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Distribution and development of the non-articulated branched laticifers of *Morus nigra* L. (Moraceae)

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SUMMARY

The origin, development and arrangement of the branched, non-articulated laticiferous system of *Morus nigra* L. (Moraceae) were studied in embryos, seedlings, and leaves, stems and roots of young and mature plants using light and scanning electron microscopy. There are two laticiferous systems present in the older plant, a primary and a secondary one. The primary laticifers arise from eight initials in the outer periphery of the future procambium near the cotyledonary node of the young heart-shaped embryo. They produce the first-formed laticiferous system of the plant. No additional primary laticifers are formed in other primary tissues. Secondary laticifers of the same type as the primary ones are produced by initials of the vascular cambium in the secondary phloem of stem and root. Their number is larger and variable. No fusions of laticiferous cells with one another or adjoining parenchyma cells were observed. The extremely elongated, thin-walled, branched laticiferous cells are devoid of pits. They exhibit a combination of intrusive and symplastic growth; penetrations into other cells were not observed. Laticifers are present in all vegetative tissues with the exception of epidermis, and primary and secondary xylem. The close developmental and distributional relationship between laticifers and phloem suggests a possible functional relationship.

Key-words: laticifer, *Morus nigra*, vegetative anatomy.

INTRODUCTION

In plants two main types of laticifers are recognized, namely, articulated (not present in genera of Moraceae) and non-articulated ones. The latter type originates from a single cell and either develops into long, more or less straight tubes (unbranched subtype), or branches repeatedly forming an immense three-dimensional system (branched subtype). Non-articulated laticifers are found in all Apocynaceae, Asclepiadaceae, Moraceae and many Euphorbiaceae (Reinders 1964). Branched ones occur in several genera of these families (Esau 1965). In the Moraceae they have been recorded in seven genera, including *Ficus, Broussonetia, Maclura* and *Morus* (Metcalfe 1989b). The type of laticifer is not constant in a given family, genus (Fahn 1969) or sometimes not even in a single species (Schaffstein 1932).

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However, the usefulness of laticiferous types in systematic comparisons between and within families has been established (Chauveaud 1891; Carlquist 1961). In *Allium*, differences in position, shape and pitting in cross walls of, in this case, non-anastomosing articulated laticifers in bulb scales, are used to distinguish subgenera, sections and subsections (Huang & Sterling 1970). On the other hand, the possible phylogenetic significance of variations in degree of specialization of laticifers is generally small (Metcalfe 1989a).

The laticiferous cell has probably evolved independently in the different dicotyledonous families, reflecting a polyphyletic origin (Mahlberg & Sabharwal 1968). The most common view is that laticifers are secretory elements (Fahn 1979). The basic nutritional requirements of the laticiferous cell are obtained from adjacent cells, possibly phloem cells (Cass 1985; Faij *et al.* 1989), since these two are often associated. Hence in some respects the laticiferous cell can be compared with a parasitic cell within the plant body (Mahlberg 1959b).

The latex is clear (*Morus, Nerium oleander*), milky (*Ficus*), yellow-brown (*Cannabis*), or yellow to orange in Papaveraceae (Fahn 1969). In non-articulated laticifers of many species the nuclei are known to undergo divisions resulting in a coenocyte (Mahlberg 1959a). In *Euphorbia marginata* Mahlberg (1959b) and Mahlberg & Sabharwal (1968) found that the nuclear divisions are not randomly distributed, but follow a successive pattern that results in mitotic waves. In *Nerium oleander* these divisions only occur in the meristematic regions of the plant body (Mahlberg 1959a).

Laticiferous cells exhibit both intrusive tip growth and growth by elongation (Mahlberg 1959b, 1961). Growing tips follow the path of the middle lamella. Pectinase has been demonstrated in the latex of *Asclepias syriaca* which may facilitate intrusive growth and may also be important for loosening wall material of the laticifer itself to simplify extension growth (Wilson *et al.* 1976). In other plants growth may be accomplished by physical intrusion of the cell tips between the adjacent cells. Growing tips have never been observed to penetrate adjacent cells, not even hydathodes (Lersten & Peterson 1974). The present study was performed to establish where and how early laticifers in *Morus nigra* are initiated, their structural type and possible changes in type, their distribution in primary and secondary tissues of the vegetative plant body, and their mutual connection.

MATERIALS AND METHODS

Anatomical features of laticifers of *M. nigra* L. were investigated in embryos of both unripe and ripe seeds, in stems, leaves and roots of seedlings up to 4 years old, and in mature trees. The material used for sectioning with a sledge microtome was either fresh, or fixed in FAE (formalin–acetic acid–ethanol), dehydrated in a graded ethanol series and impregnated in Technovit 7100.

For light microscopy, transverse and longitudinal serial sections, 6–7 μm thick, were stained with toluidine blue (contrast, cytoplasmic stain) and embedded in euparal. Laticiferous cells in sections of fresh and fixed material, were also stained with sudan III (fatty substances, latex) to facilitate their identification and embedded in Kaisers gelatin–glycerin (Johansen 1940). Individual laticifers from stem and root bark were obtained after maceration in 5% sodium hydroxide solution for 1 h at room temperature. For scanning electron microscopy (Jeol JSM-35C) bark cubes of about 125 mm^3 with clean cut surfaces were dehydrated in a graded ethanol series, critical-point dried, mounted, and

sputter-coated with gold–paladium. SEM was used to investigate possible pits in the laticiferous cell walls and to obtain a better three-dimensional image of the cells.

RESULTS

The first formed laticiferous system of *Morus nigra* originates in the embryo from eight separate initials. This number is constant for the species. The initials are situated in the cotyledonary nodal plane in the pericycle, i.e. the outer periphery of the future procambium cylinder. They are arranged in two groups of four initials each, in a plane perpendicular to the plane in which the cotyledons separate from the stem. Chauveaud (1891) gives some drawings of an early stage, whereas Fig. 1a shows a comparable situation of an older stage in which the laticifers have already branched and shifted slightly. The laticiferous initials differentiate somewhat before, or simultaneously with adjacent procambium initials. Each laticiferous cell frequently branches forming Y-shaped (Fig. 2a), and occasionally H-shaped (Fig. 2b and d), configurations. The primordia form protrusions in various directions. The tips of these protrusions find their way among the surrounding cells by intrusive growth. They probably also grow by elongation (cf. Mahlberg 1959b, 1961). They have never been observed to penetrate or anastomose with adjacent cells, and never show septations. In such a way eight separate, primary units are formed.

The branches from the nodal plane extend upward into the cotyledons and the embryonic shoot apex and downward into the root apex. They usually run parallel with the vascular tissue, but also deflect to the cortex, although never to the epidermis (Fig. 3). Young laticiferous branches in the cortex are usually triangular or quadrangular in cross-section (Fig. 1a), as distinct from those near the vascular tissue, and much smaller than the surrounding parenchyma cells. Laticiferous cells near the vascular tissues have a diameter of 10–20 μm (Fig. 1b and d). Karyokinesis regularly takes place, resulting in a coenocytic protoplast. No new primary initials originate. A schematic presentation of the ramifications of one of the eight primary laticifers in a 2-week old seedling is given in Fig. 3. The primary tissues are fully differentiated, but no secondary ones are formed yet. The figure shows ramifications in and near the cotyledonary nodal plane, but especially 600 μm lower in the transition area of hypocotyl to root. In the nodal plane areas, branches of the extravascular laticifer enter the cotyledons and leaves. Near the cotyledonary plane a branch enters the pith of the hypocotyl and epicotyl by way of the cotyledonary gap (*cf.* Figs 1d and 2a), whereas near the branch of the first leaf a ramification enters the cortex. In the cotyledons (Fig. 1c and e) and primary leaves the ramifications are frequently found remote from the vascular tissue.

Young stems (Figs 1b and 2f) and roots (Fig. 1f) possess laticifers in cortex, pericycle, primary and secondary phloem; they are absent in the xylem. In the stem pith they are also present, all entering via leaf gaps (Figs 1d and 2c); their horizontal branches remain short. No branches enter horizontally through the vascular cylinder into the pith. In the root centre laticifers are absent; the centre usually containing metaxylem (Fig. 1f). In the leaves, laticifers follow the vascular bundles and ramify in the mesophyll (Fig. 1c). In older stems branching mainly takes place in a tangential plane, not in a radial one.

New unbranched laticiferous initials with a tip to tip length ranging from 850 to 2250 μm arise in the phloem side of the cambial zone; the fusiform phloem initials show beaded walls during dormancy (Fig. 4a and c). In Fig. 4(a and b) usually only one of the tips of a single laticifer is visible; this is caused by the fact that the young laticifers are not

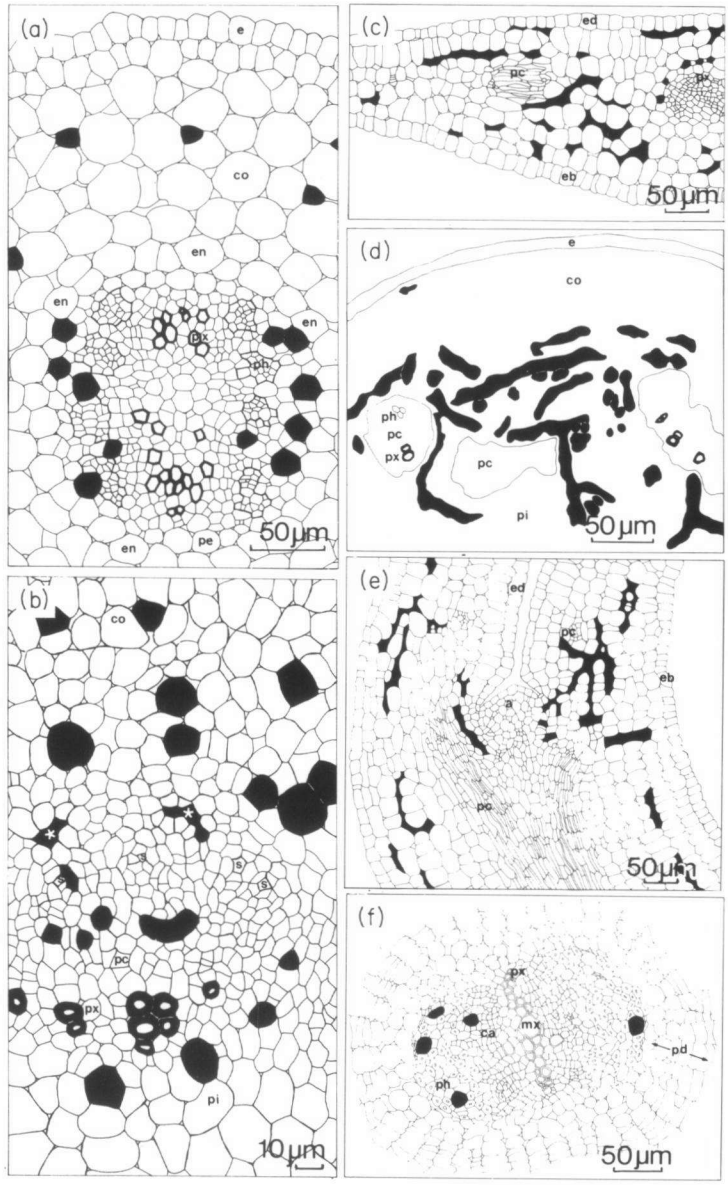

Fig. 1. *Morus nigra*.Drawings of transverse sections (a–d and f) and one longitudinal section (e). Black areas represent laticifers. (a) Shoot axis of 14-day-old seedling, 170 µm from apex. Primary phloem arranged in two areas. Each area composed of four groups of cells accompanied at first by one unbranched laticifer. (b) Shoot axis 500 µm from apex. Two laticifers (■) in pericyclic region surrounded byfibre primordia. Four protophloem sieve tubes visible (s). (c) Cotyledon of embryo in ripe seed, 300 µm above attachment to axis. (d) Leaf gap 170 µm from shoot apex. Area with strongly branched laticifers. (e) Cotyledonary node of embryo in ripe seed. Upper half of drawing shows shoot apex and two cotyledons, lower half hypocotyl axis. (f) Young root of 4-year-old plant. Periderm has appeared, cortex and epidermis have been shed. Cambium has produced some secondary vascular tissue.

Abbreviations: a = shoot apex; ca = cambial zone; co = cortical parenchyma; e = epidermis; ed = epidermis adaxial; eb = epidermis abaxial; en = endodermis; mx = metaxylem; pc = procambium; pd = periderm; pe = pericycle; ph = primary phloem; pi = pith parenchyma; px = protoxylem; s = sieve tubes of protophloem.

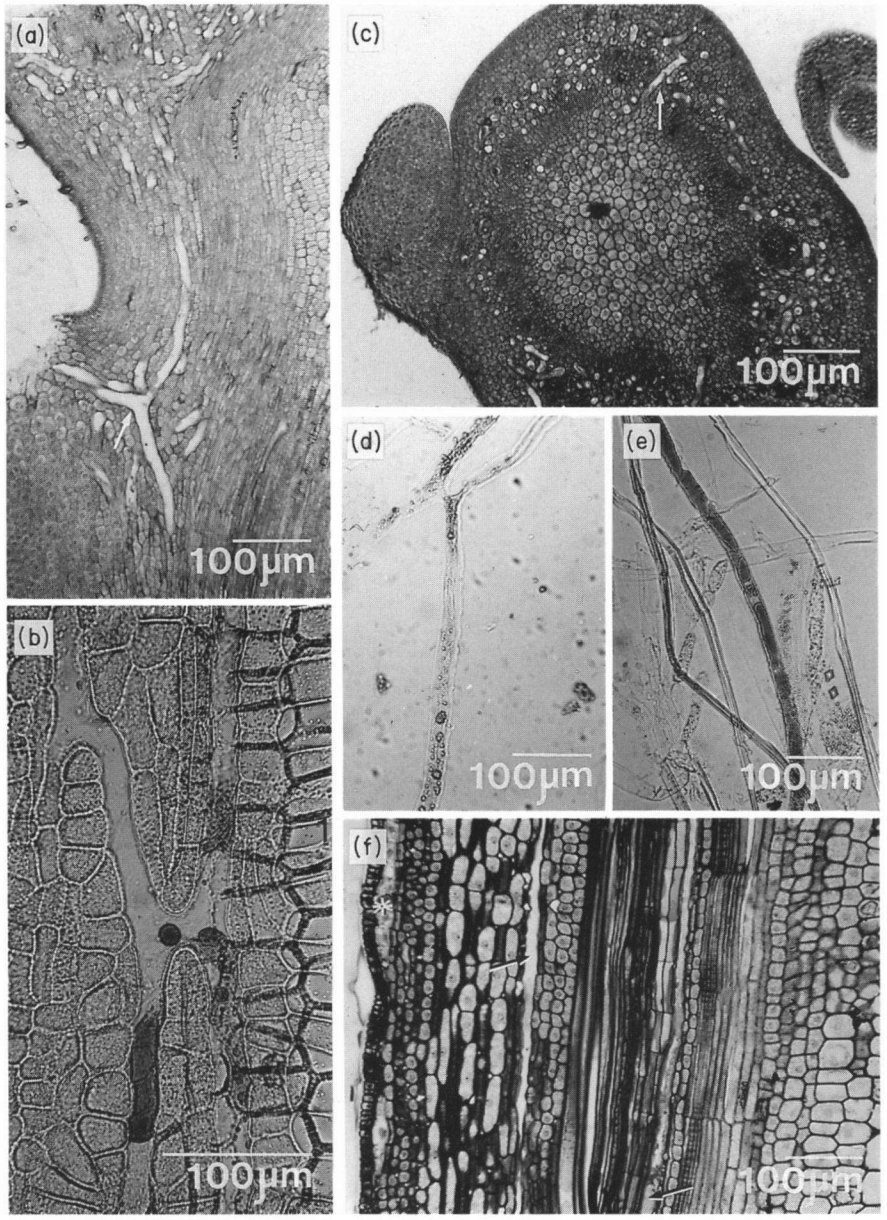

Fig. 2. *Morus nigra.* Light microscopical photographs. (a) Longitudinal section of shoot, 5 mm from apex. Branching of laticifer (↑; Y-shaped) to petiole of very young leaf. (b) Longitudinal section of 1-year-old branch at the nodal plane. Branched laticifer (H-shaped) in pith near protoxylem (left of photograph). Note remnants of latex, stained with sudan III. (c) Cross-section of shoot, 150 µm from apex. Many laticifers (white areas) outside the ring of partly differentiated primary vascular tissue. Note horizontal laticifer (↑), growing radially towards pith via leaf gap. (d) Branched laticifer (H-shaped) with remnants of latex. Maceration of primary tissues, stained with sudan III. (e) Part of unbranched laticifer, three phloem fibres and other phloem elements. Maceration of young secondary phloem, stained with sudan III. (f) Radial section of shoot, 1·8 cm from apex. Two laticifers (↑) visible; one in the cortex (left) and one in the primary phloem. Note periderm formation just below the epidermis (*).

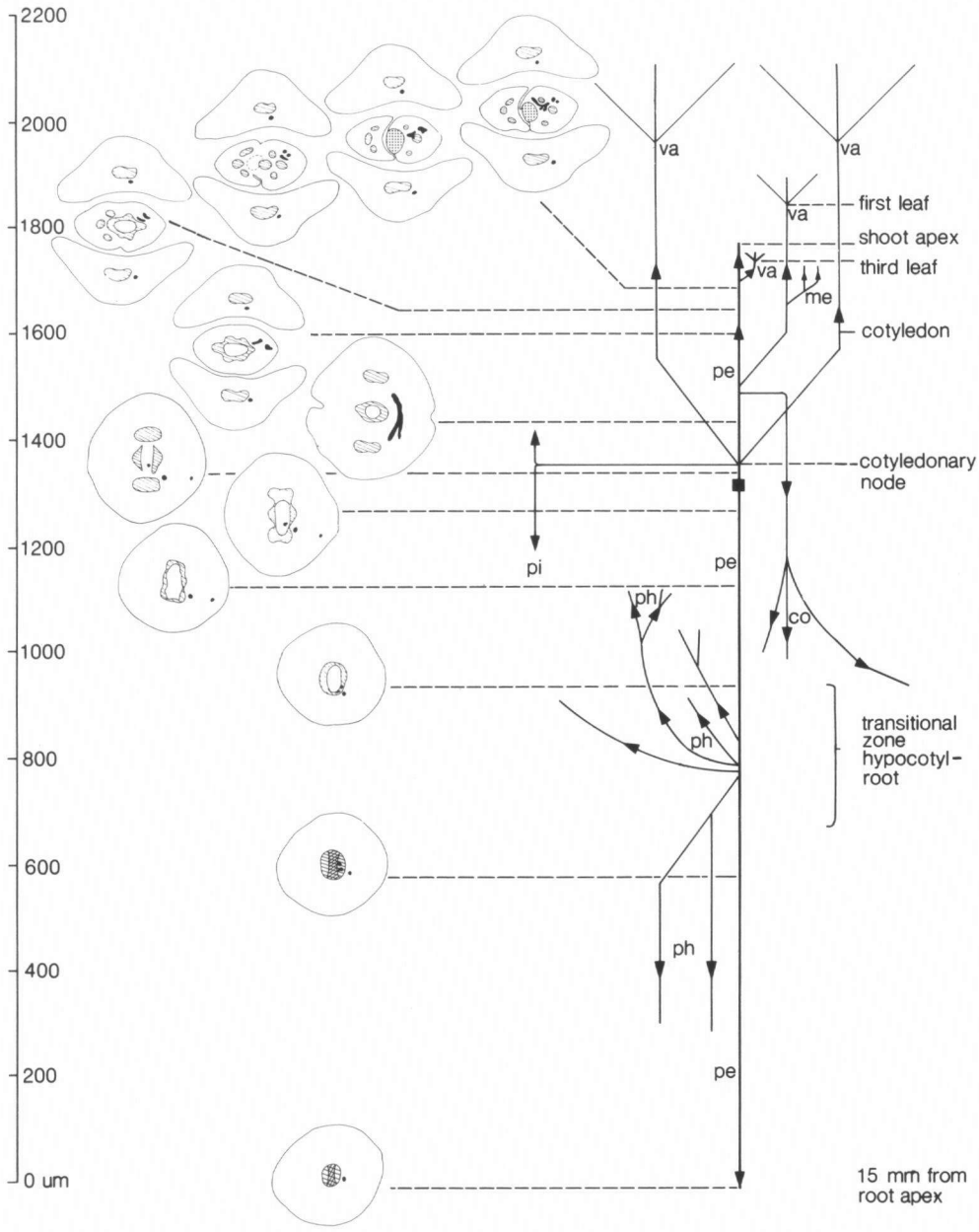

Fig. 3. Schematic representation of the upper part of one of the eight primary laticifers from a 14-day-old *Morus nigra* seedling, with its main ramifications in root, stem and leaves (right). The cotyledons and first two leaves (one not drawn because no laticifer branch was split off) have a decussate phyllotaxy, the other leaves are arranged alternately. They are all depicted in the same plane in the drawing. On the left are topographic drawings of transverse sections through the seedling at different heights (all with the same magnification), showing the position of the laticifer (black dots or black areas). The far left shows a scale (μm) starting 15 mm from the root apex.

Abbreviations: (▲) = direction of growth; (■) = starting point of laticifer; (▦) = meristematic apical region; (▩) = primary xylem; (▧) = primary phloem or vascular tissue; co = cortex; me = mesophyll; pe = pericycle; ph = primary phloem; pi = pith; va = parallel to vascular bundle in leaf.

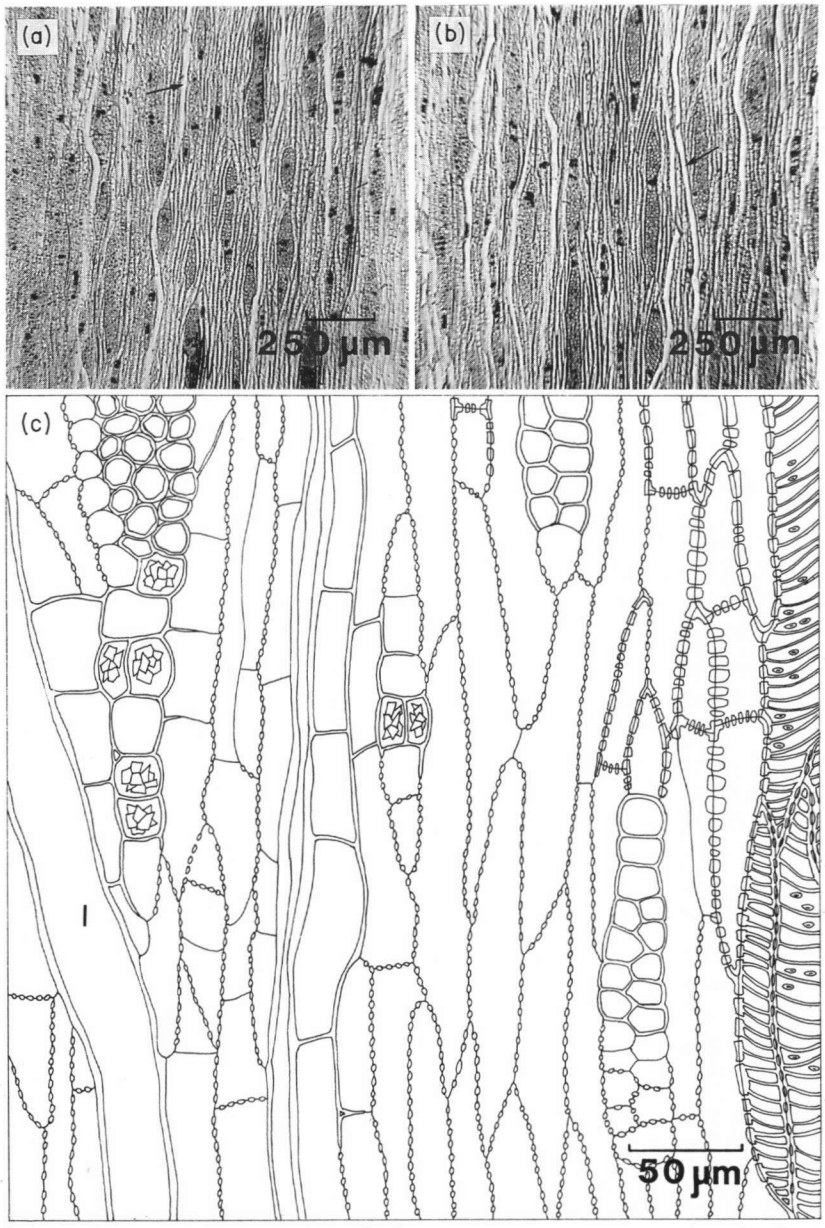

Fig. 4. *Morus nigra*. Light microscopical photographs (a and b) and drawing (c). Tangential sections of cambial zone of 4-year-old branch. (a) Cambial initials slightly below the middle of the photograph, young secondary xylem elements at bottom right. The remaining part young secondary phloem with young, secondary laticifers (one indicated with arrow; both cell tips of a single laticifer usually not visible here). (b) Young secondary phloem with young secondary laticifers (one indicated with arrow), 20 µm more outside the xylem cylinder than previous figure. (c) Initials in cambial zone with beaded wall thickenings in the middle of the drawing; young secondary phloem with secondary laticifer (l) on the left, young secondary xylem on the right.

entirely in the focal plane. The parts of the laticifers shown have definitely not grown into the secondary phloem region from primary tissues. Long unbranched (Fig. 2e), sometimes bifurcated, entire laticifers were also demonstrated in macerations of young secondary phloem. In older secondary phloem, laticifers were found with a total length of 25 mm with complete branches varying in length from 350 to 3000 μm. The diameters of the newly formed secondary laticifers range from 20 to 40 μm, those of older ones increase up to 90 μm. Their cross-section is round, stretched to oval in a tangential direction in the dilatation area where they often show a meandering course (Fig. 5a and b). Cell walls are 1–2 μm thick. (Fig. 5d and e), and with the SEM no pits could be detected (Fig. 5c and d).

Freshly cut plant parts exude a clear latex, which contains many refractive granules or globules, strongly reacting with sudan III (fatty substances; Fig. 2d and e); starch grains are absent. Criteria by which laticifers can be distinguished from neighbouring cells are: strong reaction with sudan III and toluidine blue, contents (such as fat), plasmolysis of older cell parts, cell size, cell-wall thickness, enlargement of nucleus, multinucleate condition, time of origin.

DISCUSSION

Comparison with previous research

The distribution of non-articulated branched laticifers in embryo and adult plant of *Cryptostegia grandiflora* (Asclepiadaceae) was studied by Blaser (1945), and distribution in the primary stem and leaf of *Euphorbia supina* by Rosowski (1968). Vreede (1949) elucidated the course of laticiferous elements in the genus *Ficus*, especially in the stem and their transition from stem to leaf. The origin and development of non-articulated branched laticifers has been investigated in *Nerium oleander* (Apocynaceae) by Mahlberg (1961,1963), in *Euphorbia marginata* (Euphorbiaceae) by Mahlberg (1959b) and Mahlberg & Sabharwal (1968), and in *Jatropha dioica* (Euphorbiaceae) by Cass (1985). Recently, Murugan & Inamdar (1987) described the organographic distribution, structure, ontogeny and histochemistry of non-articulated branched laticifers in *Vallaris solanacea* (Apocynaceae). In Moraceae such a laticiferous type has been recorded in *Morus* (Metcalfe 1989b). Unbranched ones are present in *Cannabis* (Esau 1965); however, this genus has been removed from the Moraceae and placed in a separate, small, closely related family Cannabinaceae (Stoffers *et al.* 1982). The non-articulated branched laticiferous system in the embryo of *M. nigra* was investigated by Chauveaud (1891). Here the laticiferous cells originate in the embryo and do not differentiate after germination as in some other species.

In *Morus*, according to Metcalfe & Chalk (1950), laticifers are present in the cortex, pericycle, primary and secondary phloem and pith. Laticifers are also present in wood rays of many Moraceae, usually in the centre of the ray (Tippo 1938).

A comparison of our findings in *M. nigra* concerning the distribution of non-articulated branched laticifers, with those of the authors mentioned above in species belonging to the families Asclepiadaceae, Apocynaceae, Euphorbiaceae and Moraceae, reveals that only vegetative material is considered with the exception of that from *Vallaris* (Murugan & Inamdar 1987). Furthermore, often only a part of the plant has been studied. Information on both embryo, seedling, and on leaves, stems and roots with secondary growth of the mature plant, is only available for *Cryptostegia* (Blaser 1945), however, this is incomplete. If secondary tissues were considered, they belonged to seedlings. The secondary xylem of young branches was only studied in *Ficus* species (Vreede 1949).

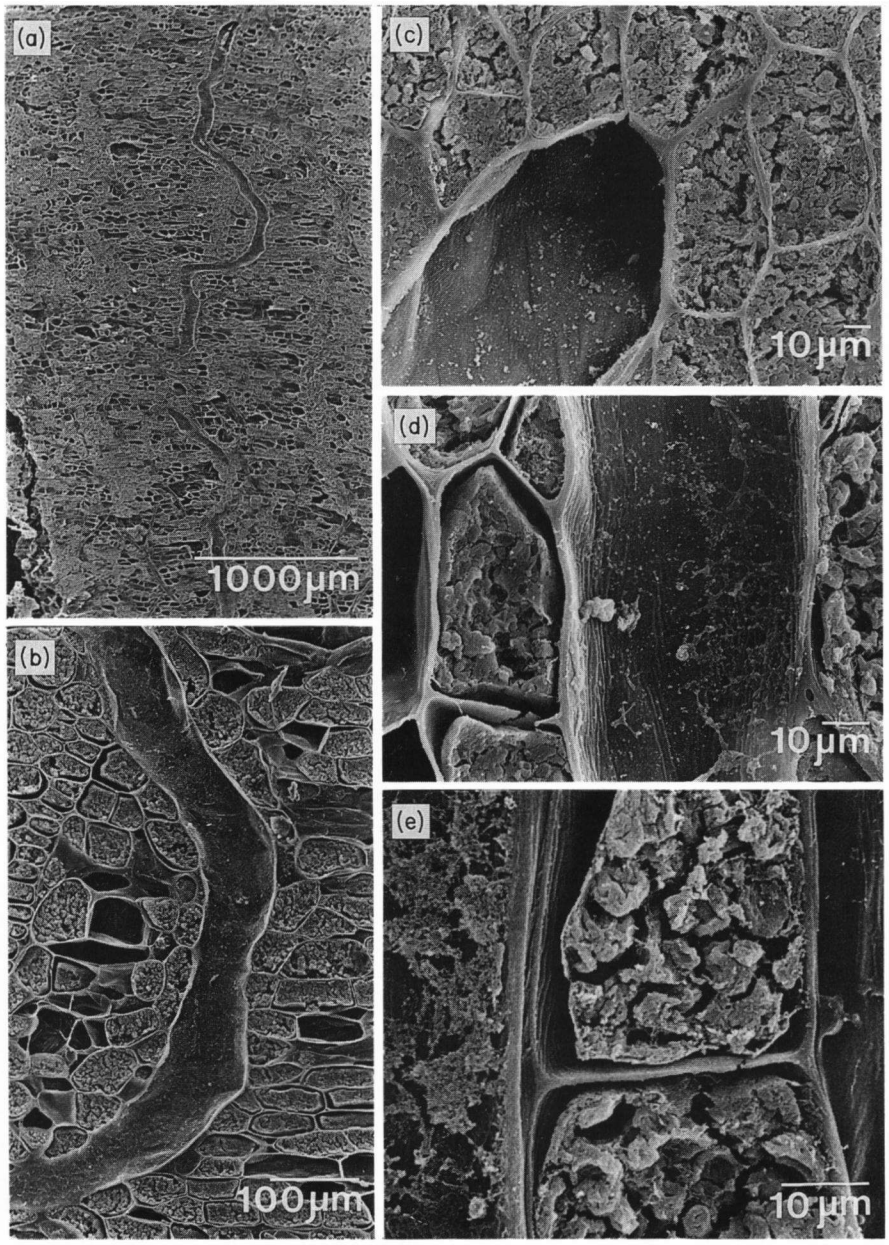

Fig. 5. *Morus nigra*. SEM photographs. Tangential sections of the secondary phloem in the dilatation zone of a 5-year-old branch. (a) Meandering laticifer between parenchyma cells (empty or with protoplast). (b) Magnification of part slightly above the middle of previous figure. (c and d) Almost empty laticifers. Note imprints of parenchyma cells seen from laticifer lumen; no pits visible. (e) Vertical part of laticifer with latex remnants (left), phloem parenchyma cells with contents (centre) and empty parenchyma cell (right).

Origin of laticifers

Chauveaud (1891) and several other authors have shown that a limited number of laticiferous initials originate in the early stage of embryo development. For instance, eight occur in the early heart stage of *M. nigra*, which is in agreement with our findings, usually 28 in the globular embryo stage in *Nerium oleander* (Mahlberg 1961), or 12 in the early heart stage in *Euphorbia marginata* (Mahlberg & Sabharwal 1968). They all arise in the outer periphery of the future procambium or vascular cylinder. The first laticifers differentiate simultaneously with or slightly before the elements of the procambium. When the seed is mature, an elaborate non-articulated branched laticiferous system is already present. The present incomplete evidence indicates that the inductive phenomena for non-articulated branched laticifers in unrelated families are generally similar. However, in *Papaver somniferum* (Thureson-Klein 1970), although with articulated anastomosing laticifers, they are not present in embryos but differentiate after germination and are found in phloem areas.

Primary laticifers

After germination, the laticiferous system of the embryo, differentiated from a limited number of initials constant for a particular species, ramifies strongly and penetrates all or only a part of the primary and later formed secondary tissues of seedlings and older plants. This pattern of origin and development of the non-articulated laticifers is typical not only for *M. nigra*, but also for other Moraceae (Chauveaud 1891). Apocynaceae, Asclepiadaceae and Euphorbiaceae species (Esau 1965).

No evidence was found that new laticiferous cells arose in apical or lateral meristems. This is in agreement with the findings of most authors mentioned earlier who investigated the subject. In contrast to this, Zander (1928) reported that new laticifers were constantly produced by the apical meristem in *Cannabis*. Also in *Vallaris*, Murugan & Inamdar (1987) reported laticiferous initials to originate in the procambium of the shoot apex towards the pith side; the embryo was not investigated.

No fusions between laticifers were observed in *M. nigra* and no other cells were penetrated during intrusive growth. The laticiferous system is a primary one. These observations were also made by all authors mentioned at the beginning of the discussion in other species.

The continuity between laticifer branches in cortex and pith in *M. nigra* is established via leaf gaps. In *Cryptostegia* (Blaser 1945) this takes place through the intervascular regions during primary growth. The laticifers are not ruptured by the activity of the vascular cambium during secondary growth, and the secondary vascular tissues even contain an extended primary laticiferous system, although none of the laticifers are derived from the cambium. The parts of the laticifer located in the cambial zone appear to extend by localized intercalary growth of primary laticifers (Blaser 1945). In the secondary xylem of Moraceae investigated by Tippo (1938), 38 out of 100 species possessed laticifers. Except for one, these laticifers all occur in wood rays only, usually in the centre of the ray. They are continuous with those in the pith and phloem and are of primary origin. Topper and Koek-Noorman (1980) demonstrated laticifers in the secondary xylem of a number of *Artocarpus* species (Moraceae), not only radial ones enclosed in ray tissue, but also as axial laticifers enclosed in the fibre tissue. We did not find any in the secondary xylem of *M. nigra*. Laticifers, especially the larger ones, most commonly lie parallel with and partially surround the vascular cylinder directly in association with, or only a few cells

removed from, the phloem (*Euphorbia supina*, Rosowski 1968; *Jatropha dioica*, Cass 1985; *Vallaris*, Murugan & Inamdar 1987), or in association with the vascular system in general (*Nerium oleander*, Mahlberg 1961). From here they ramify into other tissues. The mature hypocotyl of the embryo of *Jatropha dioica* (Cass 1985) for instance, contains two concentric rings of laticifers; the inner lies just outside the immature xylem and is separated from the outer ring by developing phloem. The inner ring is produced by inward branching of the outer ring. The close developmental and distributional relationship between laticifers and phloem suggests a possible functional relationship. In *Nelumbo nucifera* (Esau & Kosakai 1975) the laticifers, of the articulated type, occur most conspicuously in the vascular bundles but also separately from these in the ground parenchyma.

Epidermis

Laticifers in stem or leaves of *M. nigra* never penetrate between the epidermal cells to reach the cuticle. In leaves of *Ficus* species with a hypodermis (Vreede 1949) and in leaves of *Euphorbia cotinifolia* (Scott 1889), however, this seems to take place. Also in other Euphorbiaceae this phenomenon is fairly common (Rudall 1987).

Secondary laticifers

In addition to a primary laticiferous system, in *M. nigra* a secondary laticiferous system is also demonstrated, produced by the vascular cambium. The two systems do not show fusions. The reason that no secondary systems were reported in the other studies mentioned is possibly due to the fact that very young material was used. Furthermore, it was accepted up until now that non-articulated laticifers generally originate only from primary tissues as distinct from articulated ones. Recently, however, Rudall (1989) also demonstrated non-articulated, branched laticifers actually originating in the vascular cambium in *Croton conduplicatus* (Euphorbiaceae).

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