CHROMATOPHORE DEVELOPMENT, PITS, AND OTHER FINE STRUCTURE IN THE RED ALGA, *LOMENTARIA BAILEYANA* (HARV.) FARLOW

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ABSTRACT

Thin sections of the red alga, *Lomentaria baileyana*, a tubular member of the Rhodymeniales, were examined after permanganate fixation and Araldite embedding. Many of the cellular structures in *Lomentaria* were found to be similar to analogous structures in animals and higher plants. However, in the walls between cells are modified areas generally known as pits which are unique to the higher orders of red algae (Florideae). In this study the pits were found to consist of a plug-like structure surrounded by an uninterrupted membrane apparently continuous with the plasma membrane. Examination of the chromatophore revealed a characteristic limiting membrane, a relatively sparse distribution of plates, no grana, and a single disc apparently oriented parallel to the limiting membrane. In addition to their origin from non-lamellate proplastids, chromatophores were found capable of division by simple constriction. Floridean starch grains were observed outside the chromatophore and the possibility of an association of the first formed grains with portions of the endoplasmic reticulum is considered. Gland cells seem to have a high proportion of Golgi components (dictyosomes), and are believed to have some kind of secretory function. Many of the Golgi vesicles seem to open on the wall and presumably discharge their contents.

In view of the paucity of available knowledge on the fine structure of the red algae, a detailed investigation of certain features of this group has seemed warranted. Pits, gland cells, mitochondria, and the origin of chromatophores have received little attention in previous electron microscope studies, and the present work was undertaken to further clarify the structure of some of these organelles.

Brody and Vatter (1959) examined the ultrastructure of the unicellular red alga *Porphyridium cruentum* to determine the relative positions of the phycobilins and the chlorophylls in the cell as well as the influence of different light intensities on cell structure. Myers *et al.* (1959) published photographs of the pits in *Laurencia* and *Rhodymenia*, and cell wall structure has been examined to some extent by Cronshaw *et al.* (1958) and Myers *et al.* (1956), while Mitrakos (1960) observed the fine structure of pyrenoids and chromatophores in five genera. Other than these investigations there appear to be no published studies on the ultrastructure of the red algae.

The red algae are characterized by the presence of accessory phycobilin pigments, a unique reproduction system, and the absence of motile spores. Other features—the ones investigated in the present study—are the formation of the carbohydrate food reserve (Floridean starch) outside the chromatophore, the presence of pits between cells of the higher orders, and the occurrence of "gland" cells in certain members of the group. The chlorophyll-containing body in these plants has been variously referred to as the chloroplast, rhodoplast, or

chromatophore. In this paper it will be called the chromatophore.

MATERIALS AND METHODS

Electron Microscopy

Sterile (non-fruiting) plants of *Lomentaria baileyana* (Fig. 1), a tubular member of the Rhodymeniales, were collected just below low tide level in August from the jetty at Mattituck, Long Island, New York. The growing apices were cut approximately 10 mm from the tips and fixed at a pH of 9.5 in cold 0.6 per cent $KMnO_4$ diluted with veronal acetate buffer (Luft, 1956). The plants were fixed for 1 hour, then washed in 25 per cent ethyl alcohol, and subsequently dehydrated in a graded series of alcohols. Treatment for 20 minutes in each of five different concentrations did not produce the excessive shrinkage seen in other similarly treated algae. The tissue was embedded in Araldite following a 3-day soaking period (Glauert and Glauert, 1958). Gelatin capsules containing the infiltrated material were placed in an oven maintained at 48°C, and polymerization was effected within 24 hours. Thin sections were cut on a Servall Porter-Blum rotary microtome with a diamond knife. The sections were then picked up on a copper grid without a supporting film, and these were subsequently examined in a Philips electron microscope. The sections were photographed on 35 mm film (Kodak Microfil) and suitably enlarged.

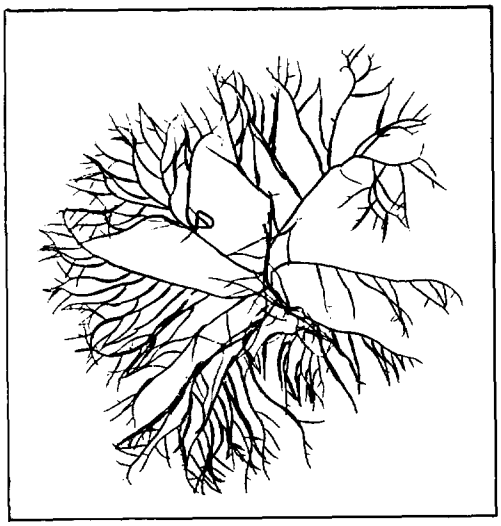


FIGURE 1

Portion of a pressed specimen of *Lomentaria baileyana*. × ⅓, approximately.

Light Microscopy

Lomentaria for light microscopy was collected at Mattituck on September 4th and some was fixed in 10 per cent formalin in sea water and the rest in a solution containing 1 gm chromic acid and 1 cc acetic acid in 100 cc of sea water. After fixation, material was run through a graded series of ethyl alcohol, sea water, and distilled water. This was followed by gradual substitution with tertiary butyl alcohol and paraffin. Sections were cut with a Spencer rotary microtome and, after removal of the paraffin, stained in acid fuchsin in 70 per cent alcohol (techniques after Johansen, 1940). Observations were made with a Leitz Dialux microscope equipped with a phase condenser and objectives. Photographs were taken with a Leitz Autophot on 3 x 5 inch sheet film.

OBSERVATIONS

Light Microscope

A longitudinal section through the tip of the plant reveals a group of elongated apical cells leading back to somewhat rounder cortical cells and ultimately to elongated hypha-like cells (Fig. 2). In the terminal growth of the alga the apical cells may first divide unevenly by a diagonal wall formed along the long axis of the cell. Then divisions perpendicular to the long axis give rise to the chains of cells which eventually expand to form the long hypha-like cells. Apical cells are uninucleate, but older internal cells become multinucleate, indicating that cell division is not synchronous with nuclear division. Chromatophores of the cortical cells are spherical while those of the inner hyphal cells are elongated, some reaching a length of 20 μ. Cells of a chain from an apical cell are "joined" by primary pits which are formed only at the time of cell division so that a cell lineage can be traced by following the distribution of pits from the apex towards the center of the plant (Fritsch, 1945). In older regions this lineage may no longer be followed due to the formation of secondary pits between adjacent chains of cells.

After staining with acid fuchsin or picric-indigo carmine, pits appear as two heavily staining "rings" separated by a light space (Fig. 6). Farther back from the tip occasional gland cells may be seen "attached" to a hyphal cell by a pit. The whole plant seems to be embedded in a mucilaginous material (Fig. 2, *Mu*).

Electron Microscope

A) Pits

In *Lomentaria* a portion of the wall between the cells of a chain has an altered appearance (Fig. 3). These areas or structures within these areas, now generally designated as pits, have been variously termed "stoppers" (Archer, 1876), "siderophilic membranes" (Mangenot, 1924), "plates" (Schmitz, 1883), "collars" (Hick, 1884), "rings" (Moore, 1885), and "condensations" (Kienitz-Gerloff, 1902). In addition to its characteristic staining properties, this region appears to have a definite fine structure consisting of a clearly defined membrane bounding a region comprised of two densities (Fig. 4). A denser zone is found immediately adjacent to the cytoplasm of the associated cell, but separated from it by the limiting membrane, while a less dense region is sandwiched in the center of the structure. Some pits show this zonation more strikingly than others. The denser areas may well correspond to the heavier staining regions seen with the light microscope (Fig. 6). Occasionally, small papillae may be seen to arise on the surface membrane as though material were being discharged into the structure or taken from it (Fig. 5). That the pit is not a static structure is evidenced by the great increase in size of pits between the large hyphal cells (Fig. 7).

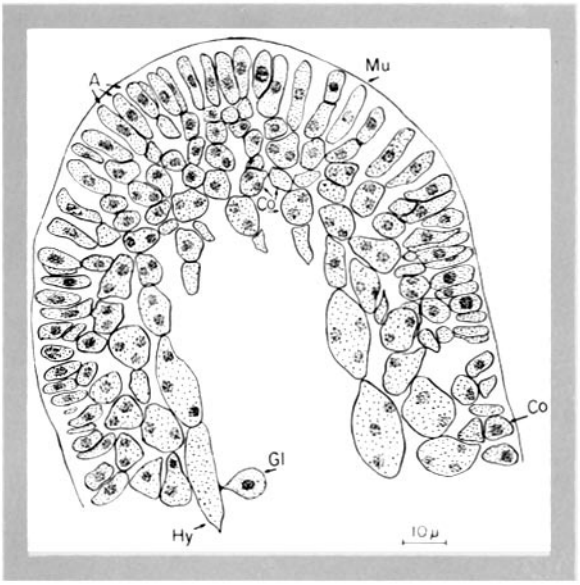


FIGURE 2

Diagram based on a camera lucida drawing of a 5 μ longitudinal section through the tip of a formalin-fixed plant. *A*, apical cells; *Co*, cortical cells; *Hy*, hyphal cell; *Gl*, gland cell; *Mu*, mucilage.

B) Chromatophores

Earliest recognizable chromatophores (proplastids) (Figs. 16, 18) appear as small (ca. 0.2 μ) spherical bodies limited by a double membrane (*ca.* 130 A thick) enclosing a homogeneous matrix (Sager, 1959). The limiting double membrane appears to consist of two closely associated membranes each with the usual two heavily staining lines separated by a light space. However, in the envelope of the proplastids the two membranes seem to share the inner electron-opaque line, thereby creating a five-layered structure of three electron-opaque lines separated by two light spaces. This construction is apparent even in the oldest chromatophores containing complete internal differentiation (Fig. 12) and serves as a convenient marker for following the various stages in plastid development. Robertson (1959) notes that there may be a sharing or fusion of the electron-opaque line in developing nerve myelin.

In the mature chromatophore the matrix is occupied in part by a series of more or less horizontal closed discs (Figs. 14, 10). These are single units and not compressed into bands as is frequently the case in other algae (*cf.* reviews in Gibbs, 1960; Heitz, 1960). Each disc is 180 to 190 A thick. The chromatophore is characterized by one disc which seems to parallel the limiting envelope. Other discs may join at their ends with

this inner limiting disc, but there is seldom any juncture with the envelope proper or between adjacent discs. Interruptions or discontinuities along the length of the disc are not uncommon (Fig. 14). The matrix remains free of the globuli characteristic of other plant chromatophores, but these globuli do appear in other genera of red algae fixed with osmium tetroxide. The reserve carbohydrate, Floridean starch, is never found within the chromatophore as is starch in plants of other groups, but is in the form of grains scattered throughout the cytoplasm of the cell. In hyphal cells the chromatophore increases greatly in length and may become as long as 20 μ (Fig. 10). The discs of these chromatophores also increase in length while their number remains fairly constant. In chromatophores from all regions the paired membranes limiting the discs frequently appear pushed apart or swollen. Such local swellings occur most often on either side of a discontinuity in the disc.

C) Nucleus

The single prominent nuclei in the cells of the apical region are 3 to 5 micra in diameter (Fig. 3). The multinucleate cortical and hyphal cells exhibit smaller nuclei relative to cell volume and the nuclei are frequently compressed between other cell components (Fig. 9). In cross-section the nucleus shows a double membrane (*ca.* 220 A thick) with occasional interruptions probably corresponding to the round pores seen in tangential sections. These pores in the nuclear envelope are similar to those described in root tip cells (Whaley *et al.*, 1960*a*; Marinos, 1960). The mottled appearance frequently observed in the nucleus after permanganate fixation (Whaley *et al.* 1960*a* and 1960*b*; Mollenhauer, 1959; Porter and Machado, 1960) is only very faintly perceptible. Continuities between the nuclear envelope and the endoplasmic reticulum may sometimes be seen.

D) Golgi-apparatus (Dictyosome)

Golgi elements consisting of stacks of 4 to 8 discs or cisternae were found in all cells examined (Fig. 17). Typically these discs appear in profile as flattened membrane-bounded vesicles such as those described for Golgi structures in root-tip meristems (Whaley *et al.*, 1959). In some cells the Golgi cisternae may be swollen to several times the thickness of those in the apical region (Fig. 19).

E) Mitochondria

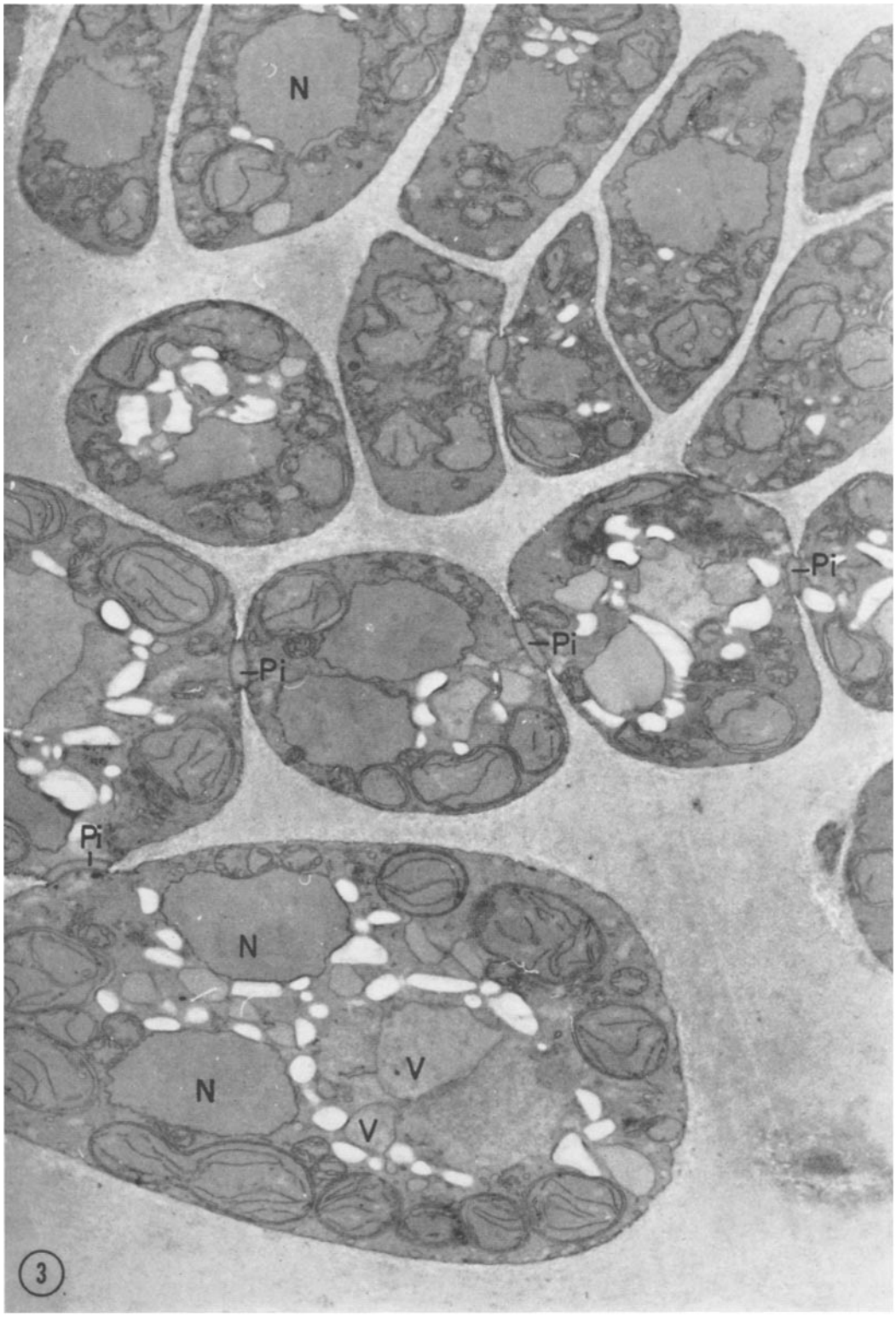
Mitochondria are found throughout the plant, but show considerable variation in appearance. Those of the apical region exhibit an irregular outline (Figs. 17, 18), while those of the cortical and hyphal cells frequently appear swollen and the cristae broken. Luft (1956) and Pease (1960) point out that permanganate often seems to cause a swelling of the mitochondria. Where these structures are better preserved (Fig. 11), they exhibit the usual cristae extending partially or entirely across the body of the mitochondrion. These cristae may apparently either anastomose with one another, or branch.

Key to Labeling

C, chromatophore
CM, cell membrane
D, chromatophore disc
ER, endoplasmic reticulum
FS, Floridean starch
G, Golgi apparatus
GS, stacks of Golgi vesicles
Hy, hyphal cell
ILD, inner limiting disc
LM, limiting envelope
M, mitochondrion
N, nucleus
Pi, pit
Pa, papilla
P, *PP*, *PP'*, *PP''*, proplastids
V, vacuole
W, wall

FIGURE 3

Longitudinal section through a region near the apex. Note the chains of cells "connected" by primary pits (*Pi*), and connection between adjacent rows through possible secondary pit (pit nearest left-hand margin). Uninucleate outer cells and multinucleate inner cells may also be seen. × 9,000.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F) Vacuoles

Vacuoles are commonly present in cortical cells, (Figs. 8, 9), and appear limited by a fine membrane (tonoplast) about 70 A thick. The contents of the vacuole tend to have a flocculent aspect in the electron microscope (Fig. 9).

Membranes are frequently seen extending from small vacuoles (Fig. 13), suggesting that parts of the tonoplast are collapsed and that an accumulation of vacuolar fluids causes a pushing apart of these membranes. Buvat (1957) has described a mechanism in higher plants whereby portions of the endoplasmic reticulum are ascribed as playing a role in vacuole formation, but it seems likely that the vacuole is a discrete organelle even in the youngest cells. Several small vacuoles may be present in the younger cells (Fig. 3), which presumably coalesce to form a single large sac in the older cells. The shape of this sac seems to be influenced by other cell components, particularly chromatophores (Fig. 8).

G) Storage Products

Floridean starch:—Grains of various shapes with very low electron-opacity, scattered throughout the cytoplasm, are interpreted as grains of Floridean starch (Figs. 3, 8, 9). They are limited by a slightly denser line which, however, does not appear to be a membrane (Fig. 13). Gibbs (1960) interprets a similar structure around the paramylum grains in *Euglena* as a denser rim of cytoplasm, probably representing a cytoplasm-starch grain interface rather than a distinct membrane. Floridean starch differs from higher plant starch in its formation outside the chromatophore and in its characteristic chemical structure (Barry *et al.*, 1949). In young cells the small starch grains frequently lie sandwiched between adjacent cisternae of the endoplasmic reticulum (Fig. 17, *ER*). This proximity may indicate an active participation of the ER in Floridean starch formation similar to that noted by Porter and Bruni (1960) in the deposition of animal glycogen. Larger starch grains no longer show this association.

H) Cell Wall and Limiting Membrane

The cell wall contains scattered fine fibrils, probably cellulose microfibrils, in an amorphous matrix. This agrees with the observations of Cronshaw *et al.* (1958) who find the microfibrillar fraction low in the red algae. Various polysaccharides composed mostly of residues esterified by sulfuric acid have been reported present in the cell wall (Haas *et al.* 1923), but these show no structural identity in the electron microscope.

The cell membrane (plasma membrane) appears as an irregular membrane (*ca.* 60 A thick) at the interface between cell wall and cytoplasm (Fig. 18). Various pockets and spheres appear at intervals suggesting that material is being released to the wall (Fig. 9, arrow).

I) Endoplasmic Reticulum

Sections of irregular membranous components (*ca.* 210 A thick) identified as elements of the endoplasmic reticulum are prevalent in young cells (Fig. 17). As noted above there is frequently an association of this structure with young starch

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Figure 4

Portion of two cells of a chain with a primary pit (*Pi*). × 29,000.

Figure 5

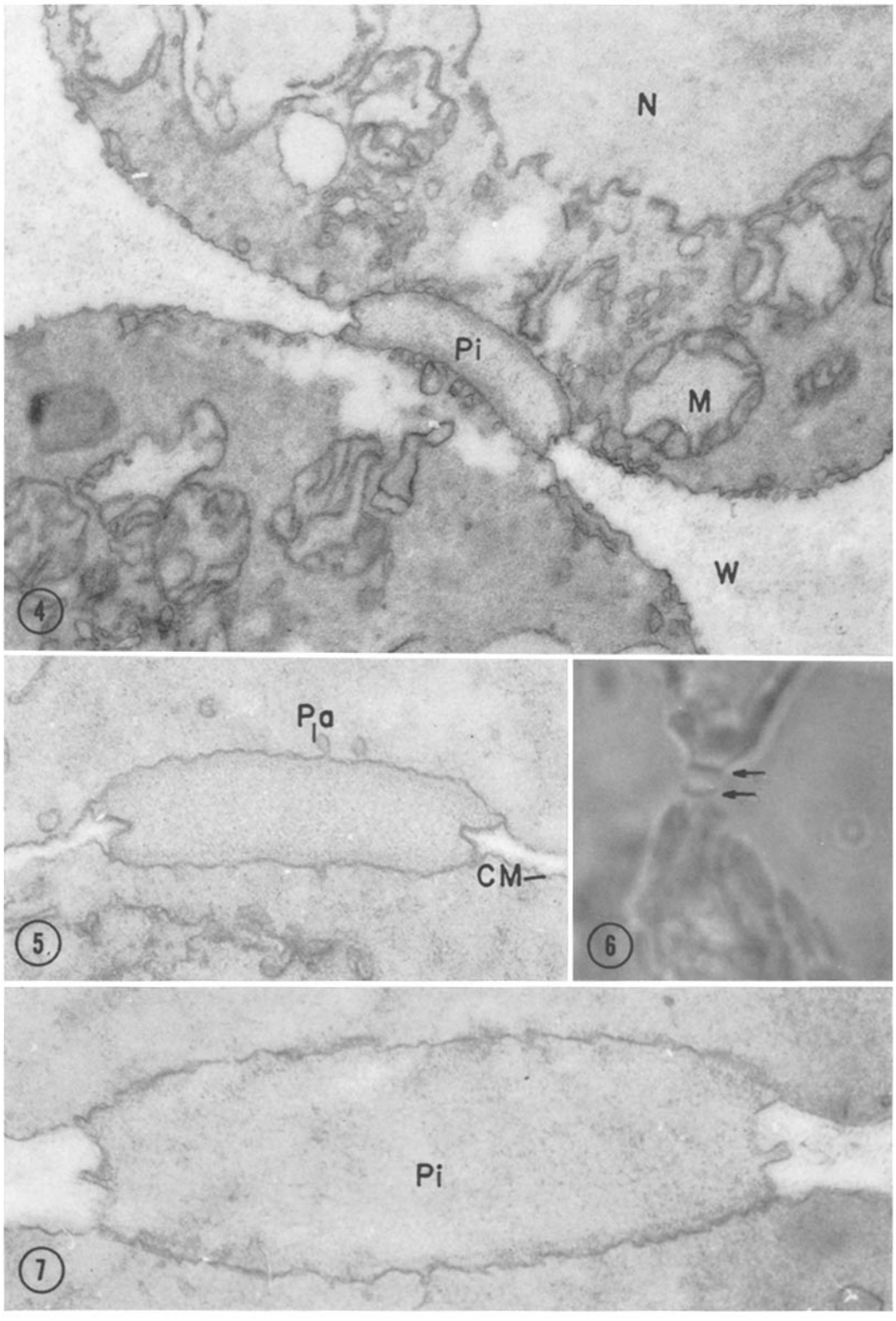
Longitudinal section through a primary pit. Note small papilla (*Pa*) arising from the surface of the pit membrane. *CM*, cell membrane. × 61,000.

Figure 6

Light micrograph of a primary pit fixed in formalin and stained with picric-indigo carmine. The two heavily staining "rings" (arrows) have pulled apart somewhat in the preparation. × 2,000.

Figure 7

Longitudinal section through a pit between two hyphal cells. Note increase in size as compared with Fig. 5. × 44,000.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grains and often a continuity with the nuclear envelope. The endoplasmic reticulum is considerably reduced in older cells, and the "Palade granules" often associated with the ER were not observed as is usually the case in permanganate-fixed material.

J) "Gland" Cells

The gland cells located along the hollow interior of the plant are characterized by many vesicles either scattered throughout the cell or in fairly regular stacks (Fig. 19). This stacked appearance indicates that the vesicles are elements of a very abundant Golgi component. A number of chromatophores and mitochondria are also apparent, and nuclei are seen in some sections either singly or paired. The gland cell is "connected" to a hyphal cell by a pit (Fig. 21). The plasma membrane of the gland cell is highly irregular and often the expanded Golgi vesicles seem to open on the wall. Similarly, small electron-opaque globules appear to be leaving the surface, suggesting a secretion of some product from these cells (Fig. 20).

DISCUSSION

It is evident that the position of a plant in a phylogenetically "lower" division need not imply an absence of a high degree of cellular organization. If the structures reported here exist in other red algae as well, it would appear that many cellular components have remained remarkably constant throughout the plant kingdom despite vast differences in vegetative appearance and reproductive cycles. However, certain features such as gland cells, pits, and the structure and development of the chromatophore do distinguish red algae from other groups previously described, and these features deserve further consideration.

Gland Cell

Spherical or pear-shaped cells which appear denser than the adjacent cells are scattered throughout the inner part of the plant. These have been variously termed "bulb" cells (Bliding, 1928), "gland" cells (Hauptfleisch, 1892) and arrested hyphae (Fritsch, 1945). They occur in many genera of the Rhodymeniaceae and Champiaceae, but a function has been assigned to them only in those genera containing diaphragms where they supposedly initiate diaphragm formation (Bliding, 1928).

The abundance of Golgi vesicles would suggest that gland cell is the appropriate name (Fig. 19), for Golgi systems seem to be especially prominent in cells showing intense secretory activity, and it therefore seems probable that these cells are concerned in the elaboration or secretion of some product. There is no evidence as to the nature of this substance, and the low incidence of starch grains would seem to rule out starch accumulation. However, there may be an association between the quantities of mucilage found in and surrounding this plant and the function of these cells. Many of the vesicles seemingly open on the wall, suggesting that there is a release of materials from within (Fig. 20, arrows).

Pits

The higher orders of red algae (Florideae) are characterized by the occurrence of pits. In previous studies, the interpretation of this structure has varied from protoplasmic to non-living, and from open, to perforated, to membrane enclosed. Its function has been described on the one hand as a region of embryonic wall formation (Mühldorf, 1937), and on the other as a region allowing the passage of nutrients and/or stimuli (Phillips, 1926; Fritsch, 1945). Jungers (1933) believed much of this confusion was the result of investigations in different genera, and it was his observation that pits could be classified into two groups: (*a*) those composed of two heavily staining discs separated by a fine membrane as in *Polysiphonia* and *Delesseria*; (*b*) those composed of a lens-shaped chromatic body set in the central orifice of the transverse wall as in *Griffithsia* and *Ceramium*.

These are interpretations which should lend themselves to verification with the higher resolution of the electron microscope. Myers *et al.* (1959) first attempted to examine the fine structure of

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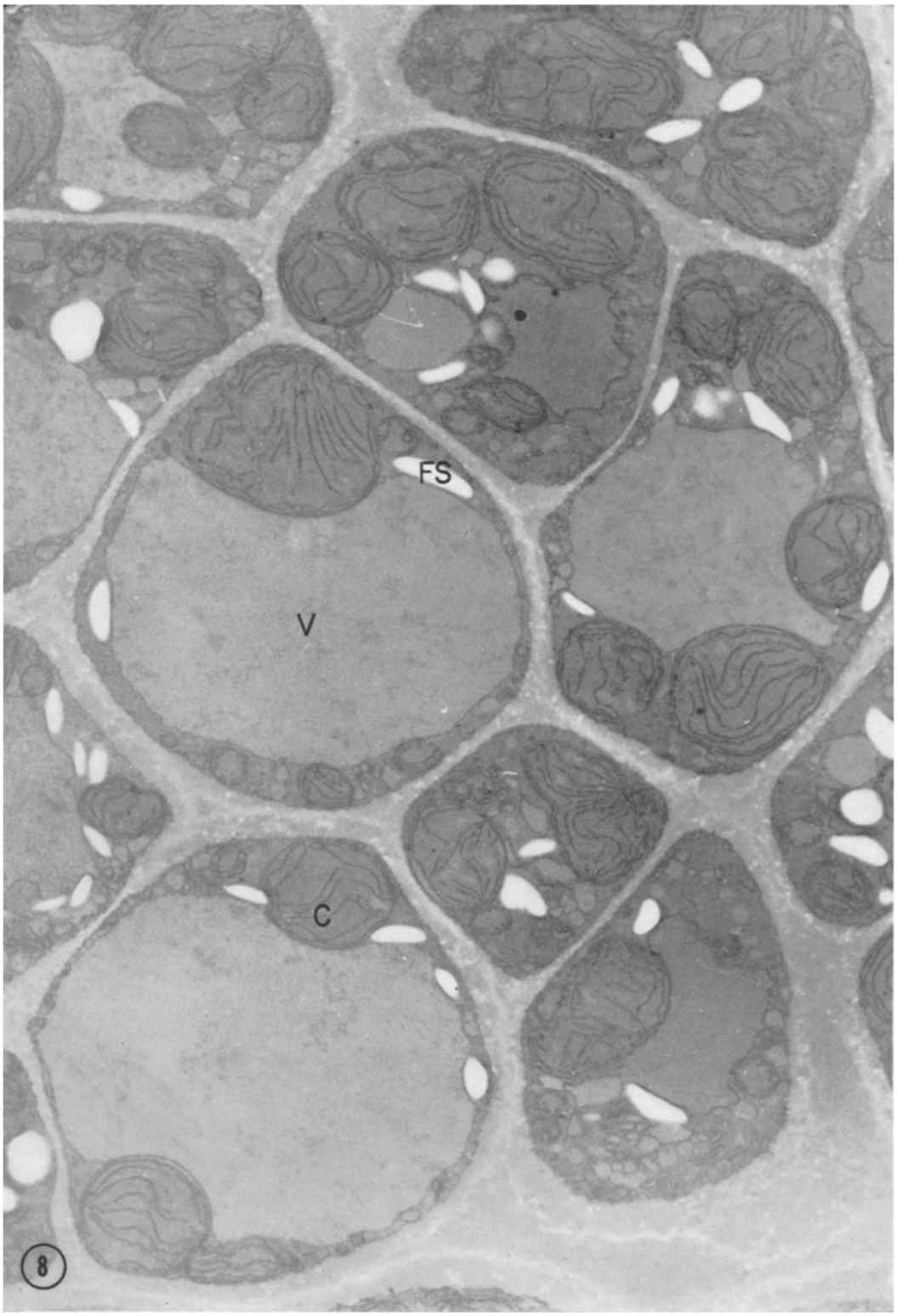
Figure 8

Tangential section through the cortical cells illustrating the prominent vacuoles. Chromatophores and other cell components apparently influence the shape of the vacuole. *C*, chromatophore; *V*, vacuole, *FS*, Floridean starch. × 10,000.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red algae pits. They believed their micrographs confirmed Jungers's earlier work, but to the present writer the resolution of their photographs leaves the problem still in doubt. The paper presented here deals with only one genus, and speculation as to the universal occurrence of the plug-like structure described is unwarranted. However, it is clear that there are no other connections or plasmodesmata between the cells of the thallus, so protoplasmic continuity must be either maintained through the pit or not at all. Furthermore, secondary pits may form between adjacent chains of cells (Kylin, 1937). In a study of *Griffithsia*, Mangenot (1924) finds a direct relationship between the size of the pit and the flow of nutrients in the reproductive apparatus, so perhaps an examination of these reproductive cells might provide additional information towards the interpretation of pit function.

Chromatophores

The first structure to appear in the enlarging proplastid is the inner limiting disc. This disc or plate closely parallels the limiting envelope providing a boundary beyond which the later formed discs rarely extend. The inner limiting disc probably originates by invagination and folding of the inner part of the limiting double membrane (Fig. 18, PP′ and PP″). Further development shows an increase in size accompanied by the appearance of additional discs which most likely arise as invaginations of the inner limiting disc, and not from the limiting envelope.

Chromatophores in the inner hyphal cells attain considerable length (Fig. 10), but those of the cortical cells apparently divide before reaching this great size. This division (Fig. 15) is accomplished through a median constriction, causing a pushing together of the discs until presumably the structure is pinched in two with the broken discs rehealing on either side of the constriction. A similar mechanism has been described by Mühlethaler (1960) for two dicotyledonous plants, while von Wettstein (1954) reports a pinching of the chromatophore in the brown alga, *Fucus*. Mitrakos (1960) believes there is an orientation of a portion of the disc parallel to the plane of division before and after division in the red alga, *Gigartina Teedii*. Thus the chromatophores in the red algae are capable not only of forming from disc-less cytoplasmic organelles (proplastids), but also by simple constriction of mature chromatophores.

It is of interest to note the great regularity of chromatophore structure in the red algae so far examined. *Porphyridium cruentum* (Brody and Vatter, 1959), *Porphyra umbilicalis*, *Nemalion multifidum*, *Kylinia* sp. (Gibbs, 1960), *Rhodochorton floridulum*, *Trailliella intricata*, *Gracilaria* sp., *Plocamium coccineum*, *Gigartina Teedii*, and *Polysiphonia nigrescens* (Mitrakos, 1960) all exhibit single-layered discs

FIGURE 9

A vacuolated cell from the cortical region with two pits (*Pi*). Note the pockets and spheres in the cell membrane and wall (arrow). × 22,000.

FIGURE 10

Chromatophore from a hyphal cell. × 17,000.

FIGURE 11

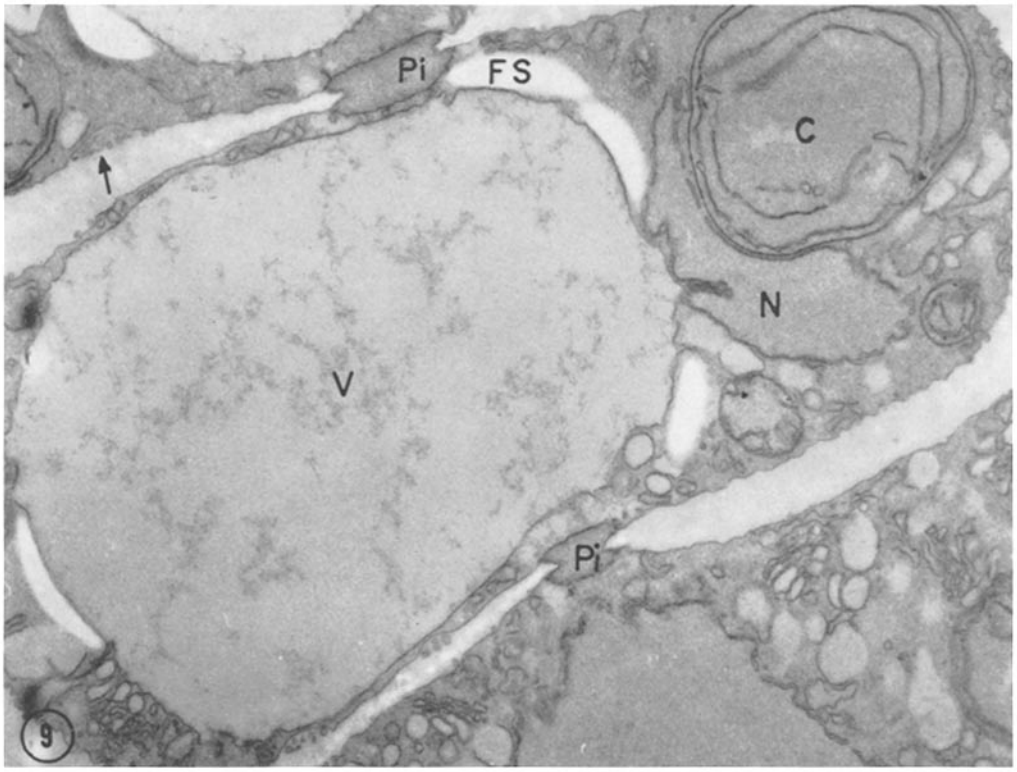
Longitudinal section through a mitochondrion. × 29,000.

FIGURE 12

Portion of the limiting double membrane from a fully differentiated chromatophore. Note the three electron-opaque lines (arrow) separated by lighter spaces as compared with the structure of the disc (*D*). × 150,000.

FIGURE 13

Starch grains bounded by a fine electron-opaque cytoplasmic interface (arrow). Extension of the vacuolar membrane may be seen just below the lower end of the starch grain. × 54,000.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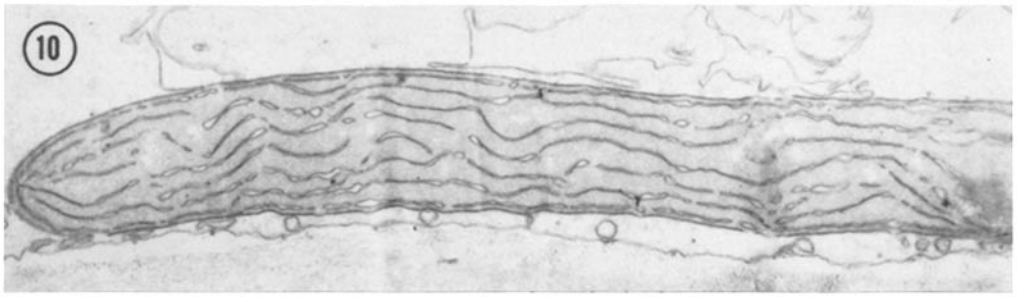
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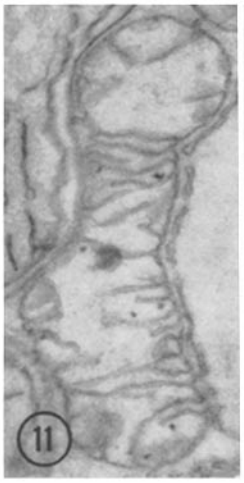
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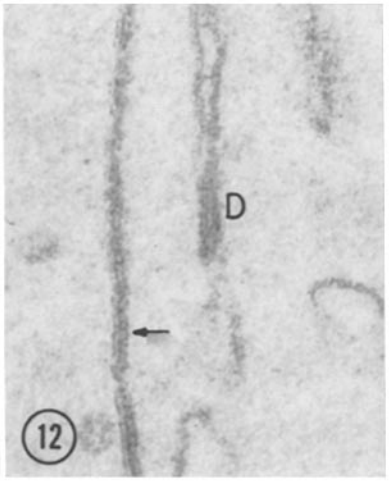
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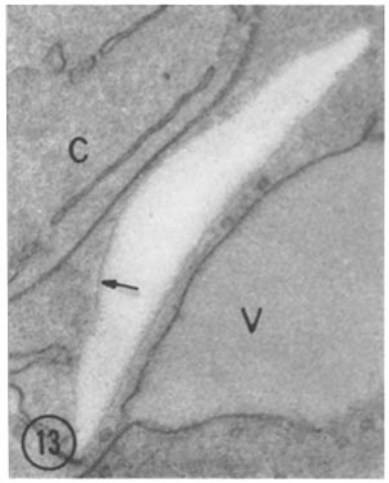
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in the chromatophore. Preliminary work by the present writer indicates that there are similar structures in *Agardhiella tenera* and *Grinnellia americana*. Other divisions of algae, such as the brown algae, also seem to possess plastids with strikingly uniform disc arrangements, although there may be considerable difference from one division to the next. Preliminary examination of the brown algae *Sargassum filipendula, Chorda filum, Chorda tomentosa* and *Sphaerotrichia divaricata*, as well as published investigation on *Fucus* (Leyon and von Wettstein, 1954), reveal the matrix of the chromatophore occupied in part by bands of discs (two to three). Additional work in other genera of red and brown algae would be most helpful in establishing to what extent this uniformity exists and, ultimately, what its relation is to the photosynthetic process.

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FIGURE 14

Section through a fully differentiated chromatophore. *ILD*, inner limiting disc; *LM*, limiting envelope. × 33,000.

FIGURE 15

Chromatophore from a cell in the cortical region illustrating division of the body through a median constriction (arrows). × 37,000.

FIGURE 16

Proplastids from a cell in the apical region showing earliest stages (*P*) and the first differentiation of the inner limiting disc. × 45,000.

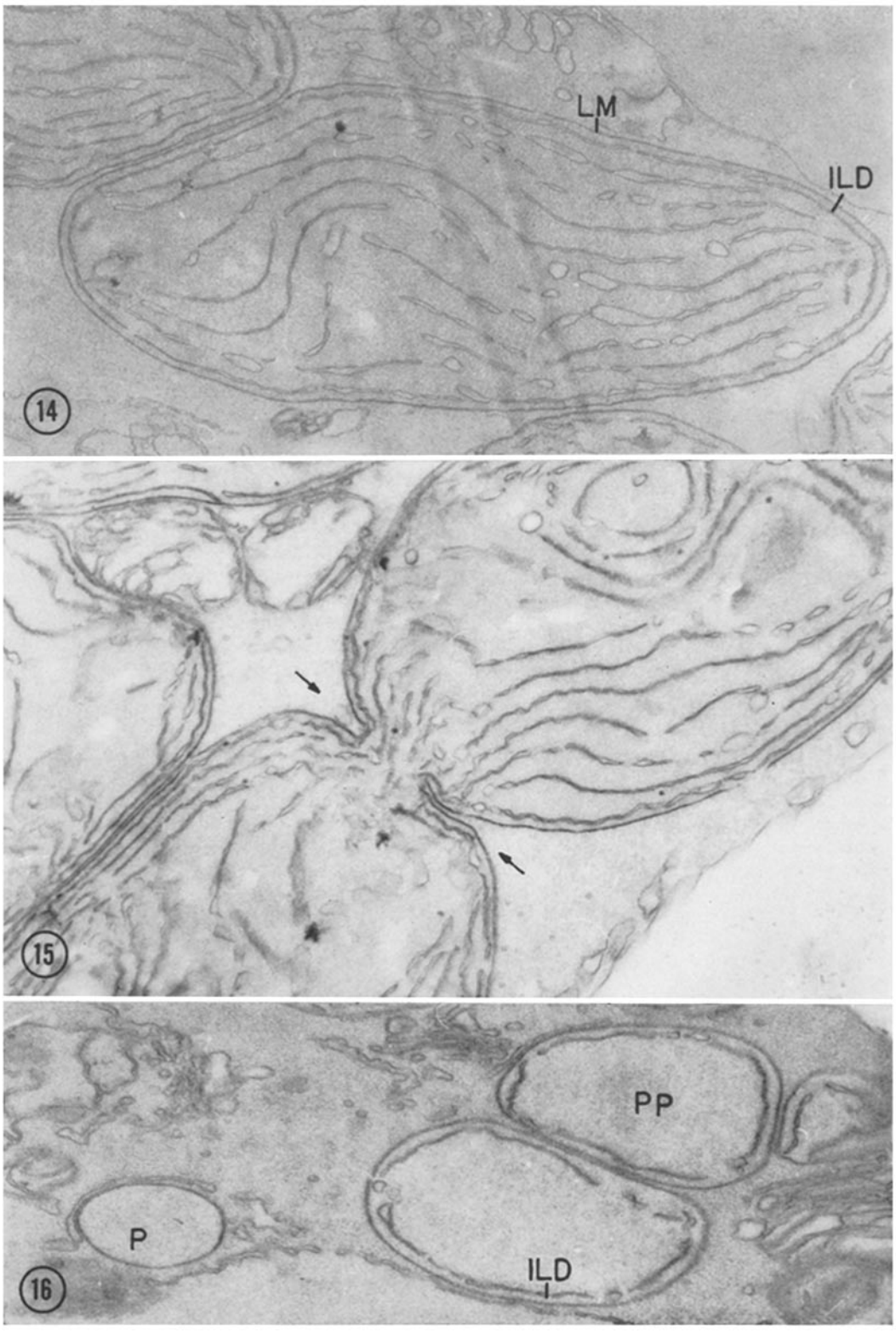
LM
ILD
14
15
PP
P
ILD
16

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FIGURE 17

Cross-section of a cell near the apical region showing the Golgi apparatus in various planes, and illustrating the association of starch with the endoplasmic reticulum. Note that starch may be deposited before the chromatophore has become fully lamellate. × 34,000.

FIGURE 18

Portion of a cell in the apical region with early stages in chromatophore development. No internal differentiation characterizes the proplastid at *P*. *PP'* shows a proplastid with foldings of the limiting membrane, *PP''* a chromatophore apparently undergoing an invagination of a portion of the limiting envelope (arrow). × 61,000.

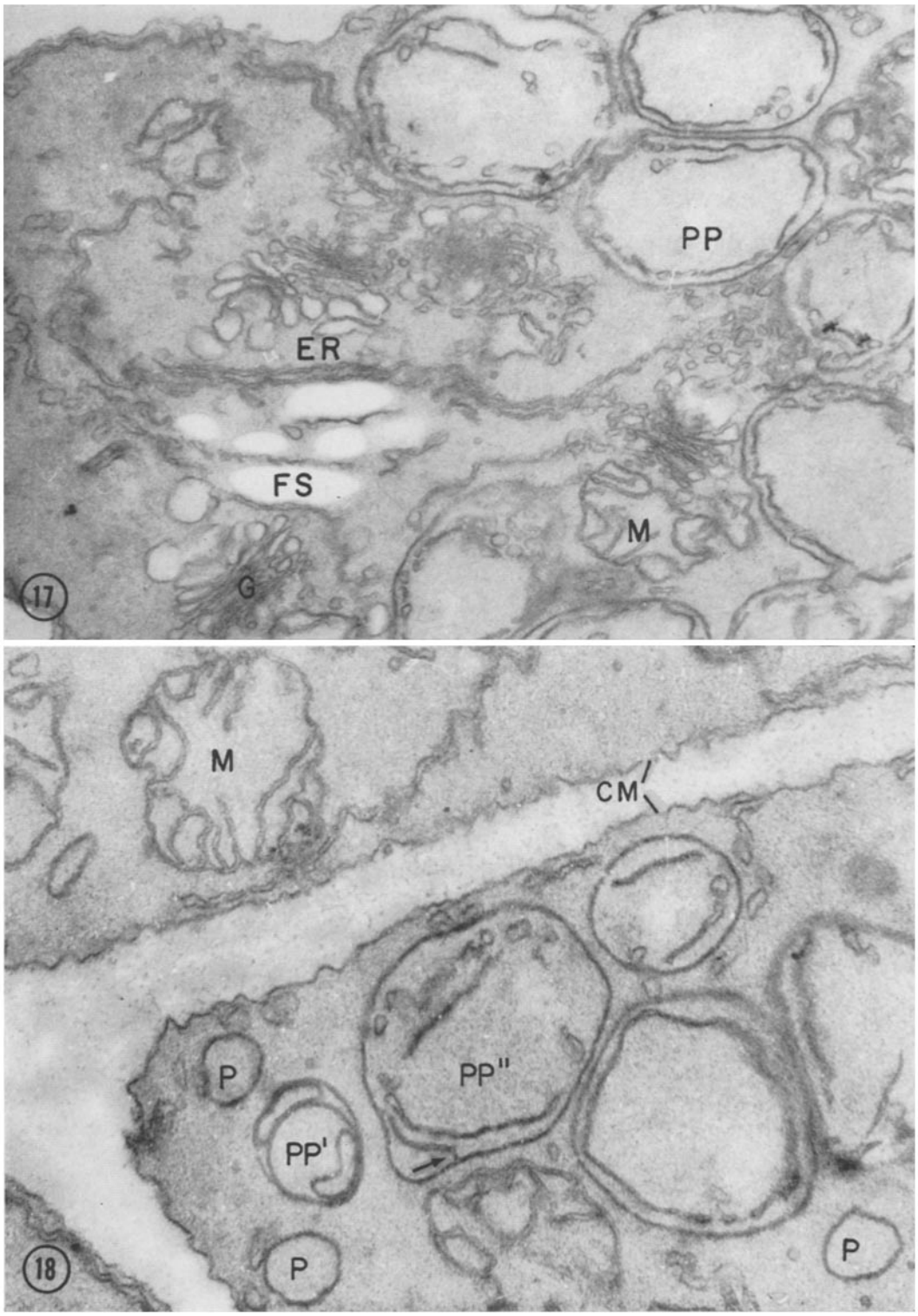

PP
ER
FS
M
G
17
M
CM
PP''
P
PP'
P
P
18

FIGURE 19

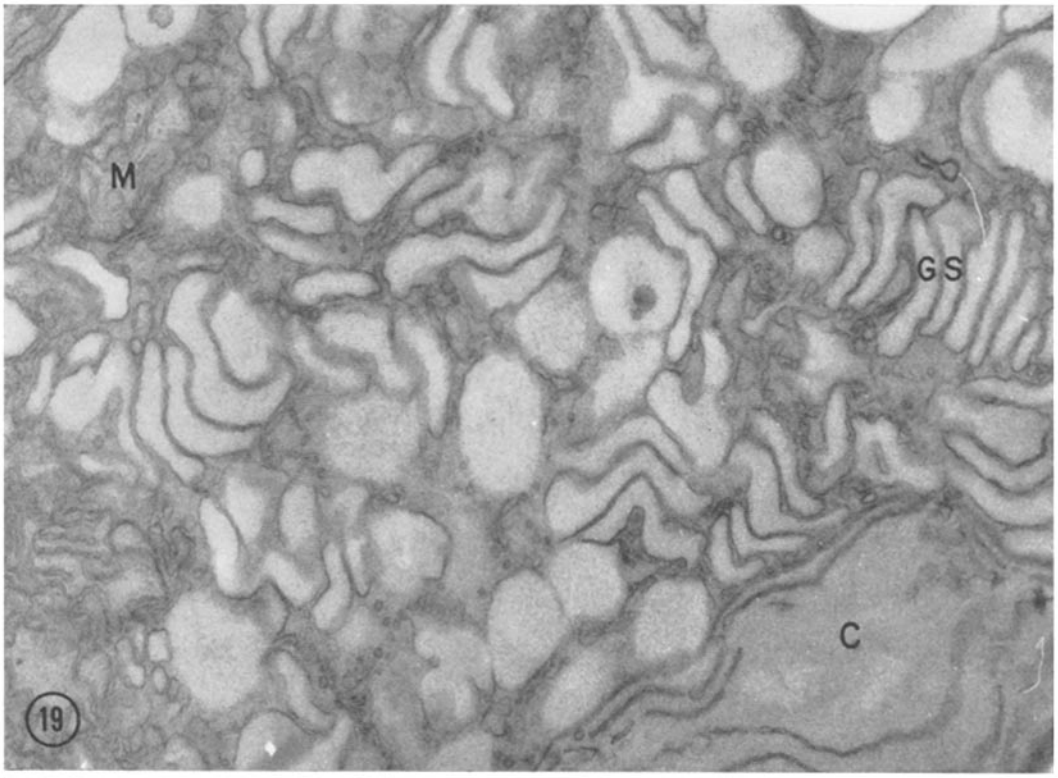
Portion of a gland cell. Stacks of Golgi vesicles may be seen at *GS*. *C*, chromatophore; *M*, mitochondrion. × 30,000.

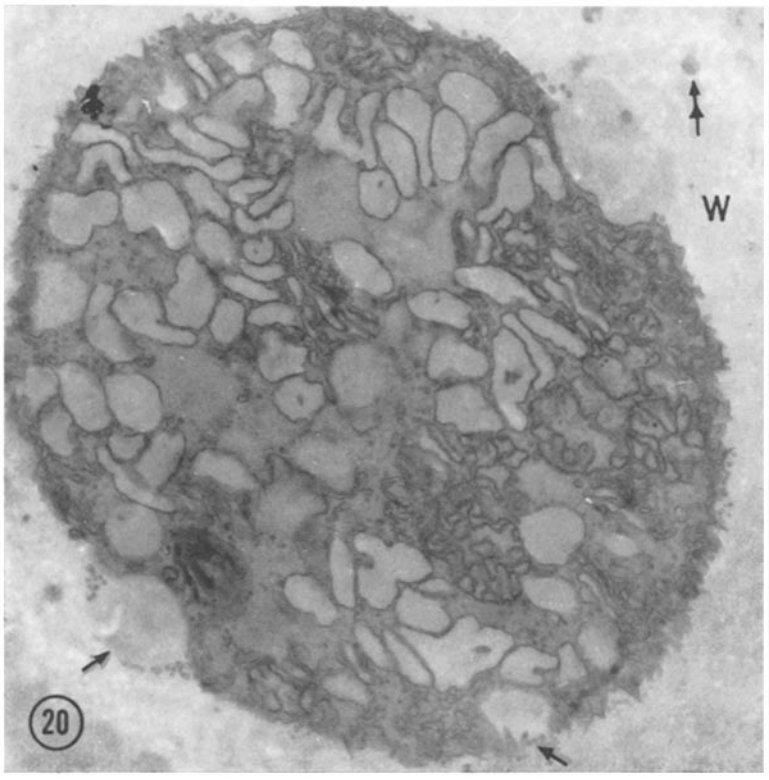
FIGURE 20

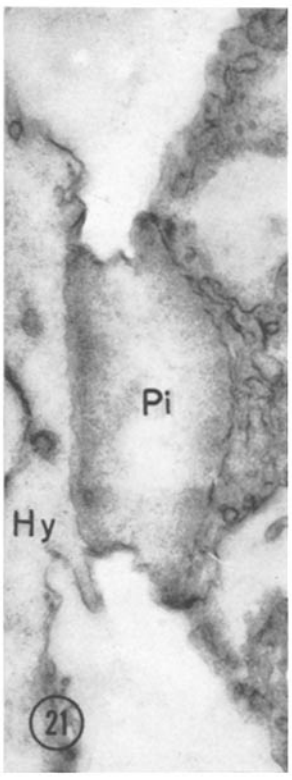
Gland cell showing possible release of materials to the wall by an opening of vesicles at the cell membrane (arrows), or through a release of small electron-opaque spheres (double arrow). × 21,000.

FIGURE 21

Pit (*Pi*) between gland cell and hyphal cell (*Hy*). × 33,000.


M
GS
C
19


W
20


Pi
Hy
21