Cytological Studies of the Nematocysts of Hydra

II. The Stenoteles*

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PLATES 28 TO 33

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ABSTRACT

Entire hydras or tentacles were prepared for electron microscopy as described in the preceding paper.

The stenotele capsule has been observed to be composed of an external membrane, a thick chitinous or keratin layer, and an inner membrane. A sac-like extension of the capsular wall into the capsule bears spines and stylets on its inner surface and evagination of this structure occurs on discharge. Profiles of tubular or membranous structures often are seen within the capsules of resting stenoteles. These structures are presumably related to the external filament. The spines often reveal a flattened aspect which suggests that at least some of them might more accurately be called "vanes." A cnidocil has been found to accompany each stenotele.

This study revealed several aspects of the developmental stages of stenoteles: A vacuole is formed which is nearly surrounded by the nematocyte nucleus. The vacuole content changes in density and a capsular wall is formed at the periphery of the vacuole. Tubules differentiate from the capsular matrix, and spines and stylets develop somewhat later. An operculum is formed from the nematocyte cytoplasm.

INTRODUCTION

Although there are four different types of nematocysts found in hydra, by far the greatest amount of interest and research has been centered about the stenoteles. This may be due to the fact that the stenoteles are, because of their armament (particularly the stylets), the most striking of the nematocyst types. The fact that they are the largest of the nematocysts may also have tended to encourage workers to choose them as subjects for nematocyst investigation.

In the present studies, as in those of workers of the past the stenoteles have proved most rewarding. This paper presents observations which have been made concerning the development, fine structure and mode of discharge of the stenoteles of hydra.

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Materials and Methods

The materials and methods used in this study of the stenoteles are identical with those described in detail in the preceding paper.

OBSERVATIONS AND DISCUSSION

A. Optical Microscope Observations.—The stenoteles, often referred to as the penetrants, are about one-tenth as numerous as the desmonemes. In the discharged state (Fig. 18), the stenotele consists of an open tubule, dilated at the base to form the so called "butt," which appears to be continuous with the capsular wall (Hyman, 1940). Three large birefringent spines, the stylets, appear on the butt curving backwards over the crown of the capsule and thus forming an angle of 130° with a line produced from the butt proper. The capsule, shaft, spines, and tubule are all positively birefringent (Picken, 1953). Kepner *et al.* (1943, 1951) and others have divided the discharged stenotele into four regions: (1) capsule and operculum, (2) shaft of the spinneret, (3)

spinneret proper, containing three stylettes, (4) filament. The shaft of the spinneret and the spinneret proper correspond to Hyman's term "butt," to Weill's (1934) term "hampe" and to the "Angelhaken," a term used in earlier papers. In the undischarged state the shaft has a median location in the capsule with the tubule coiled beneath it. The stenotele is capable of injecting a potent paralyzing substance and functions solely in the capture of prey.

B. Fine Structure of Stenoteles.—The stenoteles of hydra vary from 8 to 15 μ in length and 5 to 6 μ in diameter at their widest point (Figs. 5, 11, 16, and 18). The capsular wall (*C*) consists of chitin or keratin and is about 0.25 μ thick. In OsO_4-fixed material, the inner surface of the capsular wall appears to be limited by an 80 A thick membrane (*Mi*); the outer surface of the capsular wall appears to be limited by a 160 A thick membrane (*Mo*) (Fig. 14). Another membrane (*Mn*) of similar thickness and density appears to limit the nematocyte cytoplasm. In $KMnO_4$-fixed material (Fig. 13), the surfaces of the capsular wall show no such distinct membranes, only an increased density; the nematocyte membrane is most difficult to identify, mainly owing to its proximity to the capsular wall. (It is rather puzzling that the plasma membrane (*Pm*) in Fig. 13 is quite well preserved while the capsular wall membranes are not and that just the reverse situation obtains in OsO_4-fixed material for the preservative powers of $KMnO_4$ on cell membranes are well known.)

Phillips (1956) thinks that the capsule and the tube consist chemically of a cartilaginous material made up of eighteen amino acids and a polysaccharide. Brown (1950) detected cystine in the nematocysts of *Corynactis viridis*. This suggested to him that keratin may be a component of the nematocyst for keratin contains a high proportion of cystine. Hamon (1955), on the basis of several chemical tests, concluded that the nematocysts contained simple mucoproteins, actually glycoproteins, due to the low carbohydrate content. As no chemical analyses were included in the present studies, no further information can be provided on these points.

Study of the accompanying figures of stenoteles (Figs. 5, 10, 11 and 13) suggests that the classical terms "shaft" and "spinneret" are inaccurate or at least misleading. It can be seen from the above figures and from Fig. 16 that these terms represent different regions of a single structure. This structure, for which the name invaginated capsular wall (*ICW*)[1] is suggested, is clearly continuous with, and of similar density to the wall of the capsule, regardless of the fixative employed. The closest approximations in the literature to the *ICW* configuration occur as the structure labelled "*mj*" and called the inner margin of the gelatinous matrix by Kepner *et al.* (1951, Fig. 5, page 45) and as the structure labelled "*H*" and called the "eingestülpte Halsstück" by Schulze (1922, Fig. 4 *a*, page 392). A study of Fig. 13 and then Fig. 16 convinces one that it is an evagination of the structure labelled *ICW* in Fig. 13 that results in the classical picture of a discharged stenotele represented by Fig. 16. No other structures are involved. It seems unreasonable to apply the terms "shaft" and "spinneret" to this structure. However, the terminology of Schulze (1922), *viz.* "Halsstück" for the basal region of the evaginated structure, "Dornenstück" for the spine-containing region, and "Zwischenstück" for the region distal to the spiny region, but proximal to the filament, seems completely satisfactory. It is suggested that the name evaginated capsular wall (*ECW*) be applied in the case of the discharged stenotele to the structure called the invaginated capsular wall in the resting stenotele. This structure is labelled *ECW* in Fig. 16. It may be noted that the spines and stylets which lie within the *ICW* are found on the outside of the *ECW*. (Only the spines appear in Fig. 16. Either the stylets have broken off or they are not included in the plane of this section.) No pore at the inner end of the invaginated capsular wall was observed, as might have been expected from the report by Kepner *et al.* (1943, Fig. 6, page 587) of a pore at the fundus of the internal spinneret.

It now becomes possible to eliminate some of the misconceptions concerning the structure of the stenotele and of events occurring on stenotele discharge. Thus, Robson (1953), Jones (1947), Picken (1953), and Schulze (1922), who indicated that the spines existed on the *outside* of the "shaft" in the undischarged condition, were apparently mistaken and Hyman (1940) and Ewer (1947) were correct in indicating in their drawings that the spines occurred on the *inside* of the "shaft." It is clear that

[1] Although the terminology applied to the *ICW* is suggestive of a mode of origin, it is not intended to reflect the opinion that this is indeed how the *ICW* does originate. The term was selected upon realization of the fate of the structure.

evagination of the invaginated capsular wall places these spines on the free surface of the evaginated capsular wall where they may be readily seen in the optical microscope.

The use of the term "spine" or "thorn" to describe the short, slender processes found on the invaginated and evaginated capsular walls seems less appropriate than the term "vane" which connotes a flatness not suggested by the other terms. Fig. 17 illustrates the flat aspect of these structures. Fig. 8, page 281, in the paper by Semal-Van Gansen (1954) should also be studied. It is of course possible that some nematocysts do possess truly spiny processes, other than the stylets, which seem to have no flattened aspect.

Some uncertainty still surrounds the nature of the nematocyst filaments. The essential need here is to determine the mode of origin of the external filament. One possibility is that the external filament is derived directly from the internal filament by an eversion or extrusion. Another possibility is that the internal filament is broken down, subsequently reconstituted in conjunction with capsular matrix material and extruded to form the external filament. Kepner *et al.* (1943, 1951) have found the latter possibility to be more acceptable for several reasons. Among these reasons is the fact that they have observed the diameter of the external filament to be related to the size of the orifice formed by the partially expressed stylets. They have interpreted the filament diameter as an effect of orifice diameter. It would seem equally possible that it could be a cause of orifice diameter. In addition, they have reported that the filament advances into the external environment only so long as the stylet tips are in apposition. Furthermore, they point out that the external filament is rifled, *i.e.*, that it possesses three ridges and three grooves produced by passage through the nozzle formed by the three stylets. (It should be noted that the three stylets point towards the apex of the unfired nematocyst and towards the base of the discharged nematocyst. Jones (1947) states that stylets occur only in penetrants.)

The present study has been able to cast little light on the subject of nematocyst filaments because no representation of the external filament has been seen in any section. It may be that the external filament was broken off or that it is soluble in one of the reagents used in processing the tissue. It is difficult to interpret confidently the configurations which appear to represent the internal filament. These configurations most frequently occur as three-bladed propellers (*T* and arrows in Figs. 5, 7, 10, 11, and 13). Their surface seems to be formed by a dense membrane and the interior resembles the capsular matrix. Such forms could be interpreted as representing flattened channels formed by elaborately folded sheets of membranes or profiles of a contorted and sculptured or collapsed tubule. One is tempted to relate the three blades of the propeller to the three ridges reported by Kepner *et al.* (1951) in the external filament, and thought due to the molding action of the stylets. It should be noted that Kepner *et al.* (1951) have reported that the internal filament reveals no lumen and that the external filament appears to have a wall due to a condensation of material at its surface. Resolution of this problem seems to be at least partly dependent upon the obtaining of high quality micrographs of external filaments. In any case a relation would seem to exist between the capsular matrix with its propeller configurations and the external filament for it is seen that, in preparations in which evagination of the internal capsular membrane has occurred, the matrix and the propeller forms are absent.

The operculum (*op*) (Figs. 5, 6, 11, 13, and 16) appears to derive its substance from the cnidoblast cytoplasm, with which it is continuous (Fig. 13, at arrow), its proximal membrane from the outer capsular membrane (*Mo*, Fig. 6), and its distal membrane from the nematocyte membrane (*Mn*, Fig. 6). Some of these developmental relationships seem to be lost in the mature discharged stenotele's operculum (Fig. 16). Here the operculum shows association only with the capsule. Unfortunately, precisely how the operculum is kept closed is not revealed in the micrographs. However, the arrow in Fig. 16 points to a notch-like thickening of the capsule wall at the mouth which suggests a possible latch mechanism.

The cnidocil (*cd*) is located to one side of the longitudinal axis of the stenotele (Figs. 13 and 15). This leaves the operculum ample space into which to spring open. It also appears that additional space is provided for this essential action by an opercular chamber (*oc*) located just distal to the operculum (Fig. 13). It may be the distal border of this chamber which Kepner *et al.* (1951) have called Reynolds' membrane. Having the operculum located beneath the surface in this way may serve the added purpose of preventing its being occluded by debris.

C. Development.—Frey (1847), Moseley (1877), and Murbach (1893, 1894) as cited in Weill (1934), thought that the capsular wall was formed within the nucleus, and the entire nucleus transformed into the nematocyst. (Weill himself believed that the capsular wall is of double origin, being formed from the external protoplasm as well as from the internal capsular matrix.) Weill (1934) also states that Schulze (1873), Hamann (1882), DuPlessis (1884), and Bedot (1888) postulated a cytoplasmic origin, while Will (1909) and Kanajew (1926) attributed at least part of the development to the Golgi apparatus. The early confusion of Frey, Moseley, Murbach and others can be readily understood from inspection of Fig. 1 in which the nucleus (*N*) is nearly continuous around the entire vacuole (*Va*). It is easy to imagine how these workers could come to believe that nematocysts developed within the nucleus.

Bedot (1888) thought the vacuolar membrane to be the origin of the capsular wall, the capsular contents being the substance found between the developing shaft and the capsular wall. Chun (1881) stated that the capsular wall gave rise to the tube, the armature (stylets and spines) and the capsular contents. Finally, Ewald (1916), combining the work of previous workers (Will, 1909 and Iwanzoff, 1896), stated that the primitive vacuole transforms itself into a capsule, the wall of the vacuole forming the wall of the capsule, the contents of the vacuole forming the capsular contents and internal nematocyst structures (stylets, spines, tubules, *etc.*).

Some workers have postulated the formation of the nematocyst tube external to the capsule, followed by secondary invagination. Others considered the nematocyst tube as forming within the capsule in the midst of a primitive homogeneous matrix. The former interpretation is not generally accepted owing to the complexity of the morphological and physiological events involved. Furthermore, Weill (1934) feels that the immature nematocysts are capable of evaginating. Therefore, immature evaginated nematocysts found within their nematoblast cytoplasm are not forming tubes, but have discharged prematurely. Examples of this phenomenon have been observed in the present study.

Weill (1934) feels that the armature (stylets and spines), the capsular contents, and probably the tube are formed within the nematocyst capsule without direct contact with the surrounding cytoplasm. Presumably the tube forms first with the armature forming later, although the order may vary. The tube, however, is often difficult to distinguish within the capsule. (See Figs. 10 and 11.) The armature develops independently of the tube yet without any direct connection with the cnidoblast cytoplasm. The zone of growth of the tube seems to be localized near its end, not differentiating into the stalk and the butt proper (Weill uses the word "hampe") until it has attained a considerable length. Its development seems independent of the armature of the axial body or butt proper.

The initial stage of development can be seen in Fig. 1. The nucleus, which is of considerable size, practically surrounds a large vacuole found within the cytoplasm. The degree to which the nucleus surrounds the vacuole varies with different types of nematocysts. This vacuole has been thought by some to be derived from the Golgi apparatus (Will, 1909). No evidence relative to this point has been obtained in this study.

The next stage of development, as represented by Fig. 2, consists of a change in the vacuolar contents, with a tendency toward greater density. Few particles can be observed within the vacuole at this stage, but more are seen here than in the previous stage.

At the next stage (Fig. 3) the vacuole is differentiated into a capsule (*C*) and its contents. The capsular contents are granular and quite dense. The capsule itself is homogeneous and of low density. The nucleus has now become quite attenuated. Within the capsule proper the content exhibits a particulate nature with several different densities and sizes (Fig. 4).

This developmental sequence is followed by each of the four different types of nematocysts found in hydra. From this point on, the nematocysts develop in different ways according to their type.

The developmental sequence in the stenotele, from this stage on, is somewhat more complex than in other forms. The "tubules" (*T*) seen in Figs. 5, 7, 10, and 11 form within the capsule proper, probably from the capsular matrix (Weill (1934) and others). The armature also appears to differentiate from the capsular matrix.

In Fig. 5 the capsular wall is not complete around the entire developing nematocyst. This may be due to (1) secondary degeneration of the capsular wall, (2) preparation artifact, or (3) imperfect formation.

In the successive steps in the development of the intracapsular structures (Figs. 5, 10, and 11), a process (*ICW*) from the capsular wall near the operculum extends down into the matrix in the interior of the capsule nearly to the basal end. This forms a sort of capsule within the original capsule (see Figs. 5, 10, and 13). Within this inner capsule the stylets and spines seem to differentiate from the capsular matrix. Fig. 6 shows a peculiar configuration of this inner capsule or invaginated capsular wall. It might appear that the inner capsule splits into two layers. It seems more likely that the section has passed through a fold of the inner capsule. It is possible that the infolded capsule layer gives rise to the stylets and spines. The sequence of events in spine and stylet development can be followed from the stage where no spines and stylets are present (Fig. 5) to that in which the stylets have begun to form (Figs. 8 and 9) and then to complete differentiation of the spines and stylets (Figs. 10 and 11). (It should be noted how the spines are attached to the inner surface of the invaginated capsular wall (Fig. 10).) Meanwhile, the matrix undergoes a change from the rather coarse particles seen in Fig. 5 to the finer particles seen in Figs. 10 and 11.

The tubular forms in the capsular matrix can be seen well before the armature is elaborated (Fig. 5). They are often very difficult to make out in their earliest stage of development, since they are of the same density as the surrounding matrix. It is interesting to note the "three-bladed propeller" configuration assumed frequently by the "tubules" and shown particularly well in Figs. 7 and 13. The possible significance of this configuration has been discussed earlier. Incidentally, Fig. 7 does not represent an aberrant stenotele, these configurations having been found in many stenoteles.

The origin of the operculum has been discussed in an earlier section and need not be repeated here.

Fig. 12 shows a structure which was found in the section of a stenotele, probably near its apical end. It is a cross-section through the region of the shaft bearing the spines and stylets. The three large dense structures (*St*) peripheral to the three small central dots probably correspond to the stylets. The three, small, central structures are very likely three spines. Their nearly circular appearance in cross-section contrasts them to the vanes in Fig. 17. It is interesting to note the manner in which the three presumed stylets interlock to form a triangular lumen, in cross-section. Such a relationship has not been described previously. It would seem to support the theory of Kepner *et al.* (1943, 1951) in which the magma is squirted from a nozzle. However, one would then expect to find an external tube of triangular form rather than the grooved tube of those authors. The present authors have not observed discharged tubes. The three structures of higher density than the matrix but of lower density and more granular texture than the spines and stylets, and lying just peripheral to the latter probably represent invaginated capsular wall-enclosed masses of the matrix from which the spines and stylets differentiate. The double membrane structure which is continuous about them, the spines and the stylets would seem to correspond to the invaginated capsular wall.

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Bibliography

Bedot, M., Recherches sur les cellules urticantes, *Rec. Zool. Suisse*, 1888, **4,** 51.

Brown, C. H., Keratins in invertebrates, *Nature*, 1950, **166,** 439.

Chun, C., Die Natur und Wirkungsweise der Nesselzellen bei Coelenteraten, *Zool. Anz.*, 1881, **4,** 646.

Du Plessis, G., Observations sur la Cladocoryne floconneuse, *Bull. Soc. Vaudoise Sc. Nat.*, 1884, **17,** 119.

Ewald, A., Über den Bau, die Entladung und die Entwicklung der Nesselkapseln von Hydra und *Porpita mediterranea* nebst einigen histologischen Bemerkungen über die letztere Form, *Verhandl. naturhist. med. Verein. Heidelberg*, N. F., 1916, **13,** 303.

Ewer, R. F., On the functions and mode of action of the nematocysts of hydra, *Proc. Zool. Soc. London*, 1947–48, **117,** 365.

Frey, H., Die Bedeckung wirbelloser Tiere, Göttinger Studien, 1847.

Hamann, O., Der Organismus der Hydroidpolypen, *Jenaische Z. Naturwissensch.*, 1882, **15,** 473.

Hamon, M., Cytochemical research on coelenterate nematocysts, *Nature*, 1955, **176,** 357.

Hyman, L. H., The Invertebrates: Protozoa through Ctenophora, New York, McGraw-Hill Book Company, 1940, 1–726.

Iwanzoff, N., Ueber den Bau, die Wirkungsweise, und die Entwickelung der Nesselkapseln der Coelenteraten, *Bull. Soc. Imp. Nat. Moscow*, 1896, **10,** 95, 323.

Jones, C. S., The control and discharge of nematocysts in Hydra, *J. Exp. Zool.*, 1947, **105,** 25.

Kanajew, J., Über die histologischen Vorgänge bei der

Regeneration von *Pelmatohydra oligactis* (Pall)., *Zool. Anz.*, 1926, **65,** 217.

Kepner, W. A., Reynolds, B. D., Goldstein, L., and Taylor, J. H., The structure, development and discharge of the penetrant of *Pelmatohydra oligactis* (Pall.), *J. Morphol.*, 1943, **72,** 561.

Kepner, W. A., Reynolds, B. D., Goldstein, L., Britt, G., Atcheson, E., Zielinski, Q., and Rhodes, M. B., The discharge of nematocysts of Hydra, with special reference to the penetrant, *J. Morphol.*, 1951, **88,** 23.

Moseley, H. N., On the structure of a species of Millepora occurring at Tahiti, Society Islands, *Phil. Tr. Roy. Soc. London*, 1877, **167,** 117.

Murbach, L., Zur Entwicklung der Nesselorgane bei den Hydroiden, *Zool. Anz.*, 1893, **16,** 174.

Murbach, L., Beiträge zur Kenntnis der Anatomie und Entwickelung der Nesselorgane der Hydroiden, *Arch. Naturgesch.*, 1894, **60,** 217.

Phillips, J. H., Jr., Isolation of active nematocysts of *Metridium senile* and their chemical composition, *Nature*, 1956, **178,** 932.

Picken, L. E. R., A note on the nematocysts of *Corynactis viridis*, *Quart. J. Micr. Sc.*, 1953, **94,** 203.

Robson, E. A., Nematocysts of Corynactis: The activity of the filament during discharge, *Quart. J. Micr. Sc.*, 1953, **94,** 229.

Schulze, F. E., Über den Bau von *Syncoryne sarsi* (Lovén), Leipzig, Wilhelm Engelmann, 1873.

Schulze, P., Der Bau und die Entladung der Penetranten von *Hydra attenuata* (Pallas), *Arch. Zellforsch.*, 1921–22, **16,** 383.

Semal-Van Gansen, P., La structure des nématocystes de l'Hydre d'eau douce, *Bull. Acad. roy. méd. Belgique*, 1954, (5)**40,** 269.

Weill, R., Contribution à l'étude des Cnidaires et de leurs nématocystes, Lille, *Trav. Stat. Zool. Wimereux*, 1934, **10/11,** 1.

Will, L., Die Klebkapseln der Aktinien und der Mechanismus ihrer Entladung, *Sitzungsber. Abhandl. Naturforsch. Ges. Rostock*, N. F., 1909, **1,** 1.

Explanation of Plates

Abbreviations used on Plates

C, capsule
CB, cnidoblast
cc, cnidocil chimney
cd, cnidocil
Co, core of cnidocil
EC, ectoderm
ECW, evaginated capsular wall
F, external filament
Gg, Golgi apparatus
ICW, invaginated capsular wall
m, matrix
Mi, inner membrane of capsule
Mn, nematocyte membrane
Mo, outer membrane of capsule
N, nucleus
oc, opercular cavity
op, operculum
P, periderm
Pl, plug of matrix material
Pm, plasma membrane
S, spine
sp_1, member of group of nine outer supporting structures
St, stylet
T, tubule
Va, vacuole

In each figure the magnification mark, unless noted otherwise, indicates one micron.

Plate 28

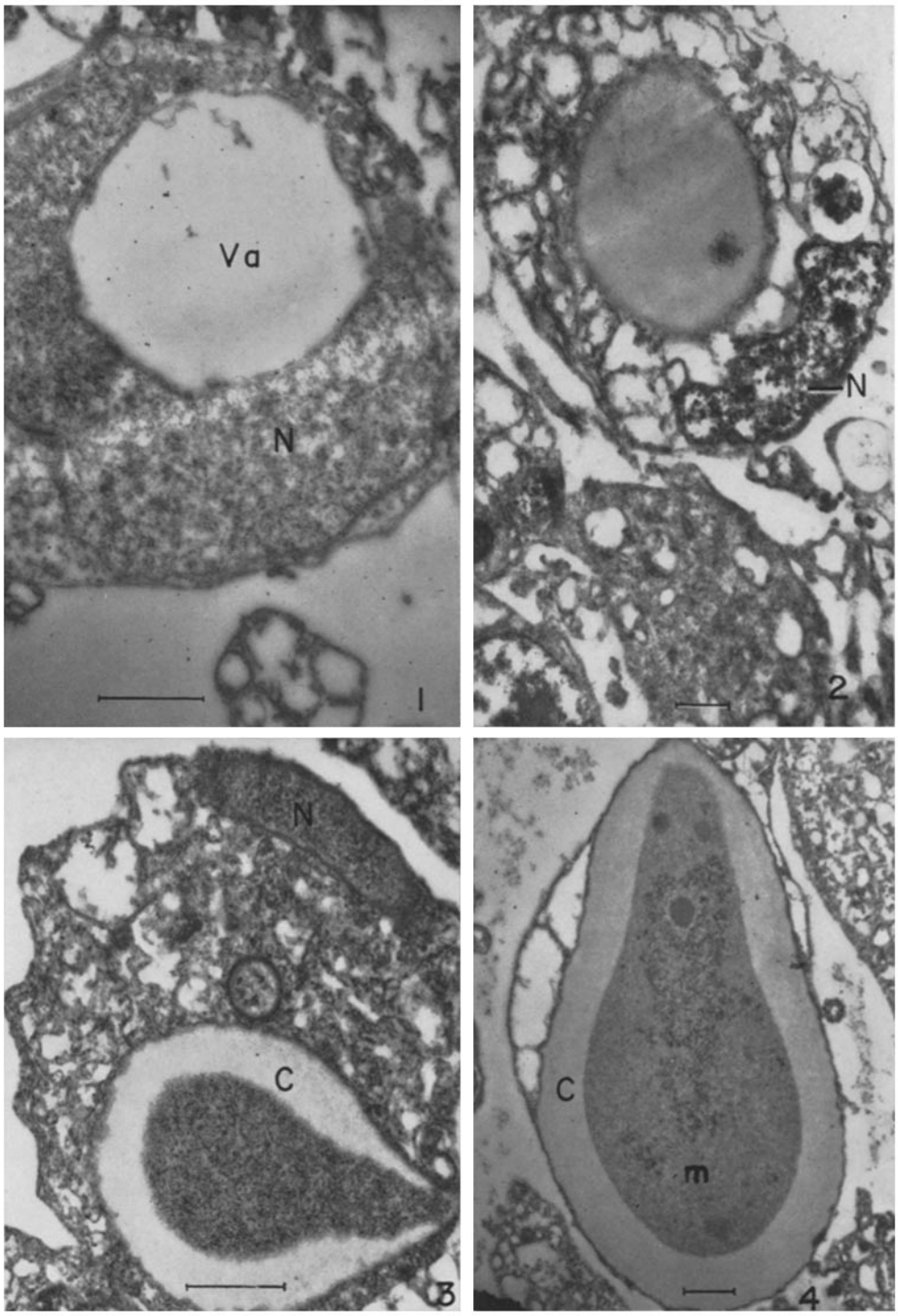
All of the figures on this plate illustrate early stages of nematocyst development, or cnidoblast differentiation.

Fig. 1. Section showing a very early stage of nematocyst formation. Note the nucleus (*N*) encircling a vacuole (*Va*). × 15,000.

Fig. 2. Section through a cnidoblast. Of particular interest is the formation of the capsule wall and the change in density of the intracapsular contents. × 7,000.

Fig. 3. Section through a cnidoblast showing a wide capsular wall with a dense granular matrix. The capsular wall is incomplete, indicating that this is probably a nearly sagittal section. × 14,000.

Fig. 4. Section through a developing nematocyst where the capsule wall is complete, indicating this is an oblique section. The intracapsular matrix (*m*) is heterogeneous. × 7,000.



(Chapman and Tilney: Nematocysts of hydra. II)

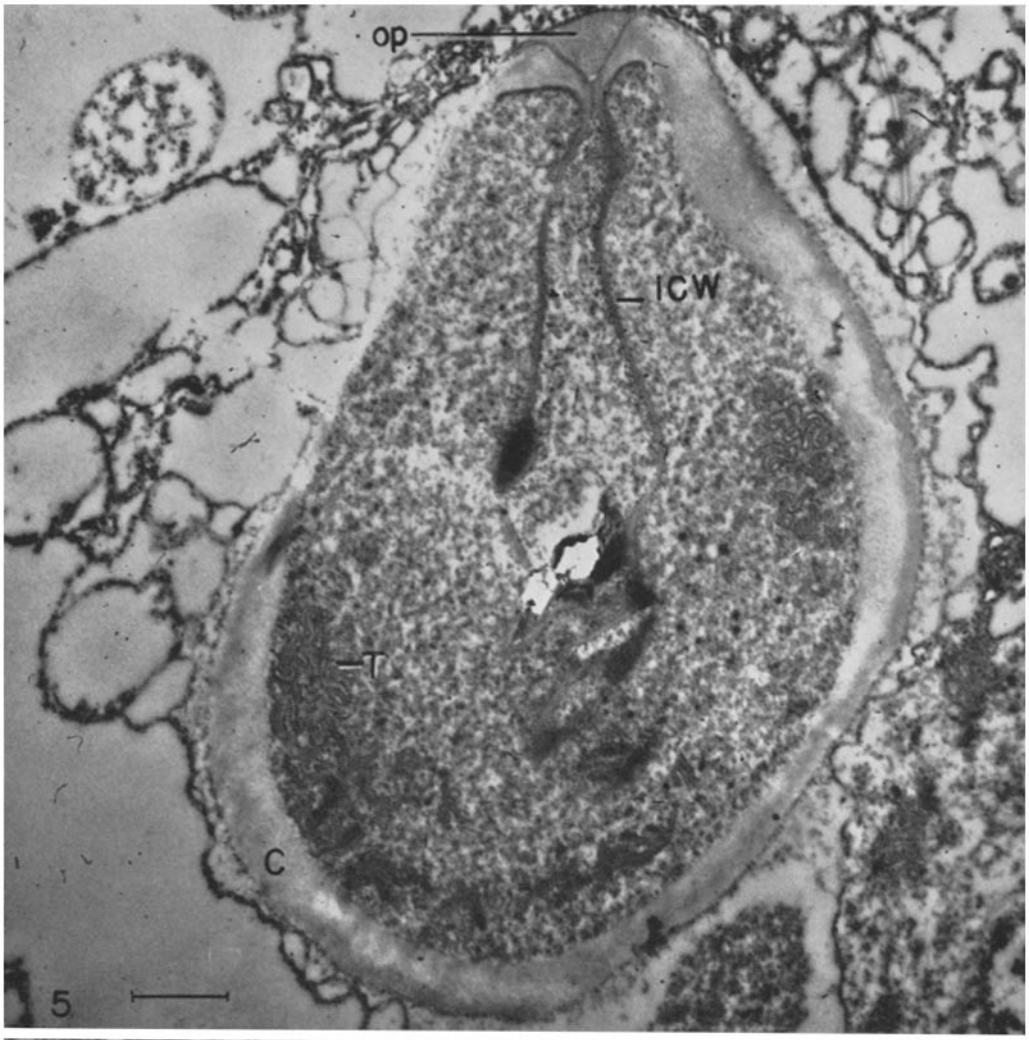
PLATE 29

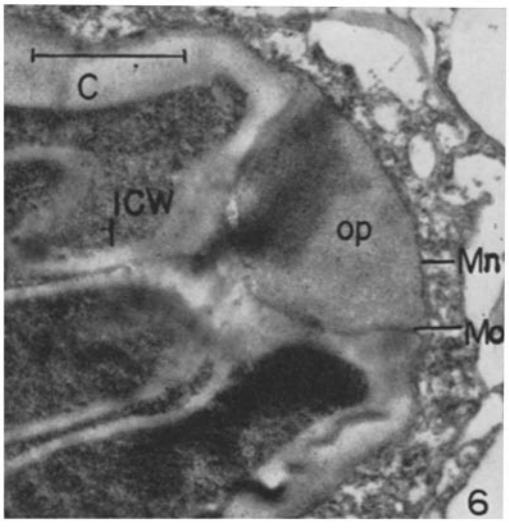
All of the figures on this plate show developmental stages of the stenoteles.

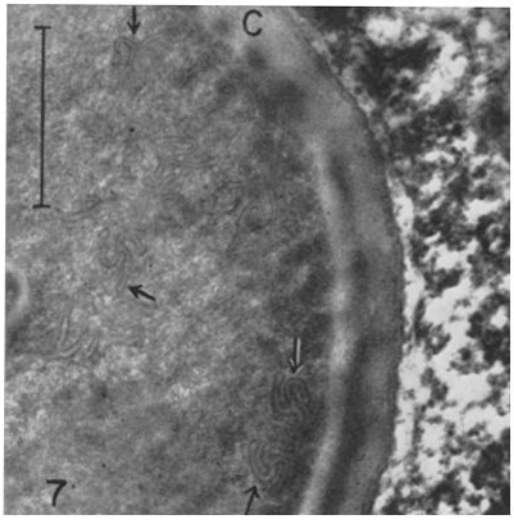
FIG. 5. Longitudinal section showing an incomplete capsular wall (*C*), an operculum (*op*) of slightly greater density than the capsular wall, and differentiating "tubules" (*T*). It appears that an ingrowth or simultaneous formation and invagination of capsular material from the apex of the capsule is responsible for the development of the "invaginated capsular wall" (*ICW*). × 13,000.

FIG. 6. Section through the opercular region of a stenotele. The distal surface of the operculum appears to be bounded by the nematocyte membrane (*Mn*). The proximal surface appears to be bounded by a continuation of the outer membrane (*Mo*) of the capsule. × 20,000.

FIG. 7. Longitudinal section through the capsule and intracellular substance of a developing stenotele. The three-bladed propeller configurations are extremely prominent and are indicated by the arrows. × 23,000.







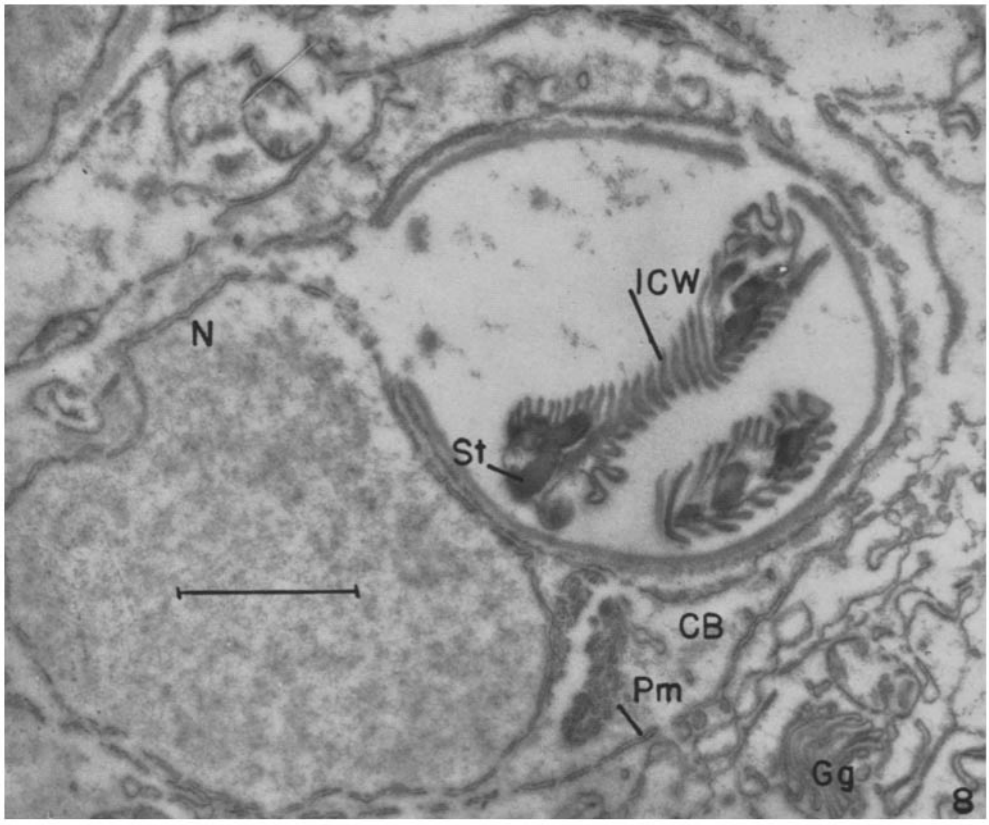
(Chapman and Tilney: Nematocysts of hydra. II)

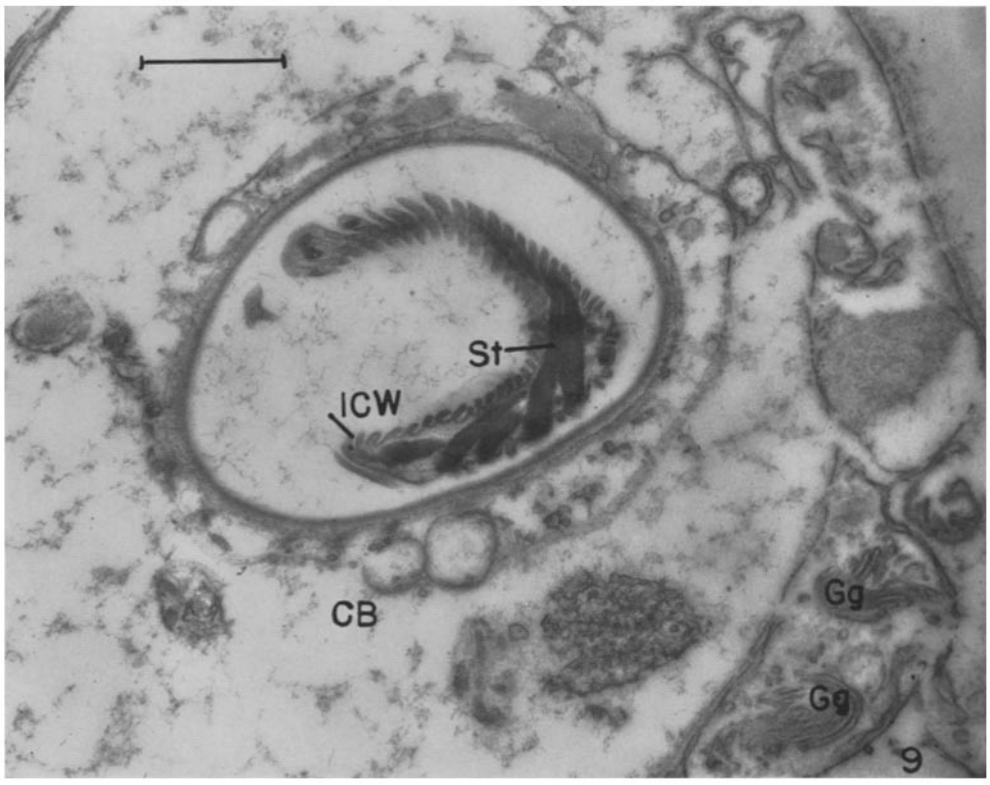
PLATE 30

The two figures on this plate (also Figs. 13, 16, and 17) illustrate the appearance of material which was fixed with $KMnO_4$.

FIG. 8. The cytoplasmic structures are better preserved than they were with OsO_4 fixation; a double nuclear membrane appears around the nucleus (*N*); the plasma membrane (*Pm*) of the cnidoblast (*CB*) is well defined. However, interruptions in these membranes and in the capsule suggest that even better fixation could be attained. A Golgi zone (*Gg*) appears in one cell. Within the capsule, the invaginated capsular wall (*ICW*) and dense bodies representing the primordial stylets (*St*) are seen. × 23,000.

FIG. 9. The immature stylets (*St*) have elongated somewhat within the invaginated capsular wall (*ICW*) shown in this figure. Golgi zones (*Gg*) appear in the small portion of a cell adjacent to the cnidoblast (*CB*). × 19,000.





(Chapman and Tilney: Nematocysts of hydra. II)

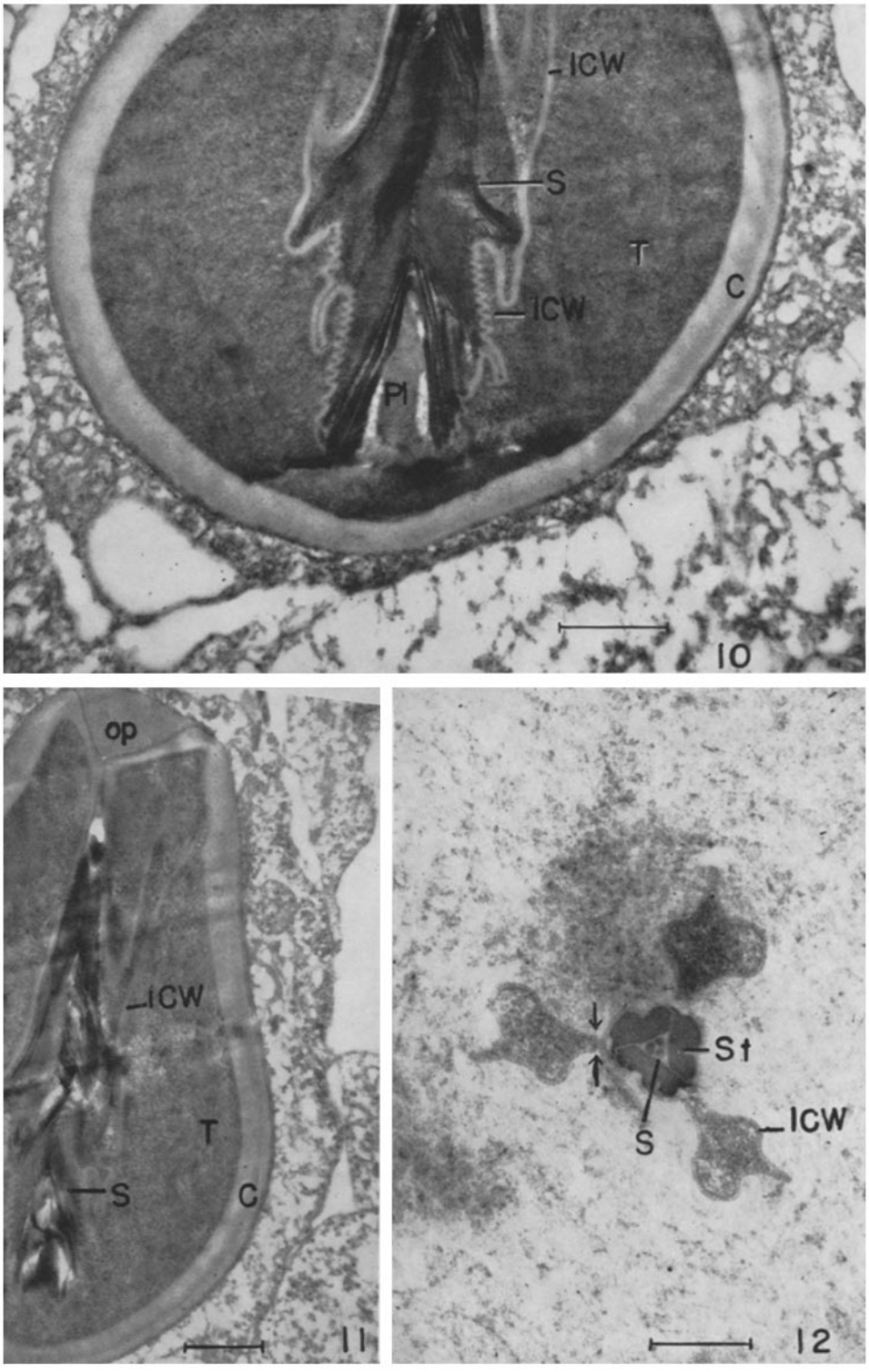
PLATE 31

Further developmental stages of the stenoteles.

FIG. 10. Longitudinal section showing the spines (*S*), the invaginated capsular wall (*ICW*), and the "tubules" (*T*) which have now attained a nearly mature state within the capsule. The plug of matrix material (*Pl*) at the base of the capsule may represent what will become the apical end of the discharged filament. × 15,000.

FIG. 11. Longitudinal section. Relationships similar to those in Fig. 10 appear here. × 11,000.

FIG. 12. Transverse section through the apical end of the stenotele. Note the dense spines (*S*) and the three structures peripheral to them which presumably are the stylets (*St*). The three structures peripheral to the stylets are considered to represent masses of intracapsular matrix enclosed within folds of the *ICW*. The connections existing between the most peripheral structures and the stylets (indicated by the arrows), are of interest. Note the method of interlocking of the stylets. × 14,000.



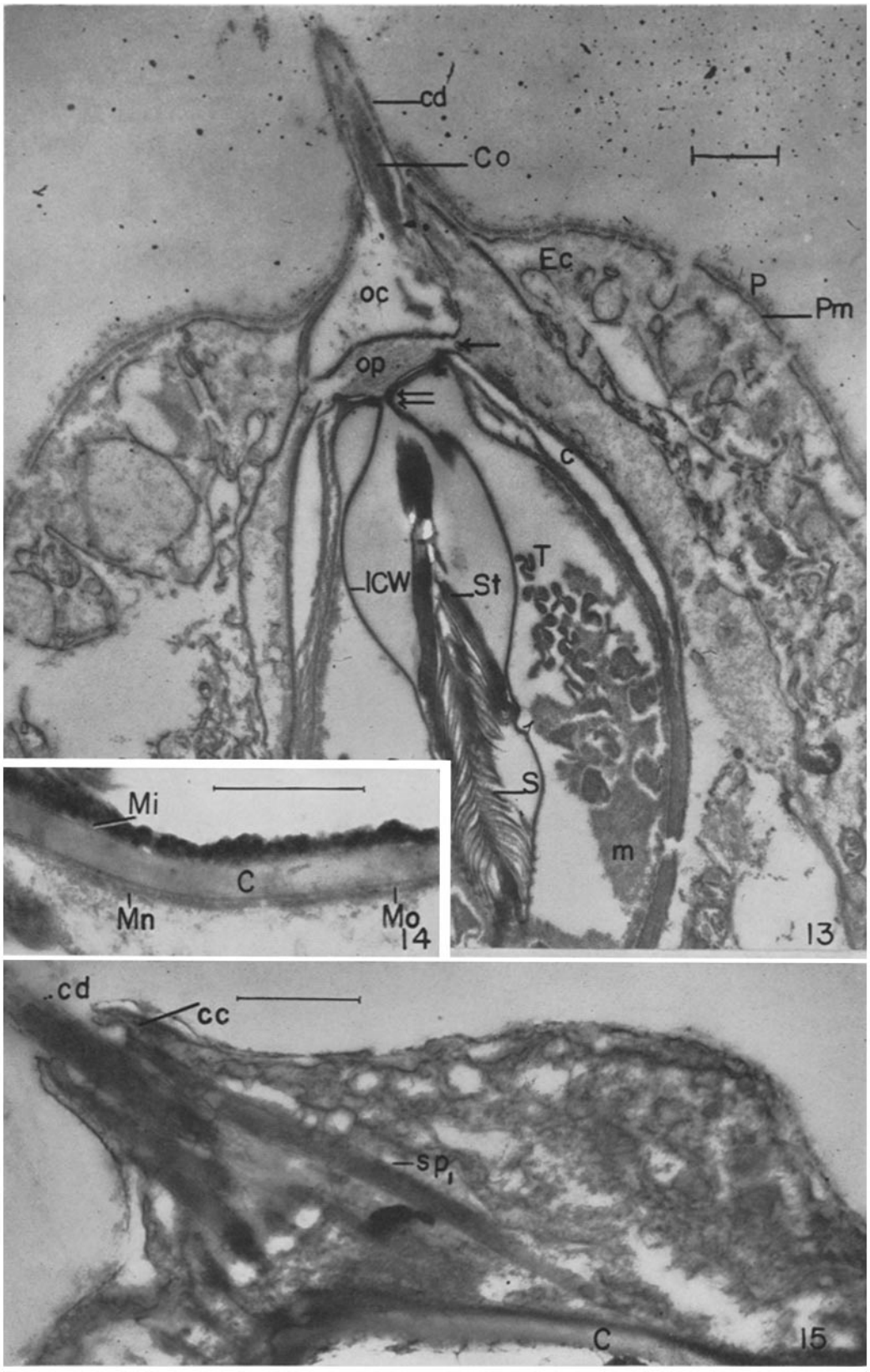
(Chapman and Tilney: Nematocysts of hydra. II)

PLATE 32

FIG. 13. Longitudinal section through a stenotele. Of greatest interest are the spines (*S*), the invaginated capsular wall (*ICW*), the capsule (*C*), and the tubules (*T*) usually surrounded by a matrix (*m*). Note that the operculum (*op*) is continuous with the nematocyte cytoplasm at the arrow, that the operculum is separated from the opercular cavity (*oc*) by a dense line (apparently two membranes), and that the invaginated capsular wall is continuous with the capsule at the position marked by the double arrow. × 14,000.

FIG. 14. Longitudinal section through the capsular wall of a stenotele showing an internal limiting membrane (*Mi*), a chitinous or keratin capsular wall (*C*), an outer capsular membrane (*Mo*), and a nematocyte membrane (*Mn*). × 24,000.

FIG. 15. Longitudinal section through the opercular region of a stenotele. Of particular interest is the arrangement of one of the nine outer "supporting structures" (sp_1) with respect to the capsule (*C*) and the cnidocil (*cd*). × 19,000.



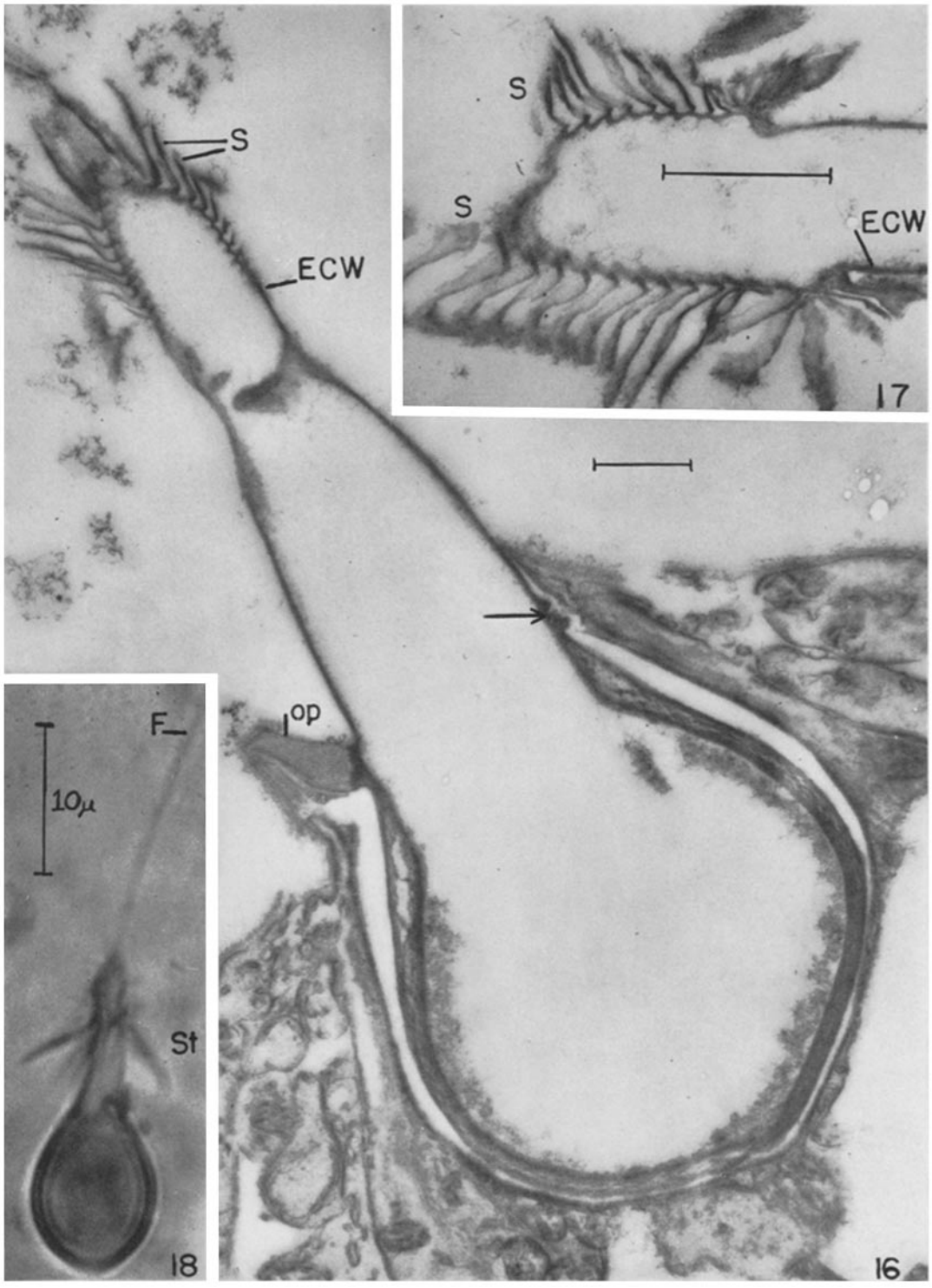
(Chapman and Tilney: Nematocysts of hydra. II)

PLATE 33

FIG. 16. Longitudinal section of a discharged stenotele. The sprung operculum (*op*) and spines (*S*) or vanes on the evaginated capsular wall (*ECW*) are readily seen. This figure indicates that the *ECW* is in continuity with the capsule. × 14,000.

FIG. 17. Longitudinal section of the spiny region of a stenotele's evaginated capsular wall (*ECW*). This figure indicates that, in this region, the armature of the *ECW* is more aptly described as consisting of vanes than of spines. (The spines or vanes are labelled *S*, however). × 25,000.

FIG. 18. Photomicrograph taken with a Baker interference microscope. The external filament (*F*) is visible, as are the stylets (*St*). × 2,200.



(Chapman and Tilney: Nematocysts of hydra. II)