THE SITE OF THE FIRST PERIDERM IN THE STEM[1]

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Abstract: The site of the first periderm in more than eighty dicotyledonous stems, both woody and herbaceous, were examined. 63 species have their initial phellogen in subepidermal layer; eight in primary phloem; four in epidermis; and still other one in second cortical layer. In other words, the development of the first periderm in most members takes place in shallow tissue layer. The deepest one was found to be from the primary phloem. The tissues located outside the vascular cambium may give rise to periderm. However it forms in either superficially in epidermis to second cortical layer or deep-seated in as deep as innermost cortical cells, and little is found to develop in the midway of the cortical tissue.

The site of the first periderm is affected by the presence of trichomes, stomata, lenticels and the shape of the outline of stem surface. The initiation of periderm always falls behind the activation of vascular cambium.

INTRODUCTION

The development of the periderm in both stem and root has long been noted in most of the gymnosperms and dicotyledons. The presence of the periderm is so common, that is necessary to analyze the developmental stages and other aspects. Comparative studies are most useful for the events leading to understand the structure which shows rather uniform in the majority of plants. But only a few studies dealing solely with the origin of the phellogen have been made. Before the observation of one of the present authores in 1978, the earliest as well as the most volumerous study was made by Douliot (1889). Furthermore the origin and the structure of the periderm in many plants were also described in the book of Metcalfe and Chalk (1950). The site of the first phellogen usually confined to a specific layer or layers in almost all the plants.

In the previous report (Chiang, 1978), it is revealed that the first periderm of the dicotyledonous stem usually initiates in rather shallow tissues and also showed a fair correlation of the location of the initial periderm with the habit of growth of the plants. The present report is to confirm the results revealed in the previous work by observing more plants. In the same time, the workers are interested in this study because the easy technique, simply by some primitive equipments, can bring the students to have opportunity to acquainted with so many plants and to recognize the related tissues during this investigation.

MATERIALS AND METHODS

Specimens studied in this investigation are listed in Table 1. Most of the collections were made in July to October, 1979 and a small part in February, 1980. All materials were obtained in Taipei area.

The young branches obtained including both woody and herbaceous dicotyledons were cut

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serially from the tip to the base by free-hand section. After the site of the first phellogen was found, the layers of secondary xylem as well as other categories were examined. Some of the materials which exhibit different characteristics other than those listed in Table 1, were fixed in FAA, followed by a traditional paraffin method. For the older twigs the sections were obtained from the fresh materials sectioned on a sliding microtome, then fixed and dehydrated through an alcoholic series. All the sections were stained with safranin and fast-green combination (Sass, 1958).

RESULTS AND DISCUSSION

The site of the initial phellogen in the young stem of the majority of plants is clearly distinguishable in a free hand sectioned specimens. The cells of the phellogen are rectangular and walls are thin with weak stain affinity when compared with their adjacent tissues. After the first periclinal division, the periderm becomes more conspicuous in appearance. All the plants listed in Table 1, the initial phellogen is developed in the first growing year of the stem. The authors failed to find the site of initial phellogen in several woody species, such as: *Eucalyptus robusta*, *E. citriodora*, *Garcinia spicata*, *Cassia fistula* and *Pyracantha koidzumii*; as well as many herbaceous members which were not listed in Table 1. The presence of the spongy cork in *Eucalyptus* has been described (Metcalfe and Chalk, 1950; Esau, 1965; Fahn, 1977). Evidently there is no reason to indicate that these plants do not form a periderm in a later stage of growth. But no further information concerning with its origin has been given. Fahn (1977) also stated that cork was never formed in *Viscum*. Most of the plants studied in the previous work (Chiang, 1978), particularly those exhibited deeper origin of the first phellogen, were also reexamined in the present investigation.

Table 1. Plant names and summary of various categories observed

Plant	Place of 1st Phellogen	Cell layer of Sec. Xylem	Plant Habit	Family
Ardisia sieboldii Mig.	epidermis	0-2	tree	Myrsinaceae
Salix warburgii O. Seem	epidermis	30	tree	Salicaceae
Euonymus tanakae Maxim. ex Mats & Hay.	epidermis & subepidermis	60	tree	Celastraceae
Cyclobalanopsis glauca (Thunb.) Oerst.	subepiderms	30	tree	Fagaceae
Elaeocarpus serratus L.	subepidermis	60	tree	Elaeocarpaceae
Schima superba Gardn. & Champ.	subepidermis	6	tree	Theaceae
Ternstroemia gymnanthera (Wight & Arn.) Sprague.	subepidermis	6	tree	Theaceae
Syzygium cumini (L.) skeels.	subepidermis	24	tree	Myrtaceae
Terminalia catappa Linn.	subepidermis	20	tree	Combretaceae
Bombax malabarica DC.	subepidermis	20	tree	Bombacaceae
Hibiscus boninensis Nakai.	subepidermis	10	tree	Malvaceae
Sapium sebiferum (L.) Roxb.	subepidermis	60	tree	Euphorbiaceae
Bischofia javanica Blume.	subepidermis	35	tree	Euphorbiaceae
Bridelia balansae Tutch.	subepidermis	12	tree	Euphorbiaceae
Gelonium aequoreum Hance.	subepidermis	70	tree	Euphorbiaceae

Table 1. Plant names and summary of various categories observed (continued)

Plant	Place of 1st Phellogen	Cell layer of Sec. Xylem	Plant Habit	Family
Glochidion honkongense M-A.	subepidermis	40	tree	Euphorbiaceae
Mallotus philippinensis M-A.	subepidermis	9	tree	Euphorbiaceae
Prunus serrulata Lindl. forma Classica Miyos.	subepidermis	15	tree	Rosaceae
Acacia confusa Merr.	subepidermis	12	tree	Mimosaceae
Bauhinia yarieqata L.	subepidermis	60	tree	Caesalpiniaceas
Pterocarpus indicus Willd.	subepidermis	70	tree	Papilionaceae
Dalbergia sissco Roxb.	subepidermis	60	tree	Papilionaceae
Erythrina variegata L.	subepidermis	30	tree	Papilionaceae
Myrica rubra Sieb. & Zucc.	subepidermis	70	tree	Myricaceae
Celtis formosana Hay.	subepidermis	40	tree	Ulmaceae
Broussonetia papyrifera (L.) L'Herit. ex Vent.	subepidermis	30	tree	Moraceae
Ficus beecheyana (Hook. & Arn.) King.	subepidermis	10	tree	Moraceae
Ficus globosa Bl.	subepidermis	8	tree	Moraceae
Ficus wightiana Wall. ex Benth.	subepidermis	12	tree	Moraceae
Ficus religiosa L.	subepidermis	5	tree	Moraceae
Morus alba L.	subepidermis	50	tree	Moraceae
Eurya japonica Thunb.	subepidermis	20	tree	Theaceae
Semecarpus gigantifolia Vidal.	subepidermis	5	tree	Anacardiaceae
Mangifera indica L.	subepidermis	200	tree	Anacardiaceae
Diospyros eriantha Champ. ex. Benth.	subepidermis	25	tree	Ebenaceae
D. oldhamii Maxim.	subepidermis	20	tree	Ebenaceae
Cordia cumingiana Vidal.	subepidermis	35	tree	Boraginaceae
Duranta repens L.	subepidermis	10	tree	Verbenaceae
Persea zuihoensis (Hayata) L.	subepidermis	50	tree	Lauraceae
Persea thunbergii (Sieb. & Zucc.) Kostermans willd.	subepidermis	55	tree	Lauraceae
Dillenia indica L.	subepidermis	25	tree	Dilleniaceae
Pittosporum formosanum Hay.	subepidermis	35	tree	Dilleniaceae
Vitex auinata W.	subepidermis	15	tree	Verbenaceae
Gordonia axillaris (Roxb.) Dietr.	Primary phloem	20	tree	Theaceae
Lagerstroemia indica L.	Primary phloem	25	tree	Lythraceae
Lagerstoemia subcostata Koehne	Primary phloem	20	tree	Lythraceae
Camelia oleifera Abel.	Primary phloem	25	tree	Theaceae
Malvaviscus arboreus (L.) Cav.	epidermis	17	shrub	Malvaceae
Hibiscus boninensis Nakai	subepidermis	10	shrub	Malvaceae
H. mutabilis L.	subepidermis	50	shrub	Malvaceae
H. syriacus L.	subepidermis	30	shrub	Malvaceae
H. schizopetalus Hook. F.	subepidermis	12	shrub	Malvaceae

Table 1. Plant names and summary of various categories observed (Continued)

Plant	Place of 1st Phellogen	Cell layer of Sec. Xylem	Plant Habit	Family
H. rosa-sinensis L.	subepidermis	30	shrub	Malvaceae
Euphorbia pulcherrima Willd. ex Klotzsch	subepidermis	20	shrub	Euphorbiaceae
Excoecaria bicolor Hassk.	subepidermis	25	shrub	Euphorbiaceae
Phyllanthus niruri L.	subepidermis	45	shrub	Euphorbiaceae
Severinia buxifolia (poir.) Tenore	subepidermis	30	shrub	Rutaceae
Ardisia squamulosa Presl.	subepidermis	30	shrub	Myrsinaceae
Thevetia peruviana Merr.	subepidermis	5	shrub	Apocynaceae
Psychotria rubra (Lour.) Poir.	subepidermis	18	shrub	Rubiaceae
Bougainvillea spectabilis	subepidermis	43	Scandent shrub	Nyctaginaceae
Boehneria formosana Hayata	subepidermis	16	shrub	Urticaceae
Thunbergia erecta (Benth.) T.	2nd Cortex	9	shrub	Acanthaceae
Lonicera japonica Thunb.	Primary phloem	3	Climbing shrub	Caprifoliaceae
Psidium guajava L.	Primary phloem	25	shrub	Myrtaceae
Buxus intermedia Kanch.	innermost cortex to epidermis	30	shrub	Buxaceae
Melastoma candidum	Primary phloem with extra phellogen at angles	15	shrub	Melastomaceae
Tournefortia sarmentosa Lam., Encycl. Meth.	subepidermis	20	Woody vine	Solanaceae
Solanum nigrum L.	epidermis	100	herb	Boraginaceae
Pouzolzia zeylanica (L.) Benn.	subepidermis	8	herb	Urticaceae
Melochia corchorifolia L.	subepidermis	40	herb	Sterculiaceae
Eupatorium formosanum Hayata.	subepidermis	90	herb	Compositae
Erigeron canadensis L.	subepidermis	75	herb	Compositae
Erigeron linifolius Willd.	subepidermis	130	herb	Compositae
Bidens pilosa L.	subepidermis	110	herb	Compositae
Eclipta prostrata L.	subepidermis	60	herb	Compositae
Crossostephium chinses (L.) Mak.	subepidermis	2	herb	Compositae
Osimum basilicum L.	Primary phloem	30	herb	Labitae

Table 2. Site of the initial phellogen related with the plant habit

habit \ site	epidermis	epidermis & subepidermis	subepidermis	2nd cortex	Primary phloem	Total
tree	2	1	40	0	4	47
shrub	1	0	14	1	3	19
vine	0	0	1	0	0	1
herb	1	0	8	0	1	10
Total	4	1	63	1	8	77

Buxus intermedia is not included in this Table.

A listing of research results are summarized in Table 1. As shown in Table 2, of seventy eight species examined, sixty three of them have their initial phellogen in the subepidermal layer. They include forty trees, fourteen shrubs, eight herbs and one vine. Eight of them show the development of the first phellogen in the primary phloem (Fig. 1, Fig. 2, Fig. 9, Fig. 11). Four in epidermis, and one in second cortical layer. In other words, the development of the first phellogen in most of the members takes place in shallow tissue layers of the stem. Only eight species are from as deep as in primary phloem. In only one case in *Thunbergia erecta*, its first phellogen is of 'second cortex origin'. Its subepidermis is definitely occupied by a layer of thick walled sclerenchyma (Fig. 3). But there is no thick walled subepidermis in some plants which have 'second cortex origin' of the first periderm (Chiang, 1978), and still another case in *Buxus intermedia*, as that occurred in *Melaleuca leucadendra* (Chiang, 1978; 1980), the initial phellogen originates very deep in about tenth cortical layer and its edges curve outward and meet the epidermis (Fig. 4). It is very commonly found the curved initial periderm cut only a small amount of the outer primary tissues (epidermis and primary cortex) in some places (Fig. 4, upper arrow), whereas another initial phellogen arises parallel with the outer surface of the branch as half of the stem circumference before its edges curve outward and meet the epidermis (Fig. 4, lower arrow). Both the localized periderm and another pattern of the development of the first phellogen are very frequently found even in the same section.

It is seems to one that all the cells laying outside the vascular cambium may become meristematic and give rise to periderm. However it is revealed in the present observation that the first phellogen develops either superficially in epidermis to second layer of cortex, or deep-seated in as deep as innermost cortical layer immediately next to the perivascular tissue. Little is found to be located in the midway of the cortical tissue.

As it is pointed out by some earlier workers that the origin and the development of the first periderm is affected by the presence of trichomes, stomata and lenticels; and the vitality of the hairs (Bowen, 1963; Haberlandt, 1928; Kauffert, 1937; Lier, 1955; Mader, 1954). The similar phenomenon was also seen in some plants examined. In the branches of *Vitex auinata* and *Broussonetia papyrifera*, it shows the superficial origin in the first cortex where a few epidermal cells grow into trichomes (Fig. 6); but it originates in second cortical layer where its surface bears dense trichomes (Fig. 7). Apparently the development of the trichome in epidermal cell cause its immediate cortical cell fails to give rise the periderm, and on the other hand, stimulates the second cortical layer to behave as a phellogen. But in other cases, it is not evident in the members which exhibit the deeper origin of the first phellogen (Fig. 11).

The place of the first periderm in these plants always parallel to the stem surface. Esau (1965) described if the stem is angled in outline or ridged, the periderm arises beneath the angles or ridges somewhat deeper than elsewhere. However the present observation demonst-

All photos are in transectional view.

Fig. 1. *Camelia oleifera*, showing the periderm originates deeply in phloic cells located under perivascular fibers. ×900

Fig. 2. *Psidium guajava*, the periderm arising beneath the phloem fiber, i. e. in the primary phloic cells. Some of its phellogen cells have undergone anticlinal divisions. ×900

Fig. 3. *Thunbergia erecta*, the periderm has developed in second cortex and beneath a sclerenchymatous hypodermis. ×900

Fig. 4. *Buxus intermedia*, one periderm arises in the innermost cortical cells and develops parallel to the surface of stem about as long as half of the stem circumference, then curve to meet the epidermis (lower arrow) and another small localized periderm in the other side of stem (upper arrow). ×150

Key to labeling: e-epidermis; h-hair; "pe"-extra periderm; pe-periderm; ped-periderm with darker cells; pel-periderm with lighter cells; pg-phellogen; sl-sclerenchyma; W-secondary xylem.


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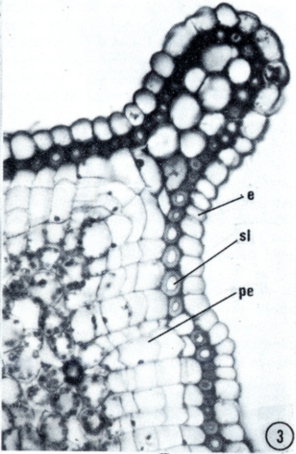
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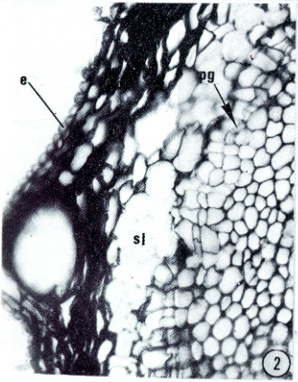
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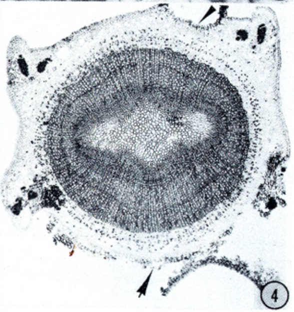
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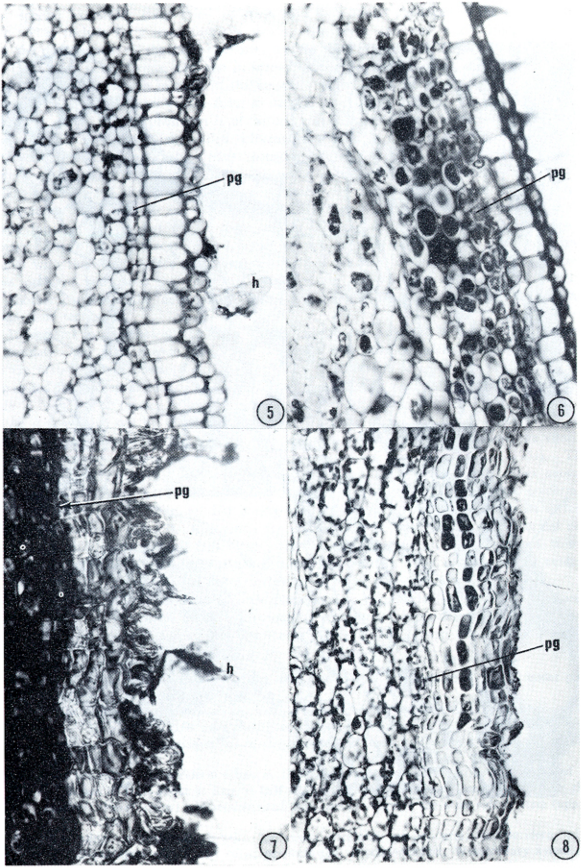
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rates that the initial phellogen originates in deeper region in some species (Fig. 9), but the extra or localized phellogen arises beneath the ridges superficially in shallow place in others, such as: *Melastoma candidum* (Fig. 9). This extra periderm commonly develops before the formation of a regular complete circmfluent periderm which arises endogenously in primary phloem. The synchronization on both periderm initiation and development is a common phenomenon in the stems with deeper origin of the first periderm. But in the stem with superficial origin of the first periderm, it always begins in localized region and develops variable amounts around the circumference in later stage (Fig. 12). Besides, the stem with superficial origin of the periderm produces more periderm and lenticel than that with deeper origin in the first growing year.

Douliot (1889) pointed out that the subepidermal origin of the first periderm was present in members of 58 out of 60 families studied and was the exclusive method of origin in 20 families. Metcalfe and Chalk (1950) discussed the cork origin with genus as an unit. It is true that species among the same genus always have the same origin of the first periderm. But exceptions also exist very frequently. *Lonicera* and *Buxus* for examples, the first phellogen originates from epidermis in *L. acuminata* (Chiang, 1978), but it arises in primary phloem in *L. japonica* (Table 1). Metcalfe and Chalk (1950) mentioned that cork in *Buxus* is of subepidermal in origin, but in *B. intermedia* it is found to be varied from innermost cortical layer to epidermis itself (Table 1).

Among 47 species of trees observed, 43 are superficial origin, four are deep-seated; 10 species of herbs examined, nine are superficial, one deep-seated; 19 shrubs observed, 16 are superficial and three deep-seated. From the data presented (Table 2), it is difficult to reach a fair conclusion to correlate the site of periderm with the plant habit. Unfortunately the authors were not able to find out the proper stage of the site of the first periderm in numerous herbaceous species. The well-timed sampling on the herbaceous members is necessary.

Most dicotyledons and gymnosperms develop the initial periderm — whether superficial or deep-seated — during the first year of growth (Esau, 1965), usually after the primary elongation is completed (De Bary, 1884). Among the plants observed, the initiation of phellogen always falls behind the activation of vascular cambium (Chiang, 1978; Table 1). The similar phenomenum also observed by Waisel, Liphschitz and Arzee (1967) on the stem of *Robinia pseudacacia.* According to the result obtained from *R. pseudacacia*, Cutter (1969) said that the strains resulting from the secondary xylem and phloem and consequently increase in girth of the stem might take part in the initiation of phellogen.

In regard to the structure of the first periderm, most species observed are homogeneous, as described by Cutter (1969), Esau (1977), and some others, it is relatively simple if compared to the deratives of vascular cambium. The heterogeneons periderm is observed in *Lagerstroemia indicum, L. japonica, Osimum basilicum* and *Diospyros eriantha.*

In *Lagerstroemia indicum, L. japonica* and *Osimum basilicum*, their periderm looks very similar in transverse section, in which the phellem is alternate by one layer of large cells and one or two layer of small cells; it is not the growth ring as described in *Rhus typhina* and *Betula populifolia* (Esau, 1977). In *Diospyros eriantha*, the phellem consists of two kinds of cells, one is light in color and the other darker. The regular arrangement of them make the phellem a lattice-work pattern in appearance (Fig. 12).

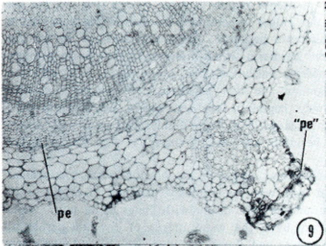
Fig. 5. *Vitex auinata*, periderm beneath the trichome, showing a little disorder in arrangement than the other place. ×900

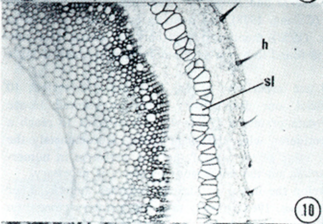
Fig. 6 to Fig. 8 all *Broussonetia papyrifera.*

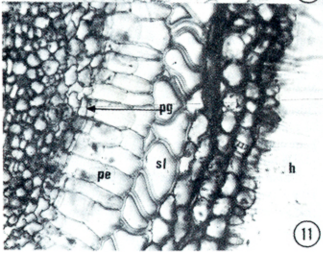
Fig. 6. The early stage of periderm development, showing the subepidermal origin. ×900

Fig. 7. The stem is covered with much denser secretory hairs than that in Fig. 6, the site of periderm seems more obscure. ×900

Fig. 8. The later stage of development, the hairs being sloughed off. ×900







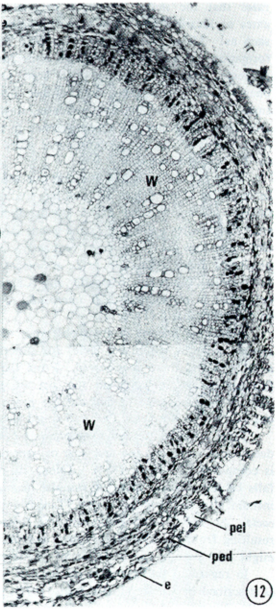


Fig. 9. *Melastoma candidum*, the main periderm is endogenously in primary phloem, and the extra periderm in the wing of stem. ×150

Fig. 10 and Fig. 11 both *Lonicera japonica*.

Fig. 10. Showing the stem tissues before the initiation of phellem, note the conspicuous ring of fibers in the inner part of cortex. ×150

Fig. 11. The periderm has established immediately beneath the ring of fibers. ×900

Fig. 12. *Diospyros eriantha*, showing the heterogeneous periderm. Two kind of phellem cells are seen, one is lighter in color, the other darker. ×150

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