THE ORIGIN OF THE FIRST PERIDERM IN SOME DICOTYLEDONOUS STEMS*

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Abstract: The first periderm of the stem in most trees is initiated superficially in the outer cortical layer (either first or second cortex), whereas in herbaceous and shrubby members it may originate from the outermost layer (epidermis) to deep-seated tissues. With the exception of *Melaleuca leucadendra*, the place of the origin of the first periderm appears in the same tissue along the entire cylinder. But the periderm of *Melaleuca leucadendra* develops in a curved or wavy band from the epidermis to the deep cortex.

INTRODUCTION

The development of the stem of both gymnosperms and dicotyledons is usually accompanied by the formation of a phellem. In an anatomical survey, one is forcibly impressed by the widespread occurrence of the periderm, and also by its place of origin which varies from an outermost layer to the very deep tissues in the stem. The behavior and the tissue constituents of the phellem are simpler than those of the vascular cambium, but the location of the first phellogen in different species is more variable. An early study by Douliot (1889) pointed out that the most common type of phellogen origin was in the first cortical layer. Later publications indicated this to be the fact for many species (Eames & MacDaniels, 1947; Esau, 1965; Lier, 1952, 1955; Waisel, 1967). During the past century further study on the origin of the phellogen has been neglected when compared with studies in other fields perhaps because of its uniformity in the majority of plants (Douliot, 1889). The intension of the present investigation was to determine the relationship of the plant habit with the place of the origin of the first phellogen.

MATERIALS AND METHODS

The specimens used in the study were collected from the plants growing in Taipei area. The observations were carried out with the materials listed in the following table. Young branches were killed and fixed in FAA, taken through a TBA series, ordinary paraffin embedding procedure, and sectioned at 8 to 10 μ. Some preparations were obtained by free-hand sections. 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. Sections were stained with safranin and fast-green combinations (Sass, 1958).

RESULTS

A listing of research results are summarized in the following table. With the exception of *Melaleuca leucadendra*, the topographical location of the first periderm is almost the same as seen in the same transection of the species.

Of the 41 species examined in the present investigation, 19 of them show that the first phellogen originates from the layer below the epidermis, i. e. first cortex (Table). Noticeably,

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Summary of periderm development

plant name	place of 1st phellogen	cell layer of sec. xylem	plant habit	family
Nerium indicum Mill.	epidermis	14	shrub	Apocynaceae
Ficus vaccinioides Hemsl. ex King	epidermis	*	woody vine	Moraceae
Lonicera acuminata Wall.	epidermis	*	woody vine	Caprifoliaceae
Galactia tenuiflora (Klein.) Willed. et Arn.	epidermis	*	herbaceous vine	Leguminosae
Ipomoea batatas (L.) Poir.	epidermis	3	herbaceous vine	Convolvulaceae
Ipomoea indica (Burm.) Merr.	epidermis	10	herbaceous vine	Convolvulaceae
Impatiens balsamina L.	epidermis	3	herb	Balsaminaceae
Ipomoea reptans (L.) Poir.	epidermis	2	herb	Convolvulaceae
Ficus elastica Roxb.	epidermis & 1st cortex	13	tree	Moraceae
Ageratum conyzoides L.	epidermis & 1st cortex	30	herb	Compositae
× × ×				
Chionanthus retusus Lindl. et Paxt.	1st cortex	8	tree	Oleaceae
Elaeocarpus decipiens Hemsl.	1st cortex	25	tree	Elaeocarpaceae
Eupharia longana Lam.	1st cortex	35	tree	Sapindaceae
Ficus microcarpa L. f.	1st cortex	1	tree	Moraceae
Grevillea robusta Cunn. ex R. Br.	1st cortex	0	tree	Proteaceae
Liquidamber formosana Hance	1st cortex	5	tree	Hamamelidaceae
Morus australis Poir.	1st cortex	5	tree	Moraceae
Pongamia pinnata (L.) Merr.	1st cortex	16	tree	Leguminosae
Prunus persica (L.) Batsch	1st cortex	34	tree	Rosaceae
Gardenia jasminoides Ellis	1st cortex	5	tree	Rubiaceae
Ligustrum japonicum Thunb.	1st cortex	4	shrub	Oleaceae
Osmanthus fragrans (Thunb.) Lour.	1st cortex	10	shrub	Oleaceae
Thevetia peruviana (Pers.) Schum.	1st cortex	4	shrub	Apocynaceae
Tithonia diversifolia A. Gray	1st cortex	15	shrub	Compositae
Ficus pumila L.	1st cortex	2	woody vine	Moraceae
Hedyotis corymbosa (L.) Lam.	1st cortex	4	woody vine	Rubiaceae
Hoya carnosa (L. f.) R. Br.	1st cortex	11	woody vine	Asclepiadaceae
Parthenocissus tricuspidata (S. et Z.) Planch.	1st cortex	1	woody vine	Vitaceae
Pueraria sp.	1st cortex	30—39	woody vine	Leguminosae
× × ×				
Olea europaea L.	2nd cortex	15	tree	Oleaceae
Syzygium samarangense Merr. et Perry	2nd cortex	25	tree	Myrtaceae
Eriobotrya japonica Lindl.	2nd cortex	7	shrub	Rosaceae
Thunbergia affinis S. Moore	2nd cortex	7	shrub	Acanthaceae
Gynostemma pentaphyllum (Thunb.) Makino	2nd cortex	0—2	herbaceous vine	Cucurbitaceae
× × ×				
Melaleuca leucadendra (L.) L.	epidermis to 10th cortex	3	tree	Myrtaceae
Rhododendron mucronatum (Blume) Don	15 cortex	35	shrub	Ericaceae
Camellia japonica L.	25 cortex	25	shrub	Theaceae
Hydrangea integrifolia Hay.	15 cortex	*	woody vine	Saxifragaceae
Zehneria mucronata (Blume) Miq.	3-4 cortex	1	herbaceous vine	Cucurbitaceae
Clematis chinensis Osbeck.	4-5 cortex	7	herbaceous vine	Ranunculaceae
Paederia scandens (Lour.) Merr.	4-5 cortex	3	herbaceous vine	Rubiaceae

* no data

all these 19 species are woody plants include trees, shrubs and vines. Furthermore 8 of the species, show that the first periderm is formed in the epidermis itself, and five of these appear to be herbaceous plants but three are woody. A third group consists of five species in which the periderm originates in the deeper cortex and four of these are woody plants, and we designate this group as 'second cortical origin member'. The plants which develop the first periderm in the deeper cortical cells are more diverse in their habit (see last group in Table), ranging from herbs to trees. Only two species, i. e. *Ficus elastica* and *Ageratum conyzoides* have their periderm originating in both the epidermis and first cortical layer. One of these is a tree and the other a herb.

The first periderm is most commonly formed in the first cortical layer. An epidermal origin is also very common and ranks next to the 'first cortical origin member'. But no arboreous tree develops its first-formed periderm from the epidermis alone. With the exception of *Melaleuca*, first periderm of all the arboreous plants is characteristically formed in the outer cortex, i. e. either in the first or second layer, occasionally from both the epidermis and first cortex. All the herbaceous species observed, develop their first phellogen in either epidermis or inner cortical layer. The deepest origin was observed in the stem of *Camellia* in which the periderm is initiated as deep as in the 25th cortical layer. No deeper-seated origin, such as from the pericycle, or phloem etc. were observed.

The radial expansion of the first formed periderm commonly occurs before a periclinal division. Two patterns of cell division are seen in the first stage of the periderm formation: equal and unequal divisions. In *Paederia, Camellia* and *Rhododendron*, with a deeper origin of the first periderm, the daughter cells are almost the same size immediately after the first division (Figs. 1, 2). At least the presence of unequal sized cells in the first and second periderm were not seen during this investigation. And another common phenomenon in the species with a deeper origin of the periderm is the synchronous formation of the first derivatives along the laterally located periderm (Figs. 1. 2). The first periderm arises almost at the same time around the entire circumference of the plant axis. So that the number of cells in early developed periderm is almost the same throughout the whole tissue, and the layer is of uniform thickness.

The unequal division of the first periderm is obvious in most of the plants having a superficial origin of the first periderm (Fig. 4). The smaller daughter cell remains as the phellogen, and the larger one undergoes differentiation to form the phellem, or phelloderm. And the first formed periderm shows slow development in some places while in other places the first periderm appears very thick and divides prolifically; consequently the periderm appears to be thicker in some places and very thin or even absent in others, thus showing several different developmental steps in phellogen activity (Fig. 3). In addition to the phellogen, its derivatives occasionally undergo periclinal cell divison thus increasing the number of cell layer (Fig. 4).

The cells located immediately below the lenticels always begin to divide earlier and divide more frequently than those in other places. The first periderm is commonly initiated parallel to the surface of the plant axis except in *Melaleuca*. In some twigs of *Melaleuca*, the first periderm originates as deep as in the 10th cortical layer and is almost parallel to the stem surface. But in some other branches the first periderm arises parallel with the outer surface of the stem in its central portion, however its edges curve outward and later meet the epidermis (Fig. 6). The periderm layer often becomes wavy within the cortical zone before meeting the epidermis (Fig. 5). This wavy pattern of the first periderm occurs very frequently in the specimens examined.

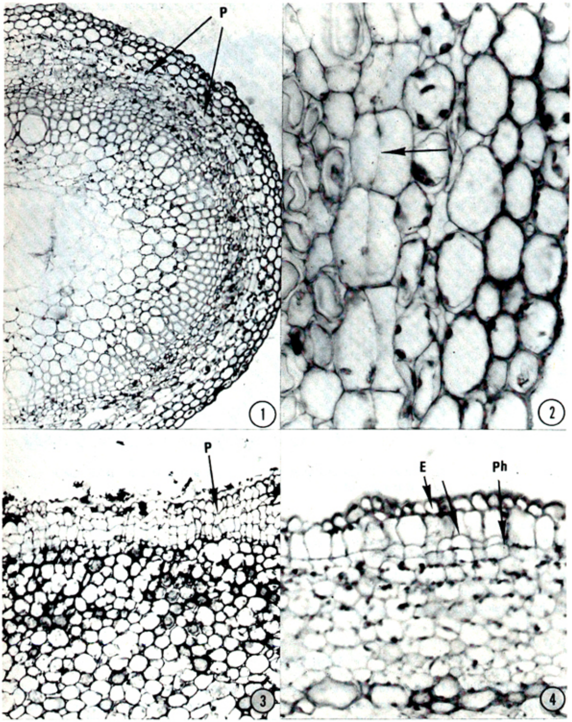

Fig. 1. Transverse section of *Paederia*, showing synchronous formation of the first periderm, ×175. E. epidermis, P. periderm; Ph. phellogen.

Fig. 2. Enlarged view of Fig. 1; arrow shows the new wall of the first periderm; ×900.

Fig. 3. *Nerium*, showing the uneven thickness of the periderm; ×175.

Fig. 4. *Hoya*, arrow show the new wall formed from the derivative of phellogen; ×350.

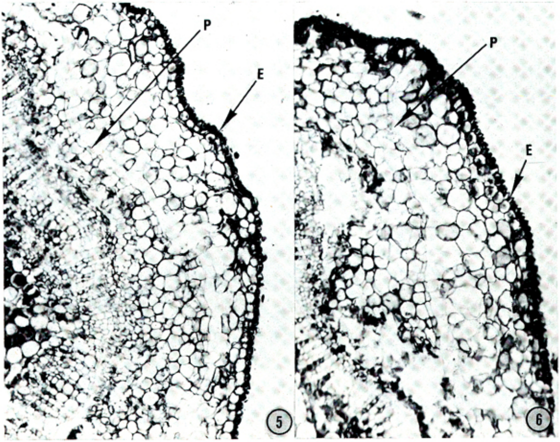

Fig. 5 & 6. *Melaleuca*, showing the wavy pattern of the first periderm within the cortical tissue; ×175.

In comparison with the formation of secondary vascular tissue the formation of the first periderm nearly always falls behind the activation of the vascular cambium in the same stem. Among the plants observed, in only three species, *Ficus retusa*, *Parthenocissus* and *Gynostemma* were found that the first periderm was initiated about at the same time as the activation of the vascular cambium (Table). The stems in which the first periderm is initiated after the stem has developed a thick secondary xylem, includes plants of all types of habit and is not restricted to trees.

DISCUSSION

As mentioned by Douliot (1889), the first phellogen in the majority of plants originates in the layer of cortical cells immediatedly below the epidermis, however many plants form their periderm in the epidermis itself, and this is the next commonest pattern. This investigation also reveals that the first periderm of the stem usually initiates superficially in the shallow tissues such as: the epidermis and the layer immediately below it. This result also shows a fair correlation of the location of the first periderm with the habit of growth rather than with the systematic position of the plants (Table). The first periderm is initiated superficially in the outer cortical layer of most trees, whereas it originates from a wide variety of tissues ranging from the outermost layers to the deep-seated tissues in both herbaceous and shrubby plants.

The place of the first division of the periderm in any given species always takes place in the same tissue along the whole cylinder, with the single exception of the stem of *Melaleuca*. The first periderm in many twigs of *Melaleuca* form a shell-shaped layer deep in the cortex (Figs. 5, 6). This behaves quite differently from that which occurs in other plants. Its periderm appears in a curved or wavy pattern in the cortex. Both shell and wing-shaped cork have been observed in other plants (Bowen, 1963; Eames & MacDaniels, 1947; Smithson, 1954), these being formed after a complete circumfluent periderm has been differentiated on the stem. Some of the localized periderms develop before the formation of a typical circumfluent periderm (Gregory, 1888). The first periderm becomes an extensive tissue in its later stage of development in *Melaleuca*, and cannot be considered to be merely a localized structure. And it appears before the subsequent periderms which are formed in the successive deeper regions.

The origin as well as the development of the first periderm is affected by several factors in addition to the environmental conditions (Bowen, 1963; Douliot, 1889; Kauffert, 1937; Lier, 1955; Mader, 1954). It is also affected by the presence of hairs, stomata and lenticels. It was observed that the time of the initiation of the periderm becomes earlier, and the amout of the periderm increases in a region below a lenticel as well as on a side of a stem which receives more sunlight. Apparently the determination of the place of periderm origin is genetically rather than environmentally controlled. An attempt was made to correlate the place of periderm origin, the cell size of epidermal cells, the number of cell layers in the cortical tissue and the density of the primary vascular bundles, but this attempt failed to reveal any significant relationship. The author examined more species than those listed in the Table, but was unable to find the periderm in some species which produced prolific secondary xylem, but there is no reason to indicate that these species do not develop a periderm in a later stage of growth. It is more than likely that the formation of the first periderm in stems of nearly all the species is somewhat delayed, as compare to the origin of the secondary vascular tissues. The earliest formation was seen in *Ficus retusa*, and species of *Parthenocissus* and *Gynostemma*. The first phellogen and the vascular cambium become active at about the same time, but in no case was the periderm initiated before the secondary vascular tissue.

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