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Corn Mitochondrial Swelling and Contraction—an Alternate Interpretation[1]

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ABSTRACT

Mitochondria isolated from 3-day-old etiolated corn shoots (*Zea mays* L.) can be categorized into three separate groups, each group characteristic of the cell type from which the mitochondria were isolated. Phloem sieve tubes and some adjacent parenchyma cells contain mitochondria that have few cristae and little amorphous matrix. Mitochondria from meristematic and undifferentiated cells have more cristae and matrix. Vaculate and differentiated cells have mitochondria with well-developed cristae and abundant matrix. Each mitochondrial type exhibits typical *in vitro* spontaneous swelling and substrate-induced contraction responses, characterized by change or lack of change in cristae size and in density of amorphous material. For the second and third types of mitochondria, swelling and contraction are characterized by a change in degree of cristae size and in matrix density. The first type undergoes few changes upon swelling or contraction. Radical changes of the inner membrane, withdrawal and infolding, are associated with cell differentiation and not with swelling and contraction of isolated corn shoot mitochondria.

Under appropriate conditions, isolated corn mitochondria can be reversibly swollen and contracted. It is generally thought that swollen corn mitochondria have very few cristae and a matrix that stains only lightly, that contracted mitochondria have many inflated cristae and a matrix that becomes densely stained, and that partially swollen mitochondria are intermediate (12, 24, 26). Swelling involves the unfolding of the inner membrane and a decrease in the amorphous matrix, while contraction involves the infolding of the inner membrane and increase in matrix density. The presence of contracted, partially swollen, and swollen mitochondria in experimental *in vitro* preparations that should contain only contracted (or swollen) mitochondria is believed to result from mitochondria responding at different rates (26). A ready reversibility has been reported to exist between swollen, partially swollen, and contracted mitochondria (24).

In vivo differences in the number of cristae and amount of amorphous matrix in different cell types for several species of plants have been reported (5, 7–9, 13, 16, 19, 22). Chrispeels *et al.* (6) indicate that mitochondria of undifferentiated cells have few cristae and large open spaces in the matrix. Mitochondria from mature cells have inflated cristae and dense matrix. Those authors suggested that *in vitro* contracted mitochondria correspond to *in vivo* mitochondria of mature cells and that *in vitro* swollen mitochondria correspond to *in vivo* swollen-degenerate mitochondria.

This paper suggests that differences observed between isolated corn shoot mitochondria are at least partially due to mitochondrial morphogenesis during cell differentiation.

MATERIALS AND METHODS

Three-day-old etiolated seedlings (*Zea mays* L. Wf9×M14 or W64A) were used for all experiments. Mitochondria were isolated by a standard procedure (18). All experiments involving isolated mitochondria were carried out in 4-ml glass temperature-controlled reaction cells fitted with a Clark oxygen electrode and positioned in the light beam of a Bausch and Lomb Spectronic 70 spectrophotometer. Oxygen concentration and percentage of light transmittance at 520 nm were recorded on a dual channel recorder. Reaction media are noted in the figure captions.

Isolated mitochondria were fixed either while they were suspended or after being pelleted at 12,000 rpm for 10 min. Fixatives for isolated mitochondria or intact shoots were 1 or 2% glutaraldehyde either in 0.1 M phosphate buffer or in 0.2 M cacodylate buffer (pH 7.4) followed by 1% OsO_4 in the respective buffer; or only 1% OsO_4 in 0.1 M phosphate buffer or 0.2 M cacodylate buffer. Dehydration was in a graded ethyl alcohol series, and propylene oxide was used as a solvent for the Epon embedment (15).

In vivo mitochondrial contractions were obtained by treating 1-mm thick sections of corn shoots with 2.5 mM 2DOG[2] for 20 min (11). The sections were then fixed in 2% glutaraldehyde in 0.2 M cacodylate buffer.

One-μm thick plastic sections of whole plant material were cut and observed with phase contrast optics for orientation purposes. Subsequently, thin plastic sections were cut from the adjacent area of the block. All thin sections were observed on an RCA EMU4 or Siemens Elmiskop I electron microscope after staining in uranyl acetate (23) and lead citrate (21).

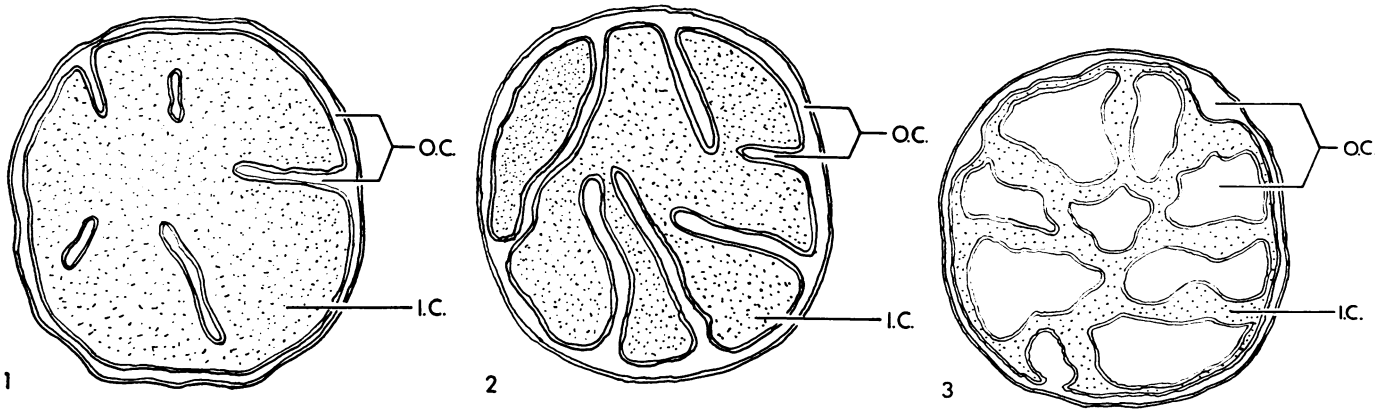
Areas of I. C. and O. C. of type III mitochondria were determined by superimposing a dot grid on a micrograph and counting dots falling in the compartments.

RESULTS

Mitochondrial profiles fell into three readily recognizable types and were classified according to the type which they most

[1] This research was supported in part by funds from the Illinois Agricultural Experiment Station.

[2] Abbreviations: 2DOG: 2-deoxyglucose; I. C.: inner compartment of the mitochondrion; O. C.: outer compartment of the mitochondrion; KBT: 200 mM KCl, 20 mM tris-HCl buffer (pH 7.4), and 1 mg/ml bovine serum albumin.



FIGS. 1–3. Line drawings defining the three types of mitochondria as defined in this paper. Fig. 1: type I mitochondrion. Outer compartment (O. C.) and inner compartment (I. C.) are shown. Fig. 2: type II mitochondrion; Fig. 3: type III mitochondrion.

closely resembled. Type I mitochondria (Fig. 1) have a small amount of matrix which stains densely, and relatively few cristae. The I. C. is relatively large in comparison with the O. C. Type II mitochondria have relatively more matrix which stains densely and more cristae than type I mitochondria (Fig. 2). The I. C. is smaller and the O. C. is larger relative to type I. Type III mitochondria have a large amount of matrix which becomes densely stained and many inflated and interconnecting cristae (Fig. 3). Of the three types, type III has the smallest inner compartment and the largest outer compartment.

Mitochondria held in 0.4 M sucrose exhibited these three mitochondrial profiles in cross section (Fig. 4). One profile had few cristae and little matrix (type I). The second type had more cristae and matrix (type II), and the third type had many inflated cristae and an abundant dense matrix (type III). Higher magnification micrographs of the three types are compared in Figures 8, 9, and 10.

Mitochondria allowed to swell for 3 min in KBT manifested three similar profiles (Fig. 5). Type I mitochondria under this treatment were no different than type I mitochondria held in 0.4 M sucrose (*cf.* Figs. 8 and 11). The cristae of type II, however, decreased in size, but the matrix was unchanged (*cf.* Figs. 9 and 12). The cristae of type III were smaller and more irregular, and the matrix stained less densely than type III held in 0.4 M sucrose (*cf.* Figs. 10 and 13). Mitochondria that had been allowed to swell passively for 15 min in KBT, actively for 5 min in potassium acetate, or passively for 3 min in 0.3 M D-ribose were essentially the same as those of the 3-min passive KBT swell, with the exception that some of the cristae within the type III mitochondria were collapsed while others remained inflated (Fig. 6).

After swelling mitochondria for 3 min and contracting them with exogenous NADH, succinate, or malate + pyruvate, the three mitochondrial profiles were still present (Fig. 7). Type I mitochondria under this treatment were unchanged from those swollen or held in 0.4 M sucrose (*cf.* Figs. 8, 11, and 14). The cristae of types II and III increased in size and approached those held in 0.4 M sucrose (*cf.* Figs. 9 and 15, and 10 and 16, respectively).

Figures 17 and 18 represent two populations of mitochondria. The section in Figure 17 came from near the surface of the pellet, while the section in Figure 18 came from near the center of the pellet. When mitochondria were fixed and then pelleted, types III and I tended to segregate. As indicated in Figure 17, 32% (28/85) were type I, 18% (15/85) were type II, and 50% (43/85) were type III. However, in Figure 18 only 8% (11/144) were type I, 5% (7/144) were type II, and type III had increased to 87% (126/144). The segregation was not as evident when mitochondria were pelleted and then fixed.

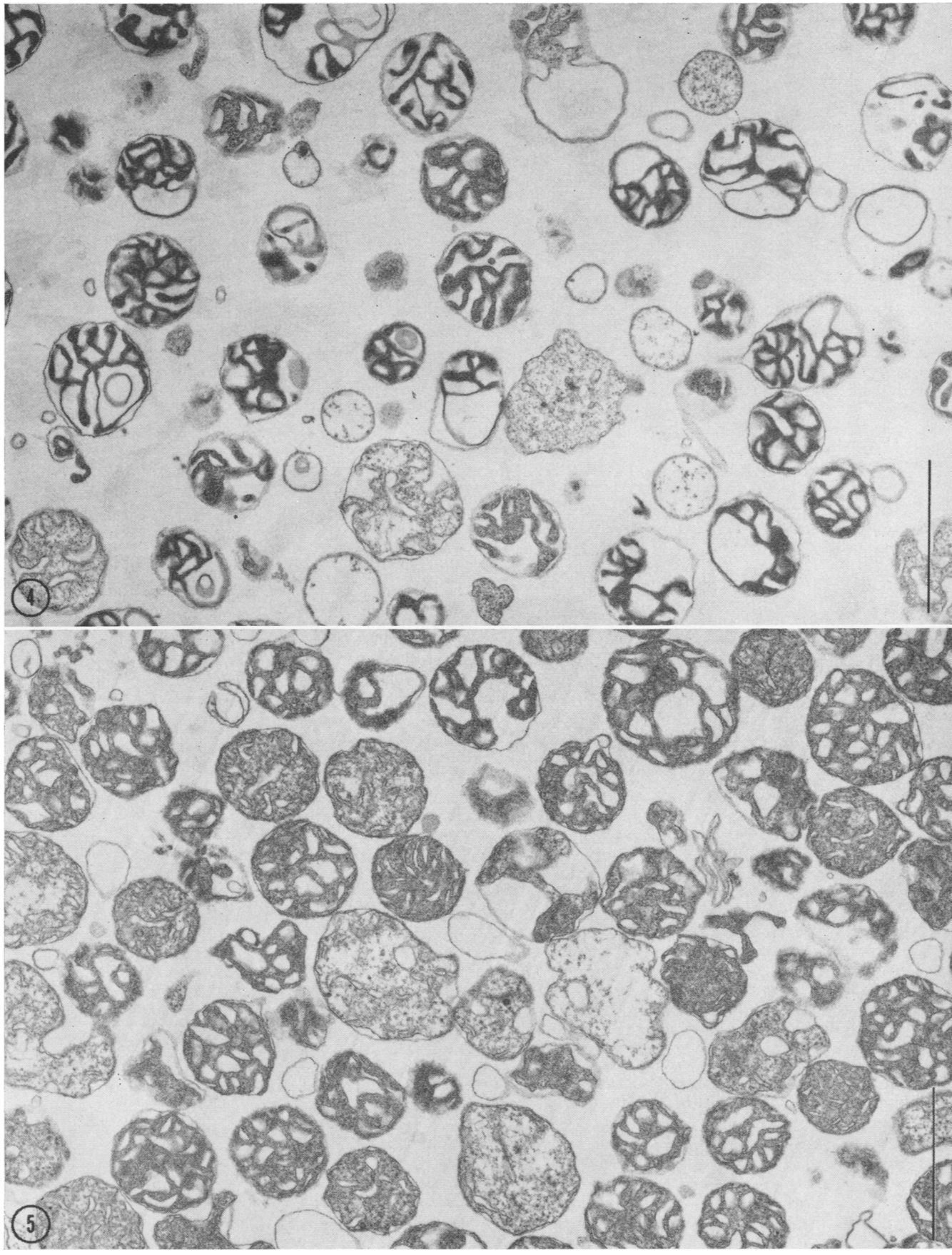
In Table I, the mean cross-sectional areas of outer compartments (of type III mitochondria) have been compared with those of inner compartments (for type III mitochondria), under experimental conditions that produce swelling or contraction. Large changes during swelling or contraction were observed in the I. C. and O. C.

The relative *in vitro* distribution of the three types of mitochondria obtained from corn roots by Chrispeels *et al.* (6) is compared in Table II with the relative frequency obtained in these experiments from corn shoots under conditions that should produce either swelling or contraction. The relative percentages of the three types remained about the same under all conditions. No statistically significant population shifts could be demonstrated.

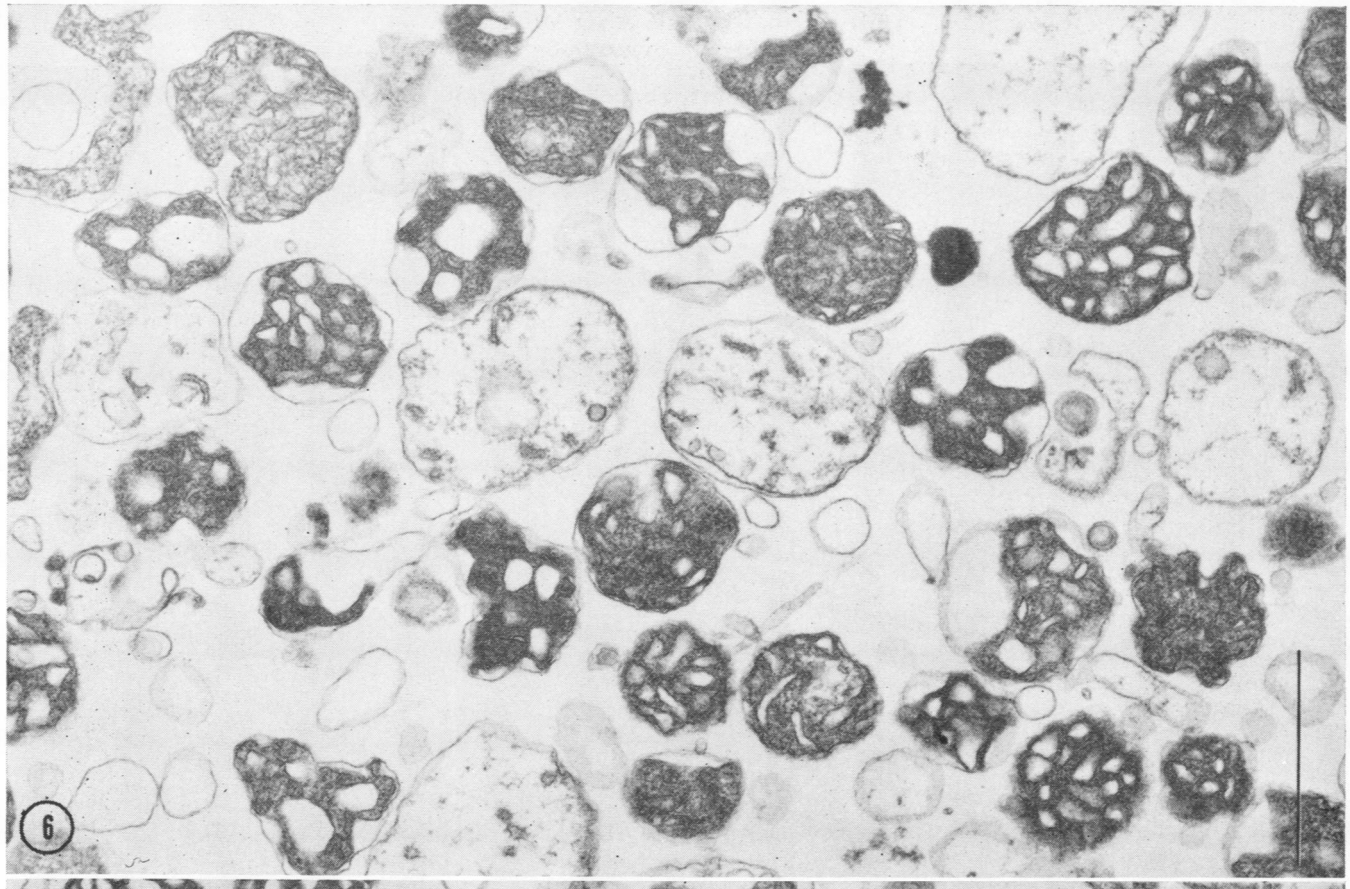
Numerous etiolated corn shoots were examined at 1-mm intervals in order to characterize *in vivo* mitochondrial morphology. Table III lists some selected cell types from three-day-old etiolated corn plants, an average cell size, the approximate total number of mitochondria computed on the respective cell size, and the mitochondrial type observed for that cell. Type II mitochondria were associated with meristematic and undifferentiated cells (Fig. 19). Types I and III were associated with differentiating and some differentiated cells (Figs. 19 and 20). As expected, some functionally mature (differentiated) cells had no mitochondria. All of the mitochondria within any given cell were usually observed to be of the same type. Since cell differentiation is a continuous process, intermediate mitochondrial types were frequently observed. While cells usually had characteristic mitochondrial types, some parenchyma cells could have either type I or III mitochondria.

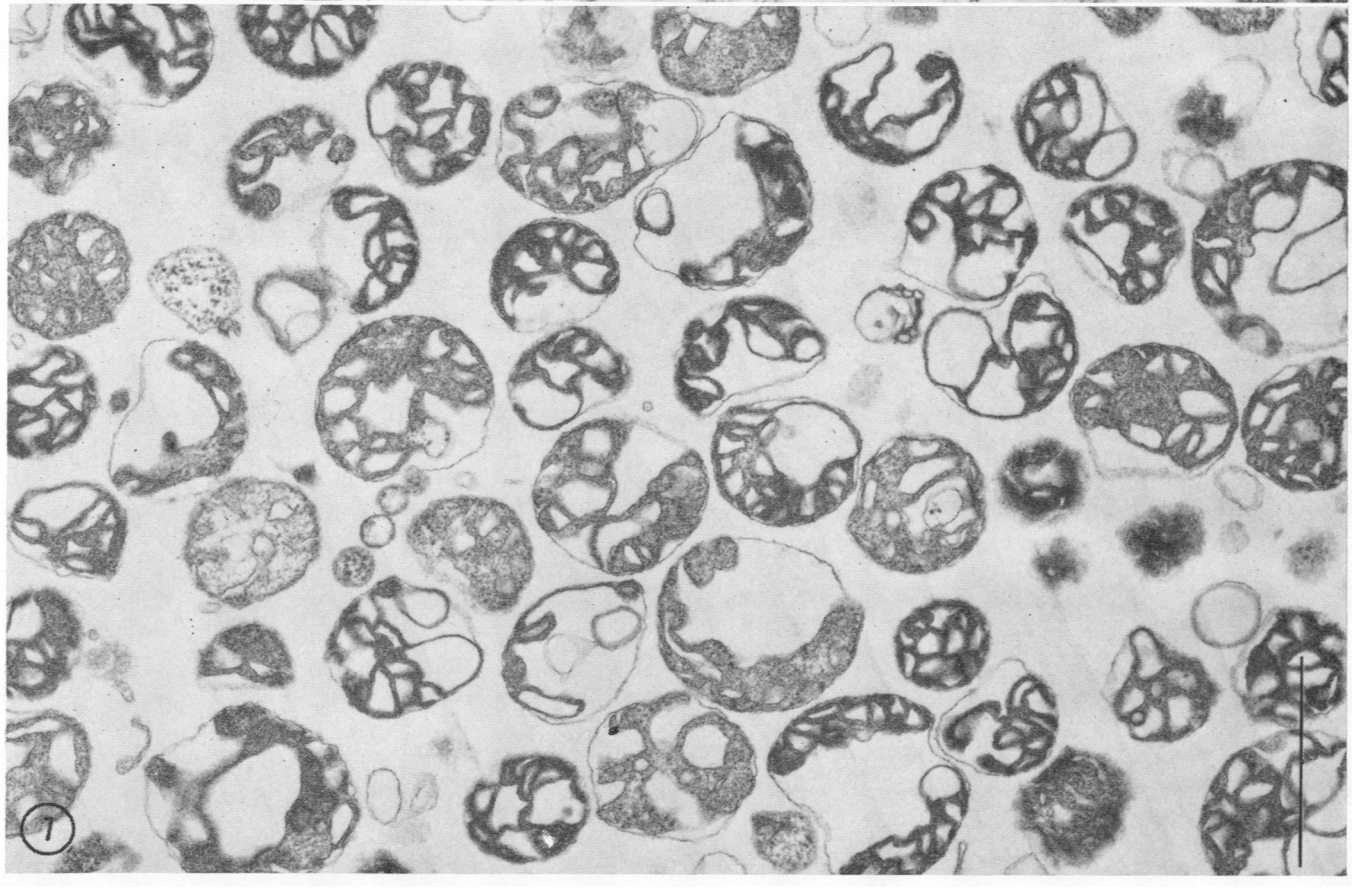
DISCUSSION

Table III presents the calculated numbers and observed types of mitochondria for selected cell types of 3-day-old etiolated corn shoots. The results should be regarded as rough guidelines obtained under a specific set of conditions and assumptions. The numbers reported here for meristematic cells are somewhat higher than those reported for other grass meristematic cells (1). With the exception of the young metaxylem vessel, the number of mitochondria per cell is reasonably constant, yet there are large differences in cell size. It is not known whether or not these differences indicate different activities.

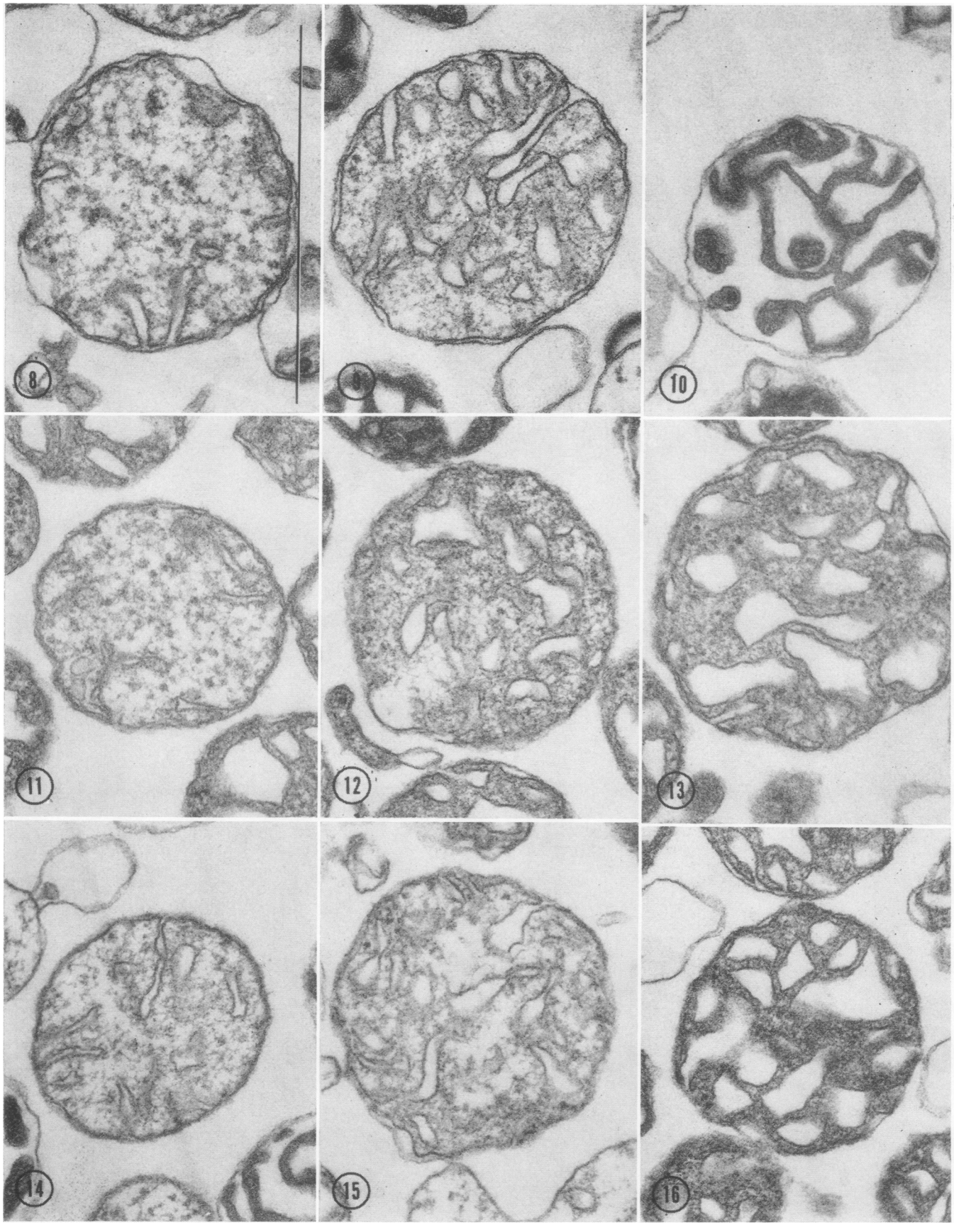


FIGS. 4–5. Corn shoot mitochondria. Line scales represent 1 μm. Fig. 4: mitochondria held in 0.4 M sucrose; Fig. 5: mitochondria swollen for 3 min in 0.2 M KCl, 20 mM tris-HCl, and 1 mg/ml BSA.

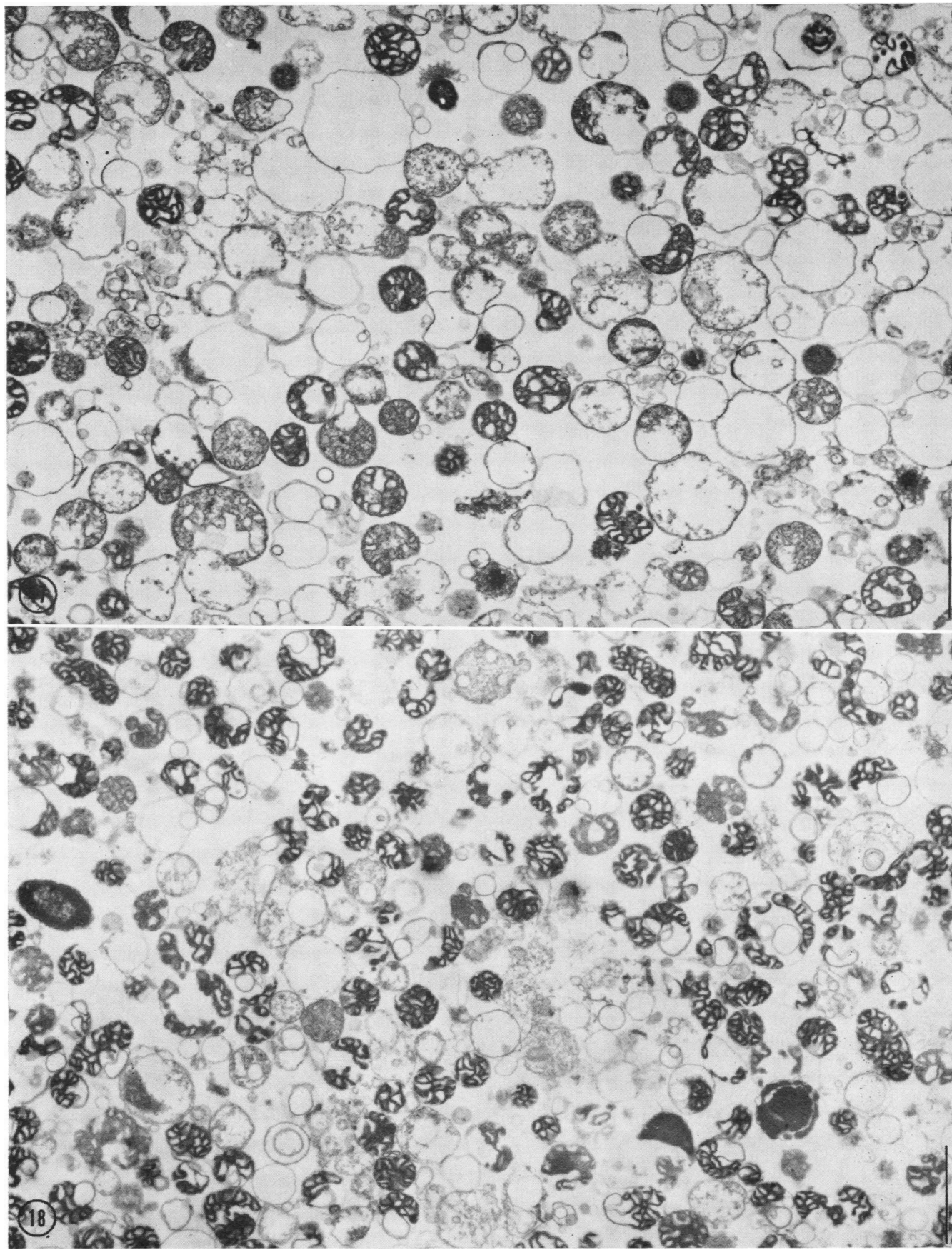




FIGS. 6–7. Corn shoot mitochondria. Line scales represent 1 μm. Fig. 6: mitochondria swollen for 15 min in 0.2 M KCl, 20 mM tris-HCl, and 1 mg/ml BSA. Fig. 7: mitochondria swollen in the above base mix for 3 min and then contracted with 2 μmoles exogeneous NADH.



FIGS. 8–16. Corn shoot mitochondria. Line scale in Fig. 8 represents 1 μm; all other figures are at same magnification. Figs. 8–10: types I, II, III, respectively, from Fig. 4. Figs. 11–13: types I, II, III, respectively, from Fig. 5. Figs. 14–16, types I, II, III, respectively, from Fig. 7.



FIGS. 17–18. Corn shoot mitochondria. Line scales represent 1 μm. Fig. 17: section near edge of pellet; Fig. 18: section near center of pellet.

Table I. *Comparison of Cross-Sectional Area of Outer and Inner Compartments of Swollen and Contracted Type III Mitochondria*

Treatment	Outer Compartment	Inner Compartment
	% of total area	
0.4 M sucrose	62.4	37.6
4 Min KBT swell	34.6[1]	66.4[1]
15 Min KBT swell	42.8[1]	57.2[1]
NADH contraction (3 μmoles)	54.7[2]	45.3[2]
Malate + pyruvate contraction (40 μmoles each)	53.8[2]	46.2[2]
Succinate contraction (40 μmoles)	49.5[2]	51.5[2]

[1] Indicates a difference between experimental treatment and 0.4 M sucrose control that is statistically significant at the 1% level.

[2] Indicates a difference between experimental treatment and both 4 or 15 min KBT control swell that is statistically significant at the 1% level.

Table II. *Relative Numbers of Mitochondrial Types under Different Conditions*

Condition	Type I	Type II	Type III	Total	I	II	III
					%		
Corn roots[1]	1151	648	624	2423	47	27	26
Corn shoots[2]	282	156	241	679	41	23	36
Corn shoots[3]	1426	957	1921	4298	34	23	44
Corn shoots[4]	374	156	462	992	38	16	46

[1] From Table III in Chrispeels *et al.* (5).

[2] Swollen *in vitro* for 4 min in KBT.

[3] Partially swollen *in vitro* in KBT and then contracted with either 2 μmoles NADH, 10 mM malate + pyruvate, 10 mM succinate, or some combination of the preceding.

[4] Held in 0.4 M sucrose since isolation with no exogenous substrate.

Type I mitochondria are found in phloem sieve tubes and some adjacent parenchyma cells, while type II mitochondria are from meristematic and undifferentiated cells. Type III mitochondria are normally found in all other vacuolate cells. Because cell differentiation is a continuum, mitochondrial morphogenesis is probably also a continuum. Therefore, it is possible to find many mitochondria that will not fit clearly into one of the three groups. Nevertheless, we have used the three groupings for convenience.

Since whole tissue contains three mitochondrial types, it is reasonable to expect isolated mitochondria to reflect the same morphological characteristics they had before isolation, unless artifacts had been introduced during isolation. Regardless of the fixative, the fixation procedure, or the reaction media conditions, the same three mitochondrial profiles were visible in all pellets. Although a single micrograph may have predominantly one mitochondrial type, there was no statistically significant difference in the proportions of types I, II, and III in a single pellet, considering many micrographs from a pellet.

Baxter and Hanson (3) demonstrated that 2,4-D influenced the morphology of mitochondria isolated from soybean hypocotyls. The hypocotyls were treated with 2,4-D 24 hr before isolation of mitochondria. The 2,4-D treatment had the effect of increasing the proportion of type II and decreasing the type III mitochondria. The effects of auxins on plant morphology are well known, and this report supports our belief that types I, II, and III are related to morphogenesis and not to swelling or contraction.

Wilson *et al.* (26) interpreted micrographs to show that the addition of substrate to KCl-swollen mitochondria increased the proportion of type III (from 37% to 72%) and decreased type I (from 43% to 6%). On the other hand, the addition of substrate to potassium acetate-swollen mitochondria decreased the proportion of type III (from 36% to 5%) and increased type I (from 59% to 68%). They interpreted these shifts in population as evidence of swelling and contraction.

Figures 17 and 18 show two populations of mitochondria, one from near the surface of the pellet and the other from near the center of the pellet. The only difference between the two micrographs is the position in the pellet from which the sections were cut. Counting only recognizable mitochondria, Figure 17 contains 32% type I and 50% type III, while Figure 18 contains 8% type I and 87% type III. When mitochondria are fixed and then pelleted, the position in the pellet can make large changes in the proportions of the types present.

Wilson *et al.* (26) fixed the mitochondria and then pelleted them, and only scored between 130 and 270 mitochondria for each treatment. Therefore, the level in the pellet at which their sections were cut could easily have influenced their counts. The

Table III. *Number of Mitochondria for Selected Cells from Three-Day-Old Etiolated Corn Shoots*

Tissue	Measured Average Cell[1]	Mitochondria[2]	Type
	size (μm) and volume (μm³)	*No/cell*	
Meristem			
Protoderm	15 × 15 × 32 = 5,652	180	II
Procambium	8 × 8 × 46 = 2,311	64	II
Ground meristem	15 × 15 × 16 = 1,885	225	II
Xylem[3,4]			
Young metaxylem vessel	20 × 20 × 117 = 36,738	2000	III
Mature protoxylem vessel	48 × 48 × 150 = 271,296	0	
Mature sclerenchyma fiber	7 × 7 ×	0	
Young parenchyma	16 × 16 × 24 = 4,823	272	III
Phloem[3,4]			
Sieve tube	16 × 16 × 78 = 15,675	160	III
Companion cell	9 × 9 × 47 = 2,988	180	I
Young parenchyma	16 × 16 × 24 = 4,823	208	III or I
Pith[3]			
Young parenchyma	16 × 16 × 24 = 4,823	304	III
Old parenchyma	47 × 47 × 78 = 135,257	235	III
Epidermis[5]			
Epidermal cell	18 × 20 × 35 = 9,891	216	III
Guard cell	4 × 5 × 47 = 738	282	III
Accessory cell	1.5 × 10 × 56 = 840	280	I

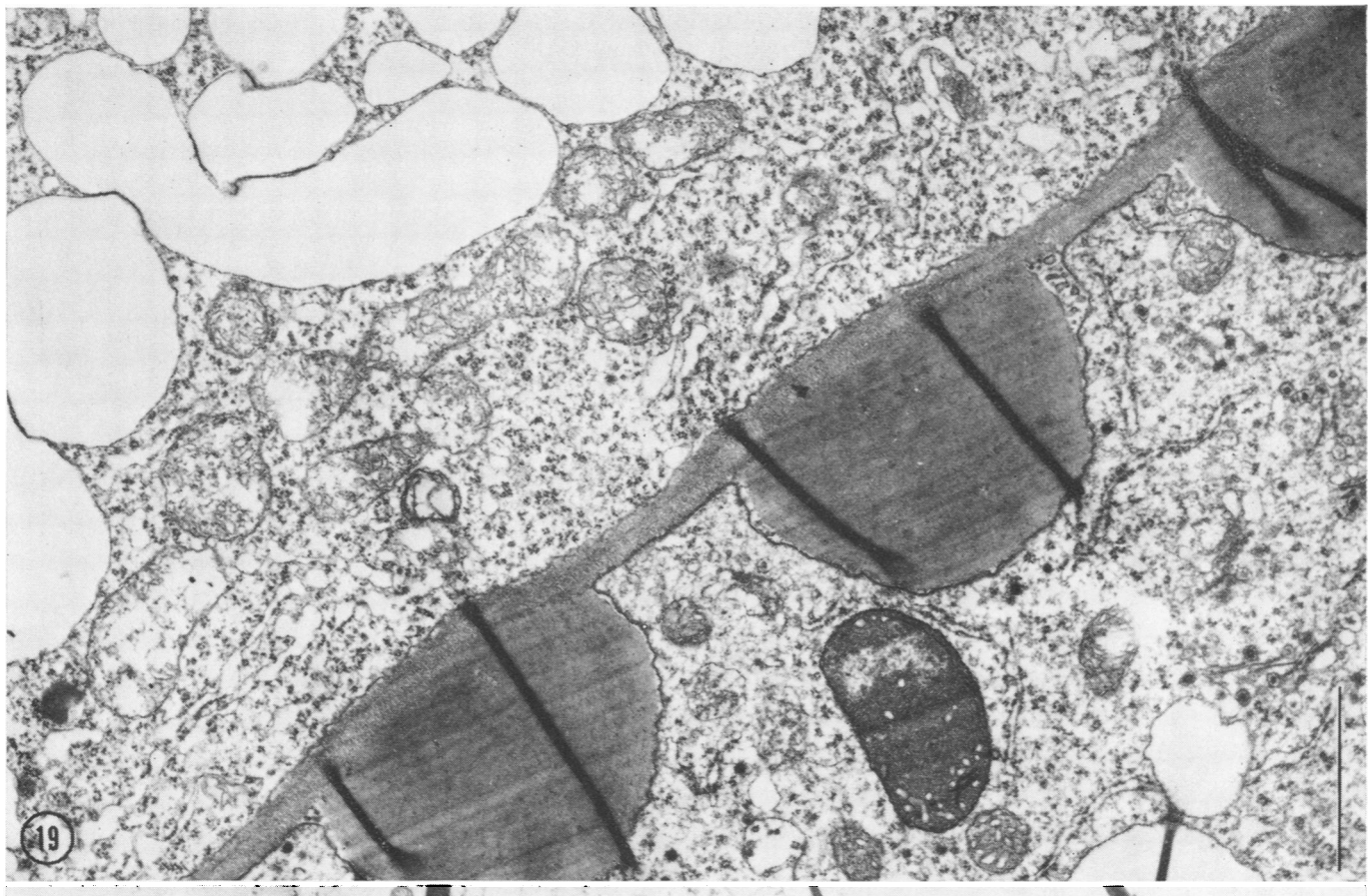
[1] Calculated by using the formula for the volume of a geometric solid that most nearly approximated the cell shape.

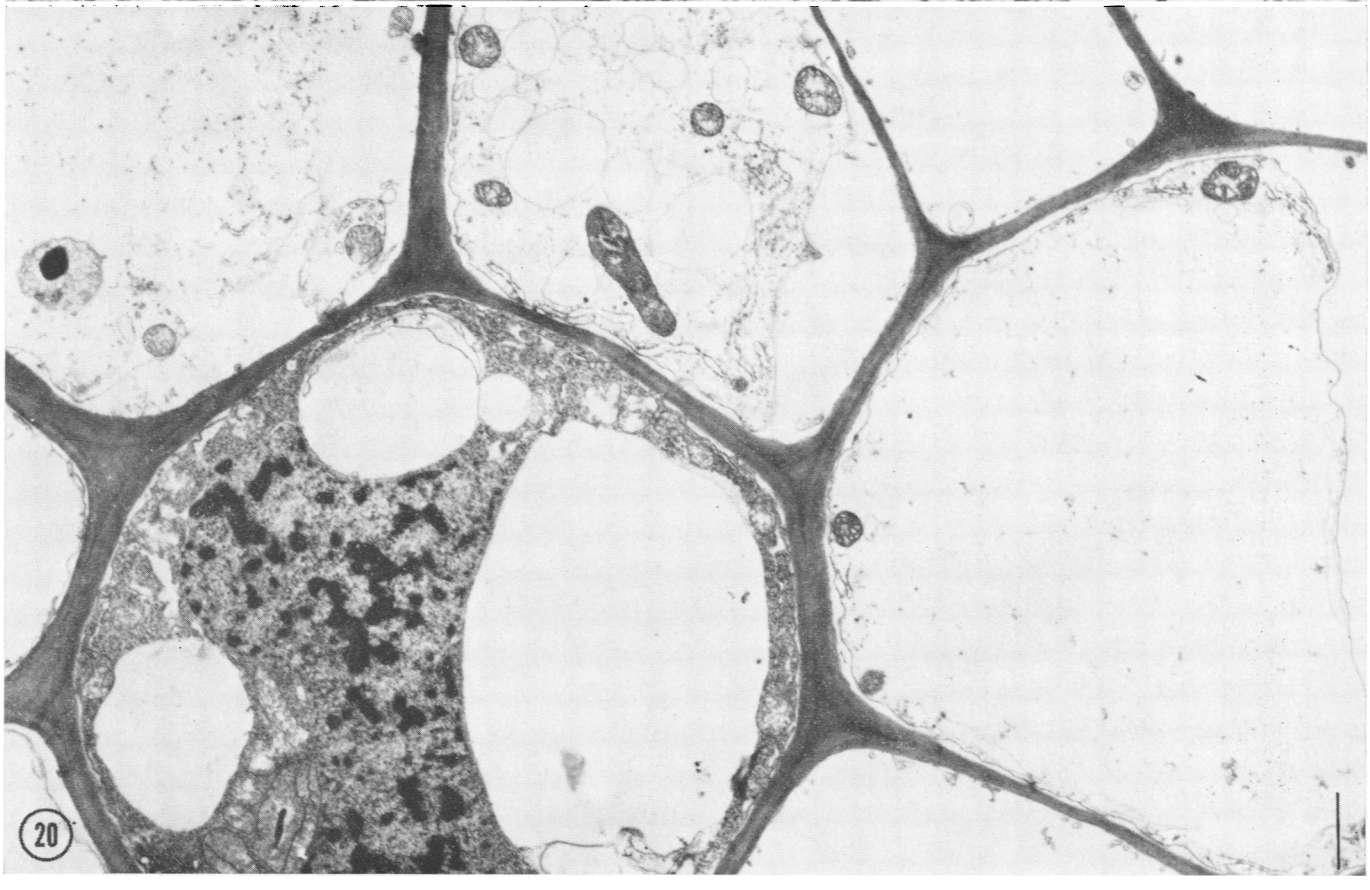
[2] Predicted on equal distribution of mitochondria within a cell and on a relatively constant mitochondrial size and shape.

[3] Stem.

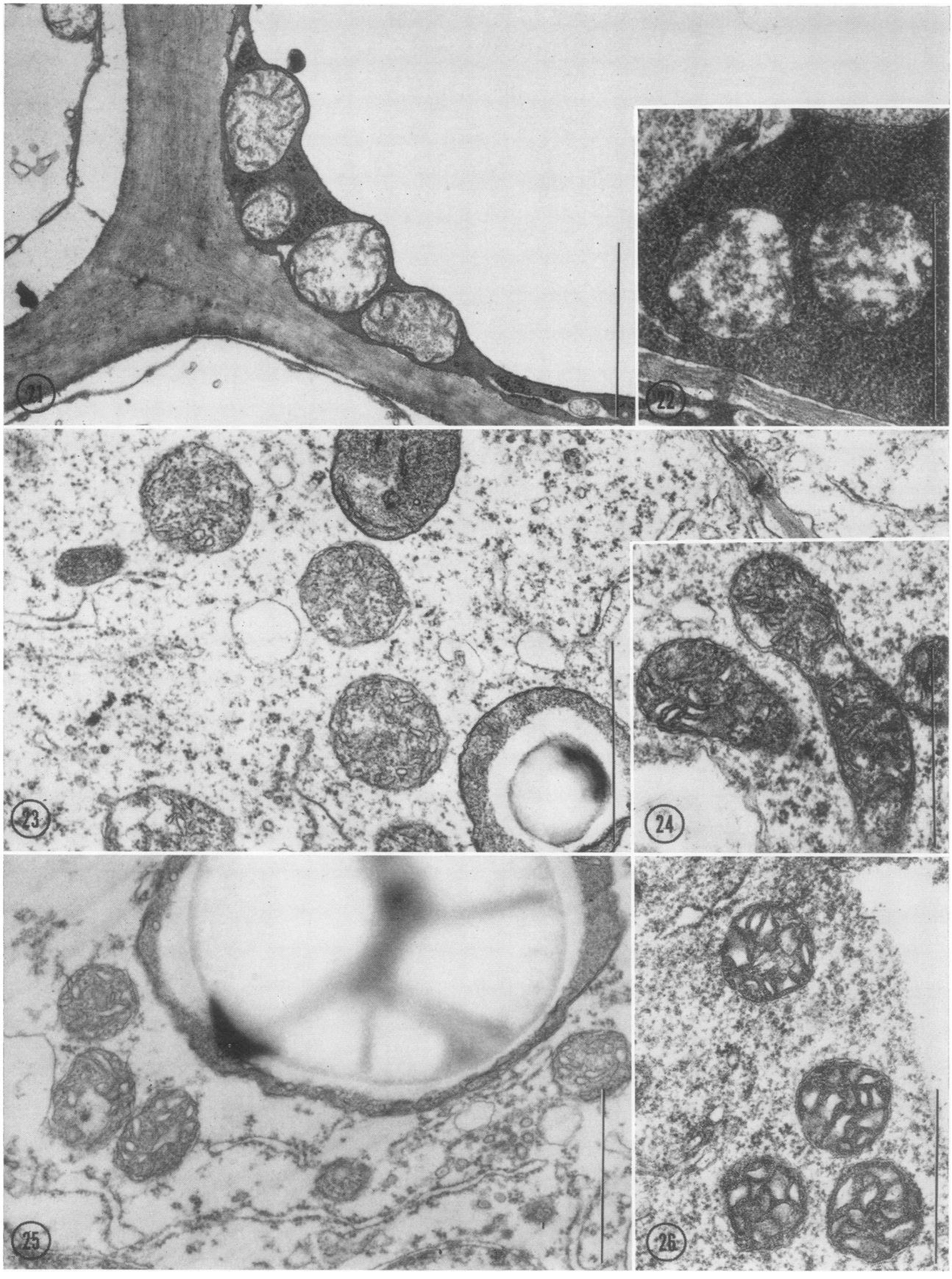
[4] Coleoptile.

[5] First leaf.





FIGS. 19–20. Whole corn shoots. Line scales represent 1 μm. Fig. 19: longitudinal section through maturing vascular bundle in first corn leaf. Metaxylem vessel on lower right and undifferentiated cell on upper left. Fig. 20: cross section through shoot 2 cm below shoot apex showing phloem companion cell (lower left) and sieve elements.



FIGS. 21–26. Cross section of corn shoots. Line scales represent 1 μm in all figures. Fig. 21: sieve tube in coleoptile; Fig. 22: same as Fig. 21 but treated with 2DOG; Fig. 23: cell of apical shoot meristem; Fig. 24: same as Fig. 23 but treated with 2DOG; Fig. 25: leaf mesophyll cell; Fig. 26: same as Fig. 25 but treated with 2DOG.

data presented in Table II were obtained by pelleting mitochondria and then fixing them, which results in a more homogeneous distribution of the three types. Furthermore, over 5000 mitochondria were scored. We interpret these data to show that there was no significant shift in population between swelling and contraction.

Hackenbrock *et al.* (11) used 2DOG to induce *in vivo* mitochondria contraction in Ascites tumor cells. Using this technique, our observations made on tissue treated with 2DOG support the interpretation that there is no shift from one mitochondrial type to another in swelling or contraction. Control tissues (Figs. 21, 23, and 25) were compared with tissues treated with 2DOG (Figs. 22, 24, and 26). Type I mitochondria are still visible in phloem sieve tubes and some adjacent parenchyma cells (Figs. 21 and 22). Type II mitochondria of the meristematic and undifferentiated cells are essentially unchanged, except that the matrix stains more densely and the membranes of adjacent cristae tend to approach one another more closely (cf. Figs. 23 and 24). Type III mitochondria are basically similar except that the cristae have increased in size, and the matrix is denser (Figs. 25 and 26).

From the preceding it can be seen that corn shoot mitochondria are morphologically heterogeneous. Similar heterogeneity in populations of isolated animal mitochondria have been observed (4, 10). However, the important difference is that this heterogeneity exists in intact plant tissue and cannot be altered by 2DOG treatment. While it is not questioned that types I, II, and III are interconvertible in the living cell, we can find no evidence to suggest that they undergo *in vitro* interconversion under various reaction conditions over short time intervals.

Since interconversion from one type to another is not associated with swelling and contraction, then what morphological change, if any, is associated with swelling and contraction? Each of the three types has its own characteristic swelling and contraction patterns: Type I is the same swollen or contracted, while types II and III show changes in the size of cristae and matrix density which very likely account for observed optical density changes. The suspending medium undoubtedly has an effect on cristae size and matrix density (2), and this is not inconsistent with anything reported here.

Changes in cristae size of type III mitochondria were readily characterized under swollen and contracted conditions. There was a statistically significant increase in the size of the inner compartment (decrease in the outer) when type III mitochondria were swollen, and a decrease in the size of the inner compartment (increase in the outer) when the same mitochondria were contracted (Table I). During the 15-min KCl swell, some cristae continued to enlarge while others collapsed, resulting in the apparently anomalous observation that 15-min swells were less effective in swelling the mitochondria than 3-min swells.

The work of Lorimer and Miller (14), Massari *et al.* (17), and Overman *et al.* (20) shows that most of the volume change of mitochondria is associated with the inner membrane. The observations presented here support their observations.

Furthermore, Weber (25) noted that the distance separating the membranes of two adjacent cristae changes, depending on the metabolic state of the mitochondrion. In our studies it was noted that the membranes of two adjacent cristae moved closer together when types II and III were contracted.

Finally, we cannot help but wonder what physiological and cytological events are associated with types I, II, and III mitochondria, if we assume that form and function are somehow related. Chrispeels *et al.* (6), Hanson *et al.* (13), Lund *et al.* (16), and Simon and Chapman (22) have noted that meristems or undifferentiated cells have lower respiration rates than more mature cells and have correlated this to mitochondrial morphology. Esau and Cheadle (7) have reported that cells transporting sugars or accumulating starch have reduced mitochondria (type I). Our observations agree with those of Esau and Cheadle, but cannot be used to suggest differences in metabolic activity. A detailed study of each mitochondrial type might reveal basic metabolic differences between the different types.

LITERATURE CITED

1. Avers, C. J. and E. E. King. 1960. Histochemical evidence of intracellular enzymatic heterogeneity of plant mitochondria. Amer. J. Bot. 47: 220–225.
2. Baker, J. E., L. G. Elfvin, J. B. Biale, and S. I. Honda. 1968. Studies on ultrastructure and purification of isolated plant mitochondria. Plant Physiol. 43: 2001–2022.
3. Baxter, R. and J. B. Hanson. 1968. The effect of 2,4-dichlorophenoxyacetic acid upon the metabolism and composition of soybean hypocotyl mitochondria. Planta 82: 246–260.
4. Burgos, M. H., A. Aoki, and F. I. Sacerdote. 1964. Ultrastructure of isolated kidney mitochondria treated with phlorizin and ATP. J. Cell Biol. 23: 207–212.
5. Buvat, R. 1958. Recherches sur les infrastructure du cytoplasme, dans les cellules du meristeme apical, des ebauches foliaires et des feuilles developpees d'*Elodea canadensis*. Ann. Sci. Nat., Bot., Ser. 11 19: 121–161.
6. Chrispeels, M. J., A. E. Vatter, and J. B. Hanson. 1966. Morphological development of mitochondria during cell elongation in the roots of *Zea mays* seedlings. J. R. Microsc. Soc. 85: 29–44.
7. Esau, K. and V. I. Cheadle. 1962. Mitochondria in the phloem of *Cucurbita*. Bot. Gaz. 124: 79–85.
8. Esau, K., V. I. Cheadle, and R. H. Gill. 1966. Cytology of differentiating tracheary elements. I. Organelles and membrane systems. Amer. J. Bot. 53: 756–764.
9. Esau, K., V. I. Cheadle, and E. B. Risley. 1963. A view of ultrastructure of *Cucurbita* xylem. Bot. Gaz. 124: 311–316.
10. Hackenbrock, C. R. 1966. Ultrastructural basis for metabolically linked mechanical activity in mitochondria. I. Reversible ultrastructural changes with change in metabolic steady state in isolated liver mitochondria. J. Cell Biol. 30: 269–297.
11. Hackenbrock, C. R., T. G. Rehn, E. C. Weingach, and J. J. Lemasters. 1971. Oxidative phosphorylation and ultrastructural transformation in mitochondria in the intact Ascites tumor cell. J. Cell Biol. 51: 123–137.
12. Hanson, J. B. and T. K. Hodges. 1967. Energy-linked reactions of plant mitochondria. Current Topics in Bioenergetics 2: 65–98.
13. Hanson, J. B., A. E. Vatter, M. E. Fisher, and R. F. Bils. 1959. The development of mitochondria in the scutellum of germinating corn. Agron. J. 51: 295–301.
14. Lorimer, G. H. and R. J. Miller. 1969. The osmotic behavior of corn mitochondria. Plant Physiol. 44: 839–844.
15. Luft, J. G. 1961. Improvements in epoxy resin embedding methods. J. Biophys. Biochem. Cytol. 9: 409–414.
16. Lund, H. A., A. E. Vatter, and J. B. Hanson. 1958. Biochemical and cytological changes accompanying growth and differentiation in the roots of *Zea mays*. J. Biophys. Biochem. Cytol. 4: 87–98.
17. Massari, S., L. Frigeri, and G. F. Azzone. 1972. Permeability to water, dimension of surface, and structural changes during swelling in rat liver mitochondria. J. Membr. Biol. 9: 57–70.
18. Miller, R. J., S. W. Dumford, D. E. Koeppe, and J. B. Hanson. 1970. Divalent cation stimulation of substrate oxidation by corn mitochondria. Plant Physiol. 45: 649–653.
19. O'Brien, T. P. and K. V. Thimann. 1967. Observations on the fine structure of the oat coleoptile. III. Correlated light and electron microscopy of the vascular tissue. Protoplasma 63: 443–478.
20. Overman, A. R., G. H. Lorimer, and R. J. Miller. 1970. Diffusion and osmotic transfer in corn mitochondria. Plant Physiol. 45: 126–132.
21. Reynolds, E. S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron mircoscopy. J. Cell Biol. 17: 208–212.
22. Simon, E. W. and J. A. Chapman. 1961. The development of mitochondria in *Arum* spadix. J. Exp. Bot. 12: 414–420.
23. Stempak, J. G. and R. T. Ward. 1964. An improved staining method for electron microscopy. J. Cell Biol. 22: 697–701.
24. Stoner, C. D. and J. B. Hanson. 1966. Swelling and contraction of corn mitochondria. Plant Physiol. 41: 255–266.
25. Weber, N. E. 1972. Ultrastructural studies of beef heart mitochondria. III. The inequality of gross morphological change and oxidative phosphorylation. J. Cell Biol. 55: 457–470.
26. Wilson, R. H., J. B. Hanson, and H. H. Mollenhauer. 1969. Active swelling and acetate uptake in corn mitochondria. Biochemistry 8: 1203–1213.