosa* and *Iphigenia* are colchicine-accumulating plants. Whether the air passage might also serve some function related to colchicine metabolism is unknown. The gloriosa-type air passage offers an interesting system for the study of gas exchange and its relation to source-sink relationship in rhizomatous plants.

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NEWS

THE SPACE INDUSTRY—TRADE RELATED ISSUES

The report now published by OECD provides in a summary form an economic view of the space industry and its markets. It attempts to give a clear definition of the sector and its links with the aeronautics and electronics industries and sets out details of medium-term market developments in the space industry—telecommunications satellites, direct broadcasting, observation satellites and other space applications.

The report highlights: 1. disparities in the space commitments of Member countries and provides comparable figures on budgets and on space related industrial activities; 2. the factors determining firms' competitiveness. The report notes that, in numerous instances, the consequences of scale are often more critical than the technology gaps; 3. the complementarity of or competition between different technologies available, *e.g.* recoverable or expendable launch vehicles for geostationary satellites, the choice of high or low powered direct broadcasting satellites, also the use of optical fibre or satellite technology for communications; 4. the co-operative and competitive strategies of firms in Europe, Japan and the United States.

The report, as its title indicates, throws light on the problems raised by trade in space products and shows how trade is affected by the lack of standardisation and by the persistance of policies based on national or regional preferences.

The report examines national policies and recent development in the marketing of space products—privatisation, deregulation, joint industry-agency involvement in space R & D work, also procurement policy. (OECD-Information Service, Paris, December 1985, OECD Press Division, 2, rue Andre Pascal, 75775, Paris).