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Laticifers: An Historical Perspective

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I. Abstract

This review describes the development of the laticifer concept, with emphasis upon the nonarticulated type, from early observations of plant exudates and "juices" to the presentation of laticifers by Esau (1953). Classical writers and herbalists described practical applications of these substances. With the advent of the microscope early investigators believed that these substances occurred in structures present in most, if not all, plants and, wrongly, equated these structures to the circulatory system in animals. Introduction of the term, latex, into botany derived from its early use as a term for a blood component by physicians, and not for analogy to milk. However, the origin of the terms, laticifer and laticiferous, remains uncertain. Initial studies of

laticifers were marked by the controversy of whether they represented intercellular spaces or elongated cells. Confirmation of their cellular character led to the designation of nonarticulated and articulated laticifers. Nonarticulated laticifers were shown to arise during early embryogeny in some plants. The ontogenetic origin of the articulated laticifer was unclear to early workers, but new laticifers were detected to be formed by cambium activity. Nonarticulated laticifers were described to develop by intrusive growth whereby tips of the cell penetrated between adjacent cells. The coenocytic condition of the nonarticulated laticifer resulted from nuclear divisions along the cell positioned in the growth region of the shoot and the subsequent distribution of the daughter nuclei along the length of the cell.

Zusammenfassung

Die vorliegende Übersicht beschreibt die Entwicklung des Milchröhrenkonzeptes, beginnend mit den frühen Beobachtungen an Pflanzenausscheidungen und "Pflanzensäften" bis hin zu ihrer Darstellung bei Esau (1953). Dabei stehen ungegliederte Milchröhren im Vordergrund. Die klassischen Schriftsteller sowie die Verfasser der Kräuterbücher haben die Nutzanwendungen dieser Stoffe geschildert. Mit der Erfindung des Mikroskops wurden frühe Forscher zu der Annahme verleitet, daß derartige Stoffe in Strukturen vorkämen, die den meisten, wenn nicht allen Pflanzen gemeinsam seien. Diese Strukturen wurden dann, fälschlicherweise, mit dem Kreislauf der Tiere homoligisiert. Die Einführung des Begriffs "Latex" in die botanische Terminologie beruht auf der frühen ärztlichen Verwendung dieses Begriffs für einen Blutbestandteil, und nicht auf einer Analogie zu Milch. Die genaue Herkunft der Bezeichnungen "Milchröhre" und "Milchsaft führend" bleibt jedoch im Dunkeln. Erste Untersuchungen an Milchröhren waren von der Kontroverse geprägt, ob es sich um sehr stark gestreckte Zellen oder um Hohlräume zwischen Zellen handelt. Mit der Bestätigung der zellulären Natur der Milchröhren fand ihre Einteilung in gegliederte und ungegliederte Milchröhren statt. Es konnte gezeigt werden, daß ungegliederte Milchröhren schon in den frühen Embryonalstadien milchsaftführender Pflanzen angelegt werden. Die ontogenetische Herkunft gegliederte Milchröhren konnte von den frühen Bearbeitern nicht geklärt werden; sie stellten jedoch fest, daß neue Milchröhrenzellen durch kambiale Aktivität abgegliedert werden. Es wurde auch beschrieben, daß ungegliederte Milchröhren während des Wachstums in bereits vorhandene Gewebe eindringen, wobei ihre Zellspitzen sich zwischen die Zellwände zweier benachbarter Zellen drängen. Die coenocytische Natur ungegliederter Milchröhren kommt durch Kernteilungen an der Spitze der Milchröhre und damit des Sprosses zustande, wobei sich die Tochterkerne nach ihrer Abgliederung entlang der gesamten Zelle verteilen.

II. Introduction

The conspicuous milky content in certain plants has attracted curiosity for many centuries. Early scholars recognized that the colored, milky substances, as well as those of a mucilaginous or resinous character, were restricted to particular plants. In the classical literature there were occasional references to the collection of these plants for their peculiar contents. Presumably such substances were utilized for various practical purposes. Theophrastus (1916) referred to the milky juices of the spurges which were collected for medicinal purposes. He also referred to the juices of other

plants, especially in the Apocynaceae (*Nerium oleander* L.), which had become well known for their poisonous character. Theophrastus very broadly suggested that these plant juices were a fundamental and essential component of all plants, an interpretation readily accepted by his students. However, the derived implication that such substances were not of a secondary origin, either secretory or excretory, provided the basis for a prolonged interpretative controversy.

Early studies were restricted to superficial descriptions of plant material, such as exemplified in herbals, while anatomical studies could be pursued only after the improvement of the compound microscope by Hooke in 1665. One of the initial topics investigated by early microscopists was the nature and the distribution of these juices. However, the inadequacies of the first microscopes, supplemented by the vivid and imaginative descriptions of early authors, resulted in the formulation of rather contradictory anatomical concepts of the form and development of structures which contained milky contents or other "plant juices."

Malpighi (1901), in his classical work on plant anatomy, described plant material as composed of two structural units; the utricles which constituted the plant body, and the tubes which were distributed within the utricular body. In the various plant materials investigated, such as fig, cypress, celery and elderberry, he distinguished two types of tubes; the *trachea,* which included the present vascular tissues, and the *vasa propria,* which contained the milky, resinous or mucilaginous substances.

It appeared that Malpighi considered all plants to possess the *vasa propria* when he stated: "There are several kinds of vessels (tubes) in plants both in the bark and in the wood in addition to the *vasa propria.*" Further, he contended that the contents of the *vasa propria* may not always be superficially visible. The liquid which appeared upon the surface of a fresh wound of some plants constituted a part of the essential plant sap contained in the *vasa propria.*

The nature of the *vasa propria* was somewhat less certain for Grew (1682), a contemporary of Malpighi. He likewise distinguished two types of vessels within the parenchymatous plant body: the air-vessels, actually the vascular conducting elements, and the lymphatic vessels which included the *vasa propria* of Malpighi and certain other structural components of phloem. The structures which he interpreted as lactiferous, resiniferous and mucilaginous vessels were included in his category of lymphatic vessels. Grew (1682) described the occurrence and distribution of lactiferous vessels in several plants, including dandelion, endive, *Scorzonera* and sumac. However, he did note that the lactiferous substance was not present in all of the plants which he studied.

III. Terminology Pertaining to Laticifer Structures

Grew's interpretation of the lactiferous substance was derived undoubtedly from its analogy to milk in animals. It was similar to milk both in color and coagulability. However, this relationship was not accepted by subsequent workers. Rather, the term latex (Latin, meaning fluid or liquid) superseded Grew's term, becoming established among English-speaking physicians as early as 1662 (Chandler, 1933). The author who initially suggested the application of it or the adjectival form, laticiferous, with reference to plant material, is difficult to determine. Schultz (1839), a German physician, was one investigator who employed the word, latex, in his botanical publications. In the field of medicine, it was used in reference to the character of blood. "Her blood appeared of a good texture, otherwise than giving off a little more than

its due proportion of latex" (Spry, 1767). Like blood, the latex in the plant was thought to be contained in a vessel system. Latex also coagulated upon removal from the plant, as did blood. Schultz communicated his observations to Lindley (1848), who published them in some detail. In this work, Lindley also referred to the milky substance as latex. The term latex remained well entrenched in the botanical literature thereafter. During the first half of the 18th century, many of the anatomical studies upon plants were performed by investigators with some medical training. Thus, it is understandable how any term with medical implications would be injected into botany.

The term laticifer also has appeared in the literature (Esau, 1953; Jackson, 1928), and was more convenient than such terms as laticiferous vessel or laticiferous structure. Since the composition of latex was quite variable, it was difficult to define as a substance (Bonner & Galston, 1947). Historically, latex was characterized by its capacity to coagulate when removed from the plant; its composition was completely unknown. Superficially, latex may appear nearly clear (*Nerium*), or white and very turbid (*Euphorbia*). It also may be colored, either yellow-brown as in *Cannabis,* yellow-orange as in *Papaver,* or red as in *Sanguinaria.* However, these observations provided no data on the chemical composition of latex. In early studies of laticifers the most precisely identified substance found in latex was starch (Hartig, 1843; Potter, 1884; Trecul, 1865a).

IV. Concepts on Formation of Laticifers

The description and interpretation of the structures, that Malpighi designated as the *vasa propria,* and the lactiferous vessels of Grew, provided the basis for the development of two distinctly different concepts of these structures. These may be designated as the intercellular space concept and the cellular concept.

A. INTERCELLULAR SPACE CONCEPT

Some investigators supported the theory that the colored, resinous, or mucilaginous substances were contained within vessels or intercellular spaces (Anonymous, 1846; Bernhardi, 1805; Link, 1824; Meyen, 1838; Mirbel, 1815; von Mohl, 1844; Schleiden, 1849; Schwann, 1839; Sprengel, 1817; Treviranus, 1835). Most often these investigators attempted to relate the supposed structures they observed to a particular function within the plant.

The great length and extensive distribution of the laticiferous system in the plant induced several investigators to compare it with the circulatory system in animals (Mariotte, 1717; Meyen, 1838; Schultz, 1839, 1841; Trecul, 1860; Unger, 1840; Wolff, 1869), which was first described in 1628 by Harvey (1941). Schultz presented a very imaginative interpretation of the latex system. The dense, colored latex of the plant body corresponded to blood of animals, whereas the plant sap was equivalent to lymph in animals. Although latex was not present in all plants, Schultz thought that he had observed it in the majority of plants he investigated. He interpreted it, like blood, to consist of a coagulum, that coagulated upon exposure to air, and also a liquid serum. Latex was derived from the sap of wood and, after rising in the wood, the sap was introduced into the leaves where it was subjected to a process of "elaboration," whereupon it was deposited in the laticiferous vessels as latex. Subsequently, it moved downward in the vessels which were distributed within the bark. During

its movement the latex supposedly permeated all the living tissues, providing them with nutritional substances. Upon exhaustion of these materials, the latex returned to the wood, as sap, whereupon the circulatory cycle was repeated.

Movement of latex and sap was attributed to both external factors (heat and light) as well as internal factors (contraction and dilation). Like Malpighi (1901), Schultz (1841) thought that he could observe the cyclosis of latex which resulted from the contraction and dilation of the walls of the laticiferous vessels. Supposedly this peristaltic movement was equivalent to the heartbeats in animals.

Several investigators interpreted the laticiferous structures as intercellular secretory cavities (Anonymous, 1846; Link, 1837; Mirbel, 1815). Rather than representing a circulatory system, they regarded laticifers as "reservoirs in which they collected their own juice" (Link). Mirbel expanded upon this hypothesis from his own observation, describing the "cannaux secretoires" as possessing a very fine limiting membrane. He was able to identify this membrane consistently in various members of the Apocynaceae, Asclepiadaceae and Euphorbiaceae that he investigated. However, the membrane appeared to be evident only in mature portions of the plant and was interpreted to arise after the formation of the secretory canals.

Presence of a membrane was substantiated also by an anonymous writer (1846) who surveyed genera from families believed to contain a laticiferous system including the Apocynaceae, Araceae, Asclepiadaceae, Campanulaceae, Caprifoliaceae, Cichoriaceae, Cucurbitaceae, Euphorbiaceae, Lobeliaceae, Moraceae, Papaveraceae, and Urticaceae. The membrane, according to this author, lined the entire intercellular cavity. Although not evident during the initial development of these cavities, it was present in later stages. The membrane, which became increasingly thicker in older canals, was interpreted to be deposited along the inner surface of the canal by the adjacent cells.

Some investigators, although adherents of the general cellular theory of plants, were unwilling to ascribe a cellular nature to the laticiferous structures (von Mohl, 1844, 1852; Schleiden, 1844, 1849; Schwann, 1839). A quotation from von Mohl is indicative of the uncertainty with which he viewed them. "In the majority of plants containing milky juices, these canals are lined with a special membrane and are then called milk vessels, but can scarcely be separated from mere canals destitute of proper membranes running between the cells, since true latex is formed in the latter in many plants, as in *Rhus.*"

A similar uncertainty was evident in Schleiden's investigation. However, he did consider the resemblances that these structures shared with cells: "The vessels of latex sap which arise with their own membrane cannot be traced back by observation to cells. Their origin is obscure, in the developed state they are similar to elongated branched cells." The incongruities in descriptions of the laticifers stimulated additional investigations and the formulation of new ideas.

B. CELLULAR CONCEPT

An elemental cellular concept of the laticifer was introduced quite early in the investigation of the plant body. Wolff (1869) formulated a theory intended to explain the formation of utricles (cells). Essentially, he maintained that the youngest part of the plant, the *punctum vegetationis,* consisted of a gelatinous matrix. The latter was saturated with a nutrient sap-like substance. Small drops of this sap very gradually increased in size, resulting in the formation of the utricle or cell. The gelatinous

matrix represented the cell wall. Elongated *vasa propria* were produced by the longitudinal extension of particular drops of the nutrient sap.

Plant growth was the result of continued formation of new utricles or cells among those already formed. The cell wall matrix was represented as a homogeneous substance, precluding the existence of any intercellular spaces. This conclusion was somewhat in contrast to that of Grew who recognized intercellular spaces. However, Grew was not certain of their relationship to his "lactiferous vessel."

The cellular nature of Malpighi's *vasa propria* was expounded by several early investigators and was contemporary with the intercellular space concept (Moldenhauer, 1812; Trecul, 1865b; Unger, 1847; Wolff, 1869). However, the concepts expressed by these investigators were quite dissimilar.

A more accurate interpretation of cellular arrangement within the plant body was presented by Moldenhauer (1812) who employed a maceration technique to isolate individual plant cells. He theorized that if cells could be isolated, then each cell must possess its own wall. Similarly, any two adjacent cell cavities must be separated by two walls. Utilizing this theory he investigated and redescribed the *vasa propria* of Malpighi with some degree of accuracy, referring to them as cells. He described the vessel-like nature of the laticifers in *Musa, Asclepias* and *Chelidonium.* However, he did not consider the resin canals of *Pinus* to be similar to the laticifer. Moldenhauer emphasized that the presence of a discrete layer of cells surrounding the resin canal and the presence of a special membrane lining the inner side of the canal suggested that the canals were not related to laticifers.

The significance of Moldenhauer's theory was not recognized immediately, but the theory did aid in defining the cellular nature of plant tissues in general. Several investigators suggested that laticiferous structures were very elongated cells (Dippel, 1865; Faivre, 1868; Hanstein, 1864; Hartig, 1862; Schacht, 1851, 1856; Unger, 1840, 1847; Vogl, 1863). The formation of the laticiferous vessel was vividly described by Unger from observations that he made on *Ficus benghalensis* L. Vessels were formed from superimposed rows of cells. The great length of these vessels was attained upon resorption of transverse walls that separated the cellular components. He noted that the walls of these vessels were initially quite delicate. During their subsequent development, the cells laid down additional, but rather irregular, thickenings upon their walls.

Laticifers were dispersed throughout the plant body and, according to Unger, the vessels were joined into a complex system by means of lateral branches. Although correct in many essentials his description of the formation of the laticifer in this plant was proven later to be incorrect. Nevertheless, since his interpretation was published during the period in which the intercellular space concept was widely recognized, it did stimulate further investigations on this topic.

Schacht (1851) investigated the laticiferous structures in various genera included in the Apocynaceae (*Vinca*), Asclepiadaceae (*Hoya, Gomphocarpus*), Caricaceae (*Carica*), Cichoriaceae (*Lactuca, Sonchus*), Euphorbiaceae (*Euphorbia*), Papaveraceae (*Papaver, Chelidonium*). In all instances he found that laticifers were of a cellular origin. He described them as resulting from the fusion of many or a few cells into a vessel. Since he was unable to find the laticiferous vessels formed into an anastomosing system in all of the plants that he investigated, he dismissed the possibility that they served any circulatory function similar to that present in animals.

Schacht (1851) clearly described the formation of the laticifer in *Carica* as arising from rows of superimposed cells, the transverse walls of which were resorbed. The

form of the laticifer present in *Euphorbia* and *Hoya* was more obscure. Its resemblance to bast cells present in surrounding tissues induced Schacht to consider it simply as a branched bast cell (also Pitra, 1860). He had become even more assertive on the nature of the laticifer, in *Euphorbia,* when he stated: "Through many investigations I have shown the non-existence of true laticiferous vessels. The latter form no anastomosing system. They are nothing more than branched bast cells bearing latex, with their ends completely closed." Schacht's correlation of the laticifer with another cellular entity, such as the bast cell, was not unique. It also was construed to correspond to sieve tubes (Dippel, 1865; Hartig, 1862; Vogl, 1863).

Hanstein (1864) supported many of the observations that Schacht had made on his materials. He expressed no doubt of the cellular nature of the laticifer. In his survey, Hanstein observed that in several families (Alismataceae, Araceae, Campanulaceae, Caricaceae, Cichoriaceae, Lobeliaceae, Papaveraceae) the laticiferous vessel was formed by the fusion of adjacent superimposed cells.

Hanstein did not consider the type of laticifer present in the Apocynaceae, Asclepiadaceae, Euphorbiaceae, or the Urticaceae to be a bast cell or a phloem element. Such factors as the very early differentiation, great length, irregular distribution, branching habit, and the moderately thickened cell wall suggested to him that the laticifer was not a latex-bearing bast cell. He did admit that transition stages between the thick-walled bast cell and the laticifer may occur. He considered the laticifer to be quite distinct. However, he thought that laticifers, collectively, formed a closed system.

Although connections may exist between the individual laticifers, no communications were evident with other cells. Nevertheless, Hanstein did not consider the laticiferous system as a distinct tissue; he was unable to ignore the superficial resemblance which it did have with the components of the bast system. Thus, he concluded that the laticifers represented constituents of the bast system.

With the publication of additional investigations upon the laticifer, all of which supported the cellular concept (Dippel, 1865; Faivre, 1868; Hartig, 1862; Unger, 1847; Vogl, 1863), the intercellular space concept of the laticifer was finally superseded by the cellular theory.

V. Classification and Distribution of Laticifers

Recognition of structural differences among laticifers in laticifer-bearing plants contributed to the development of several classification schemes. Several authors attempted to classify laticifers by their form (David, 1872; Hanstein, 1864; Hartig, 1862; Mayus, 1905; Trecul, 1865c, 1866; Unger, 1846, 1858; Vogl, 1866). In one classification laticifers were designated as the Y-form to distinguish between a simple branching pattern and the H-form which represented supposed fusion of two vertical branches. More complex patterns involving unicellular and multicellular complexes of cells and tubes were proposed by Gaucher (1902).

Hartig (1862) presented one of the initial attempts to interpret and classify the anatomical variability that he had observed in several laticiferous plants. While endeavoring to investigate the movement of latex in various plants, he described the latex system in *Acer* and *Chelidonium* as composed of articulated tubes (*gegliederten Röhren*) that he contrasted with those structures exemplified in the Euphorbiaceae, and referred to as nonarticulated vessels (*nicht gegliederten Milchgefässe*).

Utilizing macerated materials, he described the articulated latex tube as composed

of a row of superimposed cells in which the cross walls of component elements became perforated during the process of differentiation. This interpretation was similar to that presented by Unger at an earlier date (1847). The nonarticulated latex vessel, in contrast, was a very much elongated cell with no detectable cross walls along its entire length.

Hanstein concluded from his extensive survey of laticiferous plants that characteristic differences could be detected between the laticifers present in various families. In the Cichoriaceae, Campanulaceae, Lobeliaceae and Caricaceae he observed that anastomoses were present between adjacent articulated vessels. The laticiferous system appeared very much like a closed network of cells distributed in the extracambial region of the shoot. Within the Papaveraceae (*Chelidonium, Papaver, Sanguinaria*), Hanstein found that the anastomoses were quite infrequent and restricted to laticifers in leaves, cotyledons and carpels of the ovary.

Chauveaud (1891) presented a detailed classification of the forms of laticifers based upon more specific anatomical differences recorded in various genera regardless of their taxonomic position. In his interpretation the laticiferous tissues were composed either of cells or tubes. He subdivided the tubes into two types: 1) a continuous, nonarticulated tube that arose either originally in the embryo (original form), or during the post-embryonic development (subsequent form); and, 2) an articulated tube consisting of either separate, fused, or anastomosing elements. The cellular form also was subdivided according to its disposition, and was classified into types that were arranged either in series or occurred as isolated cells (Table I).

The distinction between the forms of laticifers was not as sharp as might be suggested in the tabular summary of Chauveaud's classification. The number of genera that had been investigated in detail was still minimal when compared with the approximately 800 or more genera included in the families possessing nonarticulated laticifers.

It was De Bary (1884), however, who adopted Hartig's terminology and established the two categories of laticiferous tubes: the articulated type and the nonarticulated type. The convenience and applicability of these terms was widely accepted by subsequent authors (Esau, 1953; Foster, 1949; Haberlandt, 1914; Sperlich, 1939; Tschirch, 1889).

Esau (1953) elaborated upon the classification of the laticifer, utilizing the variations observed among them. Nonarticulated laticifers were subdivided into two forms: those in which the cells developed as individual elongated tubes were termed nonarticulated unbranched laticifers; and, those in which the cells branched repeatedly during their development were termed nonarticulated branched laticifers.

Articulated laticifers also were subdivided by Esau. If no anastomoses occurred between adjacent tubes in the plant body they were designated as nonanastomosing, in contrast to the anastomosing form in which lateral anastomoses did occur (Table II).

Several studies suggested the existence of variations from these forms. These modifications may occur either in the same family, in the same genus, or even in the same individual. One such modification was exemplified by the capacity of the component cells of certain articulated laticifers (*Lactuca, Chelidonium*) to undergo a limited amount of intrusive growth. Protuberances that developed on these cells intrusively forced their way between the adjacent cells until they came in contact with another laticifer. Resorption of the cross walls at the point of contact resulted in a direct communication between the two laticifer tubes (Calvert, 1887; De Bary,

Table I

Classification of Laticifers (Chauveaud, 1891)

Laticiferous tissues	tubes	continuous	original	Beginning in embryo, traversing and being maintained throughout life of the plant: *Euphorbia, Croton, Broussonetia, Ficus.*
			subsequent	Arising during post-embryonic growth. *Urtica, Vinca.*
		articulated	separate	Occurring as one long vessel, of equal or unequal cells, but isolated one from another by transverse walls. *Cnesmone.*
			fused	Occurring as one long vessel, of equal or unequal cells; resorption of transverse walls is more or less complete. *Chelidonium.*
			anastomosing	Occurring as one long vessel, of equal or unequal cells where the resorption of cross walls is complete. In addition anastomoses are present between the adjacent tubes. *Hevea, Manihot, Papaver.*
	cells		series	*Dalechampia, Bertya.*
			isolated	*Glaucium.*

Table II
Classification of Laticifers (Esau, 1953)

Nonarticulated laticifers:	
Unbranched:	Apocynaceae, Eucommiaceae, Moraceae, and Urticaceae (in part).
Branched:	Apocynaceae, Asclepiadaceae, Euphorbiaceae (in part), and Moraceae.
Articulated laticifers:	
Nonanastomosing:	Convolvulaceae, Liliaceae, Papaveraceae, Sapotaceae, and Urticaceae (in part).
Anastomosing:	Campanulaceae, Caricaceae, Compositae (Cichoriaceae), Euphorbiaceae (in part), and Papaveraceae.

1884; Fraser, 1931; Parkin, 1900; Scott, 1884). Thus, intrusive growth may not be restricted to the nonarticulated type of laticifer.

It should be noted also that both the articulated laticifer, as in *Hevea,* and the nonarticulated type, as in *Euphorbia,* occurred in the Euphorbiaceae (Schaffstein, 1932). It had been reported by Schaffstein (1932) that both laticifer types could occur in the same plant as was the case in *Stapelia* and *Trichocaulon* (Asclepiadaceae).

VI. Origin and Development of the Nonarticulated Laticifer

Many of the investigations upon the two types of laticifers were conducted after the initial formation of the structures had occurred within the plant body. The presence of both types was readily apparent in the axes and meristems of both the seedling and mature plant. How these structures initially arose within the tissues was not understood. Trecul (1865c) and Faivre (1866) briefly described the presence of laticifers within mature embryos of the Asclepiadaceae, Euphorbiaceae, and Compositae, but neither investigated the developmental aspects in detail. Dippel (1865) and David (1872) unsuccessfully attempted to explain this fundamental aspect of their development, but neither worker became aware of the significance of the laticifers already present in the embryo of the mature seed.

Dippel contended that all laticifers arose from the coalescence of cells. He observed that the tubes could be readily followed into the young meristems where they ended abruptly. Near the ends of the so-called nonarticulated laticifer, he thought he saw the remains of wall septa within these tubes (*Ficus carica* L., *Euphorbia splendens* Boj.). It appeared to Dippel that the process of cell fusion took place in the meristematic zones and occurred very rapidly. This was in contrast to the septa that were readily detectable along a considerable length of the laticifers in the Cichoriaceae, Papaveraceae and Campanulaceae. He provided no explanation for this structural incongruity, nor indicated whether all laticifers were derived by a similar process of cell coalescence.

Dippel (1865) ascribed the origin of new laticifers to parenchymatous cells on either side of the vascular bundles in the shoot. Although he observed branches of the laticifers from the stem extending into the petiolar base of leaves, he contended that the laticiferous system within the laminae was independent of that within the stem. Rather, the laticiferous system within the blade was derived from parenchymatous cells which differentiated into laticifer cells during the development of each

lamina. These new laticifer initials, by means of coalescence with adjacent cells, progressively developed into a ramified network of tubes that extended throughout the entire leaf.

Upon reinvestigating similar genera utilized by Dippel, David (1872) was not in complete agreement with Dippel's conclusions. According to David the laticifers in the Apocynaceae, Asclepiadaceae, Euphorbiaceae and Moraceae were single cells (nonarticulated), which "elongated to a significant length by means of active and passive stretching and also by means of branching into the intercellular spaces." The laticiferous cells could be present in both the cortex and the pith (*Euphorbia splendens, Ficus elastica* L., *Nerium oleander, Hoya carnosa* R. Br.) or were confined to the cortex (*E. cyparissias* L., *F. carica*).

David (1872) maintained that new laticifers were formed progressively from certain cells of the ground tissue below the terminal meristem during the growth of the plant. Each new laticifer frequently branched as it elongated, but no anastomoses could be observed between adjacent branches. He was not certain of their relationship with the vascular bundles. In the stem the laticifers were randomly distributed, while in the petiole and the blade of the leaf they were associated with the vascular strands. David, in contrast to Dippel, observed that the branches which extended into the petiole from the stem continued into the blade of the leaf to form a continuous system (*Euphorbia*). However, in *Ficus, Nerium,* and *Hoya* it did appear to him that the "leaf specific" laticifer, as described by Dippel, did occur. Mayus (1905), in contrast to Dippel, recognized that the entire laticiferous system of the leaf was a continuation of branches from the stem. Tips of laticifer cells were observed in these plants to penetrate among mesophyll cells to and between radial walls of epidermal cells to the cuticle of the leaf (Chauveaud, 1891; Gaucher, 1902; Groom, 1889).

Both Dippel (1865) and David (1872) observed that the laticifer could be distinguished from adjacent cells in the embryo and meristems well before the cellular elements of either the xylem or phloem became identifiable. David found no indication in his material that new laticifers were produced by cambial activity, as suggested by Dippel.

A. *EUPHORBIA*-TYPE LATICIFER

Emphasis here is placed on the nonarticulated laticifer in *Euphorbia* because this genus had been studied more intensively by several investigators than any other genus and, thus, can be employed as a model for understanding this laticifer system in other euphorbiaceous genera and other laticifer-bearing families.

The divergent conclusions derived from investigations on the origin of the laticifer in the shoot stimulated a reconsideration of Trecul's earlier statement that he had observed laticifers in mature seeds of *Asclepias cornuti* Decne. and *Euphorbia lagascae* Spreng. These observations were readily confirmed by Schmalhausen (1877) and Chauveaud (1891). Both investigators intensively studied the origin and development of the laticifer in embryos of *Euphorbia.* They found that laticifers were first distinguishable shortly after initiation of the cotyledons. Only a relatively small number of laticifer initials, such as four, eight or twelve, were formed in each embryo. The only characteristics which distinguished these initials from adjacent cells were their larger size and rather refractive walls. The latter appeared to become thickened or swollen in appearance.

Chauveaud defined these cells in the following manner: "In order that these be

distinguished by their origin, let us call these the initial cells of the laticiferous system, or more briefly the initial cells, or even more simply the initials."

These initials occupied a position immediately below the primordia of the cotyledons. Chauveaud termed this region the cotyledonary node. The number of cells which develop into initials appeared to be constant within a particular species. However, the number of initials varied between species and genera. Chauveaud reported in *E. engelmannii* Bois. that only four initials were situated individually at four symmetrical points which coincided with the position of the vascular traces in the cotyledonary plane. In other species (*E. exigua* L., *E. peplus* L.) there were eight pairs at these same points, whereas in *E. segetalis* L. a larger number of initials formed symmetrical arcs at the position of the vascular traces.

In other species, as *E. myrsinites* L., he described two arcs of initials which formed a semicircle on either side of the axis, and were interrupted at the two extremities of the trace to the cotyledonary plane.

In some species the entire layer of cells located in the equatorial plane was transformed into initial cells, the latter then forming a complete circle at the cotyledonary node (*E. portandica* L., *E. lathyris* L., *E. falcata* L.).

Chauveaud described the initials as arising from the pericyclic tissue, whereas Schmalhausen (1877) found it difficult to associate their origin with a specific tissue, as evident in the following translation from his account: ". . . the line which sharply delimits the plerome from the periblem at its upper (cotyledonary) end meets directly at these cells, and these cells often appear to be wedged in between the plerome and periblem cells which border them below." The difficulty of associating nonarticulated laticifers with a particular tissue also was evident to Blaser (1945), who concluded that they were outside the vascular system.

Both Chauveaud and Schmalhausen observed that, as the young embryos continued to grow, the laticifer initials increased in length. The upper and lower ends of each initial appeared to undergo apical growth, forcibly pushing their tips between other cells. In this manner the upper protrusion which Chauveaud termed the cotyledonary tube grew into the developing cotyledon. The protrusion at the lower end of the cell extended downwardly toward the tip of the radicle, forming the central tube.

Chauveaud contended that each initial also produced lateral branches at the level of the nodal plane. Growing more or less horizontally along the intercellular spaces, these branches developed from the initials during the formation of this nodal network and grew inward and upward until the tips nearly reached the shoot meristem. These branches he termed the plumule tubes. Likewise branches developed outwardly from the plexus and grew into the cortical zone. These tubes, termed the cortical tubes, subsequently turned downward and grew toward the tip of the radicle along intercellular spaces. Other investigators confirmed the occurrence of a branched laticiferous system in the embryo (Cameron, 1936; Vreede, 1949).

Thus a cleared mature embryo of *Euphorbia* would appear to be permeated with a laticiferous system. At the cotyledonary node, it would be apparent as a ring of interwoven tubes from which branches would extend upward into the cotyledons and the shoot apex. Branches of the laticifer also would extend downward to the root meristem both along the immature vascular cylinder and along the outer periphery of the cortex.

As noted by both Chauveaud and Schmalhausen, the diameter of the laticifer when viewed in transection could vary considerably. They noted that the diameter of a laticifer in the nodal plexus of the embryo may be two or three times the diameter

of the adjacent cells. The diameter of branches developed from the laticiferous initials gradually decreased throughout their course. At the growing tip their diameter was considerably less than that of the adjacent cells. Walls of these intrusively growing branches also retained the capacity to stretch, because in mature tissues the laticifers very often were of greater diameter than adjacent cells.

Chauveaud (1891) and Schmalhausen (1877) did not agree with respect to the occurrence of fusions between the laticifer initials during their development in the embryo of *Euphorbia.* Schmalhausen contended that he had observed the fusion of the branches which developed from the initials. He thought he could detect some places where a dissolution of the common walls between two contiguous branches occurred, resulting in fusion of their protoplasts. Similarly, he described connections between the cortical and central tubes toward the tip of the radicle. Chauveaud, however, sharply disagreed with Schmalhausen. He was unable to detect the fusion of any adjacent laticiferous cells during their development in the embryo of *Euphorbia.* Likewise, he did not observe any indication of fusion in various other genera believed to contain the nonarticulated laticifer (*Aleurites, Asclepias, Croton, Hura, Jatropha, Vincetoxicum,* and others).

Chauveaud and Schmalhausen maintained that the entire laticiferous system of the mature plant of *Euphorbia* arose from the various branches produced by the initial cells formed within the embryo. No new initials were formed in the shoot during growth, as reported by Dippel (1865). Upon activation of the meristems during germination, the various branches formed by the laticiferous initials also commenced to grow. Chauveaud (1891) contended that the central and cortical tubes kept their position in the meristem region of the root by means of intrusive growth at their tips. He also stated that the cotyledonary tubes, as well as their ramifications, elongated at a rate equal to that of the elongation and development of the cotyledons. Tips of the plumule tubes also kept pace with the growth of the epicotyl and retained a position in the meristematic zone of the shoot.

In the internodal region of the stem the laticiferous branches maintained a rather straight course, exhibiting very little branching. Both Chauveaud and Schmalhausen observed that the tips of each laticifer branched at each node in the shoot. Some branches contributed to the formation of a nodal plexus similar to that formed at the nodal plane in the embryo. Several branches extended into young leaf primordia on the meristem. These branches formed the entire laticiferous system of the leaf. Tips of the remaining laticifer branches developed from the nodal plexus were observed to maintain a position in the meristematic zone of the shoot.

Nonarticulated laticifer branches in the shoot were not confined to a particular tissue, but ramified throughout the shoot (Blaser, 1945). In the shoot they formed H- and Y-configurations reflective of the branching pattern for the growing cell tip. Some tips were observed to penetrate to the epidermal layer while others were detected in contact with the cambial zone.

The presence of laticifers in roots of *Euphorbia* had been confirmed by several other workers (Chauveaud, 1891; Schaffstein, 1932; Schullerus, 1882). Schullerus emphasized that branches of laticifers did not enter into lateral roots until the lateral root had attained a diameter of 1–2 mm. In roots the laticifers were usually found to be smaller in size and more difficult to recognize than those in the shoot. Those in the root appeared to contain a considerably lower protoplasmic content along their length than the laticifer tubes in the shoot.

Both Chauveaud and Schmalhausen confirmed the earlier conclusion of David

(1872) that nonarticulated laticifers were not formed by cambium activity. The entire laticiferous system arose from embryonal initials and their intrusively growing branches.

B. VARIATIONS OF THE *EUPHORBIA*-TYPE LATICIFER

The Euphorbiaceae possess considerable variation in the form of laticifers. The genera, *Ricinus* and *Mercurialis* (Schaffstein, 1932) were reported to contain no laticifers; *Hevea* and *Manihot* contained the articulated laticifer type; the genera *Jatropha* and *Aleurites* are described (Chauveaud, 1891; Gaucher, 1902; Pax, 1884) as having both types of laticifers. However, in subsequent investigations only the nonarticulated type was identified in the latter two genera (Schaffstein, 1932; Solereder, 1908). In *Ceropegia thwaitesii* Hook. the nonarticulated laticifer was restricted to the pith; branches developed into primordia of leaves from a nodal plexus similar to the one formed in the genus *Euphorbia* (Schaffstein, 1932). The section Phyllanthoideae was reported to contain no laticifers (Pax, 1884). Gaucher (1902) contended that the articulated laticifer was the predominant form in the Euphorbiaceae.

Stapelia bella Berger (Asclepiadaceae) was reported to contain both articulated and nonarticulated laticifers (Schaffstein, 1932). The articulated system developed in the immediate proximity of vascular bundles, whereas the nonarticulated type was reported to be distributed throughout the ground parenchyma.

In several members of the Apocynaceae (*Vinca, Amsonia, Tabernaemontana*) no laticifers were evident in the embryo (Chauveaud, 1891; Schaffstein, 1932; Solereder, 1908). Observations indicated that the nonarticulated laticifers arose during postembryonal stages of growth. Presumably the laticiferous initials arose from certain cells in the meristem at the base of a young leaf primordium. These cells subsequently elongated during growth of the shoot.

Laticifers in *Cannabis* and *Humulus* originated from cells at the base of the leaf primordia in the shoot meristem, according to Zander (1928), who grouped them in the Moraceae. In this respect, laticifer origin was quite similar to that believed to occur in *Vinca.* Zander also thought that additional initials developed from other cells within the primordia themselves, and that these cells subsequently ramified throughout the lamina. These initials could be distinguished from the adjacent cells only by their somewhat more dense protoplasm and large nucleoli. Growth of the initial cells appeared to be toward the meristem only, perhaps by means of intrusive growth. Finally, according to Zander, the tip of a laticifer penetrated into leaf primordia and developed along veins of the leaf blade.

In several genera of the Moraceae (*Ficus, Dorstenia, Morus, Treculia* and *Maclura*) the branched laticifers were reported to be somewhat comparable to the *Euphorbia*-type (Chauveaud, 1891; Schaffstein, 1932; Schmalhausen, 1877). In *Maclura,* Schmalhausen observed the presence of tyloses in the laticifers. Vreede (1949) affirmed the nonarticulated structure of the laticifer in *Ficus* and described the presence of laticifers in the vascular cambium.

Several genera of the Urticaceae had been investigated for the organization of the laticifer system. Laticifers were reported to be present in the shoot of the mature plant of *Urtica,* but no initials could be detected in the embryo (Chauveaud, 1891; Gravis, 1884; Solereder, 1908; Treub, 1880). However, Schaffstein (1932) was able to detect very delicate laticifer cells in the tissues of the shoot. Presumably these cells remained unbranched during their growth and, as in *Vinca* and *Cannabis,* new initials

were differentiated from certain cells of the meristem during the growth of the shoot. Schaffstein reported that laticifers were not universally distributed in the Urticaceae because he was unable to detect them within representatives of the genera, *Helxine* and *Pilea.* However, Guérin (1923) recorded nonarticulated laticifers in the pith, cortex and secondary phloem in both the stem and root of *Laportea, Urera* and *Urtica.*

VII. Mode of Growth of the Nonarticulated Laticifer

The nonarticulated laticifer appeared to increase in length by intrusive growth of the cell tip (Chauveaud, 1891; Schaffstein, 1932; Schmalhausen, 1877; Schullerus, 1882), a process ascribed to the fiber some time earlier. The extensive development of laticifers throughout the plant body provided substantial support for this contention. In addition, when the course of any one branch of an initial was followed along the shoot toward the shoot meristem, the axis of the laticifer was observed to decrease gradually in diameter until it terminated as a narrow and rather sharply pointed tip wedged between two adjacent cells.

The walls of the laticifer conformed closely to the outlines of adjacent cells, pressing into any of the spaces which occur between the neighboring cells. Consequently, the wall of a laticifer was very irregular and jagged in appearance. Schmalhausen (1877) compared this peculiar intrusive growth habit to that of parasitic hyphae of a fungus spreading into tissues of its host, but different in that the laticifer grew and branched only in meristematic tissues of the plant.

Schaffstein (1932), in studying the growth relationships of the nonarticulated laticifer in the shoot, maintained that there was a very intimate relationship between the growth of this cell and meristematic activity of adjacent tissues. The laticifer was described as being influenced by two factors: active growth at the tip of the laticifer itself, and the influence that adjacent tissues have upon it. Information which he believed supported his hypothesis of apical intrusive growth in the laticifer was derived from grafting experiments on *Euphorbia caput-medusae* L. He attempted to determine the response of the laticifers present in the living tissues adjacent to the grafted surfaces. If a union of the various living tissues could occur, he speculated that a similar union between the laticifers of the stock and scion also may occur.

Schaffstein observed that laticifer cells in the immediate vicinity of the cut surface of both stock and scion frequently degenerated. However, some of the laticifers more distant from the cut surface remained protoplasmic. It was from these active laticifers that Schaffstein occasionally observed the occurrence of branches which penetrated into the callus. Only a few of these branches penetrated through the callus and approached the graft surface. None were observed to enter the primary callus to make contact with the grafted surfaces, or to penetrate through the graft-union into the adjacent segment of the shoot. In some instances the laticifers formed branches as they grew into the secondary callus. Schaffstein concluded from these experiments that mature portions of the laticifers, although surrounded by mature tissues, had not lost the potential to resume active growth under certain conditions. A similar conclusion also had been suggested by Schullerus (1882). The development of new branches from the laticifer suggested to Schaffstein that this growth was a response inherent in the laticifer itself. Branch formation was indicative of the active growth at the tip of the laticiferous cell. Schaffstein also contended that the occurrence and the restriction of growth only to the meristematic callus tissues supported his hy-

pothesis that growth of the laticifer only could occur in meristematic tissues, or in tissue that had regained meristematic activity. The meristematic tissues surrounding the laticifer appeared to exert control over the development of this cell type.

Similarly, Schaffstein (1932) attributed the growth of the laticifer in the normal plant to two processes: the growth and the bifurcation of the laticifer in the meristem suggested the occurrence of active growth at the tip of the cell; and, the increase in length of the laticifer concurrent with the elongation of adjacent immature cells suggested a secondary stretching of the walls of all cells. If the tip of a laticifer was to retain its position in the meristem, the growth rate of the laticifer must equal the rate of wall elongation for all cells below the meristem. However, as he pointed out, the rate of elongation of the laticifer must be greater than the rate of elongation of any one adjacent cell. This fact is derived from the consideration that within the zone of elongation each vertical tier of cells is increasing in length. Since the laticifer extends through all of these tiers, it must elongate at a rate which can be expressed as the sum of the elongation-rates in the contiguous cell-tiers. He also employed this concept to support his view that the adjacent cells somehow may influence the rate of elongation of the laticifer. Schaffstein maintained that the meristematic condition of the surrounding cells controlled the rate of growth of the laticifer. Occasionally, he observed laticifer branches which terminated after growing for only a short distance. He explained this phenomenon in the following quotation:

> *It is very possible that these laticiferous ducts have had all, or a part, of their growth arrested because they remained behind the division zone of the shoot, the only zone within which they were capable of growing. Most of the branches of the laticifer which are present in the meristem grow at a rather uniform rate. None have ever been observed to have penetrated into the distal region of the meristem immediately below the protoderm of the shoot tip. In the dormant plant, the tips of the laticifers do not grow.*

Schaffstein maintained that laticifers grew directionally toward meristematic zones. They grew along the longitudinally arranged intercellular spaces leading toward the meristem; only occasional branches developed along the intercellular spaces at right angles to the plant axis. The directional growth of the branches after their formation in the meristem responded in a similar manner. Although branching occurred in various parts of the plant, it appeared to be closely related to the formation of lateral organs. For example, branch formation regularly occurred at the base of a leaf primordium. One branch subsequently developed into the primordium while the other maintained its direction of growth upward into the region of the shoot apex. Schaffstein attributed the development of laticifer branches to stimuli from the surrounding tissues. He contended that the leaf primordium must exert an influence upon the branch of the nearby laticifer inducing it to grow into that lateral organ. Likewise, the shoot meristem was the source of a factor, or factors, that induced the second branch to maintain its course in the meristem.

The phenomenon of branching in the laticifer was not clearly understood. Meeuse (1942) suggested a mechanism whereby such bifurcations might be formed. Branch formation was preceded by division of a contiguous meristematic cell into two daughter cells. The new wall resulting from this division was perpendicular to the longitudinal axis of the laticifer. When a slight protrusion from a laticifer was interjected between the two primary walls of the two daughter cells it resulted in formation of a bifurcation. Subsequent divisions in the daughter cells facilitated the continued

development of the branch resulting in what Meeuse termed symplastic growth. Intrusive growth, according to him, did not occur, in contrast to the interpretation suggested by other authors (Chauveaud, 1891; Schaffstein, 1932; Schmalhausen, 1877; Sperlich, 1939). As Meeuse (1942) stated:

> *The latex cells therefore do not slide on the walls of their neighbor cells. The relative displacement of the tips of the young latex cells in the embryo therefore probably comes about in the same way as in the case of crystal cells of* Citrus, *i.e., the cells alter their relative position chiefly by symplastic readjustment of the whole framework of cell walls, . . .*

It was not known how the various growth processes of the laticifer were controlled. Tip growth, cell elongation, rate of growth, direction of growth, formation of branches and redifferentiation in the laticifer represented complex processes in cellular differentiation. Since Schaffstein's investigations (1932) were published shortly after Went (1928) introduced his concept of how auxin affected plant growth, it was not surprising that Schaffstein attributed the various laticifer growth phenomena to a chemotropic response.

Schaffstein suggested that auxin produced in the apical meristem formed a decreasing gradient as it diffused downwardly along the axis. He suggested that if laticifers were sensitive to auxin they would grow along the gradient in the axis toward the meristem. Similarly, an auxin gradient extending from the leaf primordium into the shoot might induce some of the branches produced by the laticifer to grow into the primordium.

VIII. Wall Structure of the Nonarticulated Laticifer

The laticifer formed a soft, plastic primary wall during its early development (Sperlich, 1939). However, the thickness of this wall was quite variable. In some plants, such as *Urtica,* it was very delicate, perhaps only as thick as the wall of the adjacent parenchymatous cells. On the other hand, in some species of *Euphorbia,* as *E. splendens,* the wall could attain a thickness of 10–16 μm (Schwendener, 1885).

The chemical and physical structure of the laticifer wall in *E. splendens* was investigated by Frey-Wyssling (1926, 1932). Upon differential dissolution of cell wall constituents, he reported that this wall was relatively high in pectic material to which he attributed its hygroscopic character.

Frey-Wyssling (1942) investigated the micellar arrangement in the walls of the laticifer. Wall birefringence and iodine dichroism indicated that cellulosic micellae were somewhat randomly arranged. In a transectional view of the cell the micellae were arranged tangentially to the wall surface, whereas in longisection the cellulosic micellae were arranged predominantly in the horizontal plane. He termed this particular arrangement the tube structure. It was not peculiar to the laticifer, but also characterized walls of sieve tubes, elongated parenchyma cells, meristematic cells, as well as the primary walls of bast fibers and all cambium derivatives (Meeuse, 1942).

The wall of a laticifer was often very irregularly thickened. This was most evident in those plants in which the laticifer wall was characteristically thicker than that of the adjacent cells (*Euphorbia* sp.). Irregularity in thickness of the cell wall appeared to be a result of the plasticity of the wall. Hence, as the tip of the laticifer cell grew along the intercellular space it conformed to the contours of the adjacent cells.

The presence of primary pit-fields in the walls of laticiferous cells has been described only by a few investigators. Haberlandt (1883) contended that he observed pits in the laticifers of *Euphorbia lathyris* where laticifers contacted palisade cells, and more obvious pits were evident where they contacted spongy parenchyma cells. Protoplasmic connections between a laticifer and the adjacent parenchymatous cells were reported in *Nerium oleander* (Haberlandt, 1886; Kienitz-Gerloff, 1891; Strassburger, 1901; Trecul, 1866), in *Euphorbia cyparissias* (Kienitz-Gerloff, 1891), in *Ceropegia* (Borscow, 1869) and also in *Codiaeum variegatum* Bl. (Böttcher, 1927). Reess (1896) reportedly observed primary pit-fields in the wall of laticifers, but was unable to detect the corresponding half of the pit-field in the adjacent cell.

IX. Cytology of the Nonarticulated Laticifer

The cytology of nonarticulated laticifers had received little attention in classical anatomical studies of the cell. Even De Bary's review (1884) on the topic of laticifers was noticeably lacking in a discussion of any cytological aspects. This quotation expresses the state of knowledge of the microscopic content of these cells at that time:

> *Within the wall neither protoplasm nor nuclei are to be seen. It is true many forms of coagulated, finely granular latex, as that of the Cichoriaceae, resemble coagulated protoplasm, or their remains here and there, in partially emptied tubes after action of alcohol, solution of iodine, etc., a coat which looks like a coagulated protoplasmic lining to the wall. Further investigations will therefore perhaps be able to prove the presence of a protoplasmic body.*

The uncertainty of the protoplasmic content within laticifers resulted in such interpretations as advanced by Berthold (1886), who temporarily resolved the problem by referring to the entire content as protoplasm. However, Schmidt (1880), Kallen (1882) and Molisch (1901) were able to distinguish a marginal protoplasm in laticifers of *Euphorbia splendens, Euphorbia pulcherrima* Willd. and *Ficus elastica.* The protoplasmic lining was not sharply distinguishable from the vacuolar content, but appeared to intergrade with it. From their investigations upon living tubes of *Euphorbia,* Bobilioff (1925) and Popovici (1926) described laticifers as possessing a marginal protoplasmic sheath which surrounded a large central vacuole. The cell sap of the vacuole consisted of various inorganic substances as well as starch and other carbohydrates.

Presence of nuclei within laticifers was observed by several workers (Buscalioni, 1898; Haberlandt, 1883; Molisch, 1901; Nemec, 1910; Smolak, 1904; Treub, 1879, 1880). Treub identified the laticifer as multinucleated, which induced Foster (1949) to describe the nonarticulated laticifer as a coenocyte. Treub, the first to describe laticifer cytology, depicted the nuclei as large and peculiarly spindle-shaped. He observed them in various genera including the Urticaceae, Apocynaceae, Euphorbiaceae, and Asclepiadaceae. The uniformity in appearance of the nuclei and the regularity of their distribution within the laticifer suggested to Treub that they were all in a similar state of development and activity. Occasionally he observed several nuclei present in a group, but usually they were quite uniformly spaced along the tube.

Origin of the multinucleated protoplast in the laticifer was ascertained only with difficulty. The most logical assumption was that the coenocytic condition resulted from repeated nuclear divisions without the formation of cell walls. However, most

of the investigators apparently were unable to detect the occurrence of any nuclear divisions within laticifers. Only a few observations of karyokinesis have been reported (Buscalioni, 1898; Nemec, 1910; Treub, 1880). Treub observed and depicted nuclear division figures in laticifers of *Urtica dioica* L., *Vinca minor* L., *Stephanotis floribunda* Brogn., *Hoya ariadne* Decne., *Ochrosia coccinea* Miq. and *Cyrtosiphonia spectabilis* Miq. Karyokinesis, as he described it, was a rhythmic process in which the nuclei divided simultaneously. Although he implied that all nuclei along the entire length of the tube performed in this manner, he did not state this explicitly. Nemec (1910) could not substantiate the occurrence of simultaneous nuclear divisions in these cells. Rather, he observed karyokinetic activity to be restricted to the plant meristem where adjacent parenchymatous cells were also dividing. No nuclear divisions were seen in the laticifer below the meristem in the region of cell elongation.

X. Summary

The classical studies of laticifers have contributed seminal information on the structure and development of these cell types in vascular plants, and provided the bases for additional investigations into their organization and interrelationships. The association of unusual cell contents with laticifers contributed to their being interpreted as secretory structures (Esau, 1953). This designation provided a working basis for studies on these cells, and the results and implications from the studies of the classical workers have raised major questions on the character and relationships of these cells.

The implications of the secretory designation suggest a functional role for cell contents or for the cell itself. There are few data to support a functional role for laticifers although one can speculate that these specialized cells do perform functions in the plant. Indeed, laticifers in different genera and families may have evolved different functions, with no one function characterizing laticifers in general.

The recognition of two distinctive laticifer types, the articulated and nonarticulated laticifers, has provided a working hypothesis for examining their ontogeny. Although this classification has been convenient, it may be too simple and, therefore, obscure subtle differences within each or both types that warrant their further separation into additional types.

The recognition of different ontogenetic origins of laticifers for plants in different families brings into question the homology between nonarticulated and articulated laticifers. Their assumed homology is typically based on the nature of their "milky" contents rather than on patterns of differentiation and ontogeny. Cell contents, as already shown by classical workers, can vary between different laticifers and may reflect selective processes independent from those controlling cell differentiation and ontogeny. The nonarticulated laticifer may be a distinctive cell type whereas the articulated laticifer may be related phylogenetically to other idioblasts.

The disjunct distribution of each laticifer type among only a few families of angiosperms as noted by the classical workers would indicate a polyphyletic origin for both articulated and nonarticulated laticifers. Although past studies indicate a limited distribution in angiosperms, future studies may reveal a more wide-spread distribution than presently recognized. Their absence in primitive angiosperms suggests that these cells are more recent in origin than most other cell types.

The great length of the nonarticulated laticifer, it being the longest of all biological cells, contributed to an interpretation that the mechanism which limits the growth

in length of other cells is absent in this laticifer. Thus, unlike other cell types, this laticifer can grow intrusively as a single cell throughout different tissues of the plant body. This feature sets the nonarticulated laticifer apart from other cells.

The detection by classical workers of a coenocytic protoplast in the nonarticulated laticifer emphasized the occurrence of an alteration in the mitotic apparatus resulting in the loss of the mechanism controlling cell plate and wall development. All nuclei in a nonarticulated laticifer, including those in the growing tips of the laticifer in plant meristems, represent progeny from the original nucleus of the laticifer initial. This laticifer, therefore, is cytologically isolated from the meristems whereas for other tissues the meristems contribute new cells with their nuclei to the developing tissue.

XI. Acknowledgments

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