Taiwania, **40**(2): 139-150. 1995

The Formation of Lenticels on the Branches of *Ficus microcarpa* L. f.

Ling-Long Kuo-Huang[1,2] and Li-Fen Hung[1]

(Manuscript received 28 April 1995; accepted 6 June 1995)

ABSTRACT: The formation of lenticels on the branches of *Ficus microcarpa* L. F. was examined. Beneath the stomata of a young branch, the division of precomplementary cells progressed from the cortex inwards and then the lenticel phellogen was formed. It was found to be continuous with the phellogen of periderm. The phellogen of the lenticel centrifugally produced a compact suberized closing layer and then one to four layers of unsuberized complementary cells. The mature lenticels are lens-shaped and convex towards both the exterior and interior. They are centrifugally composed of phylloderm, lenticel phellogen, and several strata of complementary cell layers alternated with a single closing layer. In the lenticel, some prismatic calcium oxalate crystals and several rows of radially arranged tannin cells were observed. Lenticel hypertrophy arose in the immersed mature internodes. It was characterized by large and loosely interconnected thin-walled cells.

KEYWORDS: ***Ficus microcarpa*, branches, lenticel formation, lenticel hypertrophy.**

INTRODUCTION

The most primitive type of lenticel is the parichnos (Wetmore, 1926a). It was probably widespread as the aerating channels in the ancient arboreal plants. In the Lepidodendraceae the parichnos accompanied each foliar trace into the leaf, and after the fall of leaf the paired parichnos scars were found. The parichnos-like structures have also been observed in *Ginkgo biloba, Equisetum*, and a few genera of conifers (Wetmore, 1926a).

In the large majority of gymnosperms and angiosperms lenticels are conspicuously found in the stems and roots (Eames and MacDaniels, 1947). Occasionally, they are also found in fruits (Clements, 1935). Only a few plants, e.g. *Campsis, Philadelphus, Vitis,* and some other climbers, have been reported to be without lenticels, although they form a periderm (Fahn, 1990). According to the types and arrangement of cells in the lenticels, four types of lenticels may be distinguished (Esau, 1977). In addition, depending on the orientation of the rupture on the epidermis, the lenticels are recognized as transverse or longitudinal lenticels (Wetmore, 1926a). In general, the fissures of lenticels are closely located to the phloem rays, so that abundant radial air passages are present. Lenticel

1. Department of Botany, National Taiwan University, Taipei, Taiwan, Republic of China.
2. Corresponding author.

hypertrophy has been observed on the stems of many woody plant species, when they were subjected to flood conditions (Brown and Considine, 1982; Tarkowska and Kowalska-Mueller, 1985; Larson, Davies and Schaffer, 1991).

The gross anatomy of mature lenticels in many plants has been described, but only a few reports concerning the development of lenticels have been published (Jacob, Lehmann and Stelzer, 1989). The purpose of this study is to investigate the distribution and formation of lenticels in the branches of *Ficus microcarpa*. Lenticel hypertrophy in immersed internodes was also studied.

MATERIALS AND METHODS

Young branches of *Ficus microcarpa* L. f. were collected from the campus of National Taiwan University. The branches, 4-6 cm with 5 nodes and 20-25 cm long with 10-15 nodes, were placed in beakers of water for 4-5 weeks. The lowest 2-4 nodes of each branch were immersed in water. The samples were taken at intervals of a few days, beginning when the lenticels were observed to start enlarging. The morphology and distribution of lenticels on each internode were studied with a Nikon SMZ-10 dissecting microscope. The excised small stem samples with lenticels at different developmental stages were fixed in FAA for 24 hours, dehydrated in TBA series, and then infiltrated and embedded in paraffin. The 10 μm sections were stained with Safranin O and Fast green (Johansen, 1940), and photographed with a Leitz Diaplan microscope. Some materials for SEM were fixed in 2.5% glutaraldehyde, followed by 1% OsO_4, and dehydrated in an ethanol-acetone series. The samples were then dried with a Hitachi Critical Point Dryer (HCP-1), coated with an IB-2 Ion Coater (Kuo-Huang, 1990), and then examined with a Hitachi S-550 SEM.

RESULTS

The shoot apex of *Ficus microcarpa* is enclosed in pairs of caduceus stipules. In general, the young leaves and stems are somewhat pubescent (Fig. 1a and b), but these multicellular trichomes are caduceus, therefore, the mature leaves and stems are glabrous. On the branches the lenticels are sporadically distributed on every internode. There are about 15 lenticels on each internode (Table 1), and almost all are at the same developmental stage.

The epidermis of the lowest 1-2 internodes, which were still enclosed in the stipules, was composed of ordinary epidermal cells, some trichomes and stomata (Fig. 1a, c and d). The guard cells had prominent ridges and their axes were parallel to the axis of branch (Fig. 1e). Beneath the stoma there was a group of small parenchymatous cells (Fig. 3a and c). These cells divided in different planes and formed a mass of rounded, thin-walled cells with prominent intercellular spaces (precomplementary cells). In the internodes immediately adjacent to the enclosed stipules, the division of precomplementary cells progressed from the cortex inwards and the orientation of the divisions became more and more

periclinal until the lenticel phellogen was formed. The lenticel phellogen was bowl-shaped and its margin was found to be continuous with the outer cell layer of cortex just below the epidermis. At this stage, the branches underwent the primary growth. Their outer cortex was composed of 5-7 layers of angular collenchyma.

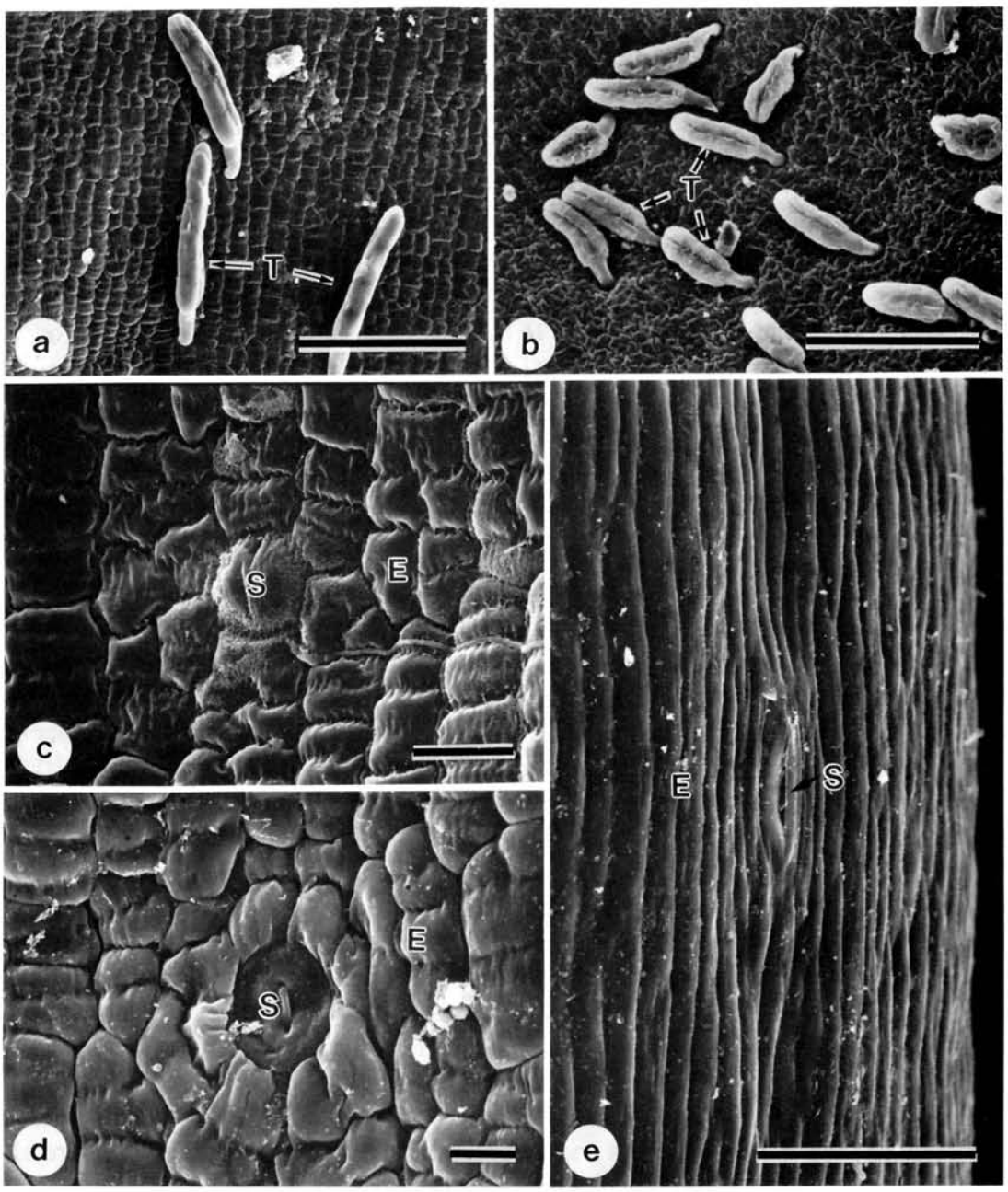

Fig. 1. a: Multicellular trichomes (T) on the surface of the young internode still included in the stipules. (bar = 100 μm). b: Multicellular trichomes on the abaxial surface of the young leaf. (bar = 100 μm). c and d: Young guard cells of stoma (S) on the epidermis (E) of a young internode still enclosed in the stipules. (bar = 10 μm). e: Stoma on the epidermis of the internode just beneath the enclosed stipules. (bar = 100 μm).

Table 1. The number of lenticels on each internode of the branches of *Ficus microcarpa*. (* : wounded internode)

		number of branch													average of the number of lenticels
		1	2	3	4	5	6	7	8	9	10	11	12	13	
number of internode	1	16	12	17	16	18	15	17	12	14	20	11	17	13	15.2±2.6
	2	21	19	20	18	13	15	23	16	22	24	15	22	10	18.3±4.1
	3	16	22	11	15	13	19	21	14	13	15	19	13	11	15.5±3.5
	4	18	23	22	23	25	14	10	9	13	18	23	9	22	17.6±5.7
	5	16	15	16	10	10	14	13	15	16	18	13	16	6	13.7±3.2
	6	16	20	16	14	*	11	*	15	15	17	17	19	14	15.8±2.4
	7	15	23	12	*	11	10	13	13	12	13	16	13	12	13.6±1.6
	8	19	13	18	*	14	12	15	21	9	10	18	21	8	14.8±4.1
	9	21	15	13	14	15	16	23	11	11	15	13	19	8	15.0±4.0
	10	12	13	12	9	-	11	-	21	13	16	12	10	10	12.6±3.2
	11	9	19	9	10	-	9	-	29	13	14	33	12	-	15.7±8.2
	12	9	14	8	14	-	*	-	-	17	21	-	18	-	14.4±3.0
	13	9	17	9	9	-	15	-	-	11	29	-	22	-	15.1±6.8
	14	15	19	-	9	-	11	-	-	9	13	-	17	-	13.3±3.6

On the internodes 1-2 nodes below the enclosed stipules, the phellogens of lenticels centrifugally produced a compact suberized closing layer (sometimes two closing layers) (Fig. 3d and f) and then one to four layers of loosely arranged unsuberized complementary cells (Fig. 3g and i). The intercellular spaces between the radial walls of complementary cells were greater than those between the tangential walls. The increase in number of these cells caused the epidermis to rupture along the stomatal pores (Fig. 2a and b) and the precomplementary cells were pushed out. The outer closing layer then replaced the epidermis as the protective layer. The phellogens of lenticels also centripetally produced 1-2 layers of phelloderm.

Soon after the formation of the lenticel phellogen, the cortex cells immediately below the epidermis non-synchronously underwent periclinal division and formed the periderm phellogen (Fig. 4a and c). At this stage the periderm phellogen centrifugally produced 2-3 layers of phellem and 1-2 layers of phelloderm (Fig. 3g and i; 4d). Also, the vascular cambium was found to be between the primary xylem and phloem of the large bundles (Fig. 4e).

The phellogens of lenticels on the internodes 3-4 internodes below the enclosed stipules, alternately produced closing layers and complementary cells (Fig. 3j and l). There after, the cells of the exposed layer died and withered away. The mature lenticels were lens-shaped, and were convex towards both the exterior and interior. Their axis was parallel to the branch and had a longitudinal fissure (Fig. 2c and d). Generally, only two compact strata of closing layers were observed in mature lenticels. In the lenticels, several rows of radially arranged tannin cells were observed (Fig. 3j and k). They were located throughout the phelloderm, lenticel phellogen, closing, and complementary cell layers. Prismatic calcium

oxalate crystals were also found in some of the phelloderm cells of the periderms and lenticels (Fig. 4f and i).

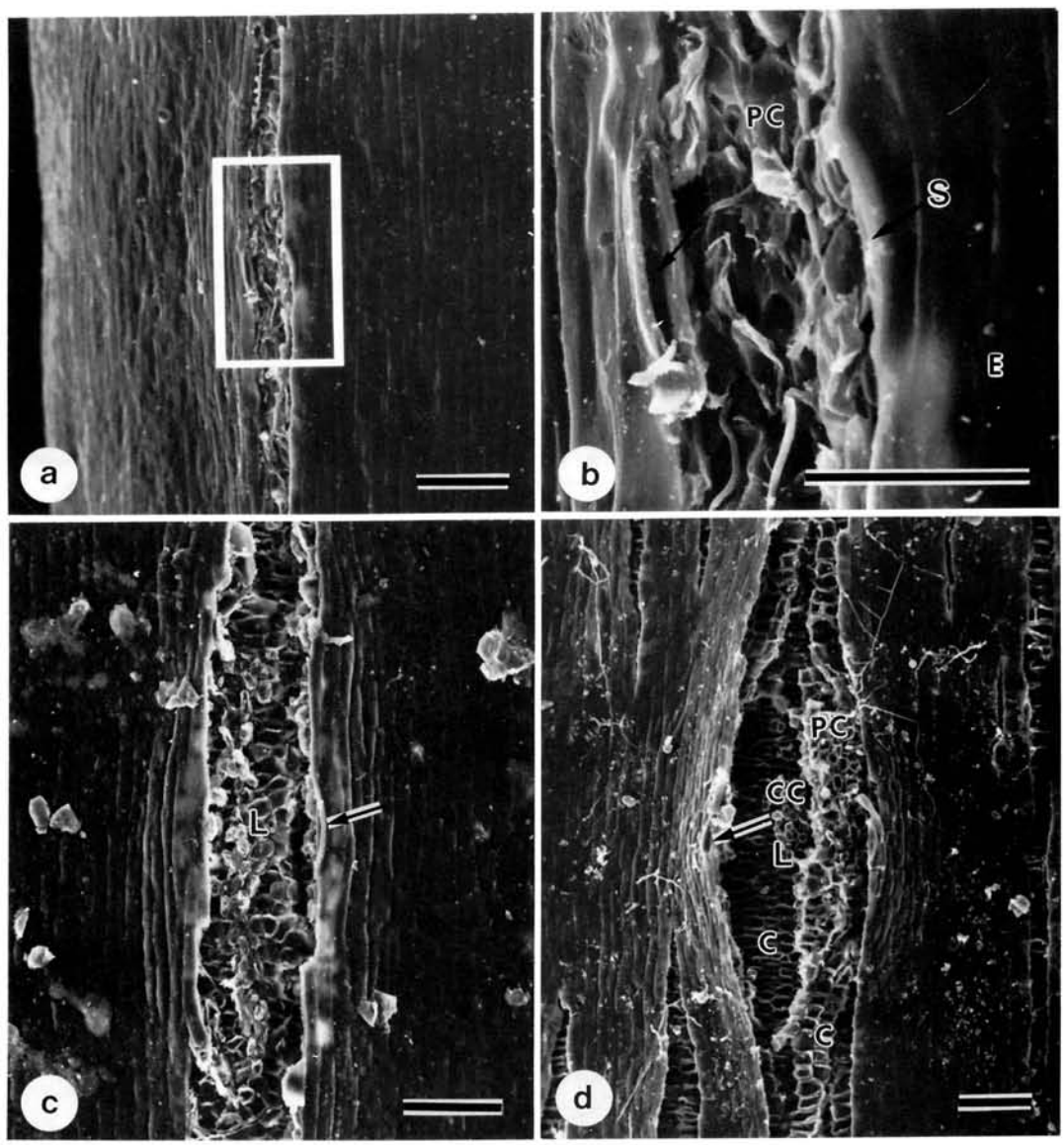

Fig. 2. a: Lenticel on the internode, 1-2 internodes below the enclosed stipule, showing the fissure of the lenticels along the stomatal pore. (bar = 100 μm). b: Enlargement of a, showing the ruptured stoma (→) and precomplemental cells (PC). (bar = 50 μm). c: Lenticel (L) on the internode, 3-4 internodes below the enclosed stipule. (bar = 100 μm). d: mature lenticel, showing the ruptured stoma (→), precomplemental cells (PC), outer compact closing layers (C), and the loosely arranged complemental cells (CC). (bar = 100 μm).

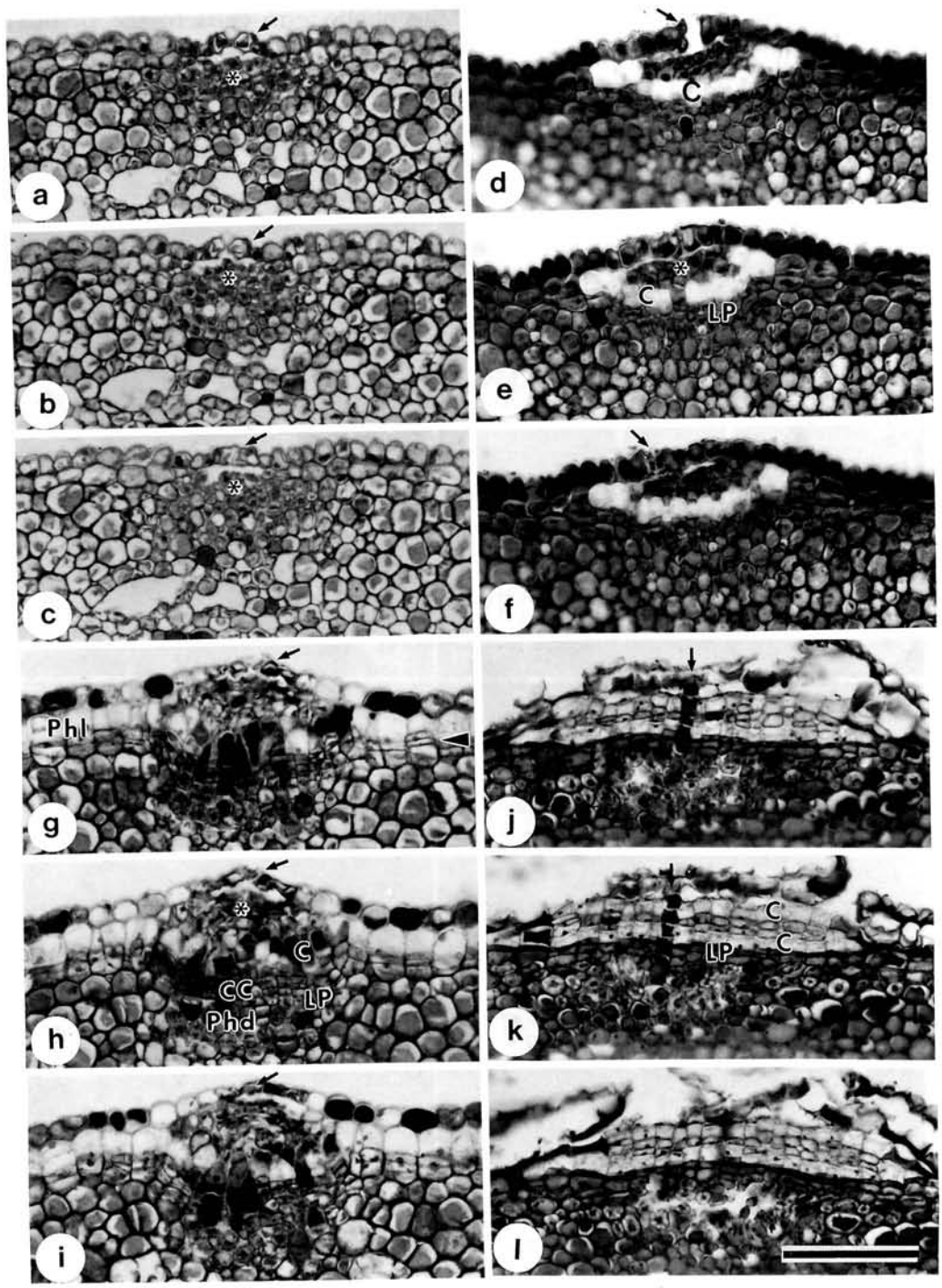

Fig. 3. Series cross sections of the lenticels at different developmental stages. (bar = 100 μm). a-c: Initiation of the lenticel showing the group of small parenchymatous cells (∗, precomplementary cells) just beneath the stoma (→). d-f: Young lenticel showing the lenticel phellogen (LP) and the first closing layer (C). g-i: Young lenticel showing the phelloderm (Phd), lenticel phellogen (LP), the closing layer (C), the complementary cells (CC), the ruptured stoma (→) and the precomplimentary cells (∗). j-l: Mature lenticel showing the fissure of the lenticels, two compact strata of closing layers (C), lenticel phellogen (LP), and rows of radially arranged tannin cells in the lenticel (→).

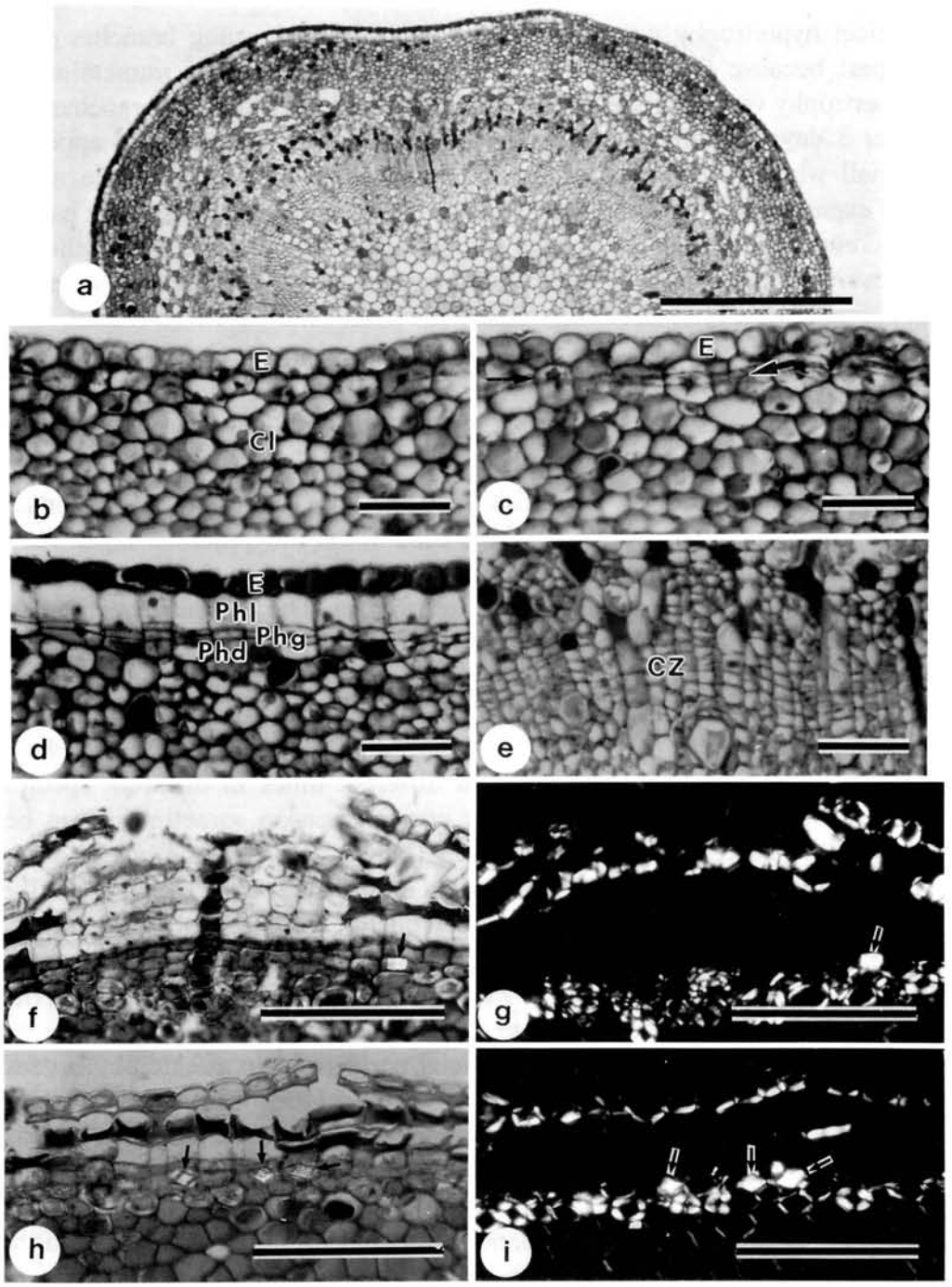

Fig. 4. a: Cross section of the internode, 1-2 nodes below the enclosed stipules. (bar = 0.5 mm). b-e: Enlargments of the portions of (a). (all bar = 50 μm). b: 5-7 layers of angular collenchyma (Cl) below the epidermis (E). c: Periclinal division in the cortex cells immediately beneath the epidermis (→). d: Phellogen(Phg) producing phellems (phl) and phelloderm (Phd). e: Cambial zone (CZ) between the primary xylem and phloem. f-i: Cross sections of the internode, 3-4 internodes below the enclosed stipules (all bars = 100 μm). f and g: Calcium crystals (→)in the phelloderm cells of the lenticel. h and i: Calcium crystals (→) in the phelloderm cells of the periderm. g and i: Photos by polarizing microscopy .

No lenticel hypertrophy was observed in the immersed young branches with only 5 nodes, in part because these branches died after several days of immersion. However, lenticel hypertrophy was clearly evident in the immersed internodes of branches with 10-15 nodes. After 3 days, the first morphological change in the lenticel sites appeared in the form of small white protrusions on the part of the stem immersed in the water. These protrusions expanded vertically and horizontally, then formed white, spongy balls (Fig. 5a). They were composed of large rod-shaped and radially interconnected thin-walled cells (Fig. 5b). There were an abundance of intercellular spaces, but no closing layers were observed (Fig. 5c). Nevertheless, rows of radially arranged tannin cells were also found.

DISCUSSION

As mentioned by Esau (1977), the first lenticels arise from below the stomata on the stems, when the periderms originate from the cells in the subepidermal layer. However, in the roots and in certain types of stems, periderms are formed in the inner layers of cortex, and the lenticels originate independently of the stomata. The present investigation reveals that on the stem of *Ficus microcarpa* the periderms originate superficially in the layer immediately below the epidermis, and the lenticels arise also only below the unevenly distributed stoma. In addition, almost all of the lenticels in a given internode are in the same developmental stage.

Lenticel and periderm initiation occur at different times in different species. In the majority of plants, it occurs during the first growing season sometimes even before the growth in length has ceased (Eames and MacDaniels, 1947). In *Ficus microcarpa* the lenticels develop very early, beneath the stomata on the internodes which are still enclosed in the stipules. After the initiation of lenticel phellogens the first periderm phellogens appear in the internodes 1-2 nodes below the enclosed stipules, and usually spread outward from the edges of the lenticels. But in *Pelargonium* (Lier, 1955) and *Kandelia* (Chang, 1984) the periderm phellogens arise from the cells beneath the trichomes.The origin and the development of the lenticels and superficial periderms are affected by several factors, including environmental conditions (Bower, 1963; Lier, 1955; Kauffert, 1937). It has been observed that the size of the lenticels and the number of layers of periderm increase on the side of a stem which receives more sunlight (Chiang, 1978).

The determination of the structural type of each lenticel is genetically rather than environmentally controlled, nevertheless, no significant similarity is revealed in the familic or generic taxa. According to the structural types of lenticels grouped by Esau (1977), the lenticels of *Ficus microcarpa* show the highest degree of specialization, producing several strata of complimentary cells and closing layers yearly. This type of lenticel is also found in the species of *Betula, Prunus* (Esau, 1977), and *Fagus* (Jacob et al., 1989),

The lenticels are assumed to function in gas exchange because of the continuity of intercellular spaces in the lenticel tissues with those in the interior of the stem. It has been reported that the orientation of the lenticels in the stems of angiosperms has clearly been correlated with the nature of the storage rays within (Wetmore, 1926b). Forms with uniseriate rays in the stem typically possess transverse lenticels. On the other hand, the

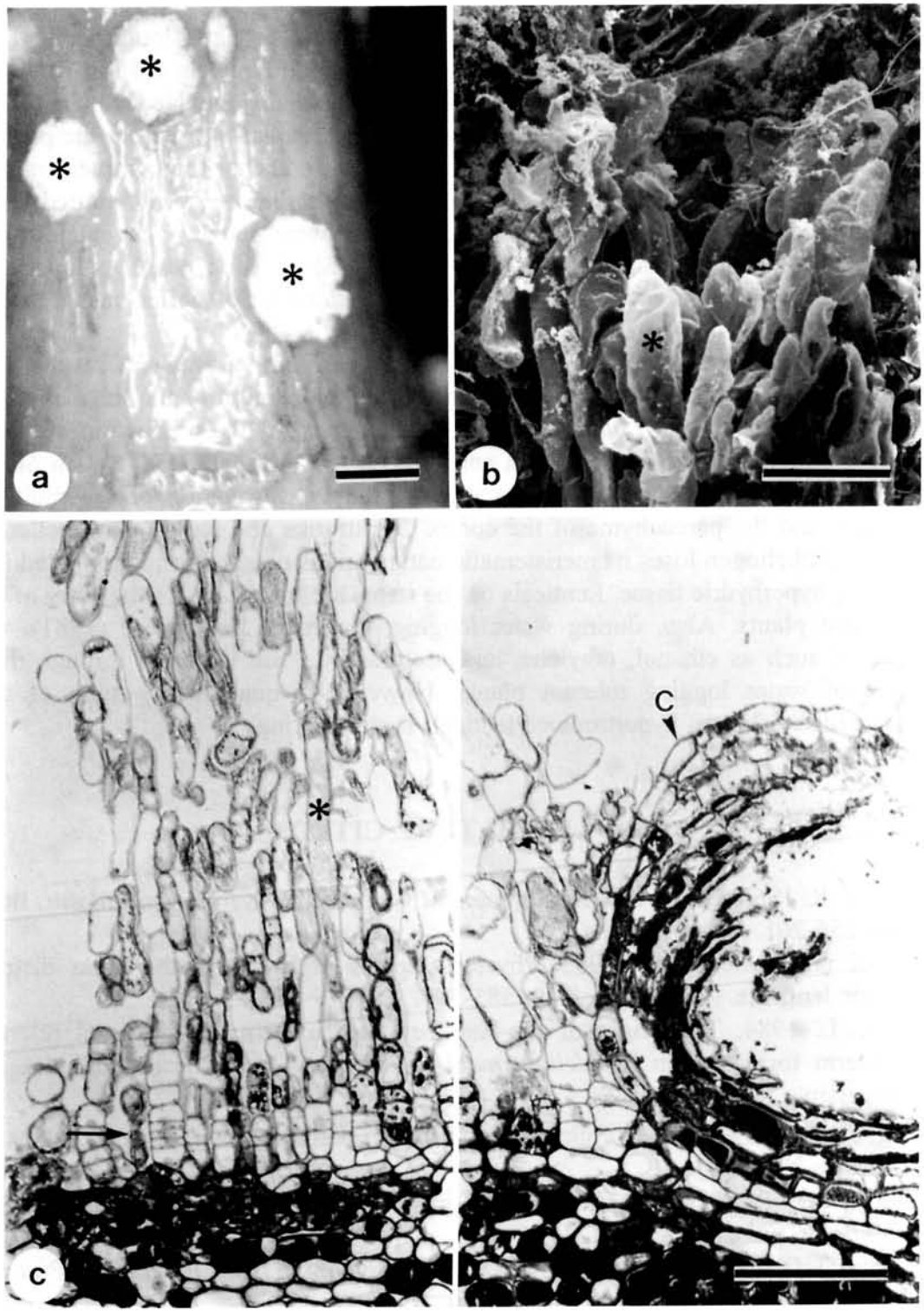

Fig. 5. a: Lenticel hypertrophy showing the white protrusions (∗) on the lenticels of the internodes immersed in the water (bar = 1 mm). b: SEM micrograph showing large rod-shaped cells in the lenticel (bar = 10 μm). c: Cross section of the hypertrophied lenticel showing the radially interconnected thin-walled cells with an abundance of intercellular spaces but without a closing layer (bar = 100 μm).

species which have multiseriate rays are usually found to have longitudinal lenticels. However, in the young branches of *Ficus microcarpa* the lenticels are longitudinal type, but the storage rays are uniseriate. Several rows of radially arranged tannin cells were observed in the lenticels of *Ficus microcarpa*. They were distributed from the phelloderm and lenticel phellogen, to the stratas of the closing layer, and of the complementary cells. The existence of tannin cells in the lenticels has never before been reported. In some phelloderm cells prismatic calcium oxalate crystals were found. The calcium oxalate crystals occur frequently in the cells beside tissues which soon cease to function, e. g. abscission zones(Chiang and Chiu, 1989), or in the stomium of pollen sacs (Horner and Wagner, 1980).

Lenticel hypertrophy in the immersed internodes of *Ficus microcarpa* results from the increased phellogen activity and the enlargement and elongation of the lenticel phellogen derived cells. In *Mangifera indica* it is also characterized by the production of additional phellem tissue via increased phellogen activity (Larson et al., 1991). But in *Sambucus nigra* the hyperphydric tissue develops through the transformation of the multilayered phelloderm and the parenchyma of the cortex (Tarkowska and Kowalska-Mueller, 1985). The lenticel phellogen loses its meristematic nature and is crushed or incorporated into the developing hyperhydric tissue. Lenticels on the stems are important for the entry of O_2 into waterlogged plants. Also, during water logging, according to Kawase (1981), volatile substances, such as ethanol, ethylene, and acetaldehyde, are liberated through the stem lenticels of water logging tolerant plants. However, a quantitative study of the gas exchange mechanism of hypertrophied lenticels is still lacking.

LITERATURE CITED

Bower, W. R. 1963. Origin and development of winged cork in *Euonymus alatus*. Bot. Gaz. **124:** 256-261.

Brown, K. and J. Considine. 1982. Physical aspects of fruit growth - stress distribution around lenticels. Plant Physiol. **69:** 585-590.

Chang, C. L. 1984. The origin of the first periderm in stem, with special reference to periderm formation in *Kandelia candel* (L) Druce. Master thesis. National Taiwan University.

Chiang, S. H. T. 1978. The origin of the first periderm in some dicotyledonous stems. Taiwania **23:** 60-65.

Chiang, S. H. T. and S. T. Chiu. 1989. Formation of abscission zone in the leaf of *Ficus wightiana*. Yushania **6:** 1-20.

Clements, H. F. 1935. Morphology and physiology of the pome lenticels of *Pyrus malus*. Bot. Gaz. **97:** 101-117.

Eames, A. J. and L. H. MacDaniels. 1947. An introduction to plant anatomy. Periderm and abscission. pp. 248-276. McGraw-Hill book company, New York, London.

Esau, K. 1977. Anatomy of seed plant. Periderm. pp. 183-197. John Wiley & Sons, Singapore.

Fahn, A. 1990. Plant Anatomy. Periderm. pp. 382-396. Pergamon Press. Oxford, New York.

Horner, H. T. Jr. and B. L. Wagner. 1980. The association of druse crystals with the developing stomium of *Capsicum annuum* (Solanaceae) anthers. Am. J. Bot. **67:** 1347-1360.

Jacob, A., H. Lehmann and R. Stelzer. 1989. Entwicklung und Struktur von Lentizellen der Buche (*Fagus sylvatica* f. *purpurea* Ait.). Flora **183:** 417- 427.

Johansen, D. A. 1940. Plant microtechnique. HcGraw-Hill book Co. Inc. New York.

Kauffert, F. 1937. Factors influencing the formation of periderm in aspen. Am. J. Bot. **24:** 24-30.

Kawase, M. 1981. Anatomical and morphological adaptation of plants to waterlogging. Hort Science **16:** 30-34.

Kuo-Huang, L. L. 1990. Calcium oxalate crystals in the leaves of *Nelumbo nucifera* and *Nymphaea tetragona*. Taiwania. **35:** 178-190.

Larson, K. D., F. S. Davies and B. Schaffer. 1991. Floodwater temperature and stem lenticel hypertrophy in *Mangifera indica* (Anacardiaceae). Am. J. Bot. **78:** 1397-1403.

Lier, F. G., 1955. The origin and development of cork cambium cells in the stem of *Pelargonium hortorum.* Am. J. Bot. **42:** 929-936.

Tarkowska, J. A. and A. Kowalska-Mueller. 1985. The development of hyperhydric tissue on the stems of *Sambucus nigra* L.. Acta Societatis Botanicorum Poloniae **54:** 361-366.

Wetmore, R. H. 1926a. Organization and significance of lenticels in dicotyledons. I. Lenticels in relation to aggregate and compound storage rays in woody stems. Lenticels and roots. Bot. Gaz. **82:** 71-88.

Wetmore, R. H. 1926b. Organization and significance of lenticels in dicotyledons. II. Lenticels in relation to diffuse storage rays of woody stems. Bot. Gaz. **82:** 113-131.

榕樹枝條上皮孔的形成

黃玲瓏[1,2]、洪麗分[1]

(收稿日期：1995年4月28日；接受日期：1995年6月6日)

摘　　要

本文研究榕樹枝條上皮孔的形成。榕樹枝條上的皮孔均起源於氣孔下方排列疏鬆的薄壁細胞（前充塞細胞群），此群細胞進行各方向的細胞分裂，而其下緣之細胞則皆行平周分裂即爲木栓形成層，其分裂面連成弧形並與一般周皮相連。木栓形成層首先在離心方向產生一至二層排列緊密的封閉層，而後爲一至四層排列疏鬆的填充細胞。成熟皮孔呈透鏡形向內、外凸出，其由栓皮層、木栓形成層、和封閉層與填充細層之由外依次交互排列而組成。皮孔內可觀察到多面體草酸鈣結晶和數排的單寧細胞。成熟枝條泡水後皮孔產生腫大的現象，是由排列疏鬆的長桿狀薄壁細胞所組成。

關鍵字：榕樹，枝條，皮孔形成，皮孔腫大。

1. 國立臺灣大學植物學系。
2. 通信聯絡員。