# Mycoplasmalike Bodies Associated with Lethal Declines of Palms in Florida

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**ABSTRACT**

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Mycoplasmalike bodies (MLB) were observed in sieve elements in tissues sampled from 21 palm species showing symptoms of lethal declines. Evidence suggested that these lethal declines are identical to lethal yellowing of coconut palms. The MLB were found most readily near the apical meristem in the bases of young petioles which had not emerged. Although MLB filled sieve elements in a few vascular bundles, their overall concentration generally was low. An analysis of measurements from 2,971 MLB photographed from thin sections, indicated that MLB populations were comprised of filamentous forms with a mean diameter of 142 nm, and nonfilamentous forms with a mean diameter of 295 nm. Filamentous forms were predominantly oriented parallel to the longitudinal axis of the sieve elements.

*Additional key words*: lethal yellowing

Several researchers (2,19,29,34) have reported mycoplasmalike bodies (MLB) associated with lethal yellowing, a destructive disease of coconut palms, *Cocos nucifera* L., in the Caribbean and neighboring regions. Presumably the disease agent is insect transmitted, but vector identity has not been confirmed (39) and transmission attempts have failed. The lethal yellowing pathogen has not been cultured, but symptom remission has been achieved with tetracycline antibiotics (25,26). The symptoms of lethal yellowing include fruit-drop, inflorescence necrosis, foliar yellowing and desiccation, root degeneration, spear leaf necrosis, and rapid death (27). Other MLB-associated diseases, possibly identical to lelthal yellowing, also have been reported in coconut palms from Togo (9,11,28), Ghana (9), and Cameroon (12). The presence of lethal yellowing was confirmed in Key West, FL, in 1955. It is presently distributed primarily along the southeastern coast of Florida where it has eliminated most susceptible coconut palms from many localities (14).

After the outbreak of lethal yellowing on the Florida mainland, numerous *Veitchia merrillii* (Becc.) H. E. Moore and *Pritchardia* spp. palms declined and died in areas of heavy lethal yellowing infection (27). Symptomatology was similar to lethal yellowing in coconut palms and a mycoplasma etiology indentical to that of lethal yellowing was postulated when MLB were found in samples from these other diseased species of palms (29). This hypothesis was strengthened by research results that demonstrated disease protection of *Veitchia* palms and symptom remission of *Pritchardia* palms after injections with tetracycline antibiotics (27). However, because techniques are not known for culture and transmission of the lethal yellowing pathogen, it is not possible to determine unequivocally whether the MLB-associated declines of different palm species are identical to lethal yellowing of coconut palms. Therefore, the term "lethal decline" has been introduced for the MLB-associated diseases in palms other than coconut (27). This terminology will be used throughout this report and expanded to include lethal yellowing of coconut palms also.

Since the report of MLB in association with *Veitchia* and *Pritchardia* palms was published, members of several additional palm species that were growing in areas with a heavy incidence of lethal yellowing infection have died displaying lethal decline symptoms. Many of these species have been surveyed for the presence of MLB and preliminary reports have been presented (36–38). This article is the first comprehensive publication of this information.

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## MATERIALS AND METHODS

The palm samples that were used for this study were collected between December 1973 and March 1978. The species and number of diseased and healthy control palms examined are listed in Table 1; these were determined largely by the availability of suitable material. The search for MLB in each palm was continued until at least 15 vascular bundles had been examined. Samples from control palms always were examined as thoroughly as those from diseased palms. Specimens from diseased coconut and *V. merrillii* palms also were included for comparison with the lethal-declined species reported earlier (29).

A limited number of attempts to locate MLB in mature leaves, roots, and inflorescences of declining palms were largely unsuccessful, so the majority of samples were taken from the bases of young, unemerged petioles within 3 cm of the apical meristem, where the MLB appeared to be more concentrated. In order to minimize trauma to the specimens, large tissue samples were collected in the field and then transported to the laboratory for further dissection. After the samples were trimmed to ~1 cm$^3$, they were quickly immersed in cold fixative in which final specimens of ~1 mm$^3$ were excised. Specimens were fixed for 18 hr in 0.1 M collidine-buffered 2% glutaraldehyde - 2% paraformaldehyde, pH 7.4, postfixed for 6 hr in 0.1 M collidine-buffered 2% osmium tetroxide, and placed in 0.5% aqueous uranyl acetate for 18 hr, all at 4 C. After dehydration in graded ethanol/acetone series, the specimens were embedded in Spurr plastic and sectioned with a DuPont diamond knife mounted in either a LKB Ultratome III or a Sorvall MT-2 ultramicrotome. Thin sections, ~60–100 nm, and thicker sections, ~250–350 nm, were collected on Formvar-coated grids and examined with a Philips EM201 electron microscope.

To determine MLB morphologies, 50 electron micrographs of individual sieve elements from members of 18 diseased palm species were studied by projecting individual negatives onto paper and tracing the outlines of randomly selected MLB. Negatives that represented several palm species and that had convenient magnifications were selected. In total, 2,971 MLB were traced with no more than 87 MLB from any individual sieve element. Most conclusions on the morphology of MLB associated with lethal declines were drawn from the analysis of data derived from these representative MLB.

The long and the short axes of each outlined MLB were measured and long/short axis ratio was calculated. If this ratio was <3, the MLB was placed into a nonfilamentous category which would conceivably include outlines of spherical, ovoid and amoeboid forms as well as transverse sections of more elongated forms. If the long/short axis ratio was >3, the MLB was placed in a filamentous category which primarily would consist of elongated forms. Short-axis measurements were used as approximations of the widths for filamentous forms, and widths for nonfilamentous forms were calculated by averaging the long and short axes of each MLB.

## RESULTS

In addition to coconut and *V. merrillii* palms (which were previously studied by Parthasarathy [29]) MLB were observed in sieve elements of 36 declining palms that included 21 species (Table 1). The MLB never were found in the 17 healthy palms which served as controls for this study. Most of the samples from the unemerged petiole bases contained mature protophloem and immature metaphloem sieve elements; some samples contained protophloem that had begun to degenerate as well as young, but apparently functional, metaphloem; and occasional samples contained nonfunctional, crushed protophloem and mature metaphloem. Assessments of sieve-element maturity were based on the developmental stages of palm phloem described by Parthasarathy (30–32). Sieve elements that contained MLB occasionally contained dictyosomes (Fig. 1) and frequently contained ribosomes (Fig. 1, 2), which indicated that MLB had invaded young sieve

TABLE 1. Species of examined palms susceptible to lethal declines

| Palm species | Declining trees | Healthy trees |
|---|---|---|
| *Allagoptera arenaria* (Gomes) O. Kuntze | 1/1[a] | ...[b] |
| *Arenga engleri* Becc. | 5/6 | 0/3 |
| *Arikuryroba schizophylla* (Mart.) L. H. Bailey | 1/3 | 0/1 |
| *Borassus flabellifer* L. | 2/2 | ... |
| *Caryota mitis* Lour. | 3/6 | 0/2 |
| *Chrysalidorcarpus cabadae* H. E. Moore | 2/4 | 0/2 |
| *Cocos nucifera* L.[c] | 2/4 | ... |
| *Corypha elata* Roxb. | 1/1 | ... |
| *Dictyosperma album* (Bory) H. Wendl. & Drude ex Schiff | 2/3 | 0/1 |
| *Gaussia attenuata* (O. F. Cook) Becc. | 1/1 | ... |
| *Howea belmoreana* (C. Moore & F. J. Muell.) Becc. | 1/1 | ... |
| *Hyophorbe verschaffeltii* H. Wendl. | 1/2 | ... |
| *Latania* sp. Comm. | 2/2 | ... |
| *Livistona chinensis* (Jacq.) R. Br. ex Mart. | 2/2 | ... |
| *Nannorrhops ritchiana* (Griff.) Aitch. | 1/1 | ... |
| *Phoenix canariensis* Hort. ex Chabaud | 2/2 | ... |
| *Phoenix dactylifera* L. | 3/6 | 0/1 |
| *Phoenix reclinata* Jacq. | 1/3 | 0/5 |
| *Phoenix sylvestris* (L.) Roxb. | 1/1 | ... |
| *Pritchardia affinis* Becc. | 1/1 | ... |
| *Trachycarpus fortunei* (Hook.) H. Wendl. | 2/2 | 0/2 |
| *Veitchia merrillii* (Becc.) H. E. Moore[c] | 2/5 | ... |
| *Veitchia montgomeryana* H. E. Moore | 1/1 | ... |
| Total | 40/60 | 0/17 |

[a] Ratio: number of palms exhibiting MLB/number of palms examined.
[b] No examinations made.
[c] Species with reports of MLB by other authors.

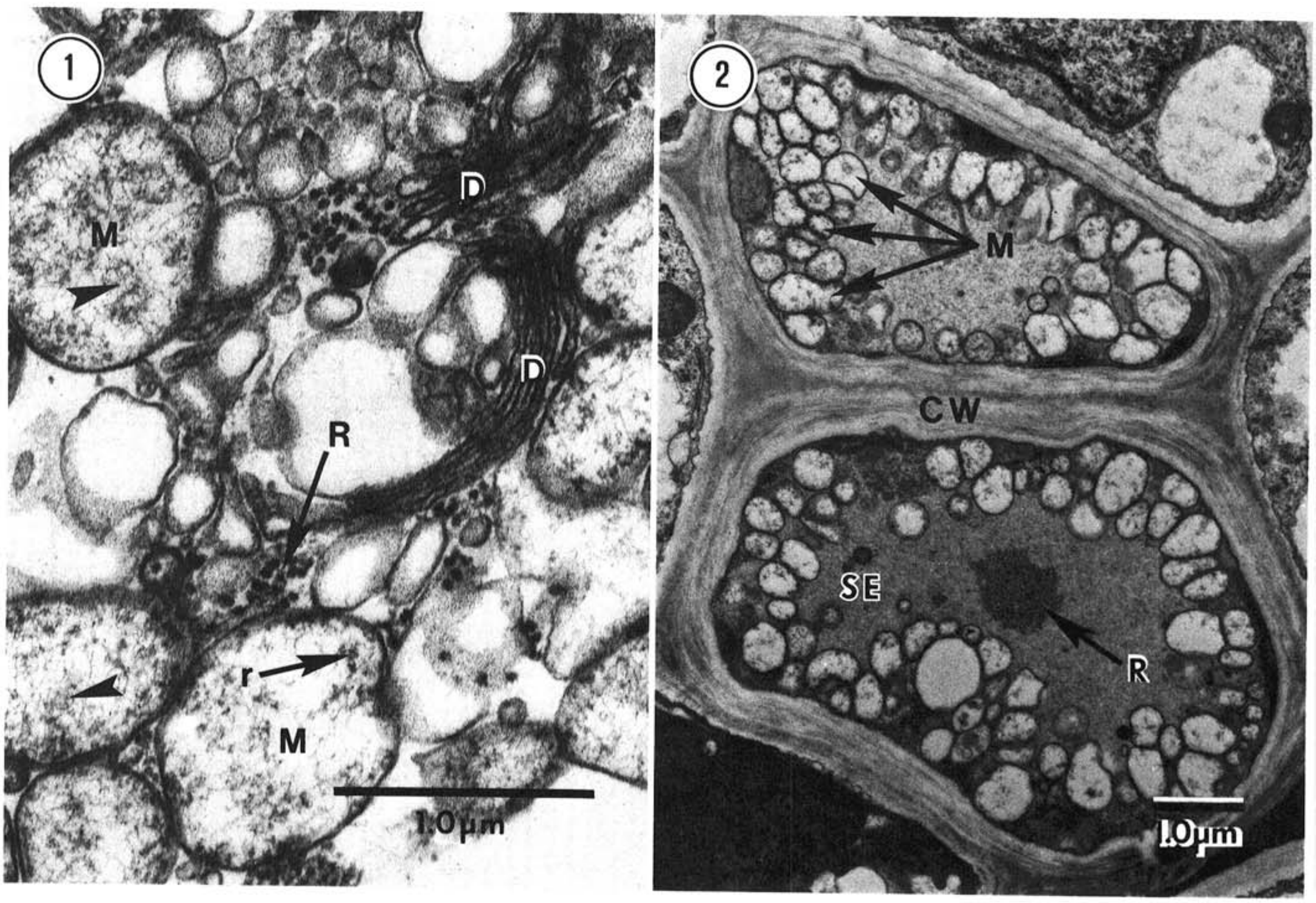


**Fig. 1–2.** Electron micrographs are of tissue samples taken from unemerged petiole bases of mycoplasmalike body (MLB)-infected palms. **1,** Dictyosomes (D) dispersed among MLB (M) in a sieve element of *Trachycarpus fortunei.* R = host ribosomes; r = ribosomelike particles in MLB; unlabeled darts = fibrillar DNA-like substance. **2,** Transverse section through two sieve elements (SE) of *Arikuryroba schizophylla* with MLB (M) in a parietal position. Most of the MLB have circular to elliptical outlines. Identification of host ribosomes (R) was confirmed at a higher magnification. CW = cell wall.

elements. However, invaded cells never were so immature that they contained nuclei, and sieve-plate pores always were present whenever sieve plates were observed. The MLB in declining palms were found most readily in petiole bases which contained the greatest number of young, but apparently functional, sieve elements. The probability of finding MLB decreased sharply as progressively older petiole bases were examined.

The numbers of MLB within palm tissues were low, although there was substantial variation among plants. No MLB were found in one-third of the declining palms that were sampled. Many diseased palms had MLB in less than 5% of the vascular bundles, but infrequently samples were examined that contained MLB in over 50% of the vascular bundles. Although the numbers of MLB found in different members of the same species varied, some species such as *Phoenix dactylifera* L. and *Latania* sp. had much lower concentrations of MLB than species such as *Phoenix canariensis* Hort. ex Chabaud and *Trachycarpus fortunei* (Hook.) Wendl. MLB concentrations in coconut and *V. merrillii* palms were among the lowest of any species examined.

The MLB within tissues generally were found in relatively high concentration in isolated areas. In most instances, individual vascular bundles either were completely free of MLB or would contain MLB in most of their sieve elements as seen in transverse section (Fig.3). Several declining palms considered to have low MLB populations overall, actually had high numbers of MLB in a few vascular bundles. Occasionally MLB were found in only a few sieve elements of a vascular bundle and in such situations, the amount of MLB within these sieve elements often was low (Fig. 4). If the number of MLB was low within a sieve element, the bodies normally would be found in a parietal position (Fig. 2), but as their numbers increased they usually were distributed thoughout the cell lumen (Fig. 5). In some sections MLB completely filled the sieve elements, assumed angular forms, and had a crowded appearance (Fig. 3).

The MLB from declining palms were extremely pleomorphic and exhibited many forms and ultrastructural details described for other plant MLB (10). In transverse thin sections of infected sieve elements, most of the MLB appeared irregularly circular to oval (Fig. 2, 3) but more elongated forms often were encountered (Fig. 5). Filamentous configurations of MLB were readily detected in thicker transverse sections (Fig. 6). Some of the MLB were branched (Fig. 6) or beaded (Fig. 7), but these forms were seen infrequently. No helices were observed even when thicker sections were studied (Fig. 6). All MLB were bounded by a trilamellar membrane and contained various amounts of ribosomelike particles and a fibrillar DNA-like substance (Fig. 1,7,8). Occasionally MLB appeared to contain membrane-bounded vesicles (Fig. 8) similar to those observed by Braun (5), but these may have been invaginations of the outer membranes as suggested by other authors (3,7).

A transverse or oblique section through a filamentous or rod-shaped MLB would be visualized as a circle or an ellipse (13). Therefore, from individual thin sections it is not possible to determine whether circular and elliptical MLB forms have resulted from sectioning spheres or ovoid bodies, or whether such forms represent sections through filaments in planes other than longitudinal. For this discussion, the terms "filament" and "filamentous" are used to describe forms which are perceived as filaments in thin sections and do not include transverse or oblique sections of tubular forms which are not recognizable as filaments. Conversely, the terms "nonfilament" and "nonfilamentous" are used for forms that do not appear filamentous in thin sections and would include some transverse and oblique sections of tubular MLB. The words "true" or "actual" are used to modify the above terms when discussing real MLB morphologies rather than those visualized in thin sections.

In infected palms, filamentous forms were recognized as 10% (149/1,501) of the total MLB population in transverse sections, 17% (153/881) in oblique sections, and 34% (203/589) in longitudinal sections, which suggests a predominantly longitudinal orientation of actual filaments. The mean diameter of filaments was appreciably smaller and showed less variation than nonfilaments ($\bar{x} \pm$ standard deviation was 142 ± 63 nm and 295 ± 166 nm, respectively). The largest diameter measured for a filament was 412 nm and only 3% of the filament diameters exceeded the median diameter for nonfilaments (240 nm). The largest diameter recorded for nonfilaments was 1,460 nm.

## DISCUSSION

Although controls were not studied for each palm species and the number of plants examined per species frequently was too low to demonstrate conclusively the constant association of MLB with each declining species, the data as a whole strongly suggest that lethal declines of palms in Florida are associated with MLB. Close chronological and geographical coincidence of the palm lethal declines with lethal yellowing of coconut palms and similarity of symptom expression further suggest that these palm maladies are synonymous, although successful culture and transmission studies are needed for final proof.

Therefore, the MLB associated with the lethal declines of all palm species have been treated as a unit when analyzing parameters such as width, length/width ratio, general morphology, and ultrastructure. This seems justified even though the full range of variability was not observed in some species for which only a limited number of samples were studied. Individual sieve elements often contained relatively uniform MLB populations. However, species that were more extensively examined, such as *Corypha elata* Roxb., *Dictyosperma album* (Bory) H. Wendl. & Drude ex Schiff, *P. canariensis,* and *P. dactylifera,* encompassed the total variation encountered in all of the species studied.

The MLB were found in two-thirds of the declining palms sampled in this study. This is comparable to a report of Granett and Gilmer (17) who found MLB in 60% of choke cherry trees showing X-disease symptoms. The failure to find MLB in all samples from palms with lethal declines is attributed either to low concentrations or to uneven distributions of MLB as has been reported for some other MLB-associated diseases (6,17,20,33,35).

The large variation in the amount of MLB observed in different palm species also is consistent with the results of investigations on other MLB-associated diseases (4,21,23). Braun (4) found that MLB populations associated with elm phloem necrosis remained low in species of elm which died soon after infection. Evidence suggests that a similar phenomenon occurs in at least some of the palm species susceptible to lethal declines. Declining coconut and *V. merrillii* palms, two of the first species to die in areas of lethal yellowing outbreaks, harbor relatively low numbers of MLB when compared to diseased *P. canariensis,* a species that shows lethal decline symptoms only after most neighboring coconut and *V. merrillii* palms have died. However, since transmission attempts have not been successful for lethal declines, it is not possible to determine whether disease incubation before symptom expression is longer in palms like *P. canariensis* or whether these palms become inoculated only after other hosts have been eliminated.

Parthasarathy (29) postulated that the apparent absence of MLB in mature parts of declining palms, and their occurrence in young tissues suggest that MLB move with the phloem assimilate stream to the "sink" regions of palms. This concept is in accord with current mass flow theories on phloem transport (eg, [8]), and would explain the presence of MLB in regions far removed from probable feeding sites of insect vectors. The distribution patterns of MLB observed in the present study are consistent with this hypothesis and further suggest that, although MLB propagules most probably are transported from older to younger tissues and would accumulate in the young "sink" regions, most of the MLB seen in younger tissues were derived from multiplication in the younger tissues. If extensive MLB multiplication occurred in older tissues, with subsequent distribution via the phloem, one would hypothetically expect a more even distribution after their lengthy passage through vascular bundles which anastomose. However, in most palms the MLB in young tissues were observed only in a few vascular bundles which had many MLB, indicating that only a few MLB had been transported into the young tissues but had undergone extensive multiplication after their arrival. Limited

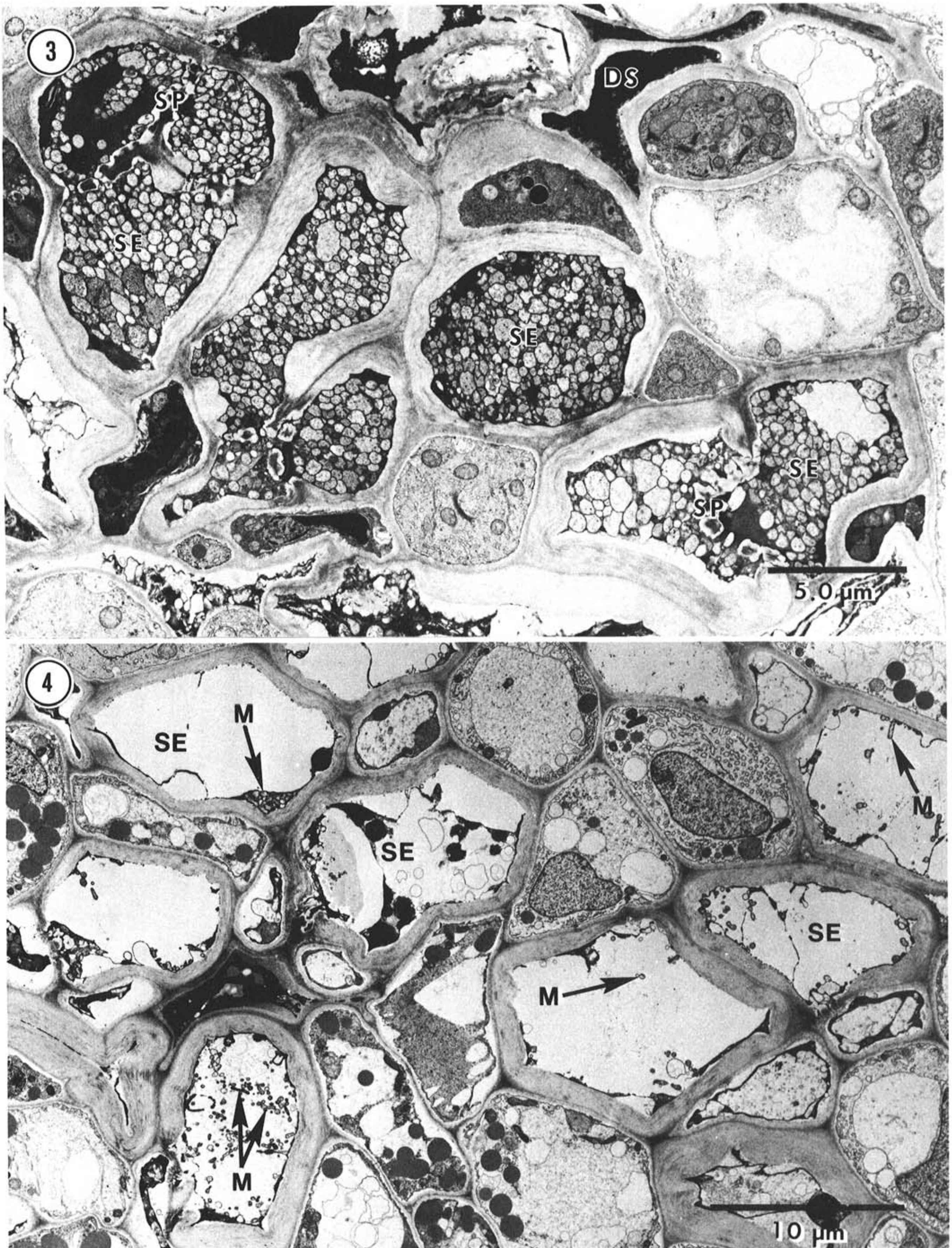


**Fig. 3–4. 3**, Transverse section through a portion of a phloem area in *Allagoptera arenaria* with high concentrations of MLB in most sieve elements (SE). Many of the MLB have angular outlines. SP = sieve plate; DS = degenerated sieve element. **4,** Transverse section through a phloem area of *Latania* sp. with low populations of MLB (M) within sieve elements (SE).

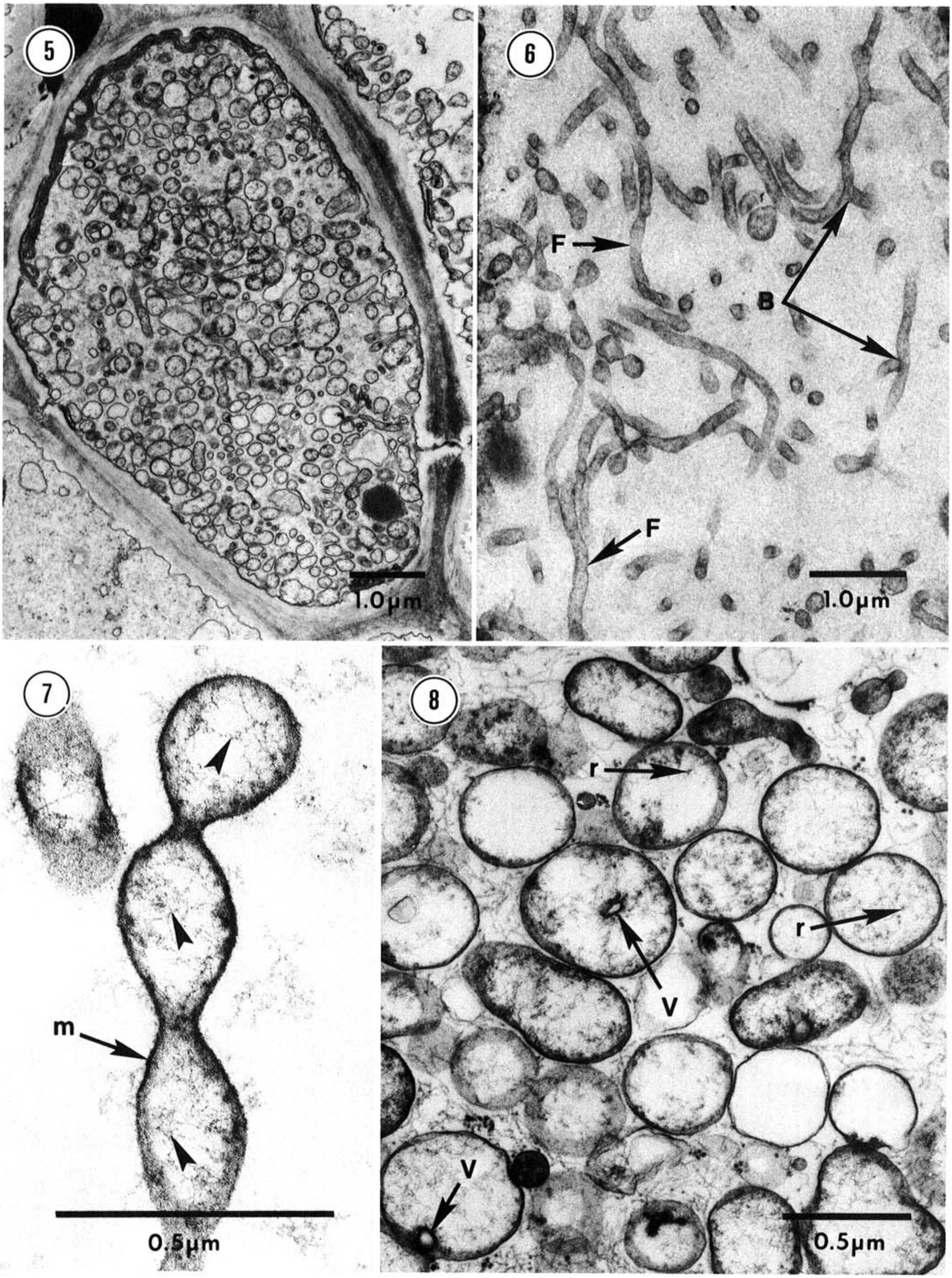


**Fig. 5–8. 5,** Transverse section through a sieve element of *Dictyosperma album* with a moderate population of MLB dispersed throughout the cell lumen. Some of the MLB have elongated forms. **6,** Transverse thick section through a sieve element of *Phoenix canariensis* showing filamentous forms (F) and branched forms (B) of MLB. **7,** Beaded MLB from sieve element of *Corypha elata.* m = trilamellar membrane; unlabeled darts = fibrillar DNA-like substance. **8,** Apparent vesicles (V) within MLB from sieve element of *Phoenix dactylifera.* r = ribosomelike particles in MLB.

MLB movement into the younger tissues might reflect a low concentration of organisms in older tissues or some restriction of propagule movement within the sieve tubes.

The criterion used to segregate filamentous from nonfilamentous MLB cannot be expected to give precise distinctions, especially when studying structures as pleomorphic and varied as MLB. It is possible that some nonfilamentous, flattened, or disk-shaped MLB were perceived as filaments when sectioned in certain planes. It is assumed that true filamentous MLB were seen as nonfilaments if sectioned transversely. A more concise interpretation of lethal decline MLB morphology might come from the analysis of serial sections (15,40) or from scanning electron microscopy (18,33), but the present analysis has been useful to help quantify some morphological features of the MLB associated with lethal declines. The method is simple and needs no special manipulations of routine samples. Also, by measuring MLB from many micrographs, a better sample of the total population was represented than would have been by studying serial sections from more limited areas.

The results of previous studies indicated that many spherical or oval forms of MLB visualized from thin sections are actually transverse sections of filamentous forms (1,17) oriented primarily along the longitudinal axis of sieve elements (22,24). Comparison between transverse and longitudinal thin sections in this study are in agreement with these conclusions. Since 34% of the MLB were depicted as filaments in longitudinal sections, it is assumed that at least a third of the total population was actually filamentous. This figure is probably conservative since 10% of the MLB which appeared as filaments in transverse sections of sieve elements would conceivably appear nonfilamentous in longitudinal sections. The number of actual filaments can best be estimated from the sum of these two figures or at least 40–50% of the total population.

Florance and Cameron (15) reported that the diameters of filamentous MLB from albino-diseased *Prunus* were at the small end of the diameter range for the entire population. Their report is in agreement with other studies which have reported dimensions for filamentous and nonfilamentous MLB separately (1,16,41). The MLB from palms with lethal declines also conform to the above pattern. Not only was the mean diameter of filaments substantially smaller than that of nonfilaments, but most of the filament diameters were below the median diameter of nonfilaments.

The data of this study help define some of the morphological features of MLB associated with lethal declines and are in accord with results from serial sections made from coconut tissues affected by lethal yellowing (40). Only 10% of the MLB population appeared to be filamentous in transverse sections of sieve elements, but half of the population is estimated to be filamentous. Also, since 97% of the filamentous MLB and 50% of the MLB visualized as nonfilaments had diameters of less than 240 nm, it is concluded that most of the MLB with diameters below this figure are actual filaments whether or not they are recognizable as such. Although the presence of filamentous MLB could be discerned from thin sections, such filaments were detected more readily from thicker sections (Fig. 6). The same data clearly show that a substantial portion of the MLB population is actually nonfilamentous and the majority of these forms have diameters above 240 nm.

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