The background of the cover is a detailed, high-magnification micrograph of graptolite fossils. The image shows a complex, branching, and somewhat circular pattern of fine, parallel lines, characteristic of the periderm and its derivatives in graptoloids. The colors are muted, with shades of purple, blue, and grey.

Ultrastructural Studies on  
Graptolites, 2: The Periderm and  
Its Derivatives in the Graptoloidea

ADAM URBANEK  
and  
KENNETH M. TOWE

## SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

*Smithsonian Annals of Flight*  
*Smithsonian Contributions to Anthropology*  
*Smithsonian Contributions to Astrophysics*  
*Smithsonian Contributions to Botany*  
*Smithsonian Contributions to the Earth Sciences*  
*Smithsonian Contributions to Paleobiology*  
*Smithsonian Contributions to Zoology*  
*Smithsonian Studies in History and Technology*

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. DILLON RIPLEY  
*Secretary*  
Smithsonian Institution

Ultrastructural Studies on  
Graptolites, 2: The Periderm and  
Its Derivatives in the Graptoloidea

*Adam Urbanek*  
*and Kenneth M. Towe*



SMITHSONIAN INSTITUTION PRESS

City of Washington

1975

## ABSTRACT

Urbanek, Adam, and Kenneth M. Towe. Ultrastructural Studies on Graptolites, 2: The Periderm and Its Derivatives in the Graptoloidea. *Smithsonian Contributions to Paleobiology*, number 22, 48 pages, 3 figures, 24 plates, 1 table, 1975.—The ultrastructure of the organic periderm in *Didymograptus* sp. (Lower Ordovician), *Pristiograptus dubius* (Suess), and in the retiolitid *Holoretiolites mancki* (Münch) (both Upper Silurian), isolated by chemical treatment, has been studied with the transmission electron microscope. In the first two graptoloids, with continuous peridermal walls in the rhabdosome, the periderm is composed of the major fusellar and cortical components which are essentially the same as those recognized earlier in the dendroid graptolites (Urbanek and Towe, 1974). In addition, both graptoloids examined show important differences in the fabric ultrastructure of some homologous parts of the rhabdosome such as the nema in *Didymograptus* sp., the virgula in *P. dubius*, as well as the prosicula in both. These occurrences of sharp differences in the submicroscopic structure of homologous parts of rhabdosomes within the Graptoloidea are suggestive of rather substantial phylogenetic changes in the history of the group at the ultrastructural level.

In addition to the peridermal materials previously recognized in the dendroids, certain parts of the rhabdosomes in graptoloids are constructed of a peculiar fabric termed the *virgular fabric*. It has been recognized so far in the virgula of *Pristiograptus dubius* and in the lists of the peridermal framework (*clathrium*) of *Holoretiolites mancki*, where it is the only component of the skeleton. It is composed of layers made of lucent fibrils with a unique substructure, embedded in an electron dense and homogeneous matrix, and separated by thin layers formed by this matrix alone. The biochemical relationships of these fibrils with extant fibrous materials are uncertain but a correlation with certain collagens has been suggested.

The structural relationships of the outer cortical deposit of thecae examined in *Didymograptus* sp. and in *Pristiograptus dubius* are indicative of different modes of secretion of the cortex in both. In *Didymograptus* sp. the cortex is formed through an accumulation of the overlapping outer lamellae of fuselli, while in *Pristiograptus dubius* the layers of the cortex are laid down over the surface of the fuselli as independent units. Moreover, other observations seem to indicate that in *Didymograptus* sp. the cortex has been formed in a somewhat different way at certain places on the rhabdosome. There does not seem to be any single, uniform pattern of secretion of the cortex in the Graptoloidea.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SI PRESS NUMBER 5190. SERIES COVER DESIGN: The trilobite *Phacops rana* Green.

---

### Library of Congress Cataloging in Publication Data

Urbanek, Adam.

Ultrastructural studies on graptolites.

(Smithsonian contributions to paleobiology, no. 20, 22)

Supt. of Docs. no.: SI 1.30:22

Contents: 1. The periderm and its derivatives in the Dendroidea and Mastigograptu. 2. The periderm and its derivatives in the Graptoloidea. 1. Graptolites. 2. Paleontology—Ordovician-Silurian I. Towe, Kenneth M., joint author. II. Title. III. Series: Smithsonian Institution. Smithsonian contributions to paleobiology, no. 20 [etc.]

QE701.S56 no. 20, etc. [QE840.5] 560'.8s [563'.71] 73-18097

---

## Contents

	<i>Page</i>
Introduction . . . . .	1
Acknowledgments . . . . .	1
Origin and State of Preservation of the Material . . . . .	1
Previous Work and Methods of Study . . . . .	2
Classification and Terminology of Peridermal Tissues in Graptolites . . . . .	2
Ultrastructure of the Nema . . . . .	4
The Nema in <i>Didymograptus</i> sp. . . . .	4
The Nema (Virgula) in <i>Pristiograptus dubius</i> . . . . .	5
Comparison and Conclusions Concerning the Nema . . . . .	6
Ultrastructure of the Prosicula . . . . .	7
The Prosicula in <i>Didymograptus</i> sp. . . . .	7
The Prosicula in <i>Pristiograptus dubius</i> . . . . .	14
Comparison and Conclusions Concerning the Prosicula . . . . .	15
Ultrastructure of the Metasicula . . . . .	15
The Metasicula in <i>Didymograptus</i> sp. . . . .	16
The Metasicula in <i>Pristiograptus dubius</i> . . . . .	16
Comparison and Conclusions Concerning the Metasicula . . . . .	18
Ultrastructure of Thecae . . . . .	18
The Thecae in <i>Didymograptus</i> sp. . . . .	18
The Thecae in <i>Pristiograptus dubius</i> . . . . .	20
Comparison and Conclusions Concerning the Thecae . . . . .	21
Ultrastructure of the Clathrium in <i>Holoretiolites</i> . . . . .	22
Literature Cited . . . . .	23
Plates 1-24 . . . . .	25



# Ultrastructural Studies on Graptolites, 2: The Periderm and Its Derivatives in the Graptoloidea

*Adam Urbanek*  
and *Kenneth M. Towe*

## Introduction

This paper is the second in a series of ultrastructural investigations of the extinct Paleozoic graptolites and related organisms having preserved organic skeletons. The first paper dealt with the dendroids, as well as *Mastigograptus*, and the microstructural features observed were classified into several structural categories. The present paper extends this work and adds some additional features as it considers another graptolite order, the Graptoloidea. As in the first paper, the well-preserved material from the rocks of Poland provides the specimens for which the ultramicrotome techniques of electron microscopy are ideally suited. Complete rhabdosomes of both *Didymograptus* sp. and *Pristiograptus dubius* are studied and compared with regard to the nema, the prosicula, the metasicula, and the thecae. The clathrium of *Holoretiolites mancki* is treated separately.

ACKNOWLEDGMENTS.—This collaborative study was made possible through a visiting postdoctoral research award from the Smithsonian Office of Academic Studies to Adam Urbanek. The preparation of the manuscript was supported by a grant from the Zoological Committee of the Polish Academy

of Sciences and the Smithsonian Foreign Currency Program. We are grateful to Professor R. Kozłowski (Warsaw) for material of *Didymograptus* sp., to Mr. C. Kulicki (Warsaw) for assistance with the scanning electron micrographs, and to Miss L. Luszczewska (Warsaw) and Mr. D. Dean (Washington) for light micrographs. Dr. Robert B. Neuman (USGS) read a draft of the manuscript and offered several helpful suggestions and criticisms.

## Origin and State of Preservation of the Material

The material selected for the present study consists of fragments of skeletal rhabdosomes of three graptoloid species: (1) *Didymograptus* sp., a representative of the suborder Didymograptina, Lower Ordovician; (2) *Pristiograptus dubius* (Suess), a representative of the suborder Monograptina, Upper Silurian; and (3) *Holoretiolites mancki* (Münch), a representative of a specialized family Retiolitidae, within the suborder Diplograptina, Upper Silurian.

The species were selected to represent quite different adaptive and structural types in an attempt to gain a representative insight into the ultrastructure of peridermal derivatives in the Graptoloidea. The first two species, representing graptoloids with a normal rhabdosome producing a kind of envelope around the zooids and made of continu-

---

*Adam Urbanek, Faculty of Geology, University of Warsaw, 02-089 Warsaw, Poland. Kenneth M. Towe, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

ous peridermal walls (a kind of "test"), are described first. The highly specialized graptoloid, *H. mancki*, with a periderm transformed into lists producing only a framework for the zooids of the colony is described separately.

All the specimens studied were etched from a limestone or marly matrix by use of acetic or hydrochloric acid. The origin, age, and state of preservation of the specimens studied are as follows:

1. *Didymograptus* sp., with numerous siculae, thecae, and proximal parts of rhabdosomes exceptionally well preserved, were obtained from marly limestone cores of the Podborowisko deep boring (Bialowieza region, NE Poland). The samples were taken from a depth of 395.10–396.30 m. This representative of the genus *Didymograptus* cannot be identified at the moment with any known species, but because of its nearly horizontal stipes, the *bifidus* stage of development, and the shape of the sicula, it bears a close resemblance to *Didymograptus* n. sp. "a," aff. *D. gracilis* Törquist as described by Skevington (1965:21–22, fig. 24). It differs, however, in the proportions and degree of overlap of the thecae.

It is found associated with *Holmograptus lentus* (Törquist) and proximal parts of a *Tetragraptus*, which on the basis of its development (initial bud arises in the prosicula, *gibberulus* stage of the isograptid type of development) may be assigned to *T.* cf. *bingsbyi* (Hall). Both forms are indicative of the age of our *Didymograptus* sp., probably being the *Didymograptus hirundo*-*D. bifidus* zones, equivalent to the Langevojan-Valastean substages of Ontikan (Lower Ordovician of Estonia and Sweden; Jaanusson, 1960; Skevington, 1965).

The siculae of this *Didymograptus* sp. have been described and figured by Kozłowski (1971:327–329, fig. 10, pls. 1, 2, and scanning electron micrographs on pl. 3).

2. *Pristiograptus dubius* (Suess), probably its subspecies *frequens* (Jaekel) = *ludlowensis* Bouček. Exceptionally well-preserved siculae and proximal parts of rhabdosomes have been etched from a number of erratic boulders of Baltic origin found in the glacial deposits of Poland. The primary boulder is number S.36 in the collection of the Institute of Palaeontology in Warsaw. It was found at the foot of a high cliff made of moraine deposits in Jarosławiec, Western Pomerania, Poland. Specimens of *P. dubius* from this boulder

were described by Urbanek (1953, 1958), and the associated fauna indicate the *Lobograptus scanicus parascanicus* zone (Ludlovian, Upper Silurian; Urbanek, 1966, pl. 1).

3. *Holoretiolites mancki* (Münch) is a retiolitid etched out of the marly limestones of the bore core at Mielnik-on-the-Bug (E. Poland), from a depth of 964.90 m, at the top of the *Lobograptus invertus* zone (Ludlovian, Upper Silurian; Urbanek, 1966, pl. 1).

### Previous Work and Methods of Study

Previous work on graptoloids using the electron microscope has been confined to only a few studies (Wetzel, 1958; Kraatz, 1964, 1968; Berry and Takagi, 1970, 1971; Rickards, Hyde, and Krinsley, 1971). Except for a very few micrographs from ultrathin sections, the nature of the techniques involved makes this earlier work difficult to compare directly. A few attempts at comparisons have been made in an earlier paper (Urbanek and Towe, 1974).

The principal methods used in the study of the present material with the transmission electron microscope were those of ultramicrotomy and have been described in an earlier paper (Urbanek and Towe, 1974).

The scanning electron micrographs of the clathrium in *Holoretiolites mancki* were made with a Cambridge Stereoscan MK.II at the electron microscope laboratory of the Polytechnic in Warsaw (Poland). The specimens were gold coated.

### Classification and Terminology of Peridermal Tissues in Graptolites

A terminology for the observed ultrastructural features of the periderm in the Graptoloidea is patterned after the present authors' earlier suggestions (Urbanek and Towe, 1974). Two main categories of structural characters are distinguished: (1) the category of *fabric*, and (2) the category of *tissue*. The fusellar, cortical, sheet, and crassal fabrics were defined by the nature of their unit elements and their particular pattern. *Fusellar fabric* is composed of slightly wavy, branched, or anastomosing fibrils, with no preserved ground substance. The characteristic pattern is a meshwork

of fibrils with a spongy appearance. The *cortical fabric* is composed of straight, unbranched fibrils, embedded in an electron homogeneous and discontinuously distributed ground substance. The ground substance itself is organized into a number of transverse rods interconnecting adjacent fibrils. The characteristic pattern is a parallel arrangement of rather loosely packed fibrils assembled into layers or plies, with frequent change of orientation of fibrils in adjacent layers. The *sheet fabric* is an electron-dense, homogeneous or very densely reticulated material, forming pellicles delimiting particular fuselli or layers of cortical tissue. The *crassal fabric* is an electron-dense and homogeneous material, sometimes with indistinct traces of layering but usually lacking a pattern. This fabric produces compact walls of considerable thickness in sheets of stolons and in secondary thecal walls in *Mastigograptus* sp. There is a close biochemical relation between the cortical and fusellar fibrils (Urbanek and Towe, 1974). More evidence to support this view is given below. The *cortical* and *fusellar tissues* differ in their predominance of a given fabric and in its origin and mode of forma-

tion. Details of this classification are given in Urbanek and Towe (1974).

The ultrastructure of the periderm and its derivatives in the Graptoloidea necessitates additional terminology for a material recognized within (1) the nema (or virgula) of *Pristiograptus dubius*, and (2) lists of the clathrium in *Holoretiolites mancki*. Similar material also occurs in the thickening of the interthecal septa and in the heavy cortical coating of the virgula in *Pristiograptus dubius*. The term *virgular fabric* is suggested to denote this particular material. The unit elements of the virgular fabric are composed of virgular fibrils with a unique substructure and embedded in matrix. Because of the presence of these two structural components, this fabric may be considered as polytypic as defined by Waddington (1962). When compared with the typical cortical fabric a characteristic feature of virgular fabric is a reversal of electron densities. The fibrous components of the virgular fabric appear lucent on a background of electron-dense matrix. The typical cortical fabric is characterized by a matrix less dense (or equally dense) than its fibrous component. In addi-

TABLE 1.—Comparison of virgular fabric

Structural Features	<u>Pristiograptus dubius</u>	<u>Holoretiolites mancki</u>
Layering pattern	Layers delimited by thin sheets of matrix	Layers delimited by wide bands of matrix
Packing of fibrils	Rather lightly packed, scarce interfibrillar matrix, frequent interfibrillar spaces	Loosely packed, abundant interfibrillar matrix, few or no interfibrillar spaces
Structural features of fibrils seen on transverse sections	Diameter within single layer uniform, "septation" rather radially arranged, darker line limited to the outer zone of fibrils	Diameter within single layer varies, "septation" more bilaterally than radially arranged, darker lines deeply penetrating
Structural features of fibrils seen on longitudinal sections	Oblique striation, darker lines crossing the fibrils transversely at an angle toward the long axis of the fibril	Oblique striation, darker lines crossing the fibrils transversely at an angle toward the long axis of the fibril
Occurrence	Outer part of virgula	All lists of clathrium

tion, and perhaps more importantly, the virgular fibrils show a unique internal substructure. Examined in transverse section they appear septate, with numerous, dense straight lines stretching toward the center (Plate 1: figures 1, 2) and continuous with the surrounding matrix. The character of this "septation" is slightly different in the virgula of *Pristiograptus dubius* and the lists of *Holoretiolites mancki*, but it is essentially similar in both (Plate 1: figures 1, 2). By way of comparison, typical cortical fibrils are either solid or have a lucent core, but always show a high electron density (compared to their background) and are usually lacking in a commonly discernible substructure. Examined in longitudinal section the virgular fibrils reveal a distinct oblique striation brought out by fine, dark lines on the lucent background of the fibrils (Plate 1: figures 3, 4). These are inclined at an angle toward the long axis of the fibrils. Here again they differ from the typical cortical fibrils, which are usually devoid of any such striation when viewed laterally. A comparison of the virgular fabric is shown in Table 1.

### Ultrastructure of the Nema

The nema is a threadlike extension of the *apex prosiculae* and is a very characteristic feature of all graptoloids. Although the function of such nemata has not been determined unequivocally, the most reasonable primary function which may be ascribed to them is that they were connected with a suspension or buoyancy device (Bulman, 1964, 1970), although Kirk (1972) considers their role as a kind of stabilizer. Whatever the primary function of the nema might be, it later acquired an additional function where it also serves in scandent graptoloids as an axis of the rhabdosome.

In *Didymograptus* sp. the nema is stretching free because of the horizontal growth of the thecae and therefore represents a primary *axonolipous* condition. In *Pristiograptus dubius* (Suess) the nema is embedded in the dorsal wall of the rhabdosome because of the scandent growth of the thecae and therefore represents a secondary *axonophorous* condition.

#### THE NEMA IN *Didymograptus* sp.

Transverse sections through the nema taken above the apex of the prosicula at a distance

equal to or greater than the length of the prosicula reveal that it is essentially a thick-walled tubule (Plate 2: figure 1). In a section of a nema whose outer diameter is about  $40\mu$ , the internal canal is about  $15\mu$  in diameter. Its cavity is filled with a loose mat of delicate fibrils. These are about  $400\text{ \AA}$  in diameter, show frequent branching or anastomosing, and are interconnected to produce a spongy appearance. They are similar to the fusellar fabric as defined previously (Urbanek and Towe, 1974), but they tend to be more delicate. The loose fibrils of the internal canal of the nema are continuous at the marginal zone with the fibrils of the innermost layer of the wall proper (Plate 2: figure 2). The ordered and highly packed fibrils of the wall of the nema pass into the loose network of the canal fibrils. This may indicate that both fabrics have a similar composition which is capable of producing two different patterns. Because of this intergradation between the fibrous components of the nema, it may be described as a system open toward its inner cavity. There is no sheet fabric delimiting the wall proper from the internal canal.

On longitudinal sections of the nema, very faint regular lines, convex toward the prosicula, were observed in the basal part of the nema (Plate 2: figure 2). These density differences seem to be faintly marked growth lines indicating a discontinuity in the formation of the material filling the internal canal of the nema. Such growth lines might be correlated with the extension of the helical line of the base of the nema in *Didymograptus* sp. Their presence in the canal above this base has not been proved. A possible relationship between these growth lines and the helical line is discussed below in connection with the problem of the diaphragm, a pellicle separating the cavities of the nema and prosicula and representing a condensation of these lines.

The wall of the nema is a distinctly layered structure with a clear cortical appearance (Plate 2: figure 1; Plate 3: figures 1, 2). On the specimens investigated the number of layers varies from 8 to about 20. The layers are deposited concentrically and the majority of them are continuous around the circumference, with only a few tapering at places. Each layer is delimited by sheets composed of densely reticulated material continuous with the ground substance between the cortical fibrils with-

in the layer. A number of intrasheet vesicles, rounded or elongated, have been recognized at places (Plate 3: figure 1). These are very similar to vesicles found within the cortex in *Dictyonema* sp. (Urbanek and Towe, 1974), each provided with its own pellicle.

The fabric within the layered structure has a distinct cortical appearance, being composed of fibrils arranged uniformly within a given layer and oriented parallel or oblique to the long axis of the nema, and a ground substance, or matrix, placed between the fibrils. Oblique sections reveal further details of the arrangement and structure of the cortical components of the nema (Plate 3: figures 1-3). Cortical fibrils lie parallel to each other and are interconnected by matrix material organized into frequent but rather irregular interconnecting rods (Plate 3: figures 2, 3). These oblique sections tend to exaggerate the thickness of the layers, showing a considerable amount of mesh material (m) composed of loosely packed fibrils and anastomosing to produce spongy intercalations between the layers of the cortical fabric (Plate 3: figure 1). The fibrils within these intercalations pass continuously into the cortical fibrils in adjacent layers, supporting the identity in the chemical nature of the fibrous component in both cases. An explanation for why the same material produces different patterns may lie in the presence or absence of ground substance. This latter seems very scanty in the area showing the mesh pattern. The interconnecting rods are reduced to small rugosities or spokes on the surface of the fibrils and only rarely do they span the fibrils. Too small an amount of matrix might result in a reduction of the ability of the fibrils to remain in register (Urbanek and Towe, 1974).

Longitudinal sections through the wall of the nema confirm that the longitudinal orientation of the fibrils is the predominant one. There is additional evidence for deviation in some layers and a shift toward an oblique arrangement of the fibrils. These sections show the organization of the matrix into numerous rods, many connecting the adjacent fibrils at irregular intervals (Plate 3: figure 3).

#### THE NEMA (VIRGULA) IN *Pristiograptus dubius*

The formation of the *nema*, which is later

embedded into the dorsal wall of the rhabdosome and therefore called the *virgula*, is a rather complicated process in the monograptids (Urbanek, 1953, 1958). Existing data suggest that the nema usually appears in two generations. An early, incipient nema, the direct extension of the apex of the prosicula (*nema prosiculae*), is present in juvenile rhabdosomes. Later, at least in some monograptids including *P. dubius*, it is subject to breakage and replacement by a regenerative nema. This latter is statistically the most common form of the *virgula* in adult rhabdosomes. Only in a minority of specimens is the *virgula* of the adult colony formed as the direct extension and thickening of the *nema prosiculae*. In both nemata the *virgula* is superficially very much the same and the two types mentioned above can be distinguished only by consideration of the structural details at the apex of the prosicula (Urbanek, 1953, 1958). They could, of course, differ in microstructure, but this has not been detected so far. The question therefore arises as to which of these two generations (or types) the *virgula* of the specimen investigated in this paper belongs.

In spite of small damage to the prosicular wall just below the apex of the prosicula, the following facts are indicative of its primary nature: (1) it is a nema of a juvenile rhabdosome (composed of the sicula and 1½ thecae). A broken nema would not have had time enough to be completely replaced by a regenerative thread and would represent only one of the known early stages of the regeneration; (2) the basal part of the nema bears traces of some extension with about five small longitudinal rods of the prosicula on it. In the case of the regenerative nema there are no more than three such rods and they are usually very broad.

Transverse ultrathin sections through the nema examined with the electron microscope reveal that at different levels of sectioning the nema may appear: (1) as a thick-walled tubule provided with a narrow internal canal (some 1μ-1.6μ in diameter) (Plate 4: figure 1), or (2) as an essentially solid rod whose central part is filled with a porous material (Plate 4: figure 2). Examination of a number of the transverse ultrathin microtome sections indicates that portions of the hollow and the filled nema may repeat along the thread, and that one of the filled segments lies close to the apex of the

proscicula. The only difference between the hollow and filled nema is in the development of the loosely packed fibrous material of the internal canal.

In all sections examined, the wall of the nema is a distinctly layered structure. Particular layers are separated by an electron-dense and homogeneous sheet fabric, which is more distinct in the peripheral zone of the nema and rather faint in the adaxial zone of the wall. Some layers extend for about half of the circumference and they taper gradually, while the two sheets delimiting them merge into a single sheet (Plate 4). The layers are not quite concentrically laid down, their number being greater on one side (about 17) and lesser on the other (about 11–12), which results in differences in the thickness of the wall.

The outline of the nema is somewhat rough because its outer surface shows a number (4–6) of gentle ridges (rugosities), which are undoubtedly the extension of the longitudinal rods of the proscicula. They rise above the surface because of a local increase in thickness of particular layers, and/or because of the local addition of some intercalary layers within the wall of the nema.

Each layer seems to be composed of a rather compact material, provided with numerous irregular, sometimes angular, sometimes rounded, or elongated holes. At places, especially along sheets, these holes are transformed into fissures. The concentration of these holes seems to increase toward the center and the layers surrounding the internal canal are thus porous (Plate 4: figure 1). At the same time the electron density of the sheet behaves in an opposite manner, becoming less distinct toward the center.

Higher magnification pictures reveal a complex ultrastructure of the main fabric within each layer (Plate 1: figures 1, 3). Transverse sections show two components: (1) electron-lucent, rounded areas, diffuse in outline, and (2) electron-dense material filling the spaces between the lucent areas and continuous with the sheet fabric separating particular layers. The rounded areas are compact and indistinct at the center, becoming clearer and separated from the background toward the outer margin of the virgula (Plate 1: figure 1). In combination with the longitudinal sections through the nema (Plate 1: figure 3), these rounded lucent areas can be identified as cross sections through fibrils, while the denser material can be considered

the matrix in which these fibrils are embedded. Moreover, each lucent area displays a rather complex substructure being penetrated by a number of denser lines that subdivide the lucent area into separate sectors and make the cross section of a fibril crudely similar in shape to an asterisk (Plate 1: figure 1). These denser lines penetrating the fibrils on transverse sections may be correlated with the delicate, oblique striations discernible on fibrils examined in longitudinal sections through the nema (Plate 1: figure 3).

Longitudinal and obliquely tangential sections through the nema show layers coated by denser sheet fabric associated with a number of intrasheet vesicles. The orientation of the fibrils in all layers seems uniform, and is parallel to the long axis of the nema. The fibrils are tightly packed together with little space left for the homogeneous matrix material. There are, however, a number of both small and rather large, longitudinally elongated fissures between some bundles of fibrils. These undoubtedly correspond to the holes recognized within the fibrous material seen on transverse sections. Smaller fissures sometimes are spanned with a number of rods interconnecting fibrils on opposite sides of the fissure. Such rods are disrupted on the walls of larger fissures and protrude into the space like lateral spokes (Plate 1: figure 3).

In spite of the presence of a number of interfibrillar spaces, the wall of the nema in *P. dubius* has a rather compact appearance, especially when compared with the ultrastructure of the nema in *Didymograptus* sp. The whole assemblage of ultrastructural features recognized within the nema of *P. dubius* is regarded as *virgular fabric*.

#### COMPARISON AND CONCLUSIONS CONCERNING THE NEMA

1. Both nemata are essentially hollow tubules. The internal canal is rather wide in *Didymograptus* sp. and filled with a loose fibrous material, while in *P. dubius* the nema is very narrow and empty except for the occasional loosely packed material continuous with the wall.

2. Both nemata differ fundamentally in the ultrastructure of their walls. In *Didymograptus* sp. the nema is made of cortical fabric, while in *P. dubius* it is composed of the virgular fabric.

3. These differences in the ultrastructural com-

position of the walls of the nema are paralleled by corresponding differences in the structure of the wall of the prosicula. It will be shown later that in *Didymograptus* sp. the loose fibrous material inside the nema is an equivalent of the middle component of the prosicula, while the wall proper is a direct extension of the outer component of the prosicula. In *P. dubius* the relation of the wall of the nema to the prosicular wall has not been established in detail, but there is a substantial difference in the ultrastructure of the fabrics involved.

4. The considerable differences in the ultrastructure of the nemata seem to be correlated with fundamentally different adaptive types represented by the species examined. The compact virgular fabric making up the virgula of *P. dubius* is consistent with a secondary supportive function for the scandent growth of the theca, while the rather loose cortical fabric of the nema in *Didymograptus* sp. is consistent with a less supportive role for the horizontal direction of thecal growth. A primary function for either is unclear, but in each case the nema in reflecting the consequences of an axonolipous or axonophorous condition is a key element in determining the adaptive type of the colony.

5. The present study does not provide any data to help solve the problem of the function of the internal canal of the nema. The opinion that the hollow nema might be filled in life with soft tissues has been expressed many times. Such a supposition cannot be denied entirely for *Didymograptus* sp., where the diameter of this canal and the fibrous loose nature of the diaphragm do not preclude the presence of a cord of soft tissues obtaining nourishment via the prosicula. But if we consider the loose material filling the canal as an equivalent of the middle component (mesh) of the prosicular wall, there is little reason to suggest that both were filled with some cellular matrix. This seems even less probable for the internal canal of the virgula in *P. dubius*, which is extremely narrow (1–1.6 $\mu$  in diameter) and at places filled by rather dense material, even in the youngest stages of development. The diameter of this internal canal may be compared with the diameters of the stolons in *Rhabdopleura*, which according to Kulicki (1971) are 17 $\mu$ –53 $\mu$  (31 $\mu$  in average); or with stolons of *Podoryne*, which

according to the data of Braverman (1971) are 40 $\mu$  diameter; a single wall of the stolon is 10 $\mu$ . The nourishment and growth of cellular tissues only 1 $\mu$  in diameter and several centimeters long seems improbable.

The interpretation of the internal canal of the nema most consistent with the data is that it is primarily a *structural space*. Its appearance is simply the result of a particular mode of formation and it probably served no special physiological function. The nema and virgula were most probably formed by soft tissues enveloping them from the outside, the deposition of each successive layer being external. There is no evidence in our studies to support a recent hypothesis of Kozłowski (1971), suggesting the internal centripetal deposition of the layers inside the primary outer wall of the nema.

### Ultrastructure of the Prosicula

The prosicula, conical in shape, is a proximal, early formed part of the sicula—a theca of an initial zooid of the graptolite colony. In contrast to the metasicula, a distal part of the sicula formed later, the bleached prosicula appears under the light microscope on total preparations as being composed of a thick, structureless membrane. The only discernible features are the *helical line*, a spiral line, probably embedded into the wall of the prosicula (intramural), and a number of longitudinal rods or threads, which are external ridges believed to be cortical in nature.

#### THE PROSICULA IN *Didymograptus* SP.

The morphology of the prosicula in *Didymograptus* sp. has been described and figured by Kozłowski (1971:327–329, pls. 1–3: fig. 10). Transverse microtome sections taken from different levels in the prosicula in *Didymograptus* sp. and examined with the light microscope (Plate 5: figures 1, 2) reveal that it is made of three main components. These are: (1) a dark, laminated *outer* component (o), with occasional ridges which correspond to the longitudinal rods of prosicula; (2) a light, *middle* component (m), with distinct swellings or protuberances that penetrate into the longitudinal rods of the prosicula. Arcuate lines of greater density within this component of the prosicular

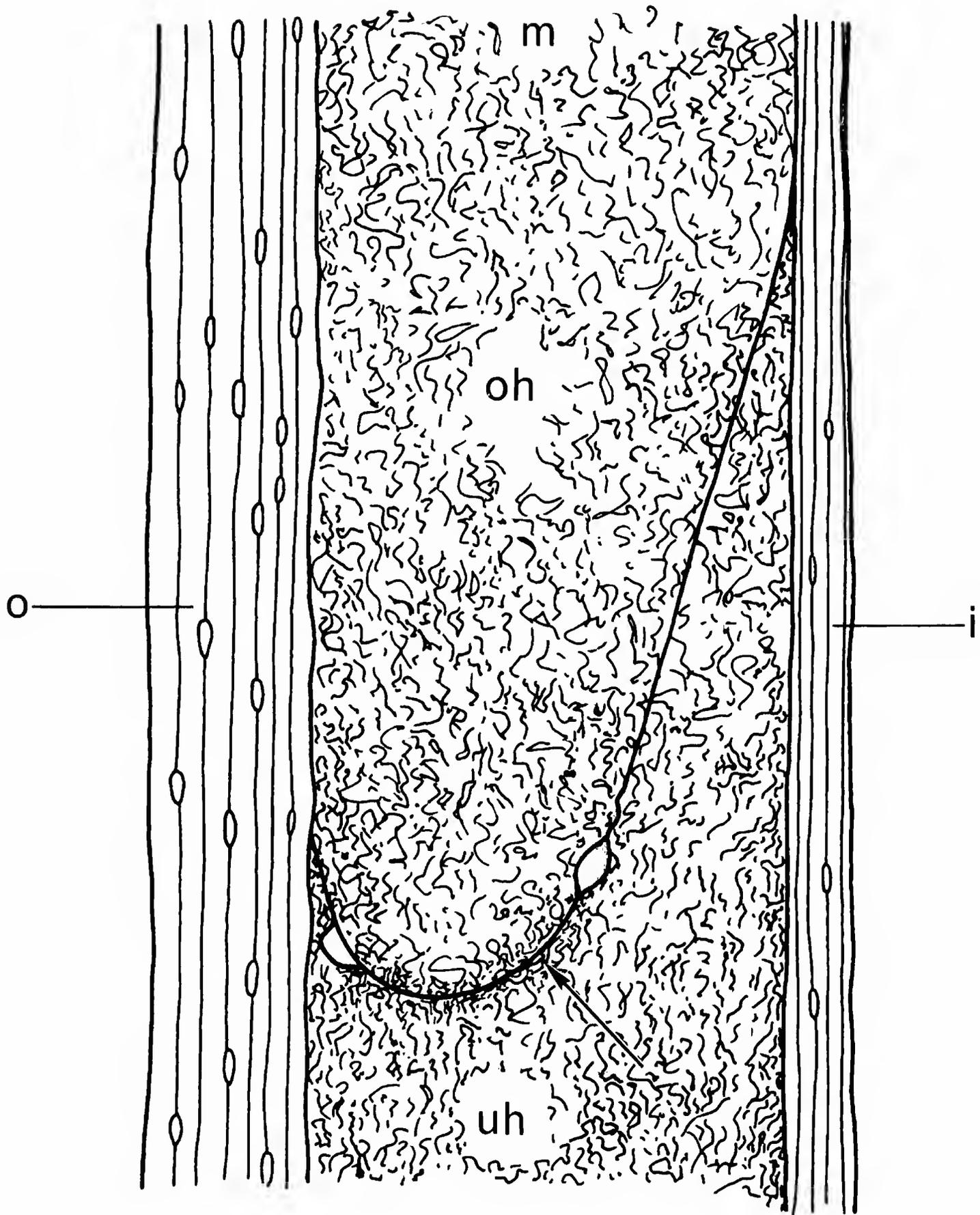


FIGURE 1.—A longitudinal section in three dimensions through the wall in the middle portion of the proscicula in *Didymograptus* sp., showing an obliquely oriented growth line delimiting two adjacent helical bands (arrow). It appears in transparencies of the proscicula in side view as the helical line (i = inner component of the proscicular wall, m = middle component, o = outer component, oh = overlying helical band, uh = underlying helical band).

wall mark certain discontinuities in the fabric; (3) a dark, *inner* component (i), delimiting the cavity of the proscicula and having a smooth surface but rather variable in thickness around the circumference. The thickness of these components varies along the proscicula, showing a distinct adapical increase for the outer component and a slight adapertural increase for the inner component. The middle component changes little as it tapers very gradually toward the apex of the proscicula. All three components of the proscicula may be easily recognized with the electron microscope.

In transverse ultrathin sections the outer component of the wall in the proscicula appears as a distinctly layered structure made of cortical fabric (Plate 5: figures 3, 4). In the adapical part of the proscicula this component is made of some 10–12 layers of cortical fabric, producing in this way a heavy coating on the surface of the proscicula. In sections through the more adapertural parts of the proscicula, the outer component consists only of about five layers and is not much thicker than the inner component. The fibers within the outer component are rather densely packed, as well as uniformly oriented within a given layer. The predominant orientation seems to be oblique and longitudinal with respect to the long axis of the proscicula. Rarely are they transverse. The layers are separated by sheet fabric with numerous vesicles. These are elongated laterally and few of them occupy an intersheet position. Most are scattered within the cortical layers (Plate 5: figures 3, 4o).

The middle component of the proscicula is made of a loose mat of fibrils producing an irregular network. The diameter of these fibrils is about the same as in the fibrils of the outer component, the difference being in their mesh pattern. This spongy material in the middle component produces swellings or protuberances entering into the longitudinal rods, acting in this way as a foundation. There is a gradual passage within each protuberance (which is in fact a list or keel) from a loose mesh into a more condensed packing of fibrils, thus giving them a cortical appearance. The whole structure is a combination of both fabrics with a considerable share of vesicular tissue on the slopes and at the top of the protuberance.

Growth lines within the middle component (Plate 6: figure 1g) were identified with the electron microscope as arcuate lines representing a

greater condensation of fibrous material, not unlike fusellar boundaries. These lines, which mark certain discontinuities in the formation of the middle component, are the only structural details in the wall of the proscicula that might be correlated with the helical line. This would result from their oblique orientation within the wall and spiral continuation along the proscicula. This is illustrated schematically in the diagram of Figure 1. The only difficulty with this conclusion is the repetitive occurrence of these lines with rather short spacings, at least in the adapertural part of the proscicula and close to the porus (Plate 6: figure 2g).

The inner component is adapically very thin, being composed of one to three layers of cortical fabric only (Plate 5: figures 1, 3i). Particular layers are separated only by sheets without vesicles, thus giving this structure a compact character. Each layer is composed of very tightly packed fibrils, which have a uniform orientation within any given layer but are different in adjacent layers. At certain places the inner component is strongly reduced and appears transformed merely into a condensation of fibrous material. At the middle of the proscicula the thickness of the inner component increases to be almost equal to that in the outer component. It is made of about five or six layers containing a few vesicles.

This simple structural pattern of the proscicula is modified to some extent at two places: at the apex and at the aperture (Diagram: Figure 2A,B; Figure 3). At the apex of the proscicula the outer component of the proscicular wall passes gradually into the wall of the nema with continuity in most layers. Additional layers are added, or intercalated, to accommodate the increase in thickness as the diameter of the proscicula gradually decreases. There is no doubt therefore that the wall of the nema is an extension of the outer component of the proscicular wall (Plate 7: figure 1).

The fate of the two remaining components of the wall at the apex of the proscicula is less clear. Longitudinal sections reveal that the middle and inner components taper gradually toward the apex, the latter already quite thin within the apical part of the proscicula. The diagram (Figure 2A,B) shows a wedge-shaped layer of the middle component decreasing gradually toward the apex and coated by a thin, denser layer that is a continuation of the inner component. Examination of additional

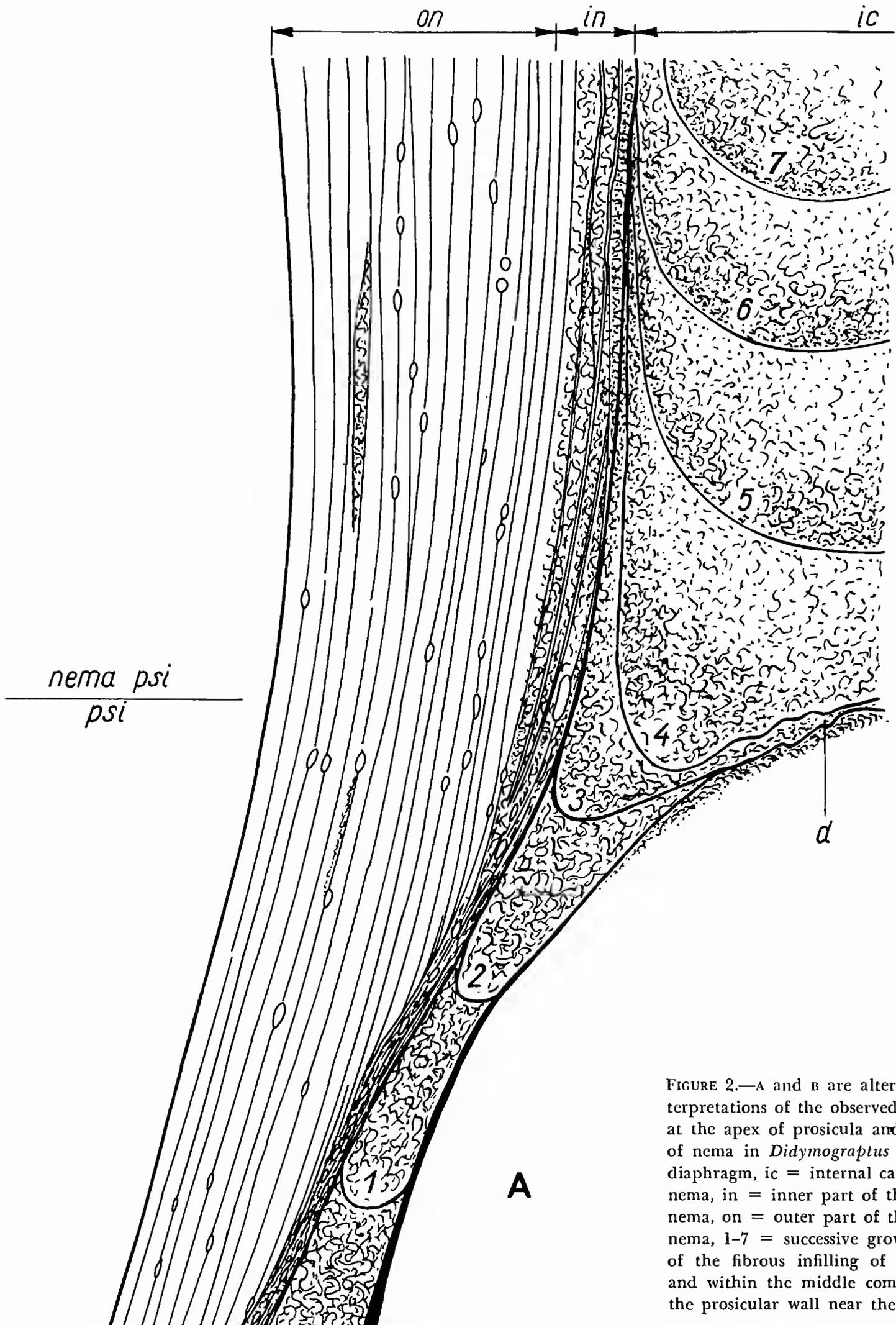
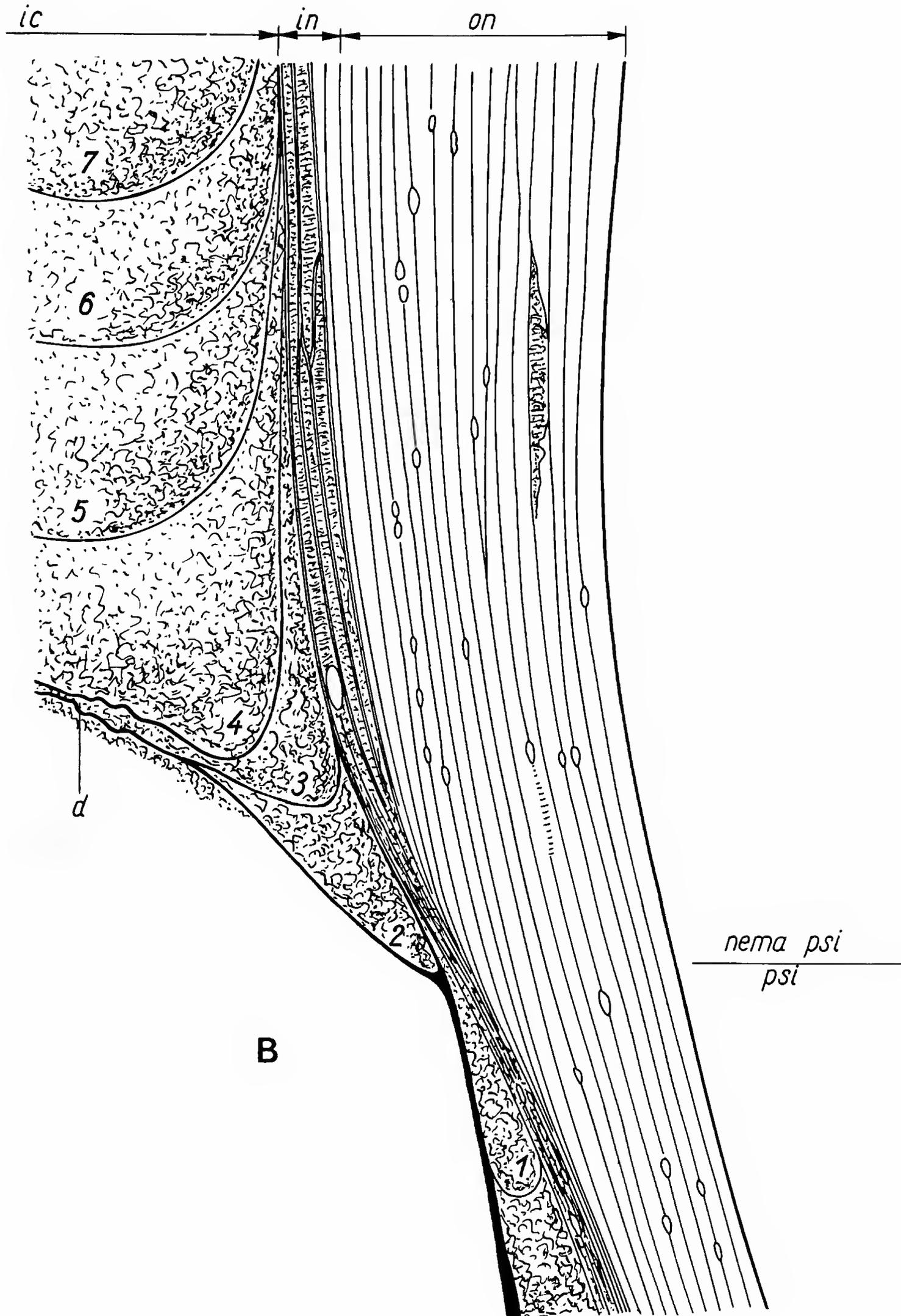


FIGURE 2.—A and B are alternative interpretations of the observed structure at the apex of prosicula and the base of nema in *Didymograptus* sp. (d = diaphragm, ic = internal canal of the nema, in = inner part of the wall in nema, on = outer part of the wall of nema, 1-7 = successive growth bands of the fibrous infilling of the nema and within the middle component of the prosicular wall near the apex).



sections has proven that the middle component either tapers almost completely at the apex (Figure 2B) or meets it as an extremely narrow strip with overlying loose fibrous material, which appears to fill the internal canal of the nema (Figure 2A). There is not, however, any sharp line to delimit both fibrous materials, producing a situation somewhat difficult to interpret. Because of the coincidence in the decrease of the middle prosicular component and the simultaneous appearance of the fibrous infilling of the nema canal and because of the lack of a sharp discontinuity between them, the data can be interpreted in two ways.

The first alternative is that the middle and inner components taper at the apex and the fibrous material is independent in the cavity of the nema in spite of its close contact (Figure 2B). In this case the nema is continuous only with the outer component of the prosicular wall. The second possibility is that, in addition to the outer component, the middle component is also continuous with the nema, specifically with the fibrous material filling the canal of the nema (Figure 2A). After a strong reduction in thickness the middle component expands rapidly in combination with a loosening up in the packing of the fibers—a factor responsible for the difference in appearance of the fibrous material within the middle component of the prosicula and within the canal of the nema. The second interpretation is more compatible with the observed continuity of the helical line, which is probably linked with the growth lines in the middle component of the prosicula and the fibrous canal material in the nema.

Another difference in the structural pattern of the fibrous material filling the internal canal at the very base of the nema is the presence of the faint but easily discernible growth lines marking some discontinuity in the formation of this material (Plate 7: arrows). These are delicate densities of arcuate outline when examined on longitudinal sections. At the bottom of the internal fibrous infilling of the nema there is a dome shape where growth lines merge and condense together. The central part of this structure is made of two growth lines joined together, forming a double layer. The position and nature of this condensation of fibrous material locates the so-called *diaphragm*, a membrane supposed to separate the cavities of the nema and prosicula, at least in some graptoloids.

Kraft's (1926) first description of the diaphragm in *Orthograptus gracilis* (Roemer) as a "membranartige Abdichtung" agrees with the situation recognized with the electron microscope in *Didymograptus* sp. The presence of a diaphragm in the apex of the prosicula has been reported by Kozłowski (1971:329, fig. 10 and pl. 1: fig. 1). His observations indicated that the diaphragm is a concave-convex membrane with its concave side facing the cavity of the prosicula, and pierced in the center by a small, round opening. These observations may be restated on the basis of the electron microscopic studies, but with some modifications. The diaphragm is not a single structure of the membrane type, but consists of a number of dense growth lamellae fused together. This membrane-like condensation of the fibrous material is not completely continuous, but shows a number of disruptions filled by loose fibrous material (Plate 7: figure 1d). A transverse microtome section through the center of the diaphragm, and examined with the light microscope only, showed the diaphragm to be a delicate substance, straw-yellow in color, with a number of irregular openings (Plate 7: figure 2d). The presence of a single, centrally placed opening, occupying one-third of the diaphragm as mentioned by Kozłowski (1971) was, however, not confirmed. Moreover, the irregular openings recognized in the diaphragm do not seem to be ducts (or similar anatomical foramina), but rather appear as either primary imperfections in construction or as secondary preservational features.

A number of delicate growth lamellae in the material filling the internal canal at the base of the nema may be correlated with the extension of the helical line onto the basal part of the *nema prosiculae* (comp. Kozłowski, 1971, fig. 10 and our Plate 7: figure 1, arrows). It is suggested here that these growth lines on bleached specimens are seen through the wall of the nema to produce the effect of a spiral thread within it. It seems therefore that the helical line is connected with discontinuities within the fibrous component of the prosicula and the *nema prosiculae*.

At its aperture the structure of the prosicula is shown in Plate 8 and Figure 2. The middle component of the prosicula has a blunt end made of a mesh of fibrils, discontinuously displaced and separated by extensive empty spaces. The outer

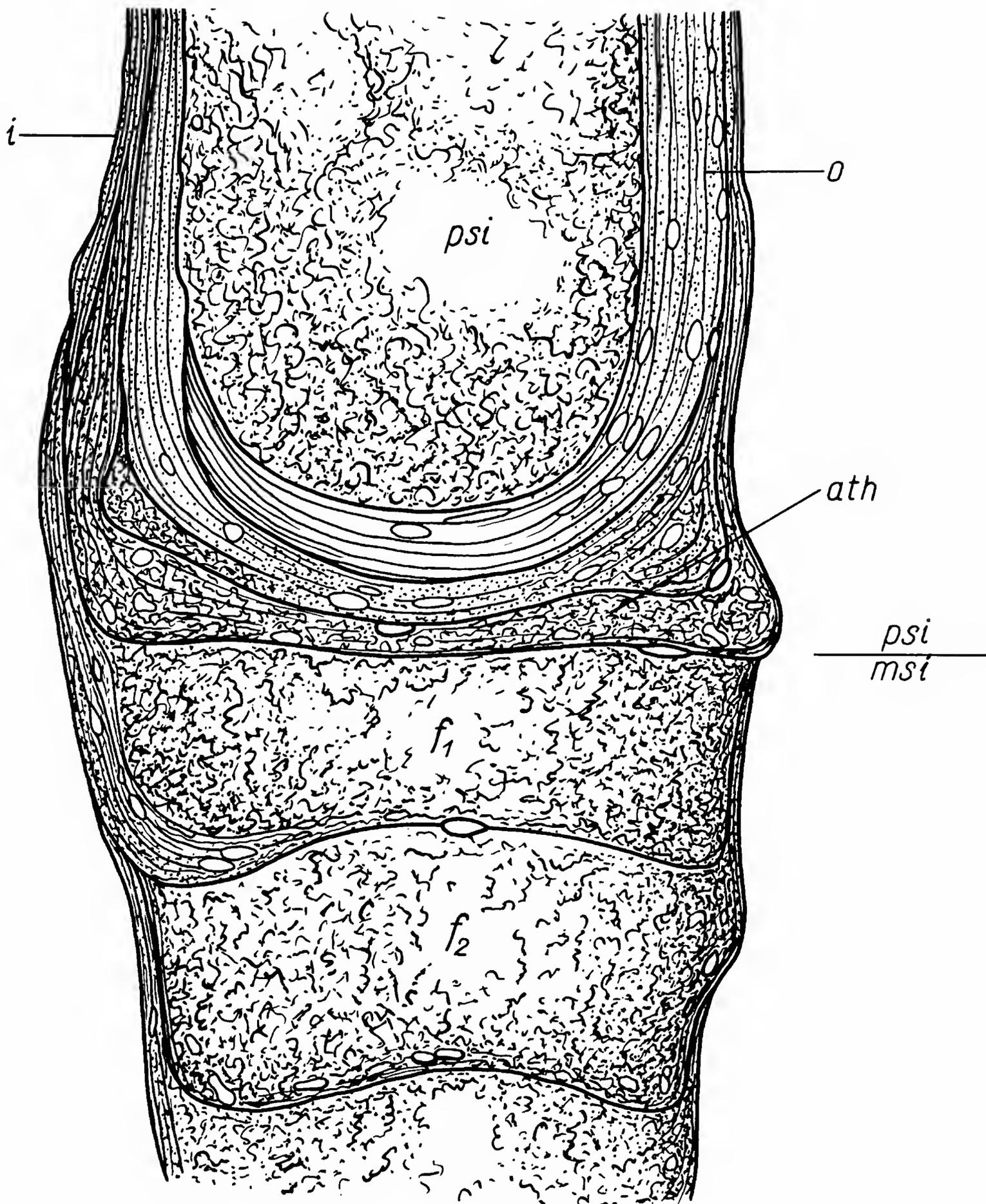


FIGURE 3.—An interpretation of the structure at the aperture of prosicula and at the boundary of pro- and metasicula (ath = apertural thickening of the prosicula,  $f_1$ - $f_2$  = successive fuselli of the metasicula, i = inner component of the prosicular wall, o = outer component of the prosicular wall, psi = prosicula, psi/msi = boundary between pro- and metasicula).

component (o) is rather thin and composed of a number of strongly condensed layers of sheet fabric accompanied by strongly elongated vesicles and containing few cortical fibrils. It overlaps the apertural border and tapers rapidly on the inner side. The aperture is provided with a number of layers of cortical aspect, which are densely crowded and provided with numerous elongated or rounded vesicles. To some extent the layers overlap the apertural margin from both sides. This structure undoubtedly corresponds to the apertural thickening (ath) of the prosicula described in a number of graptoloids. Although slightly angular in cross-section, it produces a cylindrical appearance when viewed laterally in the light microscope, and it has a similar look on deep tangential microtome sections (Plate 8: figure 1a). The apertural thickening is overlain by successive fuselli of the metasicula and the outer lamella of the first one is placed on it directly (Plate 8: figure 2f; diagram: Figure 3f<sub>1</sub>,f<sub>2</sub>). The inner component (i) of the prosicula wall does not constitute a continuation of the outer component but is formed independently as a rather thin, compact condensation of fibrous material as an extension of the inner arm of the apertural thickening.

A number of thin-walled, membranaceous external "blisters" (Plate 9) have been observed on the prosicula of *Didymograptus* sp., some of them being as large as the prosicula itself (comp. Kozłowski, 1971, pl. 2: fig. 3). They may represent the results of some pathological effects on the soft tissues surrounding the periderm (inflammations caused by foreign bodies or parasitic organisms?). A small protuberance of this kind situated just above the initial bud and sectioned transversely is shown. It is made of loosely displaced fibrous material, coated as well as divided obliquely by a thin, dense layer. The considerable thickness of the underlying outer component of the prosicula implies a late appearance of this "blister" after the formation of the initial bud.

#### THE PROSICULA IN *Pristiograptus dubius*

Ultrathin sections made at different levels through the prosicula in this species (Plate 10) reveal a picture surprisingly different from that recognized in similar parts of the rhabdosome in *Didymograptus* sp. The wall is distinctly layered,

usually composed of seven or eight layers. The number of layers increases at the position of the longitudinal rods where there are 14 to 18. A cross section through the prosicula halfway along its length shows six or seven well-defined rods, represented by swellings of the wall, and producing ridges on the outer surface.

The innermost layers recognized within the wall are made of a distinctly fibrous fabric with a cortical appearance (Plate 10: figure 2 on left). Each layer is delimited by electron-dense sheet fabric associated with a few intrasheet vesicles. Some of these are modified into fissures enveloped by pellicular material, producing locally a doubled sheet surrounding these intrasheet fissures. More of them, however, have similar fissure-like extra sheet spaces formed as a result of a disjunction between the underlying fibrous material of a given layer and the sheet coating it. The layers composing the wall commonly taper, producing at places wedge-shaped terminations.

The fabric within the innermost layers may be classified as cortical, since the fibers examined on longitudinal sections do not show the oblique striations characteristic of the virgular fabric in the adjacent nema.

The outer layers of the prosicula wall are made of a rather compact material with a less well-defined fibrous appearance. It is separated by distinct sheets devoid of vesicles or fissures (Plate 10: figure 2 on right). The main part of the longitudinal rods is composed of this material, which is not unlike the material, also characteristically "porous," recognized in the central part of the virgula. The lateral transition of the longitudinal rods into the virgula and the relationship between this material and the components of the virgula proper have not been established on the sections examined.

The outer surface of the prosicula is smooth, being coated with sheet fabric. The inner surface is made of fibrils without sheet fabric, but in spite of this it is also rather smooth. There are no filamentous outgrowths on the inner surface similar to those in the nema (Plate 10: figure 1).

The somewhat vesicular and rather loose material recognized at the base of the longitudinal rods extends transitionally within the same layer into normal cortical fabric (Plate 10: figure 3). This is probably the result of a local loosening of the

fibrils. The structure of the prosicula in *P. dubius* is much simpler than that in *Didymograptus* sp. But surprisingly no features were recognized within the wall which could be correlated with the helical line.

#### COMPARISONS AND CONCLUSIONS CONCERNING THE PROSICULA

1. In spite of a great similarity in the gross morphology of the prosicula in *Didymograptus* sp. and in *P. dubius*, a closer examination reveals remarkable differences in their micro- and ultrastructure. The prosicula of the former is thick-walled and made of three different components: (a) an *outer*, made of layered cortical fabric, (b) a *middle*, of fibrous mesh material, and (c) an *inner*, again of cortical appearance. The mesh material of the middle component seems to represent the primary prosicular tissue, as the others are added at somewhat later growth stages. The prosicula in *P. dubius*, on the other hand, is thin walled and simpler in composition, its inner layers being made of cortical fabric, covered by an outer compact layered material, not unlike such material within the central part of its virgula. Both prosiculae thus reveal fundamental differences in ultrastructure that are paralleled by differences in the ultrastructure of their nemata.

2. The only structures which might be correlated with the helical line in *Didymograptus* sp. are the growth lines observed within the middle component of the prosicular wall. These growth lines (Figure 1) can be interpreted in the light of Kozłowski's observation (1971:327) that the helical line is in fact a sort of suture between the whorls of a spirally coiled band of which the prosicula is composed (see also Andres, 1961). Individual whorls are sometimes separated as a result of disintegration of the prosicula (Kozłowski, 1971, pl. 2: fig. 2). Our studies indicate, however, that these sutures are confined to the middle (primary) component of the prosicula. Thus elongation of the nema cannot be related to the growth of the spiral band alone because the nema proper is an extension of the outer component of the prosicula (comp. Kozłowski, 1971:327).

3. Recognition that the growth lamellae inside the middle component of the prosicula in *Didymograptus* sp. may correspond to the sutures of the

helical line agrees with its position as intramural. Scanning micrographs of the prosicula in this species (Kozłowski, 1971: pl. 3: figs. 1, 2) show the helical line in the form of hoops slightly protruding over the external surface. This could be a secondary mechanical effect ascribed to a slight collapse of the periderm between the adjacent sutures as a result of desiccation.

4. No traces of any structures which could be positively correlated with the helical line have been found in the prosicula of *P. dubius*. Although the helical line has been recognized in some monographtids (Kraft, 1926; Walker, 1953), it is always very faint and barely discernible or even lacking (Urbanek, 1953, 1958, 1959, 1966, 1970). In *P. dubius*, neither Cox (1934) nor Urbanek (1951, 1958) were able to find reliable traces of the helical line. This was explained at the time as a result of an unsatisfactory state in the preservation of the specimens. But the absence of mesh material from the prosicular wall in *P. dubius* provides another interpretation. At least some monographtids may lack a helical line because of a reduction in the primary prosicular component with which this structure may be linked. Further ultrastructural study should clarify this problem.

5. In contrast to the internal position of the helical line, the position of the longitudinal threads (rods) of the prosicula has been shown to be external.

#### Ultrastructure of the Metasicula

The metasicula is formed after the prosicula and constitutes a distal portion of the sicula. Both portions differ distinctly in their structure and the metasicula is composed of fusellar growth bands, the growth lines of which produce a ventral and a dorsal zigzag suture. The sharp contrast in the structure of the prosicula and metasicula has been interpreted as the result of a metamorphosis of the siculozoid (Kozłowski, 1949). Although this interpretation seems reasonable, electron microscope studies indicate that this sharp difference has in some cases been based on a change in the mode of secretion of the peridermal substance rather than on a substantial difference in the nature of the fabric. The fusellar material of the metasicular tissue does not differ much in ultrastructure from the mesh material recognized in the middle com-

ponent of the prosicula in *Didymograptus* sp., although both are quite differently organized at the microstructural level. The fabric of the prosicula in *P. dubius* differs sharply from that in the metasicula.

#### THE METASICULA IN *Didymograptus* sp.

A young metasicula examined in *Didymograptus* sp., made of some 25 fuselli, has at its aperture ventral and dorsal shovel-like processes (Plate 8: figure 1m). The first fuselli laid down over the apertural thickening of the prosicula are rather low and provided with flattened, or even slightly concave tops (Plate 8: figure 2). Later fuselli are taller, their tops being inclined toward the inner side of the wall and at the interfusellar suture on the outer side is a prominent ridge (Plate 11: figure 2).

Each fusellus is composed of the *body*, made of loose fibrils with a typically fusellar appearance, and of the outer *lamella*. The latter is produced at the margin of the fusellus as a result of the condensation of the fibrils. Although the outer lamella contains fibrils that are not always well ordered and straight, some being wavy and irregularly displaced, it resembles cortical fabric. The thickness of the outer lamella varies. It is very thin at some places, especially at the top of the fusellus, but slightly thicker on the lateral sides. There is no well-defined sheet to border the fuselli and distinctly delimit their outer lamellae (Plate 11). Fuselli are superimposed, with the body of one fusellus resting immediately on the top of the preceding one without producing its own outer lamella at the base. The outer lamellae, however, show some overlap on the lateral sides and this tends to be greater at the inner surface facing the cavity of the metasicula (Plate 11). This overlap results in some accumulation of outer lamellae, so as to produce two, or in some places even three, layers of cortical-like deposit on the inner side. The analogous structure on the outer side is generally thinner, insofar as it is seen by transverse ultrathin sections (Plate 12: figures 1, 2). The outer cortical deposit formed in this way in the young metasicula is usually less well preserved, being damaged and composed of somewhat distorted fibrils.

Both longitudinal and transverse sections through the metasicula show the presence of nu-

merous vesicles, many linked with the outer lamella at the top of the fuselli (interfusellar sutures, Plate 12: figure 1), and with the outer lamella situated at the oblique suture of the fuselli.

#### THE METASICULA IN *Pristiograptus dubius*

As in *Didymograptus* sp. the metasicula is made of a number of fusellar growth bands laid down alternately on one side and then the other. The main differences are: (1) the presence of peculiar "black rings" of the metasicula in *P. dubius*, which are internal, secondary thickenings showing traces of lamellar structure when examined with the light microscope; and (2) a greater elaboration of the aperture, which in *P. dubius* is provided with a prominent ventral apertural spine called the "virgella," and a short, shovel-like dorsal process.

Transverse ultrathin sections through a proximal portion of the metasicula reveal two structural patterns. One is combined with cross sections taken at the level of the internal thickenings (Plate 13: figure 1), and the second is obtained when such sections pass between these internal "black rings" (Plate 13: figure 2).

The outer components correspond to cortex and fusellum. The metasicula of the young rhabdosome (stage of 1½ thecae) is already coated in its proximal region by about five layers of cortex with well-defined sheets. A number of fissure-like spaces, adjacent to the sheets, or occasionally of an intrasheet nature are present, giving the cortex an appearance peculiar to *P. dubius* (see below). The cortical fibrils within the layers are longitudinally arranged with respect to the main axis of the sicula. Only in one or two layers are they transverse.

The fusellar component of the metasicular wall is made of a rather dense felt of fibrous material, the fibrils being somewhat coarser than those in *Didymograptus* sp. This fibrous material which constitutes the body of the fusellus is coated by the transversally arranged fibrils corresponding to the outer lamella of the fusellus. The fibrils are oriented normal to the outer pellicle of each fusellus. Some fuselli display a considerable overlap of their oblique sutures, and at places delicate traces of an outer pellicle, in addition to the outer lamella, are discernible.

On both longitudinal and transverse sections

through the internal ring (Plate 13: figures 1, 3) a dense, almost homogeneous, deposit covers the inner surface of the fusellar component. It shows only faint traces of layering due to greater densities, which are as dense as the sheet material within the cortex. These densities and some very fine fissures are the only recognizable features within this material. Cross sections taken between the metasicular internal rings reveal a heavy internal deposit, their inner surface covered by one to three thin layers of cortical fabric separated by thin sheets.

A distal, apertural part of the metasicula sectioned longitudinally (Plate 14) shows that the wall of this part of the metasicula, at the growth stage of the rhabdosome of  $1\frac{1}{2}$  thecae, is devoid of an outer cortical deposit (although its proximal part is already coated by about five layers of cortex). The only component of the wall is therefore the fusellar tissue. The fuselli are rather tall, quite variable in outline, and usually provided with a broader base that overlaps the underlying fusellus. A rather narrow "trunk" and a much wider "head," which is clublike in section, can be seen (Plate 14: figures 2, 3). Structurally each fusellus is composed of (1) a *body of the fusellus* made of the fusellar fabric (a dense mesh produced by coarse fibrils as compared with *Didymograptus* sp., (2) a distinct, wide *outer lamella*, which by its dense packing of fibrils produces a rather sharp contrast to the material within the body, and (3) a distinct *outer pellicle* made of homogeneous and electron-dense material (Plate 14: figure 3, arrow). The outer lamella is especially well developed within the "head" and the "trunk" of the fuselli and is less distinct or absent at the base of a given fusellus, where it is covered only by the outer pellicle (Plate 14: figure 3). The fibrils of the outer lamella are arranged normal to the outer membrane of the fuselli. The fuselli show a considerable overlap at their interfusellar sutures, the base of each fusellus overlapping the "head" of the subjacent one at some distance. Spongy, fusellar fabric of the base rests immediately on the outer membrane of the "head." A thin and, at places, damaged, discontinuous coating made of one or two layers of dense cortical fabric has been recognized on the inner surface of the distal part of the metasicula, producing in this way a delicate lining.

Elaborations of the apertural margin of the

metasicula are: the dorsal process and the virgella formed at the ventral zigzag suture. The dorsal process is a slightly introverted shovel-like outgrowth of the margin (Plate 15: figure 1). Ultramicrotome sections reveal an indistinct production of one or two fuselli and a number of layers (7–10) of dense cortical fabric, enveloping the last fuselli to produce a distinct cylindrical thickening at the border (Plate 15: figure 2). Some of these cortical layers taper within the thickening, some gradually decrease in thickness toward its base.

The virgella, a prominent spine, is formed on the ventral zigzag suture by a special arrangement of the fuselli, which involves a rapid widening of each fusellus close to its oblique suture. This, combined with the alternate overlap of the fuselli, results in an arcuate shape, thus forming a lobe on the margin. This becomes thickened later so that the growth lines on it cannot be seen, even on strongly bleached specimens. The virgella belongs to the class of fusellar structures that may be considered a derivative of the ventral wall, and therefore to which two series of fuselli contribute (difusellar; Urbanek, 1958). This difusellar nature of a thickened, distal part of the virgella is difficult to prove with the light microscope. However, ultramicrotome transverse sections through it reveal a clear picture confirming the difusellar foundation of the virgella (Plate 16: figure 1). The central part of the virgella is composed of fusellar fabric and one can distinguish two fuselli—a larger one and a smaller one ( $F_1$ ,  $F_2$ ). The larger fusellus ( $F_1$ ) has a body made of loose fusellar fabric, and a dense outer lamella coated by a sheet which is the outer membrane of the fusellus. The smaller fusellus ( $F_2$ ) is similar, with a rather indistinct outer lamella of densely crowded fibrils, and a thick outer pellicle made of a strongly electron dense material. The larger fusellus almost entirely overlaps the smaller one as is indicated by the outer lamella of the former which embraces the latter (o). Both fuselli meet in the middle with their outer pellicles producing by fusion a heavy, double, electron-dense line.

This central fusellar component of the virgella is coated by a thick cortical component made of three to six layers unevenly distributed around the virgella. Some layers delimited by electron-dense membranes are made of a material very similar to the virgular fabric. The latter consists of tightly

packed, less dense fibrils and scanty, but electron-dense interfibrillar matrix, which seems continuous with the sheet material, giving a "cellular" appearance to the tissue (Plate 16: figure 2). Although the fusellar component is clearly present in the strongly thickened distal part, the tip of the virgella is probably made of cortical fabric alone.

#### COMPARISON AND CONCLUSIONS CONCERNING THE METASICULA

1. Examination of ultrathin sections of the metasicula in *Didymograptus* sp. and in *P. dubius* reveals that considerable differences exist within their respective fusellar tissues. The fuselli of the metasicula in the former are uniform and regularly shaped, while in the latter they are more variable. Longitudinal cross sections show that the fuselli in *Didymograptus* sp. are parabolic in shape and lacking an outer pellicle, while in *P. dubius* they are pear-shaped and provided with a distinct outer pellicle. In both cases the fuselli have a distinct outer lamella that resembles the fuselli in *Acanthograptus* sp. but differs from those in *Dictyonema* sp. (Urbanek and Towe, 1974).

2. There are indications of a considerable difference in the onset of corticalization of the metasicula. The metasicula of the *Didymograptus* sp. rhabdosome at the initial bud stage already has a thin cortical coating made by an accumulation of overlapping outer lamellae of the fuselli. In *P. dubius* the metasicula, at the growth stage of 1½ thecae, has an incipient cortex in its proximal part but still lacks one in its distal part. This coating is made by the deposition of layers of cortical fabric independent of the fuselli. Thus, *the formation of the cortical deposit over the outer surface of the metasicula proceeds in two different ways in the species examined.*

3. In both species the metasicula has an inner cortical deposit which shows the same differences in its mode of formation as does the outer one.

4. Internal ringlike thickenings of the metasicula (metasicular black rings) in *P. dubius* are composed of a homogeneous (crassal) fabric showing only faint traces of layering.

5. Apertural thickening of the metasicula examined on its dorsal apertural process in *P. dubius* consists of numerous layers of compact material resembling virgular fabric.

6. The thickened, distal portion of the virgella in *P. dubius* has a difusellar foundation and an outer, layered envelope made of a compact fabric, also resembling that of the virgula.

#### Ultrastructure of Thecae

Thecae are zooidal tubes or lodgings for blastozoids in a graptoloid colony. They display the same fundamental structure as the metasicula, being composed of fusellar growth bands produced by a regular superposition of ventral and dorsal zigzag sutures. The budding of the thecae (order of appearance, direction of growth, and final arrangements) displays considerable differences within graptolites (Bulman, 1970). In the graptoloids the thecae are essentially nonpolymorphic but may be biform.

*Didymograptus* sp. represents a dichograptid type of development at the primitive *bifidus* stage (see Bulman, 1970:75 for definition), and *Pristiograptus dubius* represents the most advanced monograptid type of development (see Bulman, 1970:79 for definition).

#### THE THECAE IN *Didymograptus* sp.

As is the case in the dichograptid type of development, the first theca appears by means of a so-called *perforational budding* (Kozłowski, 1949). This is accomplished by the production of a circular opening situated at the prosicula close to its aperture. This opening or *porus* serves as a passage to the exterior for the newly formed first blastozoid. Further deposition of fusellar strips around the porus results in the formation of the early portion of the first theca, the *initial bud* (Plate 17: figure 2). The porus and the proximal portion of the initial bud situated on the prosicular wall, studied with the light microscope in transverse microtome sections, show that the wall of the prosicula is interrupted to produce the porus, which in turn is covered by the domed wall of the initial bud. Ultramicrotome sections taken at about the same level and examined in the electron microscope show additional details. The wall of the prosicula at the margin of the porus ends unevenly.

The outer and inner components terminate first, while the middle one composed of spongy fabric extends short filaments (f) from both sides into the

porus (Plate 17: figure 1). The inner surface of the corners of the initial bud and the prosicula are filled by a spongy fabric delimited into triangular fields by distinct growth lines (c) (Plate 6: figure 2). This material has a fusellar aspect. In one case it was deposited in the form of a wedge-shaped strip on the inside of the prosicula close to the porus, producing a rather long brushlike outgrowth of spongy fabric penetrating the foramen.

The wall of the initial bud proper (B), as seen on Plate 6: figure 2, is composed almost exclusively of cortical fabric, with very faint indications of remnants of spongy fusellar fabric on the inner surface. This is almost certainly the result of preservation since longitudinal sections through the initial bud in its very early stages of formation (some nine fuselli) clearly show its fusellar structure (Plate 17: figure 2). This figure is, moreover, highly informative with respect to the cortical component of the wall of the initial bud (o). It is continuous with the main part of the outer component of the prosicula. The outer component of the prosicula wall, preserved close to the porus and hidden beneath the initial bud, is extremely thin and probably made of only one layer of cortical fabric. But the outer component on the exposed outer surface of the prosicula and on the initial bud is much thicker, with seven layers of the cortical material. This cortical envelope is common to the prosicula and the proximal part of the initial bud and layers pass from the bud into the prosicula without interruption. Judging from the superposition of the layers in the outer component of the wall of the prosicula at an area close to the porus, the bulk of the cortical fabric has been deposited after the formation of the porus and simultaneously with the growth of the initial bud. Prior to the formation of the porus the early prosicula was most probably covered by a very thin outer component. The layers at the boundary of the pro- and metasicula show that a thin layer of the outer component is overlain by the apertural thickening of the prosicula, and next to it by the first fusellus of the metasicula. These relationships seem to indicate that the degree of corticalization of the outer surface in the early prosicula is rather low. Further deposition of cortical fabric over the outer surface of the prosicula coincides with the budding of the first theca. These sections, through an early growth stage of the initial bud, reveal that the first fuselli

are superimposed over the adapical margin of the porus. The prosicular wall overlapped by the first fusellus has a very thin outer component that is thicker on the free part of the prosicular wall. Additional layers of this thicker cortical envelope of the prosicula seem to be continuous with the outer lamellae of the two most proximal fuselli of the initial bud. The outer lamellae of the adjacent fuselli overlap one another and extend farther into successive layers of the outer component of the prosicula. The remaining fuselli do not participate in the formation of the cortical envelope in the same way. This results in a decrease and eventual disappearance of the cortical coating toward the growing margin of the initial bud. In this specimen the last formed fusellus seems incomplete, consisting of the body of the fusellus alone, with the outer lamella still lacking (Plate 6: figure 2).

The ultrastructure of the thecal wall has also been examined in a distal, strongly carbonized theca. Here longitudinal sections through the ventral wall reveal a series of surprisingly well-preserved fuselli (Plate 18: figure 1). The thickness of the wall increases distinctly toward the aperture, the fuselli being initially tall and narrow and later short and wide. Each fusellus is composed of the body proper and a rather thin outer lamella. The former is made of a mesh of loose and delicate fibrils, giving this fabric a definite fusellar aspect. The latter, as in the fusellar tissue of the metasicula, is produced by a condensation of fibrils, and it delimits particular fuselli since the outer pellicle enveloping the fuselli is lacking. Fuselli traced on the longitudinal sections through the theca display a distinct asymmetry. The outer lamellae gently slope toward the inner surface and steeply slope toward the outer surface of the theca. Moreover, on the inner surface of the theca the outer lamellae show very limited overlap and are sometimes very attenuated (Plate 18: figure 1). On the outer surface, however, they overlap a number (5-6) of the underlying fuselli (Plate 18: figure 1). This results in an accumulation of outer lamellae over the external surface of the thecae, producing a peculiar kind of cortex (Plate 18: figure 2). It is composed of five or six layers of cortical-like fabric, with an essentially ordered arrangement of fibrils. Each layer is an extension of an outer lamella of a given fusellus. Particular lamellae taper out at some distance below the base of one fusellus and give

way in the next layer to an extension of the outer lamella of an overlying fusellus. In this way a cortical coating of rather uniform thickness is formed on the outer side of the ventral wall of the thecae.

The mode of formation of this particular cortical coating in *Didymograptus* sp. differs distinctly from that in the outer cortical tissue (cortex) in *Dictyonema* sp. (Urbanek and Towe, 1974). In the latter the fuselli on both sides are completely closed systems devoid of the addition of any outer lamellae. In the former, fuselli provided with a distinct outer lamellae are closed systems on their inner surface but open systems on their outer surface, thus producing through considerable overlap a separate layer of outer cortical fabric, which is in fact an extension of the outer lamella. Although this coating differs from true cortex in its mode of origin, it is nevertheless composed of cortical fabric. The chief structural difference is the uniform orientation of the fibrils in all layers transverse to the long axis of the theca. In the cortex of the dendroids their orientation is variable.

The outer cortical deposit of the thecae in *Didymograptus* sp. is generally rather thin, and in spite of the strong "carbonization" the fuselli are generally discernible without bleaching. As seen in the light microscope, bleached specimens show a greater accumulation of the outer deposit on the dorsal surface of the stipe. Whether this deposit was formed by condensation of the overlapping outer lamellae or was deposited in the form of independent layers of cortical fabric has not been established from the sections studied.

#### THE THECAE IN *Pristiograptus dubius*

The ultrastructure of a heavily corticalized thecal wall has been studied in longitudinal sections through strongly carbonized proximal parts of an older rhabdosome (Plate 19: figures 1, 2). It consists of: (1) a cortex (c), composed of six to ten layers of cortical fabric deposited over the outer surface of the fuselli, (2) a fusellar component (f), and (3) a rather thin, and not always preserved, inner cortical deposit (i) made of one or two layers of cortical fabric laid down over the inner surface of the thecae.

The cortex is surprisingly uneven, showing numerous local swellings that express themselves on the external surface as distinct elevations followed

by depressions (Plate 19: figure 2). In places the cortex exceeds the fusellar component twice or three times in thickness. Each layer is composed of loosely packed fibrils, uniformly arranged within each layer, but showing different orientations in successive layers. The prevailing orientation of the fibrils is oblique or transverse. Rarely is it parallel with respect to the main axis of the theca. Adjacent cortical fibrils are interconnected by numerous transverse rods that span the interfibrillar spaces. At some places these spaces are transformed into larger fissures between the fibrils. The fabric within the layers of the cortex in *P. dubius* is therefore genuinely cortical. The delicate oblique striation observed on the fibrils in the virgular fabric is not seen here. The layers of the cortex are separated by distinct sheets associated with fissure-like admembrane spaces, the presence of which is a special feature of the cortical tissue in *P. dubius* (see above description of the cortex in the metasicula). This feature is probably primary but could also be preservational. In a few cases an electron-dense sheet is associated with one layer but the adjacent layer is lacking it. This could result from a mechanical separation (detachment) of the two primarily fused layers. In the majority of cases, however, both layers are separated by a fissure and are provided with their own electron-dense sheets. The origin of the fissure separation may be related to a process involving the formation of these structures by coalescence of the vesicles along zones of weakness. The origin of the numerous dark and irregular bodies within these zones is unknown and they appear to be restricted to the cortex.

Tangential sections reveal additional details of the ultrastructure of the cortical fabric. The exaggeration of the thickness on such sections shows that the cortical fibrils pass just beneath the sheet into an irregular network (m) and that the sheet fabric is not quite homogeneous but rather very densely reticulated (Plate 20: figure 1). Such details are not readily discernible in transverse or longitudinal sections.

Elevations observed on the outer surface of the cortex are due to either an increased number of layers of cortical fabric or a greater thickness of the layers or both. The fusellar component provides some input in the formation of such elevations through the protrusion of the "heads" of the

fuselli outward, thus producing a projection which is later emphasized by the overlying cortex.

The fusellar component of the thecal wall consists of fuselli that are similar to those observed in the distal part of the metasicula. Morphologically they could be subdivided into a lower *base*, a middle *trunk*, and an upper *head*, while structurally they consist of a *body*, an *outer lamella*, and an *outer sheet* (Plate 19). The body is made of fusellar fabric, which marginally gives way to the cortical fabric of the outer lamella. The transition of a single fibril of mesh material within the body of the fusellus into one of the uniformly oriented fibrils of the outer lamella has been observed many times (Plate 19: figures 1, 2, arrows). The fabric within the outer lamella is genuinely cortical and the outer lamella does not differ from the adjacent layers of the cortex. The outer lamella is rather thin within the base, is better developed within the trunk, and is thickest within the head. A distinct outer sheet, produced by an electron-dense, homogeneous material always coats each fusellus. Few intersheet vesicles have been observed in association with the outer sheet of the fuselli. Since the degree of overlap of the fuselli at their interfusellar sutures is usually slight, the inner cortical deposits are probably formed primarily through independent deposition of a few layers of cortical fabric, differing from that in the cortex only by its less distinct sheets.

Longitudinal sections through an interthecal septum (between thecae 1 and 2) of an old rhabdosome reveal it as a very thin lamella that has not been formed at a single fusellar wall. It shows traces of a bilayered or even multilayered structure, which most probably is the result of the secondary deposition of fusellar strips over the primary wall (Plate 21: figure 2). The small, wedge-shaped, so-called "intercalary fuselli", described by Walker (1953) and Urbanek (1958) in the interthecal septa of some monograptids, might be thus only partly intercalary and partly the result of additional fuselli laid down over the surface of the primary interthecal septum.

The free edge of the interthecal septum is usually strongly thickened to produce a characteristic club-like structure (Plate 21: figure 1). It is composed of about 15 layers of a compact material, each layer being separated by a distinct electron-dense sheet, frequently associated with a number of vesicles or

perimembrane fissures. The compact material in these layers is not unlike that of the virgular fabric. This compact layered material surrounds the margin of the interthecal septum and is discernible in the center of the thickening as an accumulation of the spongy material.

The prothecal portion of the theca first shows a finger-like outgrowth stretching toward the thecal cavity (Plate 20: figure 2). Although the nature of this appendage is obscure, it recapitulates the peridermal materials being composed of an intercalation of fusellar and cortical fabrics, the latter in both a loose and compact form. The structure in question demonstrates the zooidal potential for a local reversal from the secretion of fusellar fabric to the secretion of cortical fabric and vice versa, and shows also the transition from loose into compact cortical fabric.

Transverse microtome sections through a young rhabdosome (at 1½ theca stage) illustrate the mode of junction of theca 2 to the sicula. A growing margin of the prothecal portion of theca 2 is shown. This somewhat obliquely oriented section through the last formed fusellus shows its mode of fusion with the wall of the metasicula. A thin wall that corresponds to the trunk of the fusellus is made of a compact material, the two outer lamellae leaving little space for dense mesh material (Plate 21: figure 3). This compact wall divides at the junction with the wall of the metasicula (S) to produce a characteristic bifurcation (Plate 21: figure 3, arrow). Each wall is made of an outer lamella and some subjacent spongy material, both of which merge with the wall of the metasicula to become its outermost layers. The triangular space outlined by the bifurcation of the fusellus and the wall of the metasicula is filled with a very loose fibrous material. The head of the fusellus is seen as a clublike extension having a somewhat larger amount of the dense mesh material within it (Plate 21: figure 3).

#### COMPARISON AND CONCLUSIONS CONCERNING THE THECAE

1. The specimens studied reveal a somewhat contradictory picture for the formation of the cortex in *Didymograptus* sp. Ultrathin sections, through a growing initial bud, show that the earliest fuselli produce a thin cortical coating through an overlap

of their outer lamellae. This is continuous with that over the prosicula. At the growing margin, however, they show no such overlap and no other outer cortical deposit. Any subsequent cortical fabric, therefore, could be laid down only over these fuselli. In contrast to this, the distal thecae show formation of the cortex simultaneously with the growth of the fuselli through a subsequent overlap and accumulation of their outer lamellae. Consideration of these data, together with the results obtained for the metasicula where the primary outer cortical coating is very thin, indicate a heterogeneity in the formation of the cortex at different places within a single rhabdosome. Further study is necessary, however, to establish this conclusion.

2. It seems safe to conclude that the formation of the cortex in the distal thecae of *Didymograptus* sp. is different from that of *P. dubius*. In *P. dubius* the entire cortex is formed independently from the outer lamellae of the fuselli, while in *Didymograptus* it is produced as a result of the overlapping of the outer lamellae of the fuselli.

3. The present study supplies more evidence to support an earlier hypothesis by the authors (Urbanek and Towe, 1974) for a close chemical relationship between the cortical and fusellar fibrils. In a number of cases within a single fusellus, a continuous passage from irregularly arranged fusellar fibrils of the body of the fusellus into the more or less ordered fibrils of the outer lamella of the fusellus has been observed (comp. Plate 19: figures 1, 2, arrows). A single wavy fusellar fibril may pass in this way into a straight fibril in the outer lamella, this having a distinct cortical appearance. Such a passage may be indicative, in spite of the differences in physical appearance, for an essentially similar chemical nature for both fibrous materials in the graptolite periderm. The cortical fibrils within the outer lamella are occasionally spanned by transverse rods considered to be related to the ground substance, but the fusellar fibrils lack such traces. This supports the concept that the matrix was responsible for the ordered arrangement of fibrils and for keeping them in register (Urbanek and Towe, 1974).

### Ultrastructure of the Clathrium in *Holoretiolites*

In marked contrast to the graptoloids described above, the periderm of *Holoretiolites* exists only

as a skeletal framework (the *clathrium*) composed of delicate lists. The skeletal lists are arranged according to a regular geometric pattern, which is characteristic of particular genera and species of this group of retiolitids (Plectograptinae). For details of the construction of the clathrium in *Holoretiolites*, see Münch (1931), Eisenack (1951), Bouček and Münch (1952).

Scanning electron micrographs (Plate 22: figures 1, 2) show that the surface of the lists producing the clathrium in *H. mancki* is covered by numerous blunt spines arranged in parallel longitudinal rows. Each row is separated by grooves from the adjacent ones, and the spines within a particular row situated one over the other are connected by ridges. This produces the characteristic spinose appearance of the lists.

A series of ultramicrotome sections through the middle part of the clathrium brings out the ultrastructural pattern of the lists (Plate 22: figure 3; Plate 23). Transverse sections through diagonal and ventral lists and longitudinal sections through arched, upper lists of the apertural loop (Brücke, in Eisenack's (1951) terminology) demonstrate that the different rods of the skeletal network in *H. mancki* are made of the same fabric and show the same pattern. Both of these deviate from "normal" graptoloid periderm, being constructed of virgular fabric as earlier defined.

The lists are composed of a number of layers made of two different materials. Fibrous layers are made of a polytypic material composed of peculiar fibrils (F) (Plate 23) embedded in a homogeneous and electron-dense matrix. They are separated by layers made solely of homogeneous and electron-dense matrix (M) and are therefore monotypic.

Transverse sections through diagonal and ventral lists of the clathrium reveal that these are rods that are rounded or reniform in outline, concave on the internal surface, and convex on the external surface. Each rod is composed of some four to six well-defined fibrous layers and a few additional, rather thin, "intercalary" fibrous layers (Plate 22: figure 3). These layers were deposited hemiperipherally on the outer surface of the internal groove, which results in a crescentic shape of each fibrous layer. Adjacent fibrous layers are separated by a rather wide layer made of homogeneous matrix material. The formation of each

list started with the deposition of the first fibrous layer outlining the internal groove and ended with the secretion of the most external homogeneous layer. The spines present on the surface of the rods are made entirely of this latter material. These were formed in the later stages of the growth of the list. Since traces of their presence appear only on penultimate (or rarely on next to penultimate) homogeneous layers (Plate 22: figure 3, arrows), the external surface of the lists in the early stages of their formation were smooth and the surface of the internal groove was smooth as well.

The structural details of the fibrils within the fibrous layers of the lists of the clathrium deserve special attention. Transverse sections show the fibrils to be rounded, slightly elongated, or in certain cases somewhat angular (Plate 24: figure 1). In contrast to the cortical fibrils, or to the fibrils in the virgula of *Pristiograptus dubius*, they are not uniformly thick. Thinner fibrils are scattered among the thicker ones (Plate 24: figure 1). The lateral ends of the crescent-shaped fibrous layers are usually made of somewhat thinner fibrils than those in the main portion of the fibrous layer. Some fibrils are rather loosely dispersed and separated from each other by abundant matrix. This material fills the interfibrillar spaces as a compact mass without being organized into interfibrillar rods, and this is another notable feature of the fibrous material encountered in the clathrium of *H. mancki*.

Transverse sections bring out the ultrastructure of the fibrils. Each fibril appears as an electron-lucent spot on a background of electron-dense matrix (Plate 24: figure 2). Each is provided with numerous delicate septations, made of an electron-dense material probably continuous with the matrix (Plate 1: figure 2; Plate 24: figure 1). These septations are not quite radially arranged, but show a more or less pronounced, bilateral arrangement, being frequently V-shaped, stretching toward the center of the fibrils from two sides. The same feature examined on longitudinal sections

(Plate 24: figure 2) produces a uniform pattern of delicate electron-dense bands obliquely oriented with respect to the main axis of the fibril. The vertical repeat distance is approximately 700 Å.

Towe and Urbanek (1972) have emphasized that the fibrils of the cortical fabric are collagen-like and may represent one of many varieties of invertebrate collagen materials. However, the fibrils of the virgular fabric discussed here and throughout this paper present difficulties as regards their biochemical or biophysical affinity with extant fibrous materials. Obliquely banded fibrils are a structural feature of the keratin class of proteins and have been observed in reconstituted cartilage collagen (Bruns, Trelstad, and Gross, 1973), as well as in paramyosin filaments (Elliott and Lowy, 1969; Cohen, Szent-Györgyi, and Kendrick-Jones, 1971). But no materials known to us, including the above-mentioned fibrous proteins, show a cross-sectioned pattern identical to that displayed by the virgular fabric. This stellate-septate ultrastructure is, as far as we know, unique.

The similarities with keratins are few and the paramyosins, being muscle proteins, can be ruled out because of functional considerations. The vertical d-repeat of the oblique bands measures approximately 700 Å and this compares favorably with collagens (B. Doyle, personal communication). The packing of the fibrils together, with their cross-sectional diameter averaging 1500 Å, provides additional features in common with collagens. Their structural support function is also consistent. In extant organisms, the presence of strongly oblique banding in *native* collagens is uncertain because of the possibility of mechanical deformations induced during fixation and specimen preparation, but its presence in reconstituted cartilage collagen (Bruns, Trelstad and Gross, 1973) shows that undistorted structures of this type are possible. The alternative to a collagen-like fibril for these graptoloid materials would be a new type of fibrous material, unknown to date in living organisms.

### Literature Cited

Andres, D.

1961. Die Struktur von Mastigograpten aus einem ordovizischen Geschiebe Berlins. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 12:636-647.

Berry, W. N., and R. S. Takagi

1970. Electron Microscope Investigations of *Orthograptus quadrimucronatus* from the Maquoketa Formation (Late Ordovician) in Iowa. *Journal of Paleontology*, 44:117-124.

1971. Electron Microscope Study of a Diplograptus Species. *Lethaia*, 4: 113 pages.
- Bouček, B., and A. Münch  
1952. The Central European Retiolites of the Upper Wenlock and Ludlow. *Sbornik Ústředního Ústavu Geologického*, 19: 151 pages.
- Braverman, M.  
1971. Studies on Hydroid Differentiation, VII: The Hydrozoan Stolon. *Journal of Morphology*, 135:131-152.
- Bruns, R. R., R. L. Trelstad, and J. Gross  
1973. Cartilage Collagen: A Staggered Substructure in Reconstituted Fibrils. *Science*, 181:269-271.
- Bulman, O. M. B.  
1964. Lower Palaeozoic Plankton. *Geological Society of London, Quarterly Journal*, 119:401-418.  
1970. Graptolithina with Sections on Enteropneusta and Pterobranchia. Part V in R. C. Moore, editor, *Treatise on Invertebrate Paleontology*. 2nd edition, XXXII+163 pages. Boulder, Colorado: Geological Society of America.
- Cohen, G., A. G. Szent-Györgyi, and J. Kendrick-Jones  
1971. Paramyosin and the Filaments of Molluscan "Catch" Muscles, I: Paramyosin: Structure and Assembly. *Journal of Molecular Biology*, 56:223-237.
- Cox, I.  
1934. On the Structure of *Monograptus dubius* (Suess). *Annals and Magazine of Natural History*, 10:421-425.
- Eisenack, A.  
1951. Retioliten aus dem Graptolithengestein. *Palaeontographica*, 100:129-163.
- Elliott, A., and J. Lowy  
1969. Helicoidal Structure of Paramyosin. *Nature*, 224: 1105-1107.
- Jaanusson, V.  
1960. Graptoloids from the Ontikan and Viruan (Ordovician) Limestones of Estonia and Sweden. *The Bulletin of the Geological Institutions of the University of Uppsala*, 38:289-366.
- Kirk, N. H.  
1969. Some Thoughts on the Ecology, Mode of Life, and Evolution of the Graptolithina. *Proceedings of the Geological Society of London*, 1659:273-292.  
1972. More Thoughts on the Automobility of the Graptolites. *Journal of the Geological Society*, 128:127-133.
- Kozłowski, R.  
1949. Les Graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. *Palaeontologia Polonica*, 3: 235 pages.  
1971. Early Development Stages and the Mode of Life of Graptolites. *Acta Palaeontologica Polonica*, 16: 313-342.
- Kraft, P.  
1926. Ontogenetische Entwicklung und Biologie von Diplograptus und Monograptus. *Paläontologische Zeitschrift*, 7:207-249.
- Kraatz, R.  
1964. Untersuchungen über die Wandstrukturen der Graptolithen (mit Hilfe des Elektronenmikroskops). *Zeitschrift der Deutschen Geologischen Gesellschaft*, 114:699-702.
1968. Elektronenmikroskopische Beobachtungen an Monograptus-Rhabdosomen. *Der Aufschluss*, 12:357-361.
- Kulicki, C.  
1971. New Observations on *Rhabdopleura kozłowskii* (Pterobranchia) from the Bathonian of Poland. *Acta Palaeontologica Polonica*, 16:415-428.
- Münch, A.  
1930. *Retiolites mancki*: Ein neuer Retiolites aus dem norddeutschen Geschiebe. *Berichte der Naturwissenschaftlichen Gesellschaft zu Chemnitz*, 23: 8 pages.
- Pease, D. C., and M. Bouteille  
1971. The Tridimensional Ultrastructure of Native Collagenous Fibrils, Cytochemical Evidence for a Carbohydrate Matrix. *Journal of Ultrastructure Research*, 35:339-358.
- Skevington, D.  
1965. Graptolites from the Ontikan Limestones (Ordovician) of Öland, Sweden, II: Graptoloidea and Graptovermida. *University of Uppsala, Bulletin of the Geological Institutions*, 43: 74 pages.
- Towe, K. M., and A. Urbanek  
1972. Collagen-like Structures in Ordovician Graptolite Periderm. *Nature*, 237:443-445.
- Urbanek, A.  
1953. Sur deux espèces de Monograptidae. *Acta Geologica Polonica*, 3:277-297.  
1958. Monograptidae from Erratic Boulders of Poland. *Palaeontologia Polonica*, 9: 105 pages.  
1959. On the Development and Structure of the Graptolite Genus *Gymnograptus*. *Acta Palaeontologica Polonica*, 4:279-336.  
1966. On the Morphology and Evolution of the Cucullograptinae (Monograptidae, Graptolithina). *Acta Palaeontologica Polonica*, 11:291-544.  
1970. Neocucullograptinae n. subfam. (Graptolithina)—Their Evolutionary and Stratigraphic Bearing. *Acta Palaeontologica Polonica*, 15:163-388.
- Urbanek, A., and K. M. Towe  
1974. Ultrastructural Studies on Graptolites, I: The Periderm and its Derivatives in the Dendroidea and in *Mastigograptus*. *Smithsonian Contributions to Paleobiology*, 20: 48 pages.
- Waddington, C. H.  
1962. *New Patterns in Genetics and Development*. XII+271 pages. New York and London: Columbia University Press.
- Walker, M.  
1953. The Development of *Monograptus dubius* and *Monograptus chimaera*. *Geological Magazine*, 90: 362-373.
- Wetzel, W.  
1958. Graptolithen und ihre fraglichen Verwandten im elektronenmikroskopischen Vergleich. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 7:307-312.

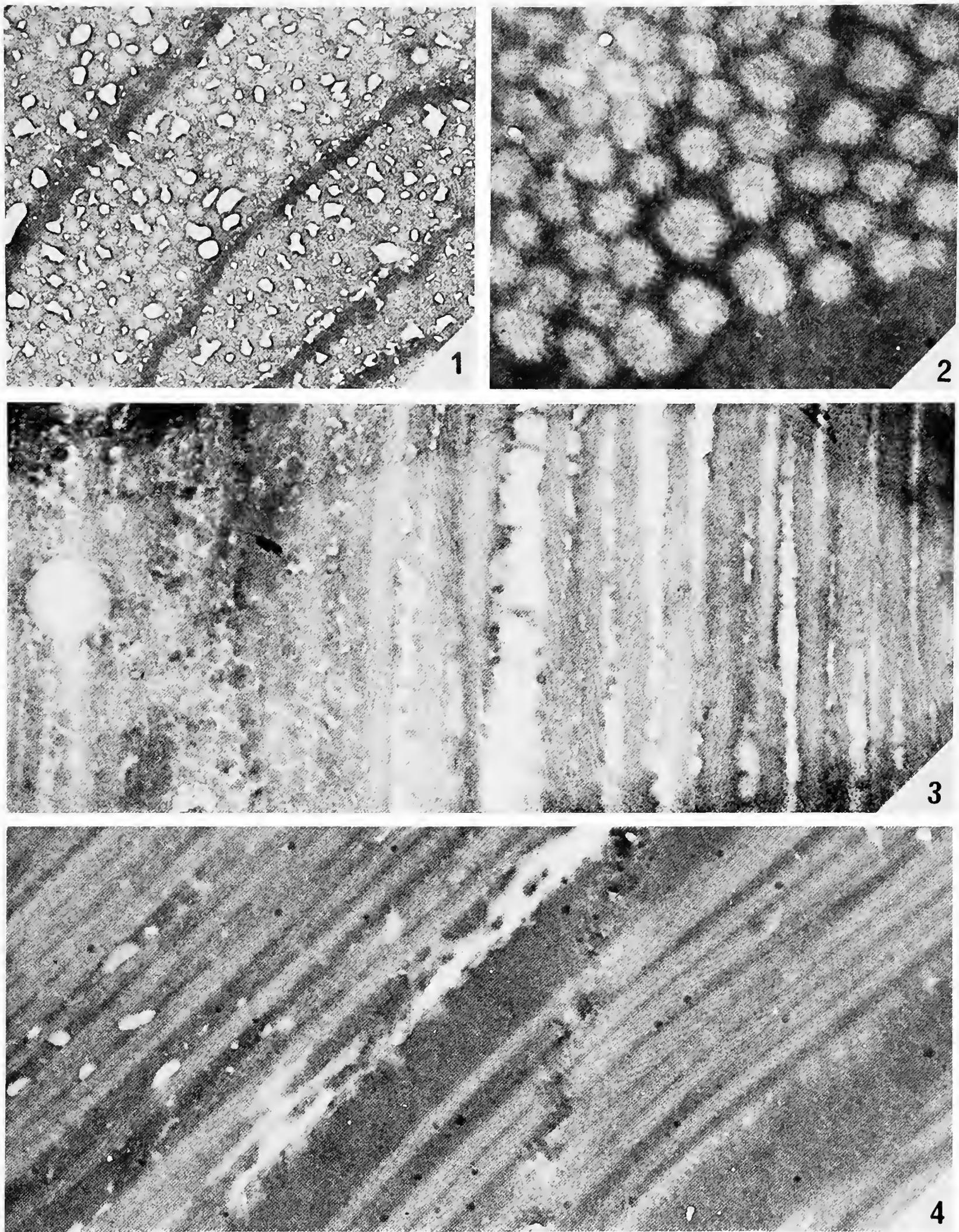


PLATE 1.—Ultrastructural features of the virgular fabric: 1, 3, On transverse and longitudinal sections of the virgula in *Pristiograptus dubius* ( $\times 35,000$ ;  $\times 45,600$ ); 2, 4, on transverse and longitudinal sections through rods of the clathrium in *Holoretiolites mancki* ( $\times 72,100$ ;  $\times 45,600$ ).

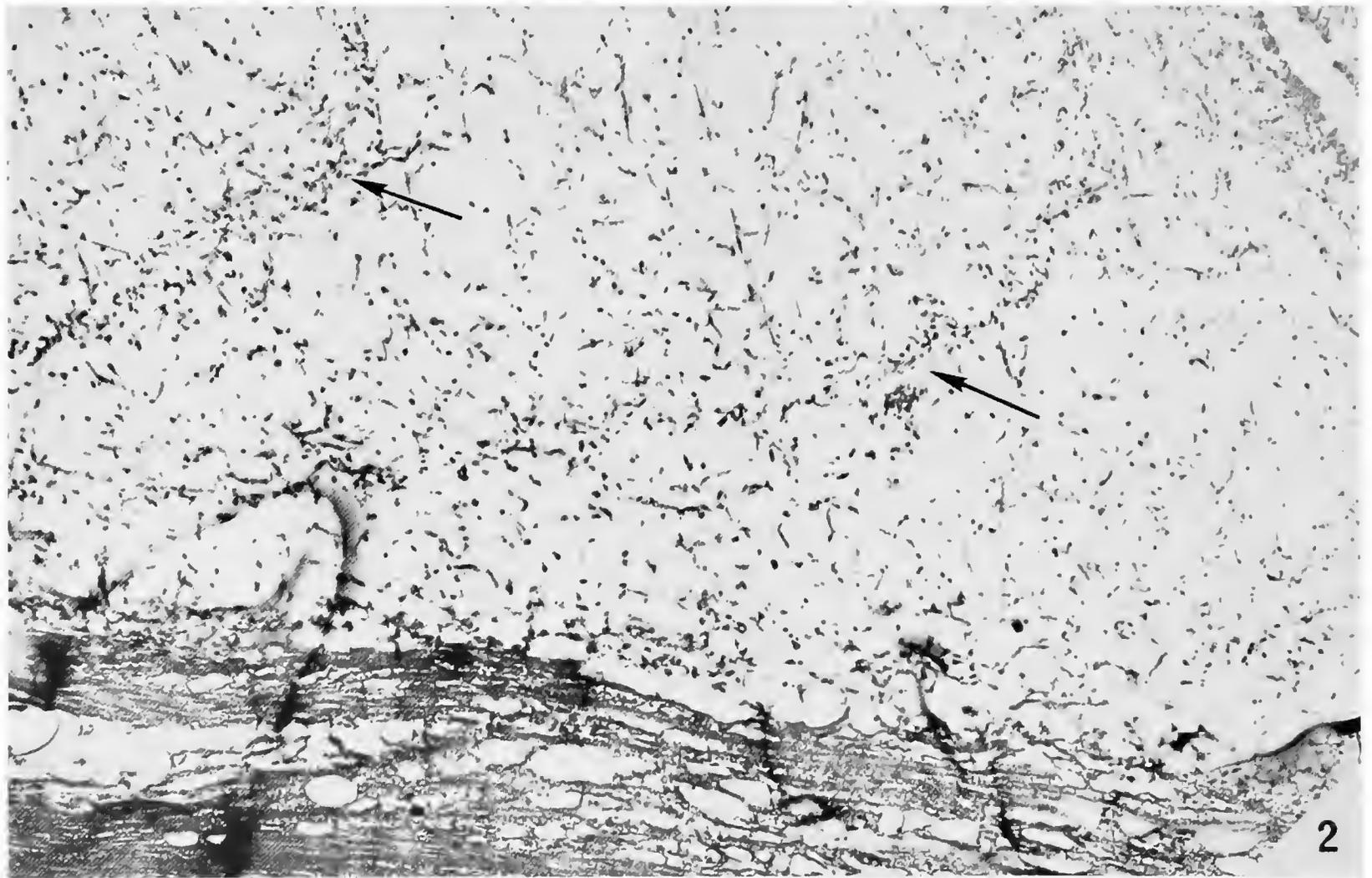
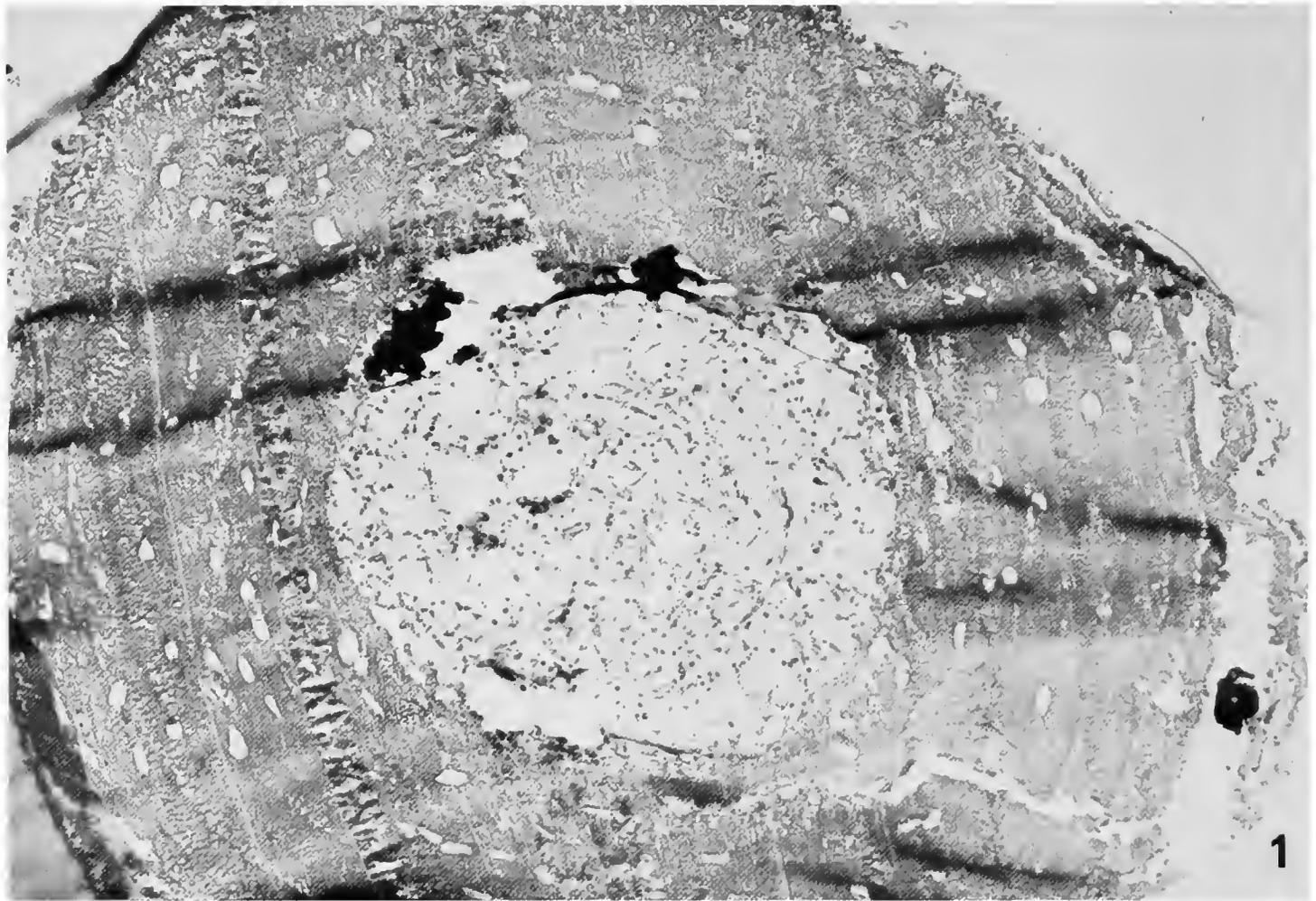


PLATE 2.—*Didymograptus* sp.: 1, Transverse section of the nema ( $\times 3,800$ ); 2, longitudinal section of the nema near the apex of prosicula ( $\times 14,000$ ), showing growth lines in the material that fills the internal canal (arrows).

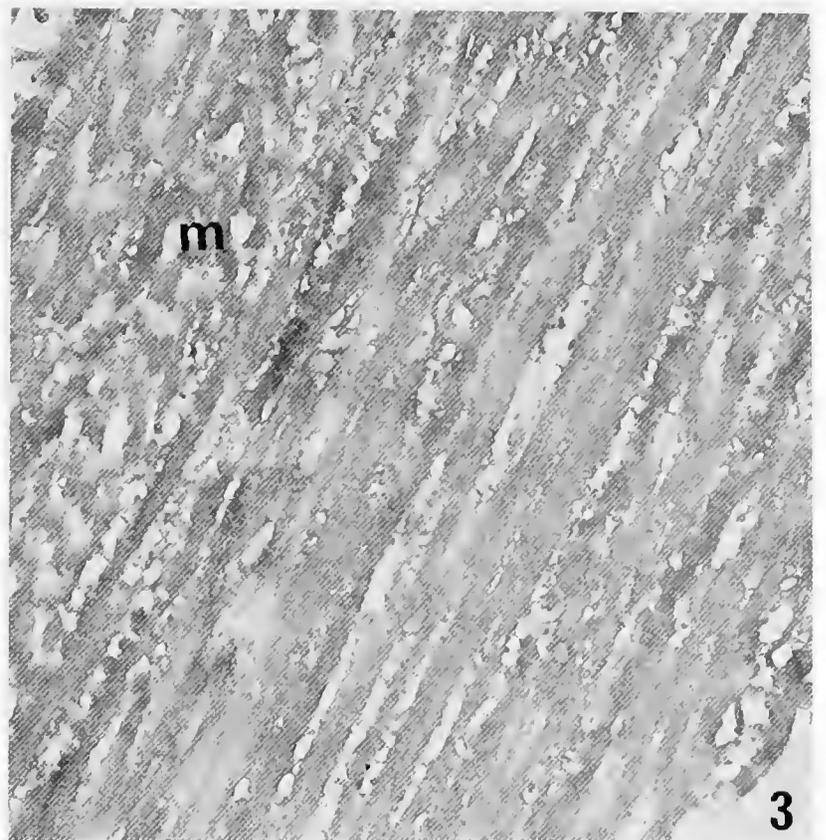
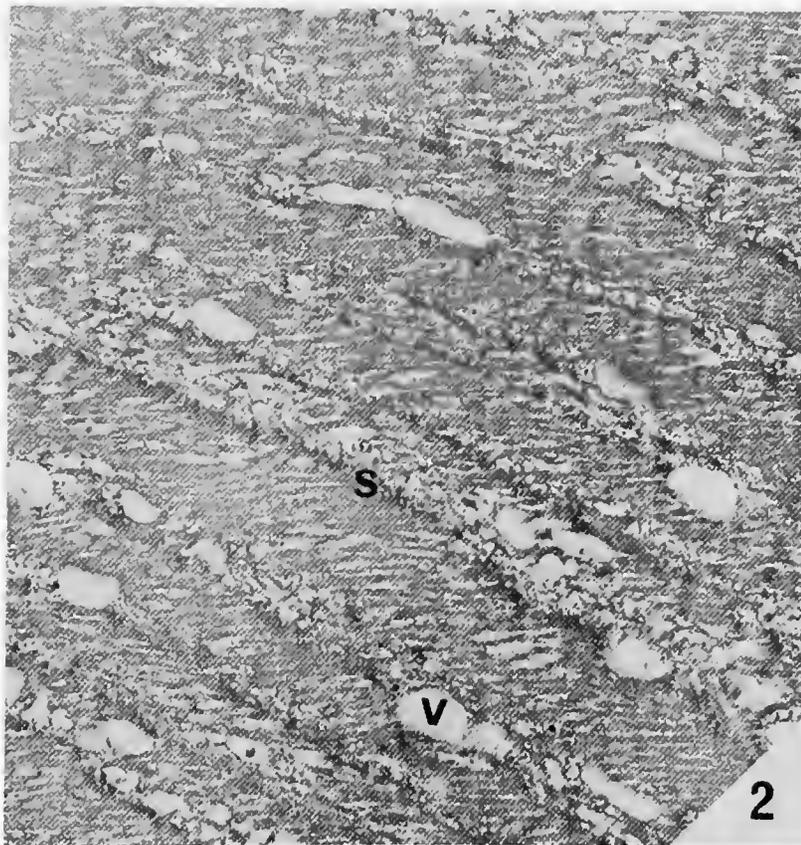
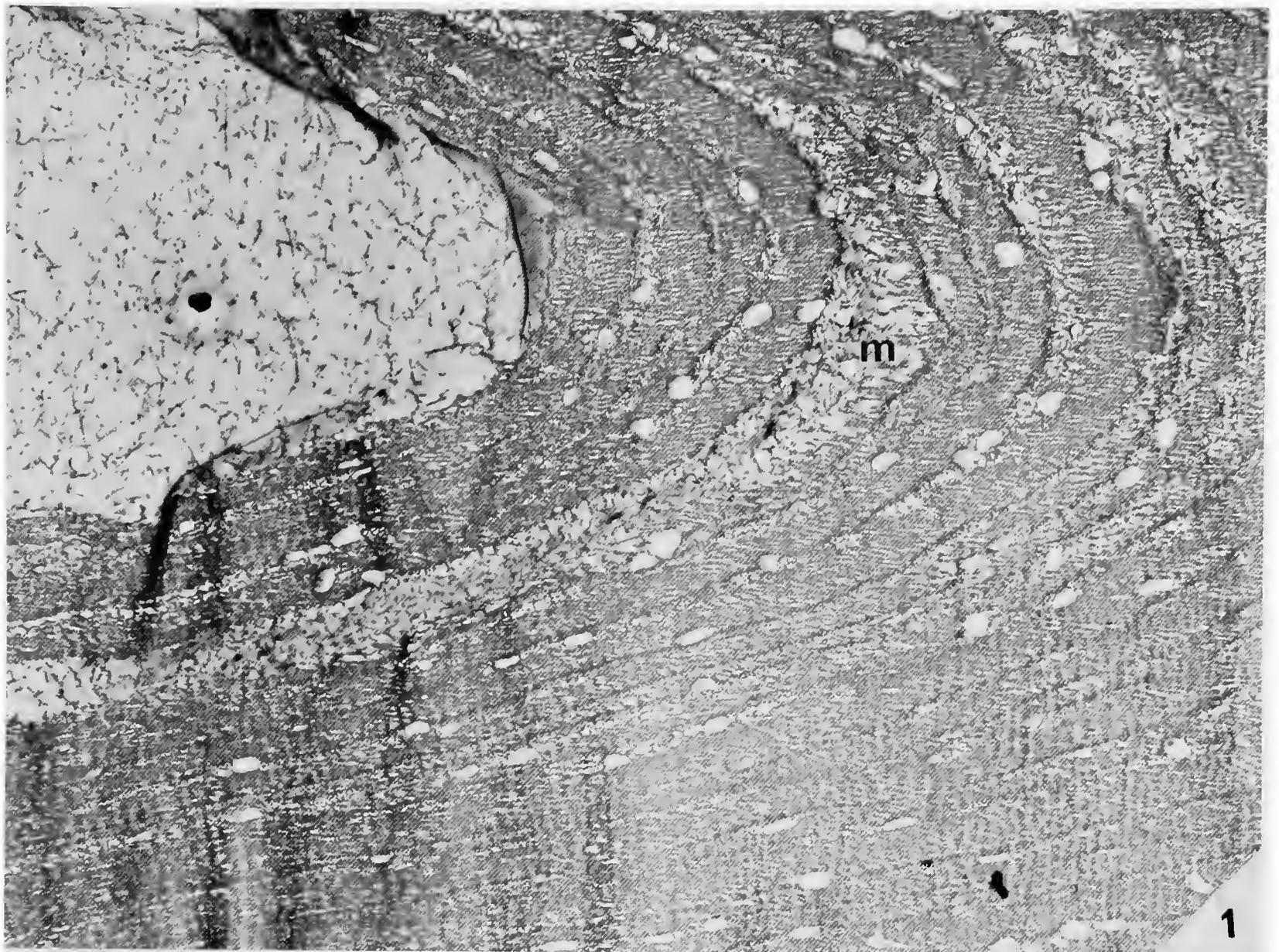


PLATE 3.—*Didymograptus* sp.: 1, Structural features of the wall of nema, as seen on oblique section ( $\times 7,000$ ) (m = mesh material); 2, details of particular layers showing sheet fabric (s) and intrasheet vesicles (v) ( $\times 11,500$ ); 3, cortical fibrils recognized within a layer ( $\times 32,500$ ).

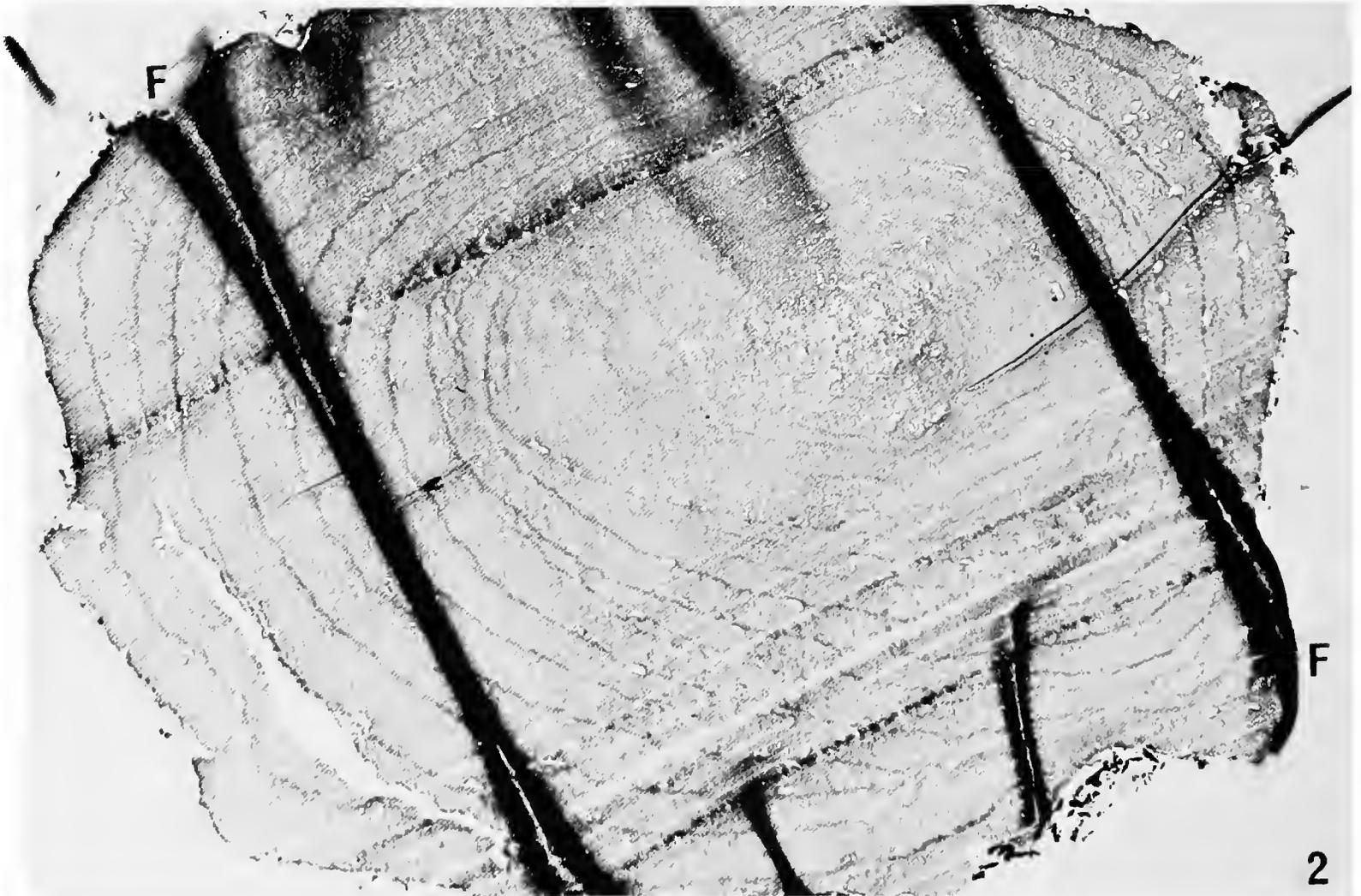
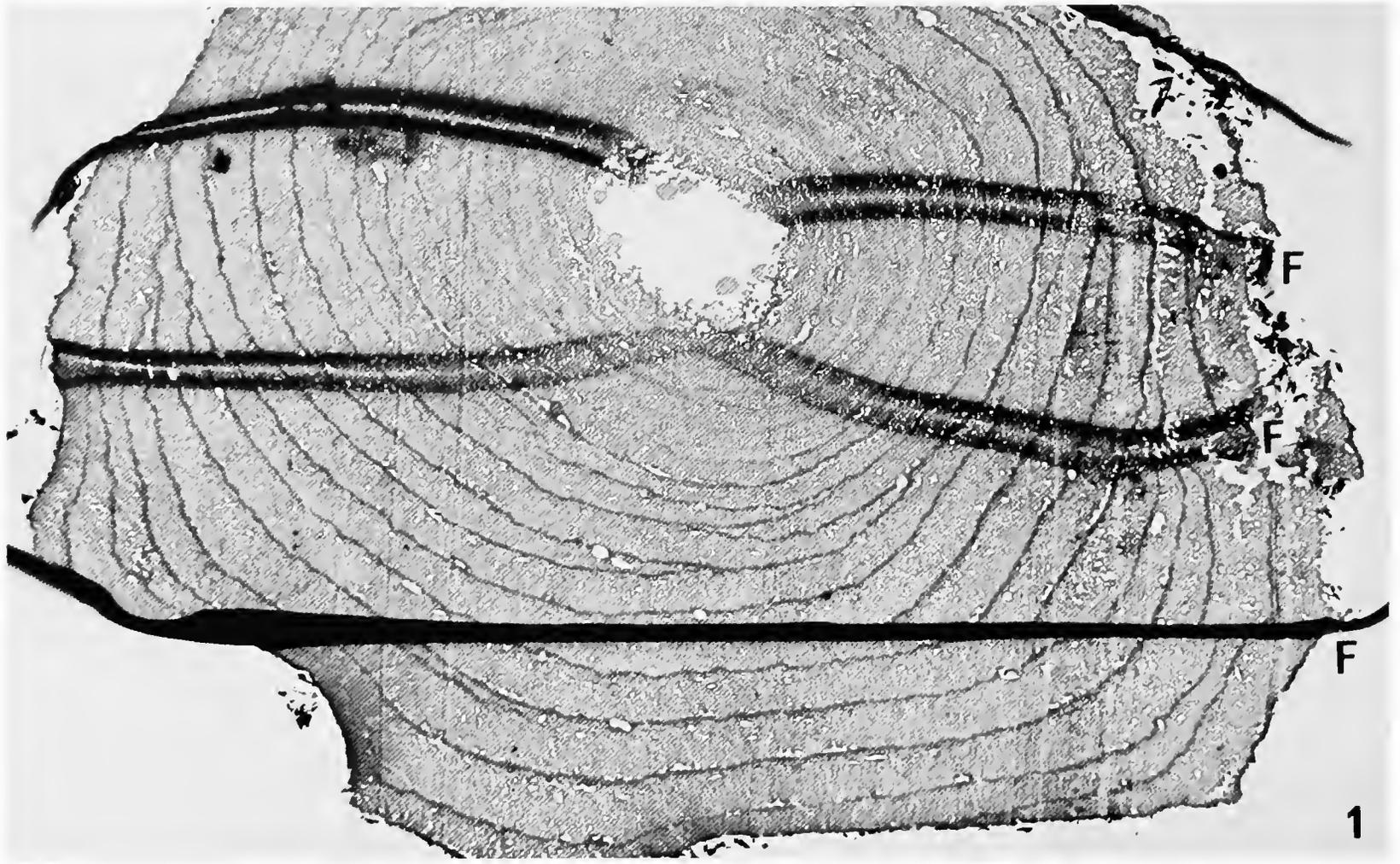


PLATE 4.—*Pristiograptus dubius* (Suess): 1, Transverse sections of the virgula showing a narrow internal canal ( $\times 8,100$ ); 2, porous material filling this canal ( $\times 8,600$ ) (F = artifacts produced by folding of the ultrathin section over the grid).

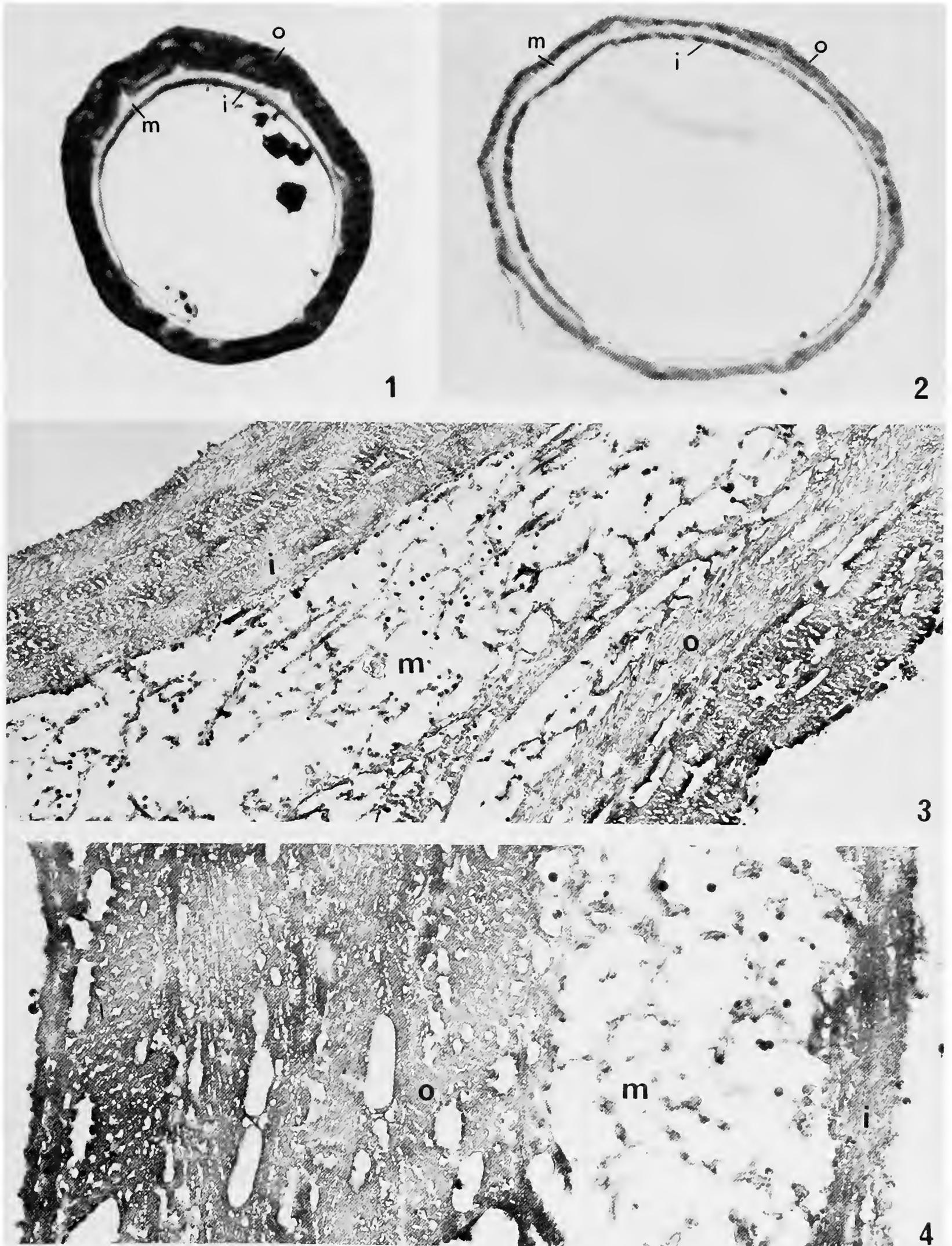


PLATE 5.—*Didymograptus* sp., structure of prosicula: 1, 2, Light micrographs showing transverse sections near the apex ( $\times 800$ ) and in the middle part ( $\times 600$ ); 3, 4, electron micrographs showing transverse sections through the prosicular wall with a relatively thick ( $\times 5,500$ ) and thin ( $\times 8,300$ ) inner component (i = inner component, m = middle component, o = outer component).

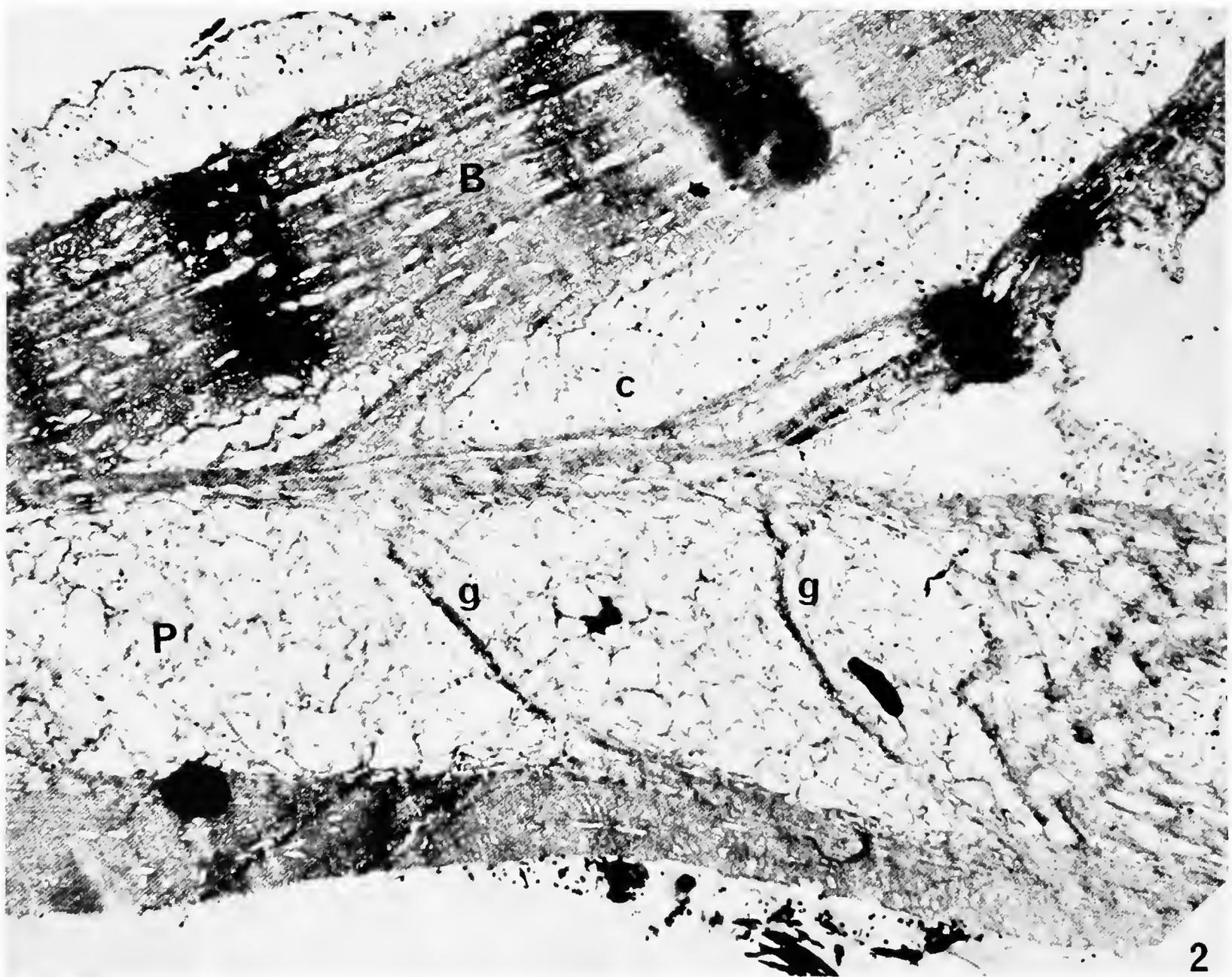
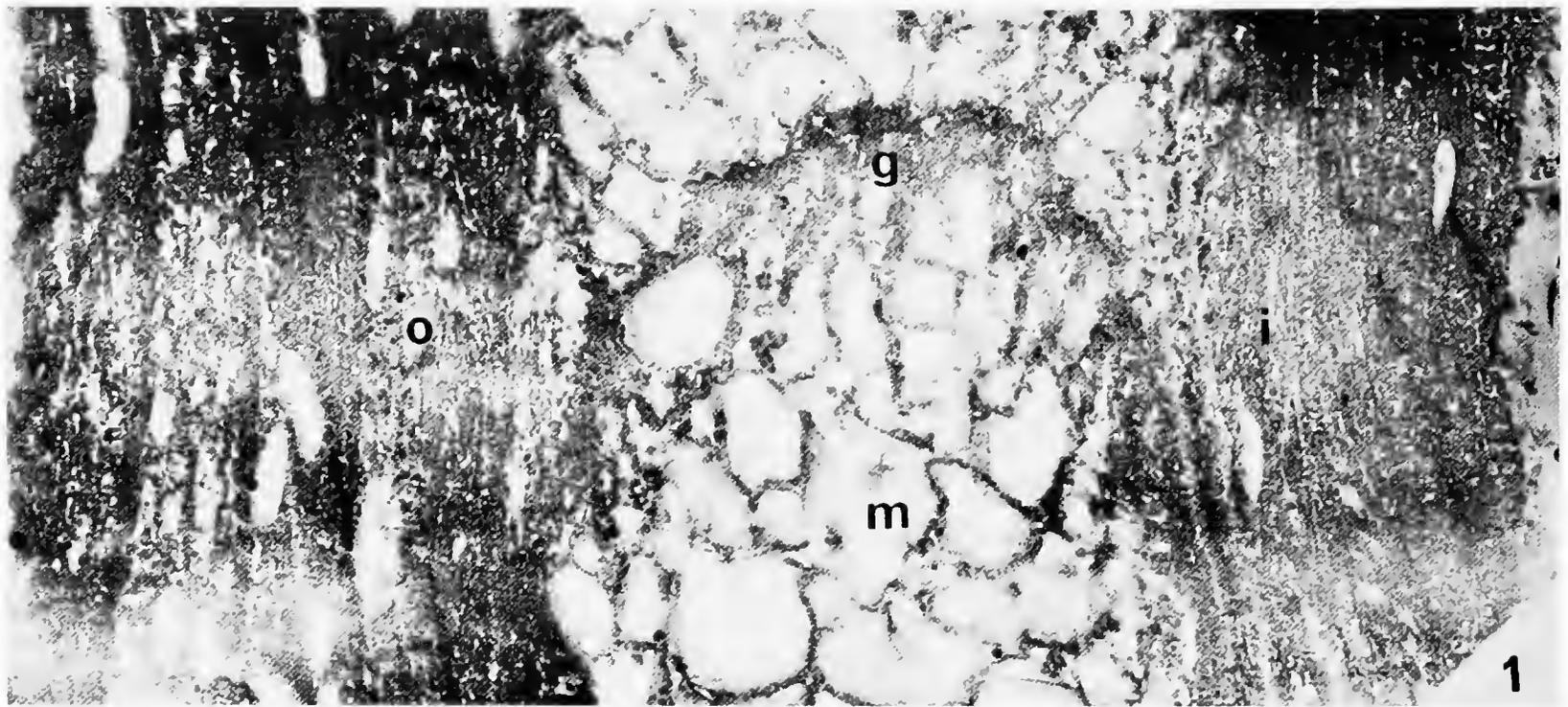


PLATE 6.—*Didymograptus* sp., structural details of the prosicula: 1, 2, Growth line recognized within the middle component of the prosicular wall ( $\times 32,200$ ) and wall of prosicula near porus and the initial bud ( $\times 10,600$ ) (B = wall of initial bud, c = material filling the corner of the initial bud, g = growth lines, i = inner component, o = outer component, P = wall of prosicula, m = middle component).

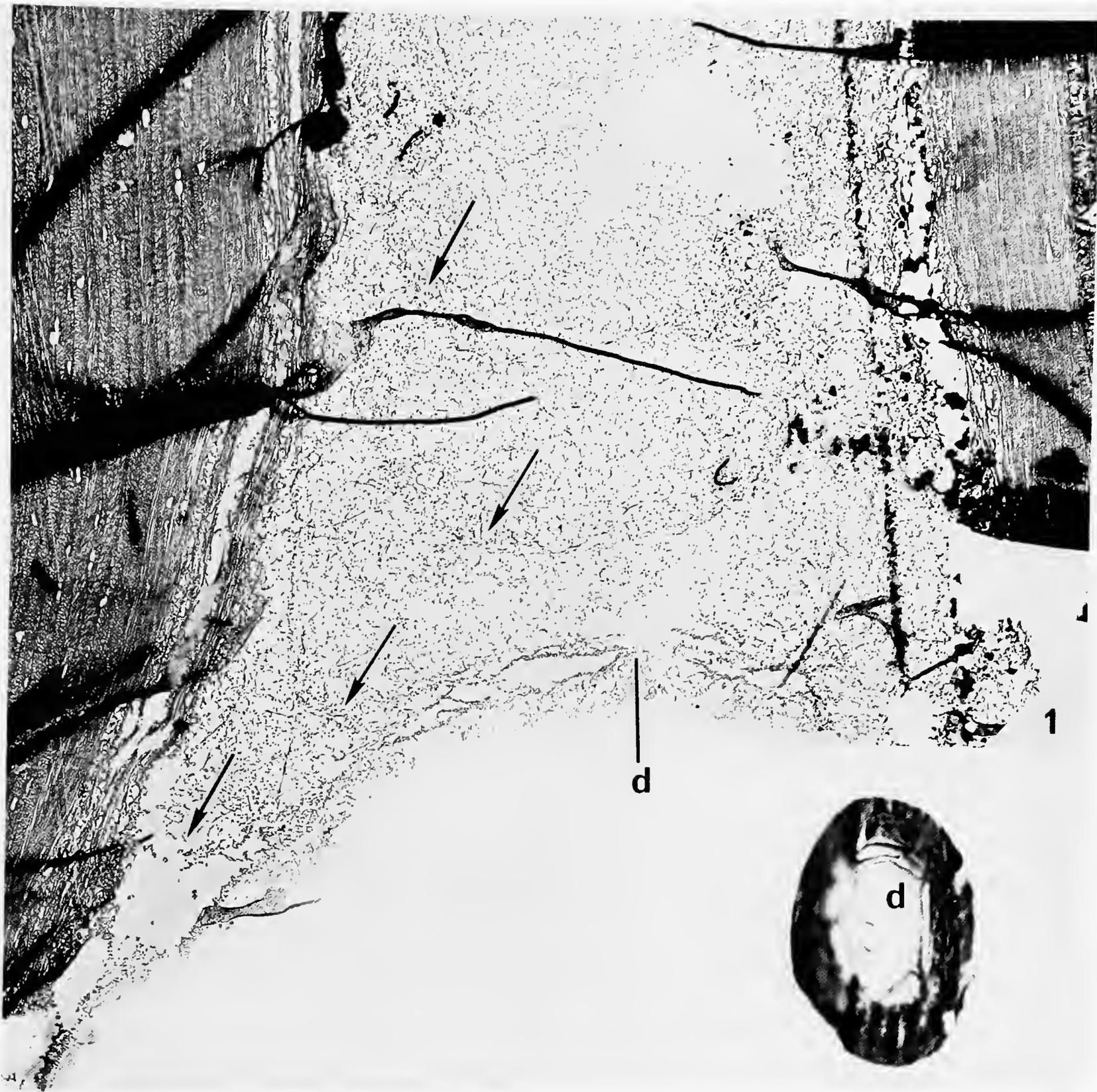


PLATE 7.—*Didymograptus* sp., structure of the apical part of the prosicula and the base of nema: 1, Electron micrograph showing longitudinal section near the apex of prosicula ( $\times 4,400$ ); 2, light micrograph showing a transverse section through the apex prosiculae and revealing the diaphragm ( $\times 800$ ) (d = diaphragm, arrows indicate growth lines within middle component of prosicula and loose material filling the canal of nema).

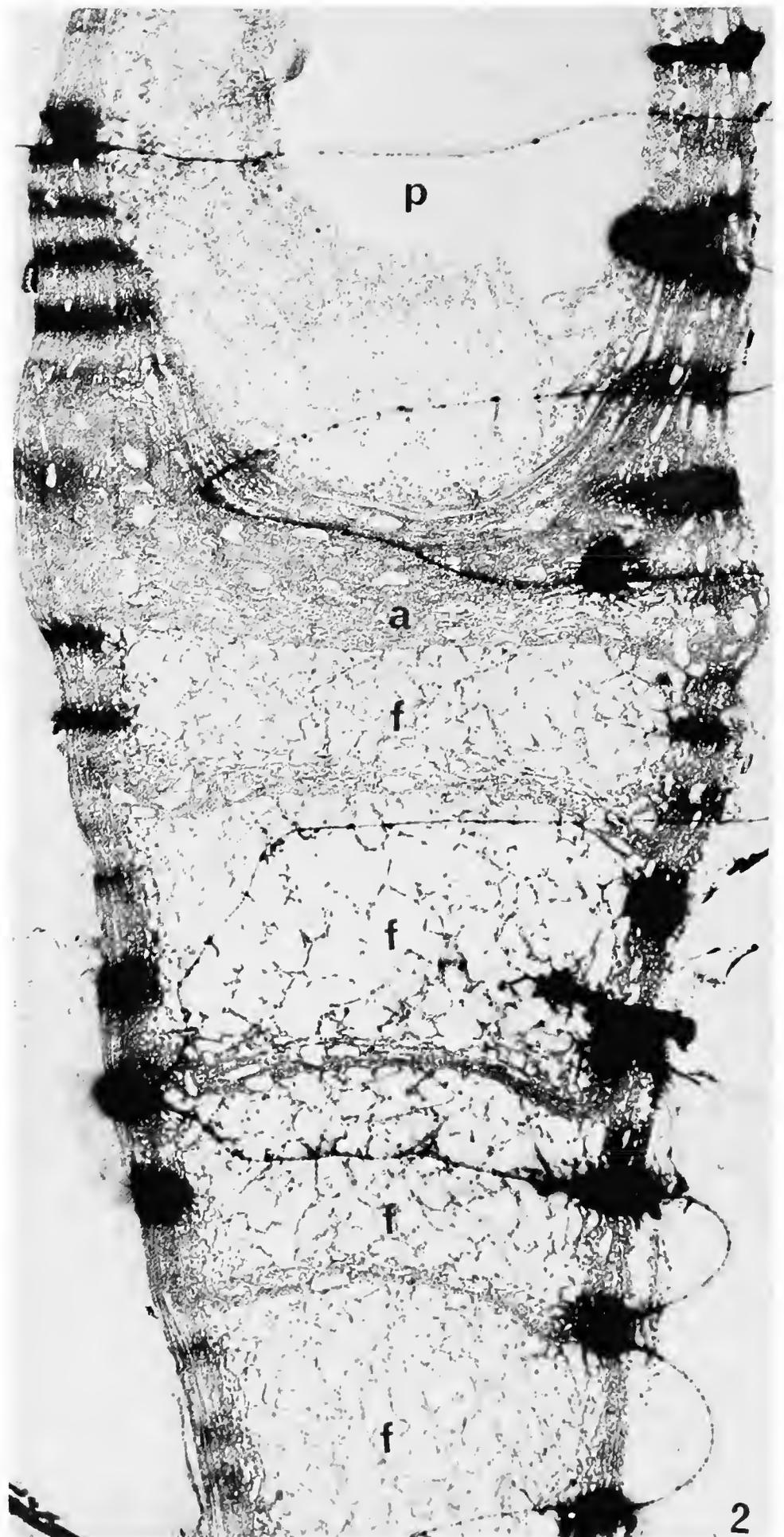
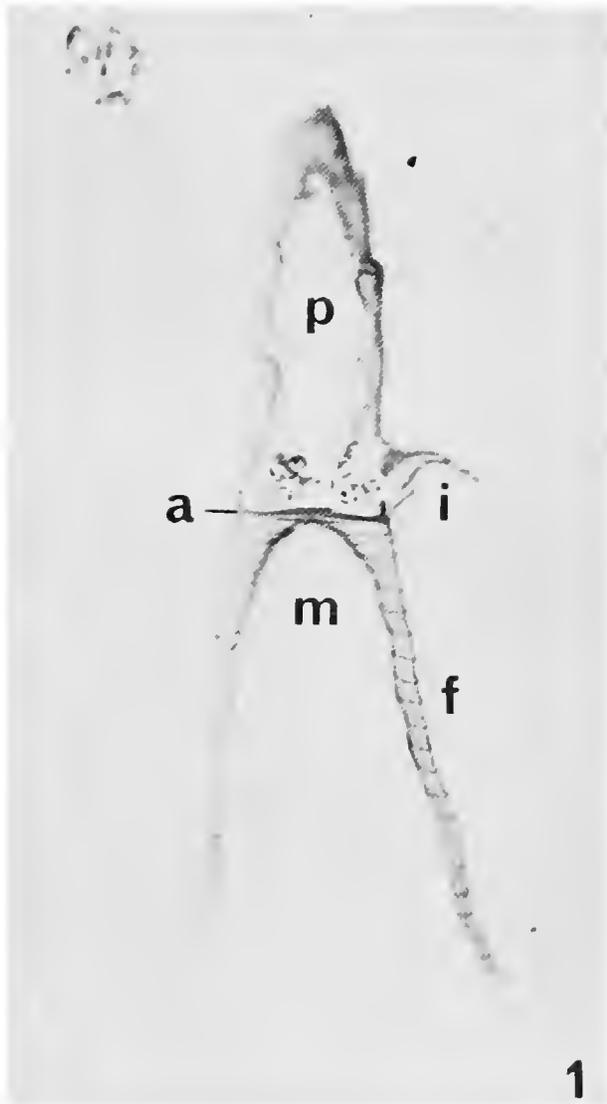


PLATE 8.—*Didymograptus* sp., structure of apertural part of the prosicula: 1, Light micrograph showing longitudinal section of the sicula with distinct apertural thickening of the prosicula ( $\times 130$ ); 2, electron micrograph showing longitudinal section at the boundary of the prosicula and metasicula ( $\times 26,700$ ) (a = apertural thickening of prosicula, f = fuselli, i = initial bud, m = metasicula, p = prosicula).

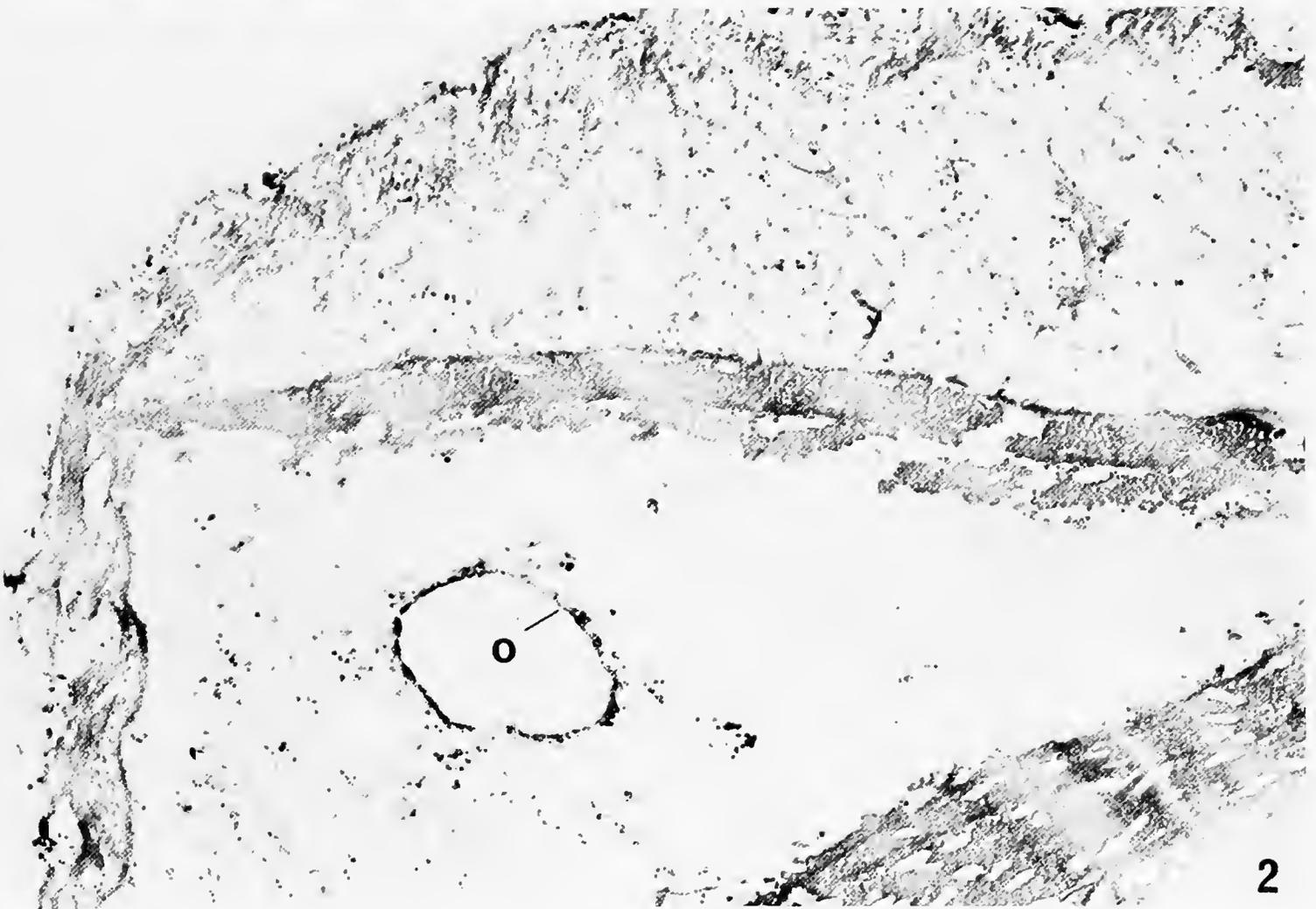
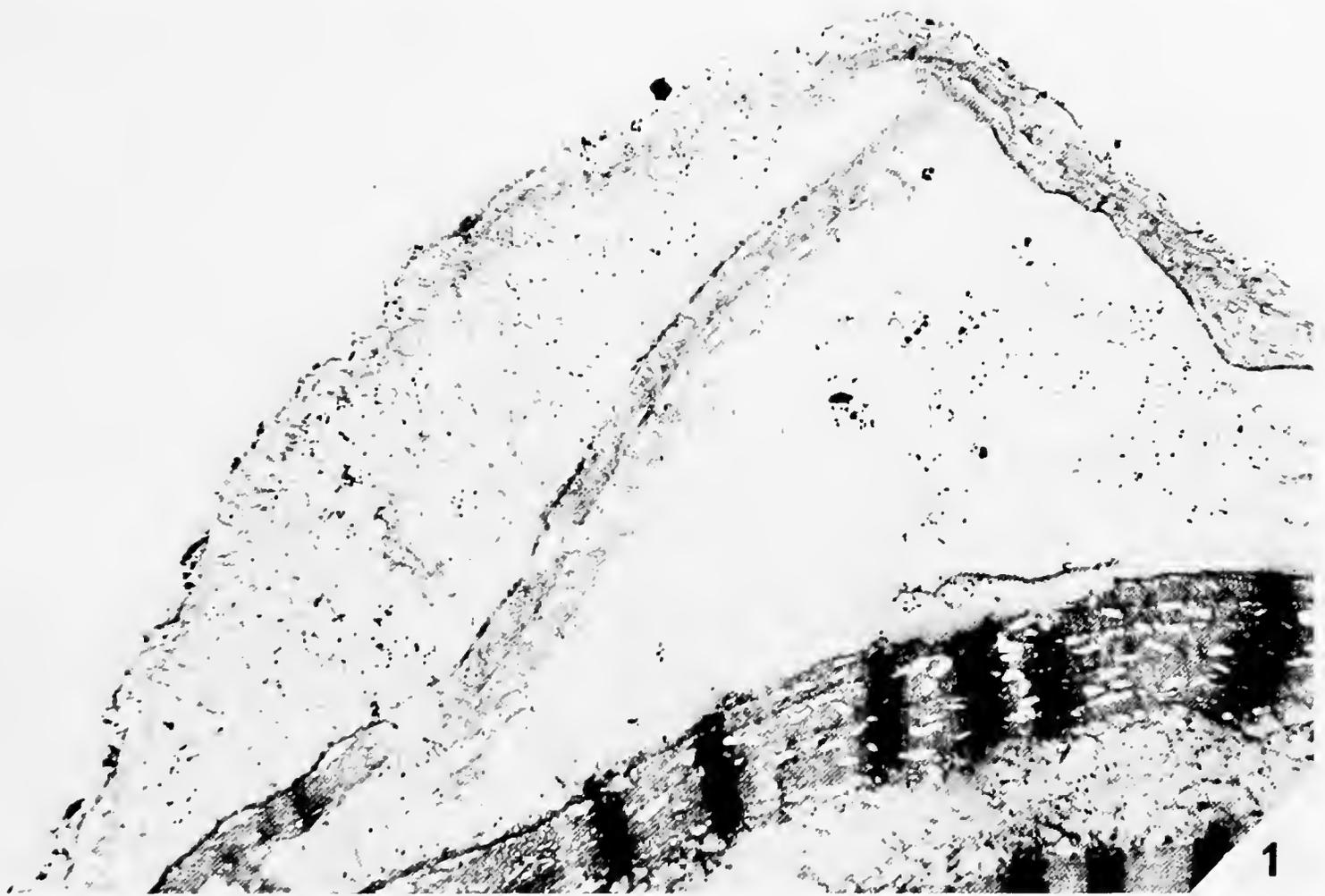
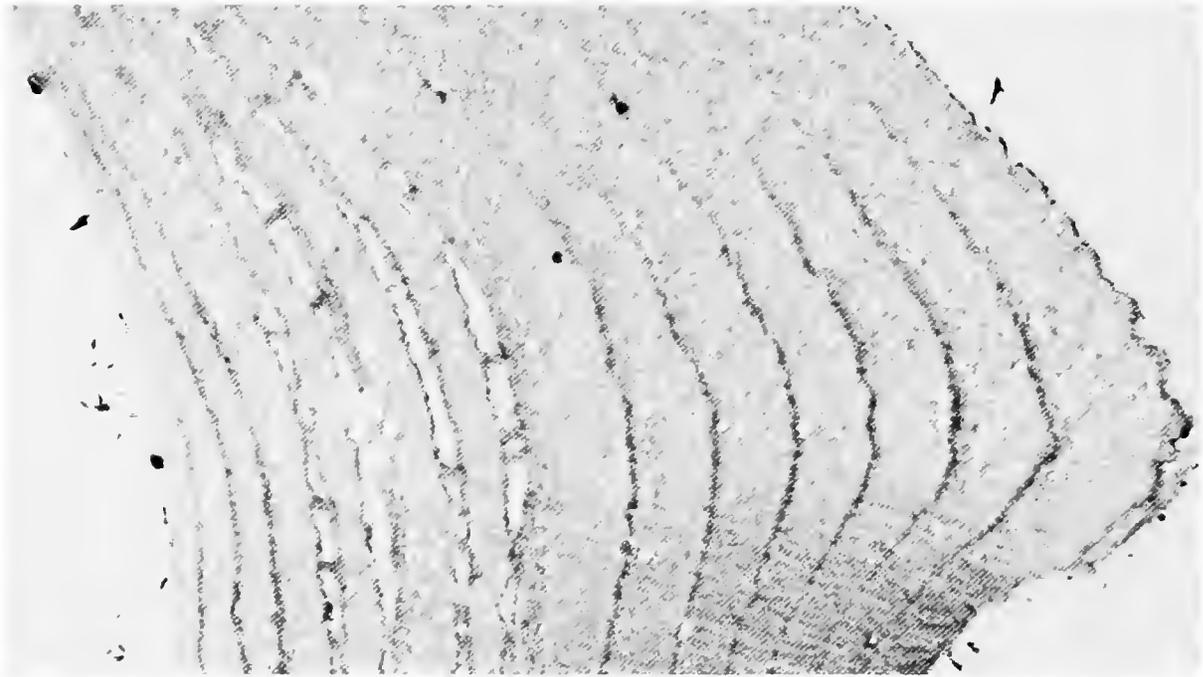
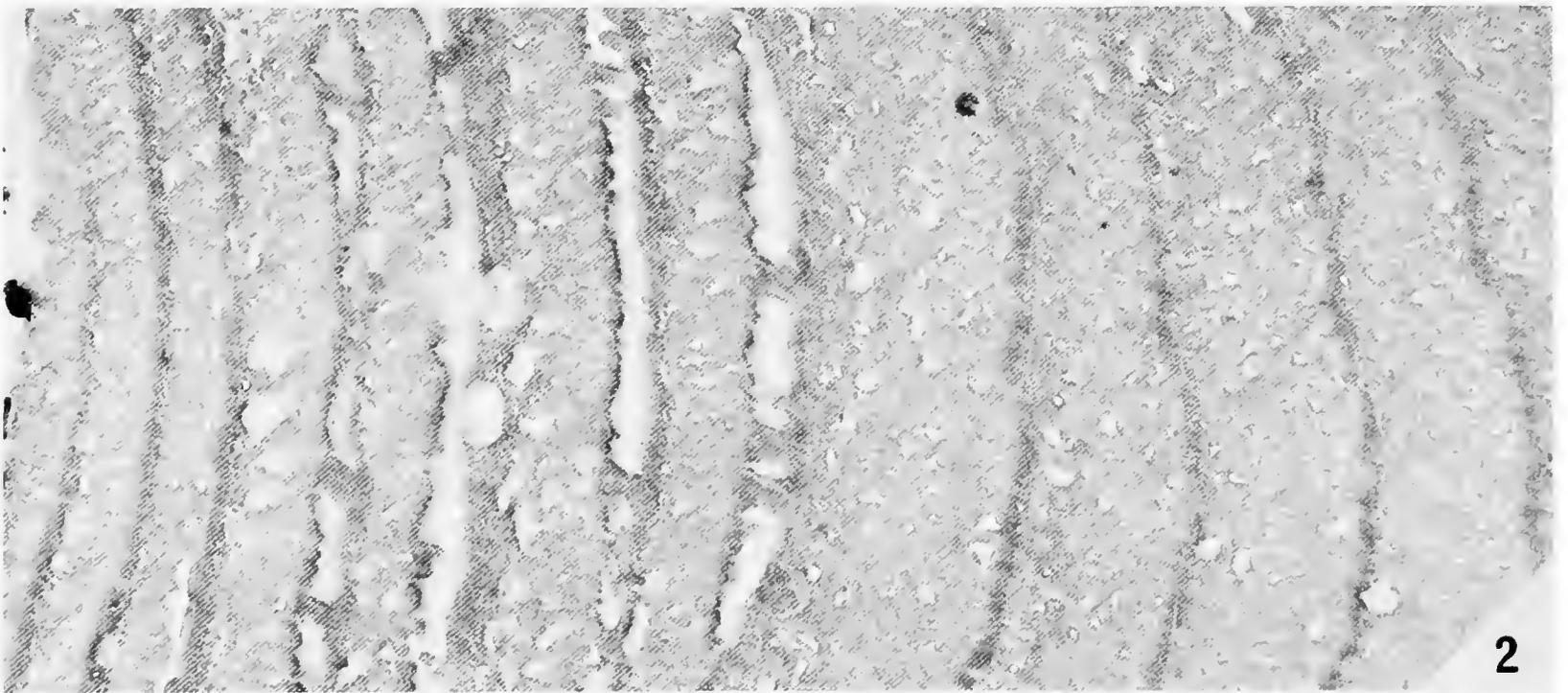


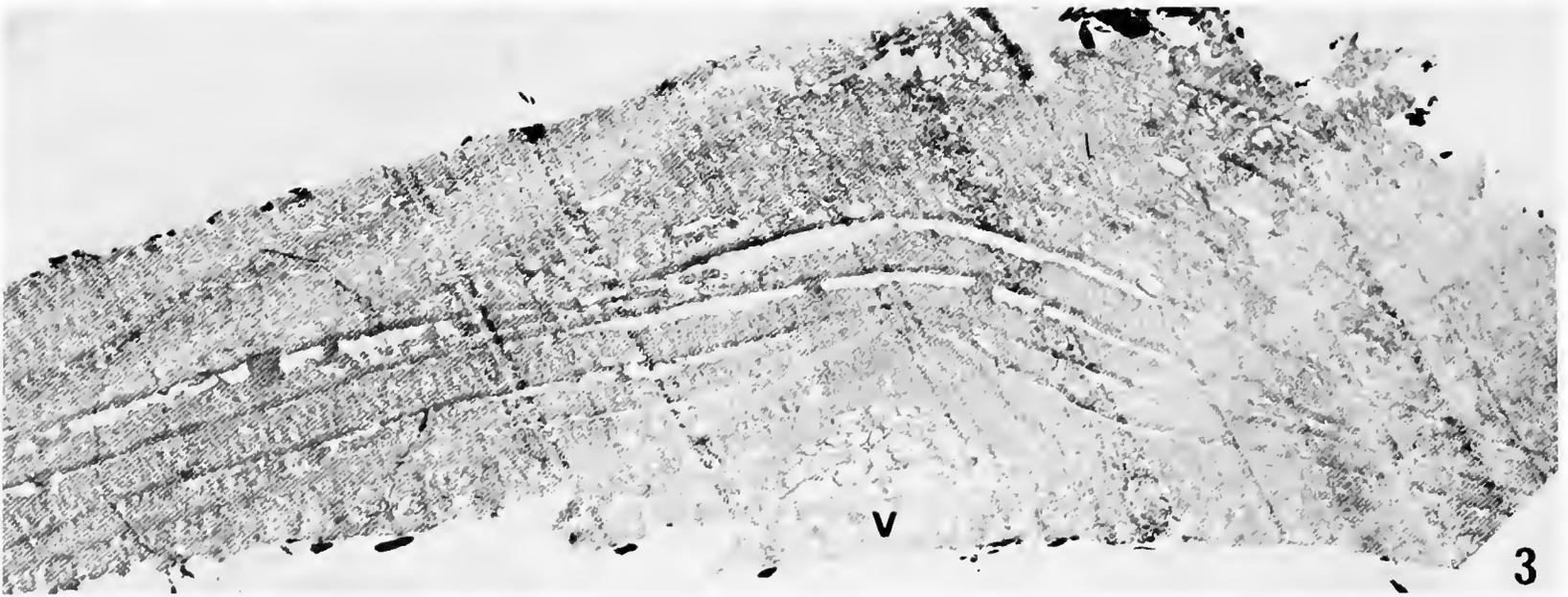
PLATE 9.—*Didymograptus* sp.: 1, 2, Ultrastructure of membranaceous vesicles ("blisters") as seen on transverse sections ( $\times 7,000$ ;  $\times 8,400$ ) (O = enigmatic ovoid body).



1



2



3

PLATE 10.—*Pristiograptus dubius* (Suess), ultrastructural features of the prosicula as seen on transverse sections: 1, Section through a longitudinal rod of the prosicula situated in the apical part ( $\times 12,200$ ); 2, some details of the prosicular material ( $\times 27,600$ ); 3, vesicular material recognized within middle part of the prosicula ( $\times 14,300$ ) (v = vesicular material).

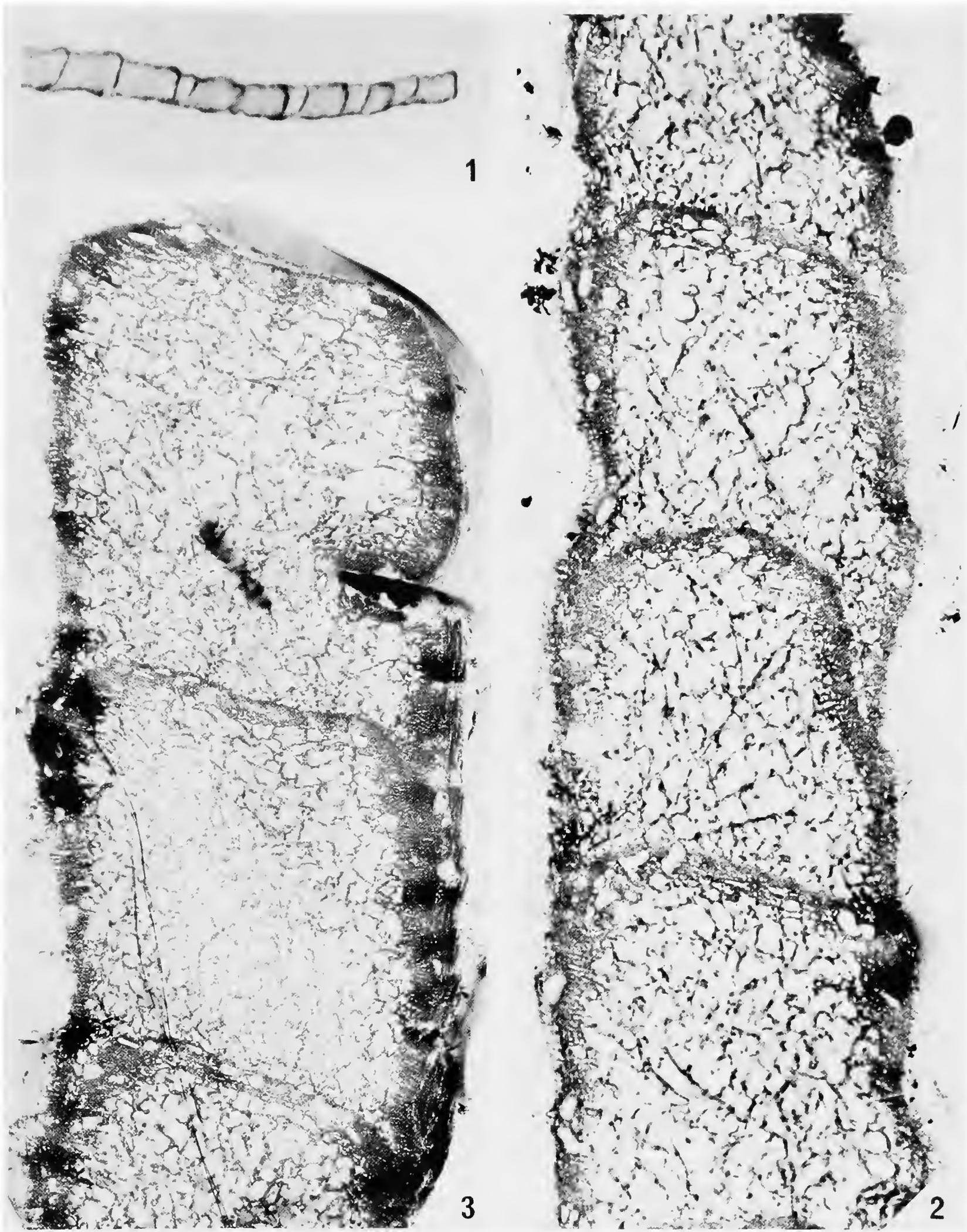
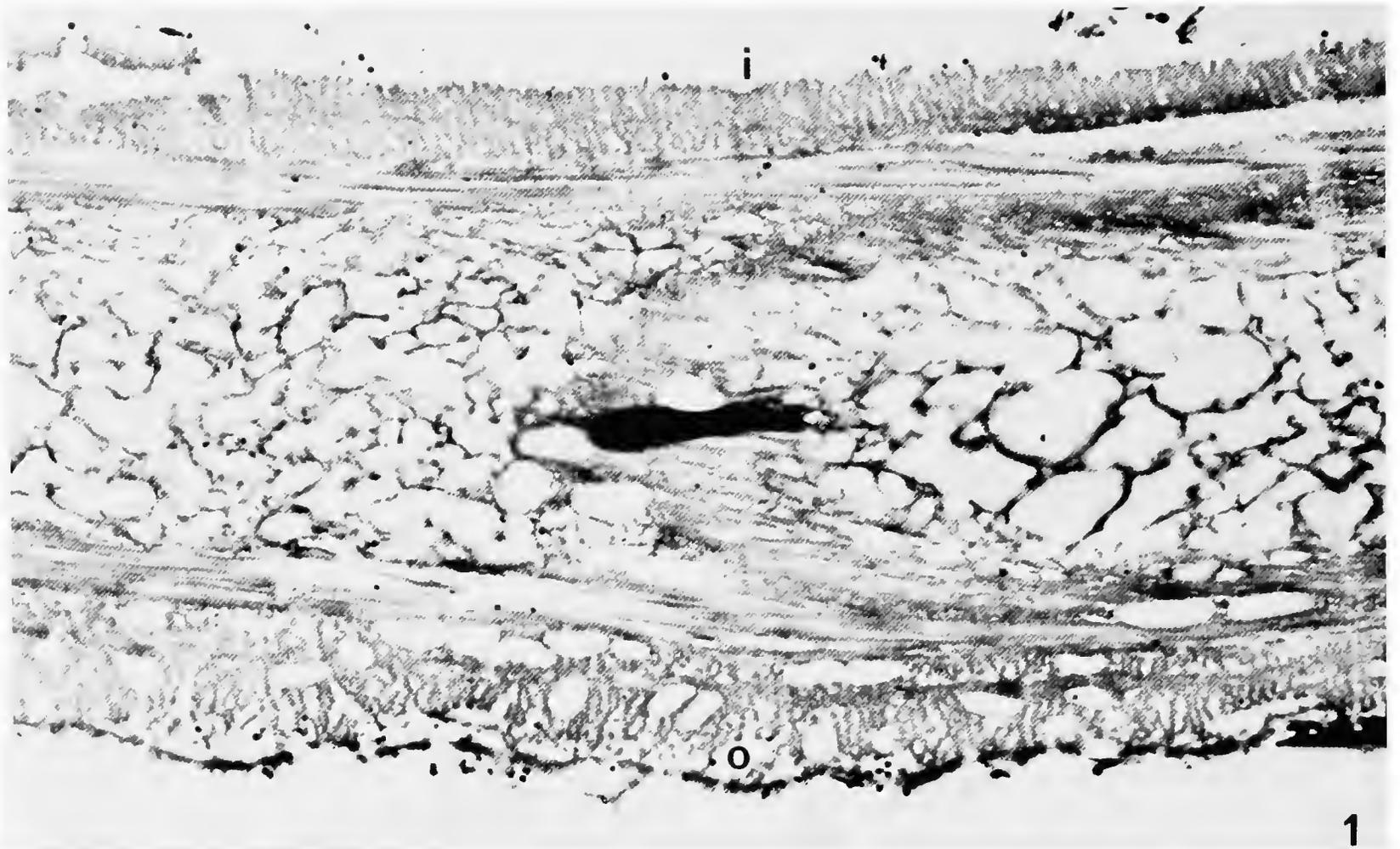
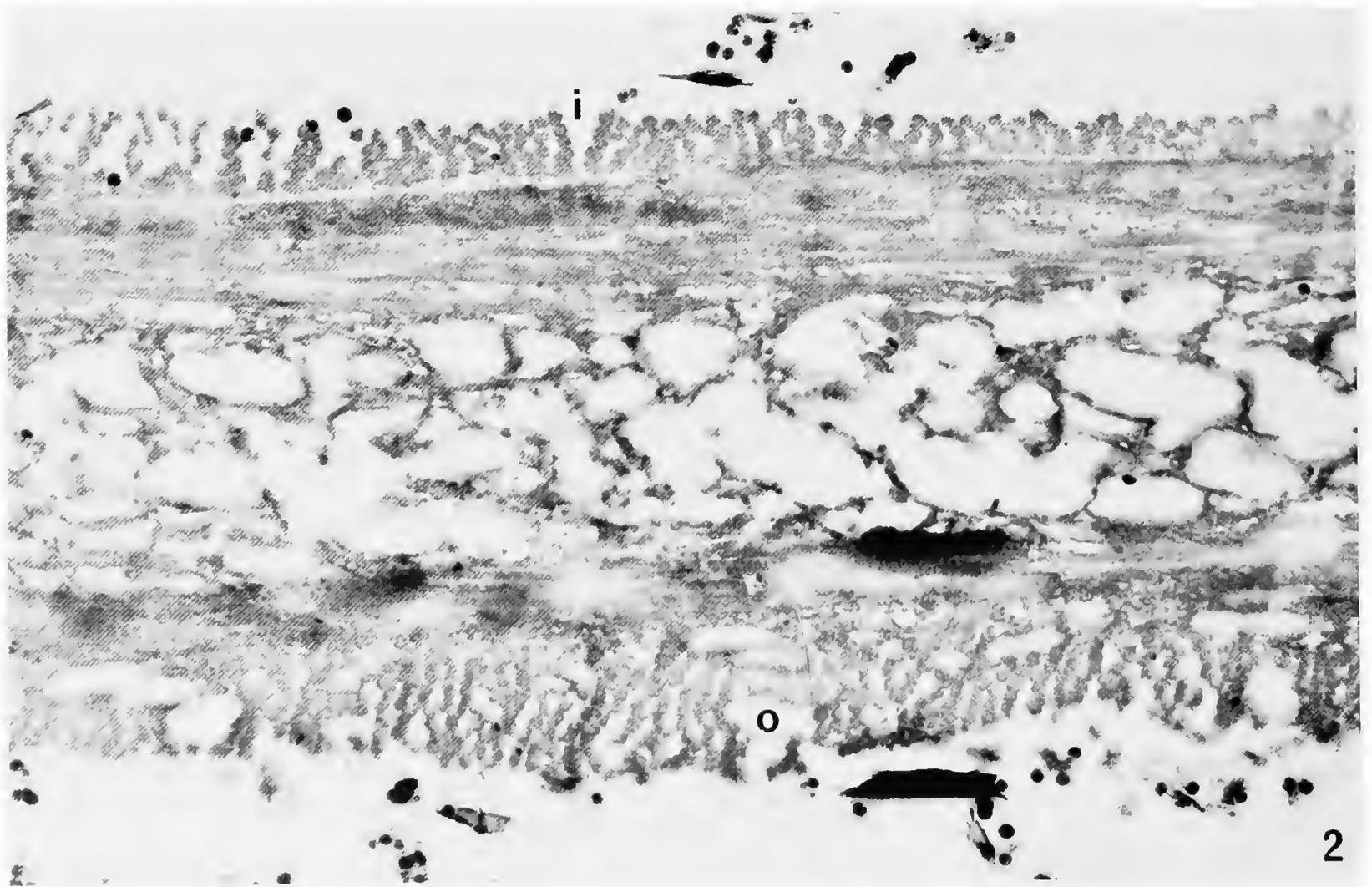


PLATE 11.—*Didymograptus* sp., longitudinal sections showing the structure of metascicula: 1, Light micrograph showing the fuselli of the metascicula ( $\times 800$ ); 2, 3, electron micrographs showing the fuselli of the metascicula in the middle part of the wall ( $\times 10,200$ ) and at the aperture ( $\times 4,000$ ).



1



2

PLATE 12.—*Didymograptus* sp., ultrastructure of the metasicula as seen on transverse sections: 1, Shows a boundary between fuselli ( $\times 15,300$ ); 2, reveals a middle part of the fusellus ( $\times 14,000$ ) (i = inner surface, o = outer surface).

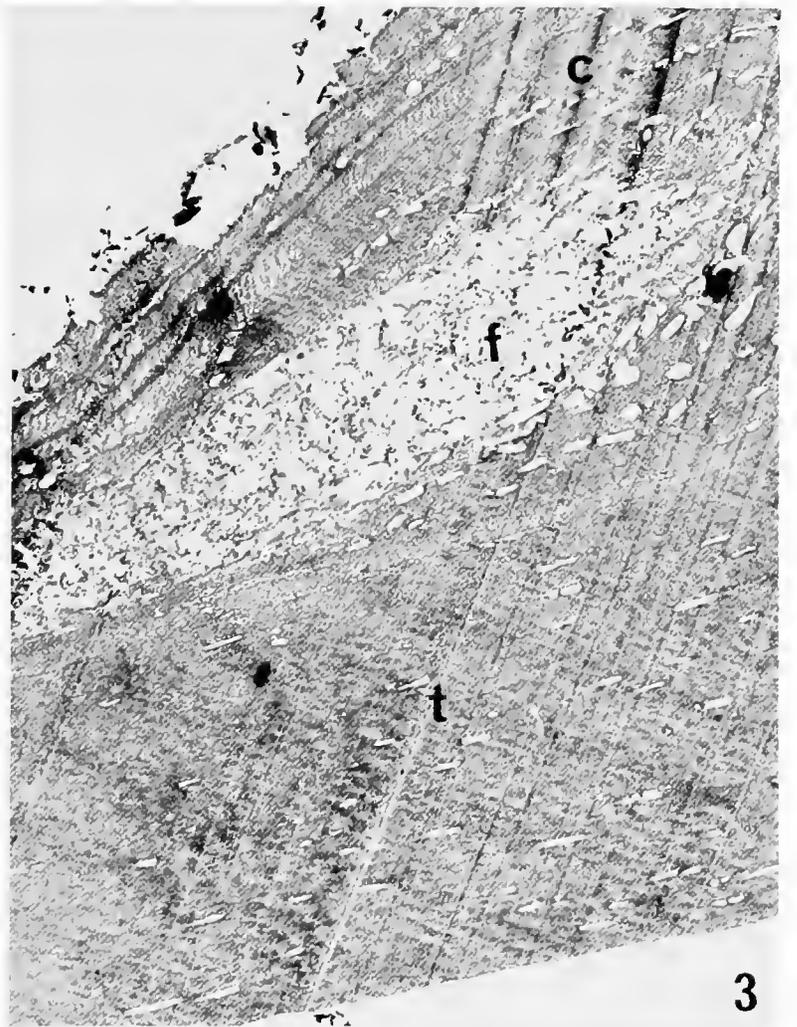


PLATE 13.—*Pristiograptus dubius* (Suess), ultrastructural features of the metasicula: 1, Transverse section at the level of the internal thickening ( $\times 16,300$ ); 2, transverse section between the adjacent internal thickening ( $\times 18,700$ ); 3, longitudinal section at the level of internal thickening ( $\times 9,000$ ) (c = outer cortical deposit (cortex), i = inner cortical deposit, f = fusellar fabric, t = internal thickening).

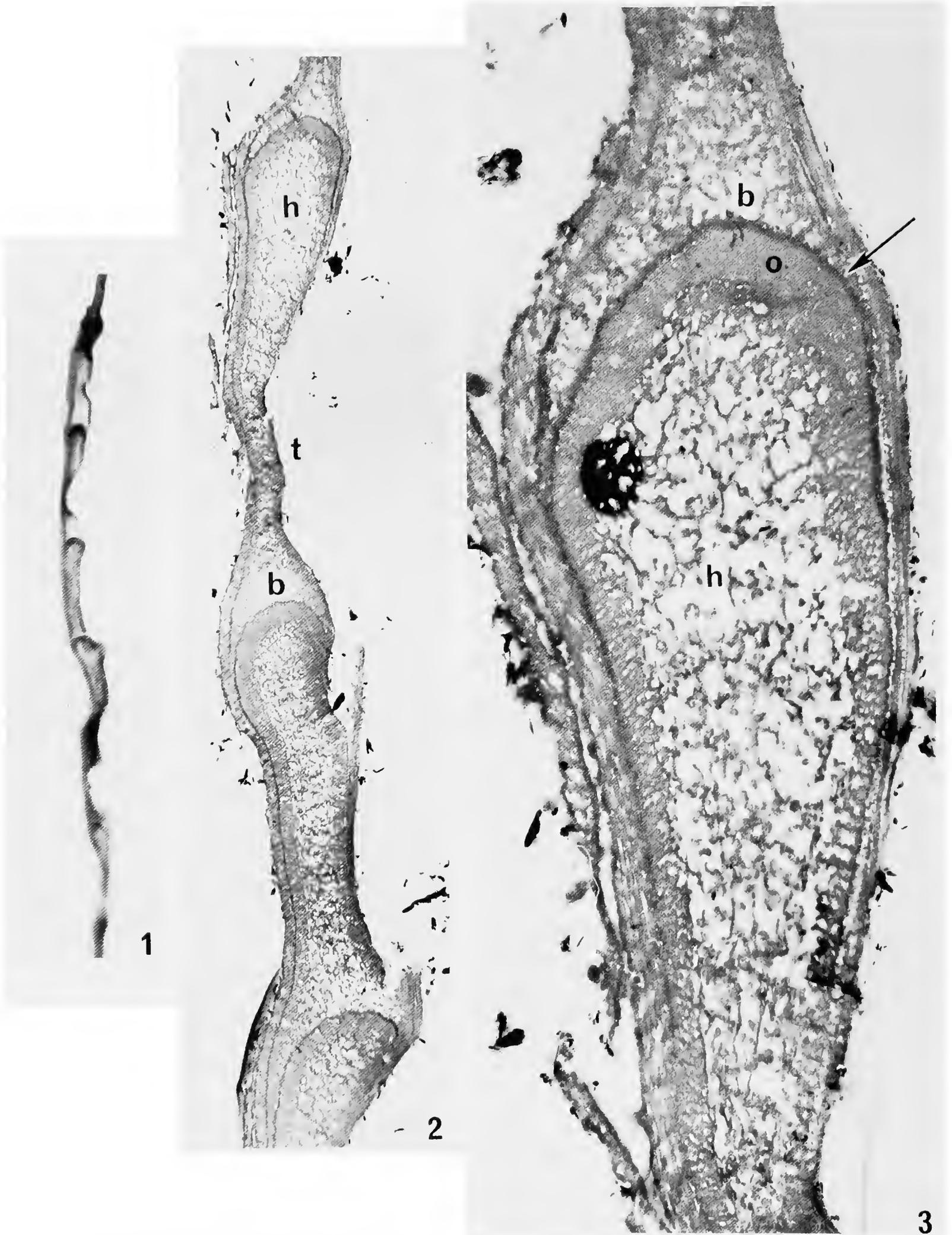


PLATE 14.—*Pristiograptus dubius* (Suess), structure of metasicula as examined on longitudinal sections: A light micrograph showing wall of metasicula ( $\times 800$ ); 2, 3, electron micrographs showing fuselli ( $\times 5,100$ ) and structural details on their boundary ( $\times 17,000$ ) (b = base of the fusellus, h = "head" of the fusellus, t = "trunk" of the fusellus, o = outer lamella, arrow indicates the outer pellicle).



PLATE 15.—*Pristiograptus dubius* (Suess), longitudinal sections showing the thickening on the dorsal apertural process of the metasicula: 1, A light micrograph ( $\times 800$ ); 2, an electron micrograph ( $\times 10,400$ ).



PLATE 16.—*Pristiograptus dubius* (Suess), ultrastructure of the virgella: 1, As examined on transverse section ( $\times 10,000$ ); 2, details of its cortical coating ( $\times 30,000$ ) (c = cortical coating, F<sub>1</sub>, F<sub>2</sub> = larger and smaller fusellus, o = outer lamella of the larger fusellus).

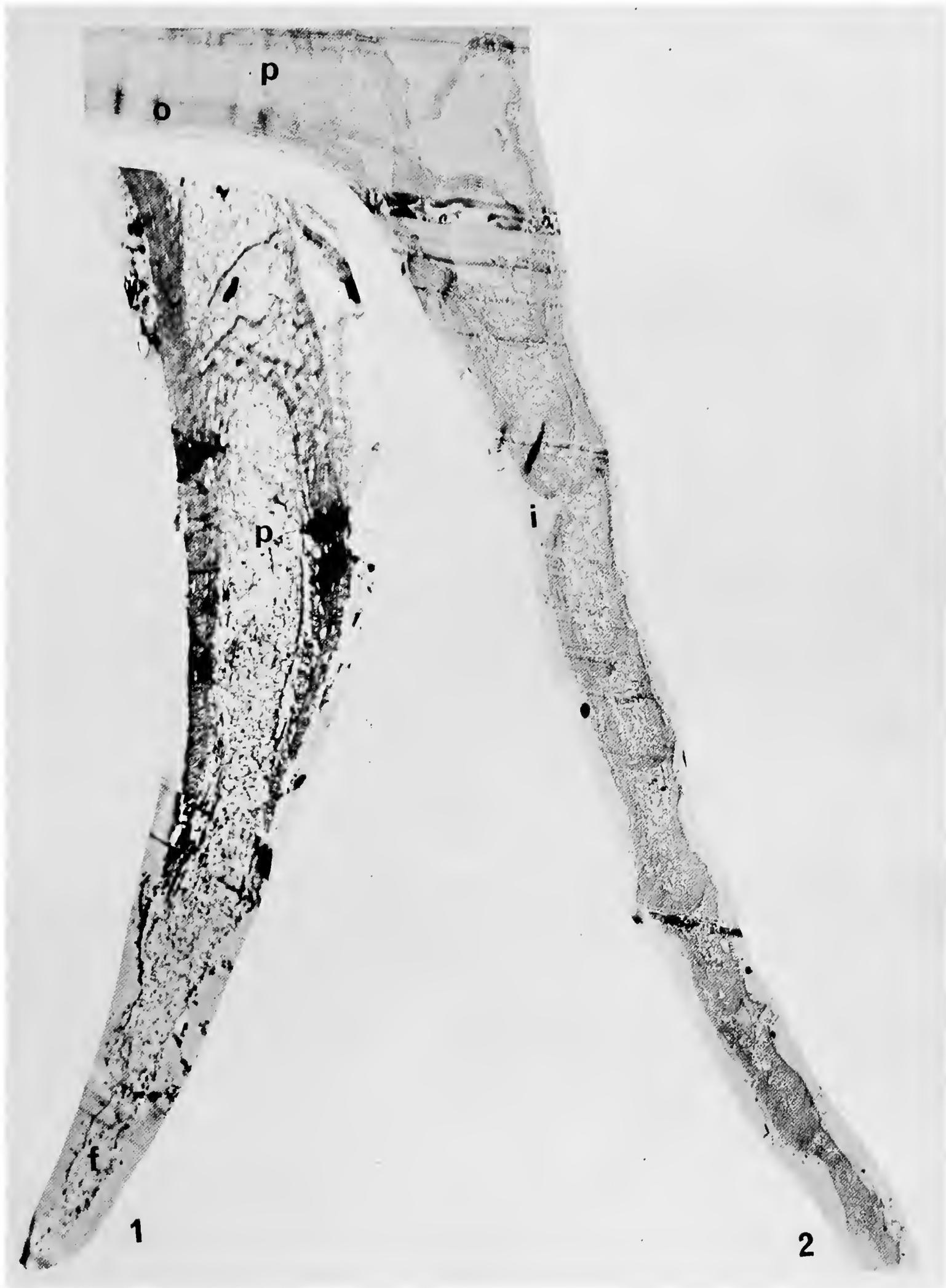


PLATE 17.—*Didymograptus* sp., prosicular wall at the porus region: 1, Shows filaments of the middle component inside the porus ( $\times 4,400$ ); 2, shows initial bud in its relation to the wall of prosicula as seen on transverse section ( $\times 4,100$ ) (f = filaments of the middle component, i = initial bud, o = outer component of prosicula, p = wall of prosicula).

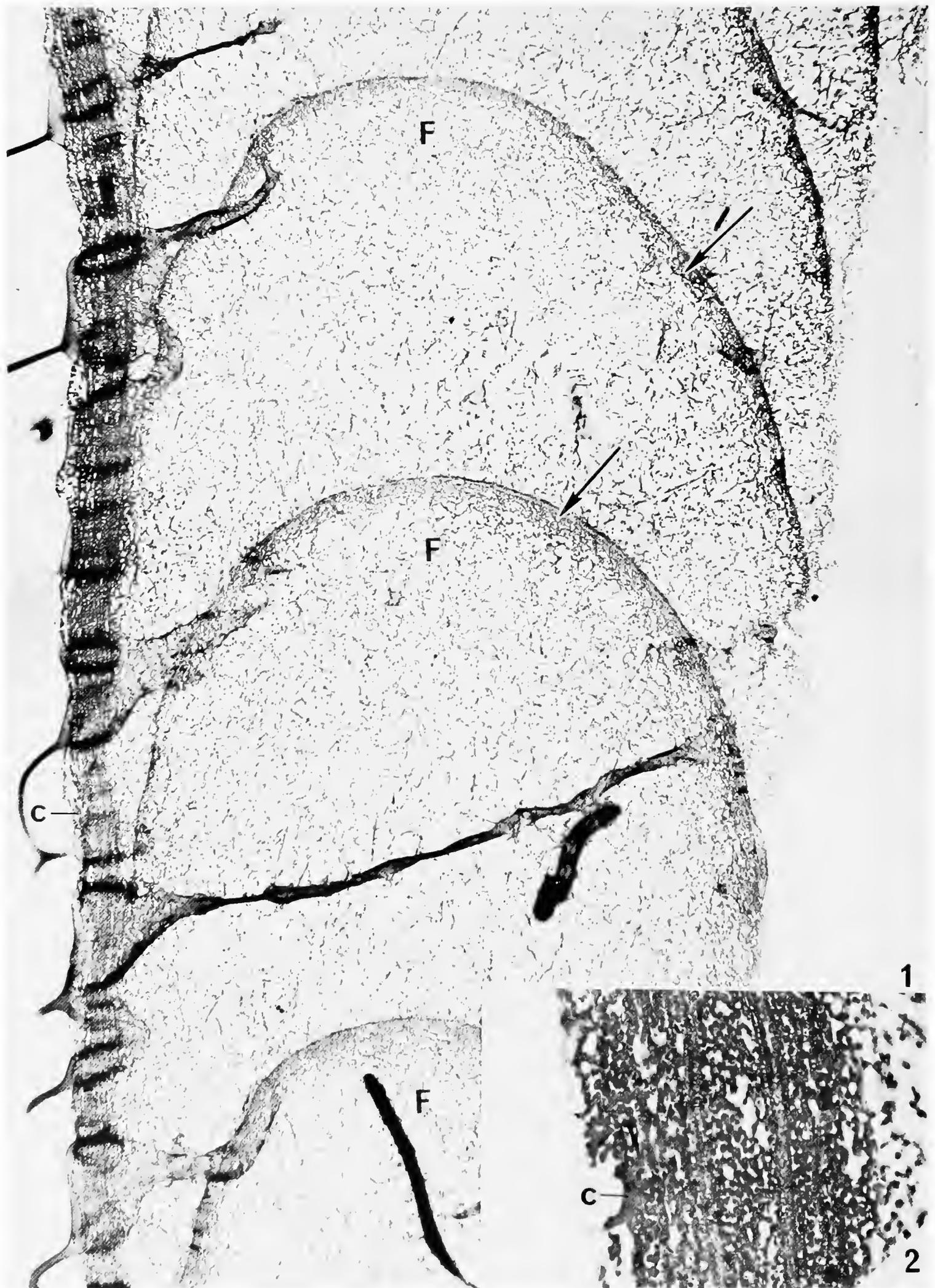


PLATE 18.—*Didymograptus* sp., ultrastructure of thecal wall as examined on longitudinal section: 1, Arrangement of fuselli and outer cortical deposit ( $\times 5,500$ ); 2, structural details of the cortex ( $\times 35,300$ ) (c = cortex, F = fuselli; arrows indicate outer lamellae).

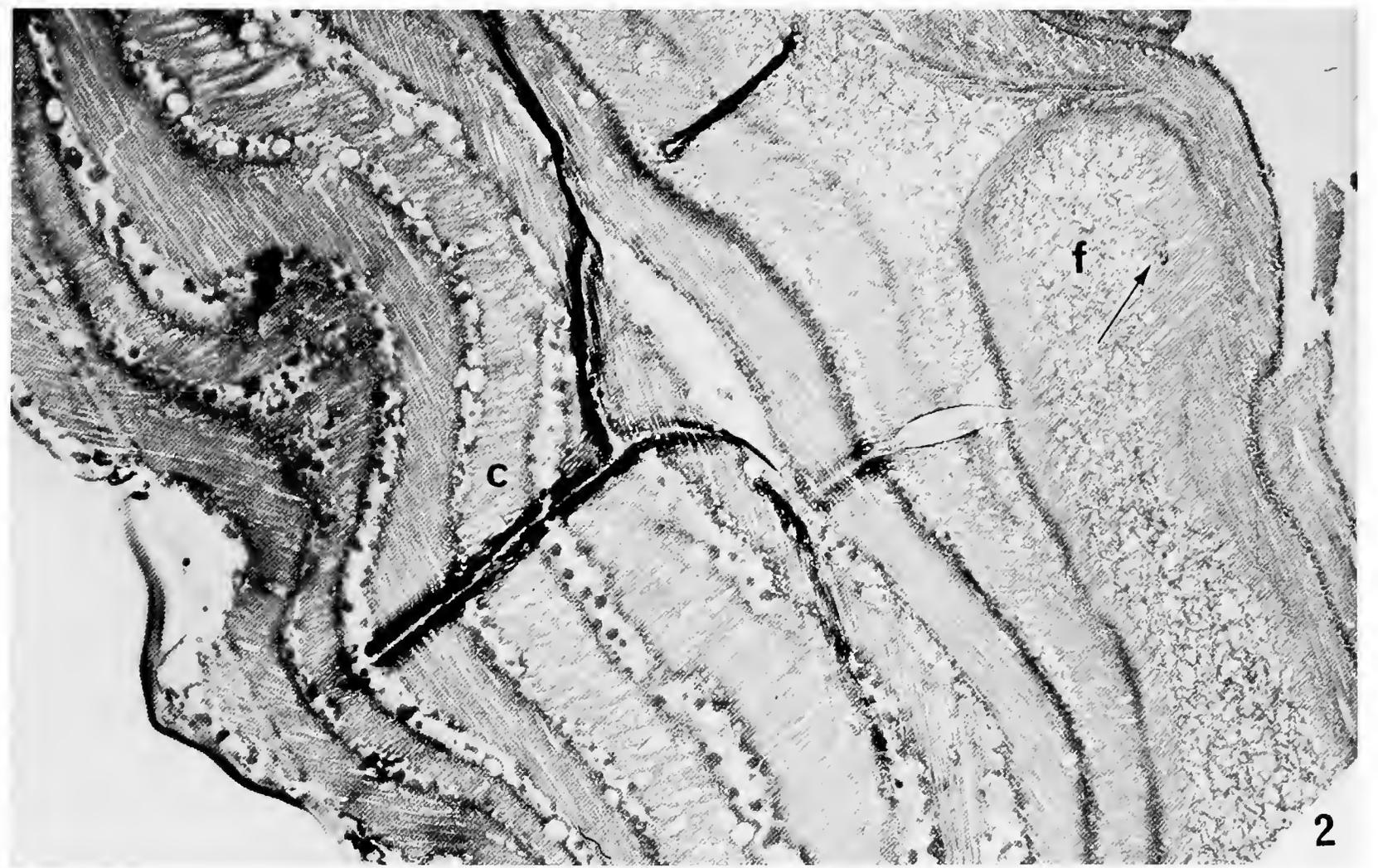
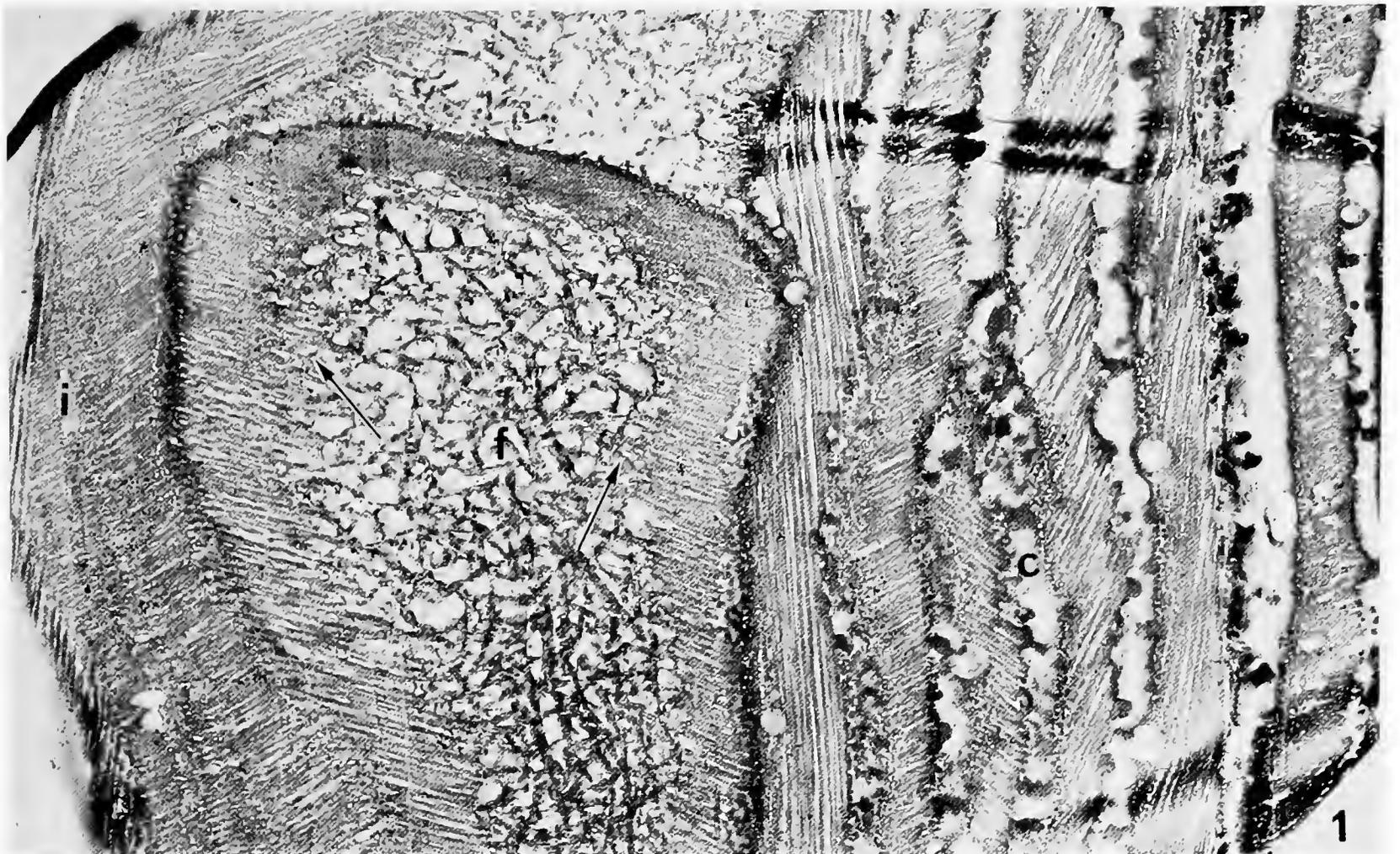


PLATE 19.—*Pristiograptus dubius* (Suess), ultrastructure of thecal walls as examined on longitudinal section: 1, Shows main components of the thecal wall ( $\times 9,800$ ); 2, shows uneven surface of the cortex ( $\times 6,700$ ) (i = inner cortical lining of the thecae, f = fusellar component, c = cortex, arrows indicate a passage of fusellar fibrils in the main body of fusellus into cortical fibrils in its outer lamella).

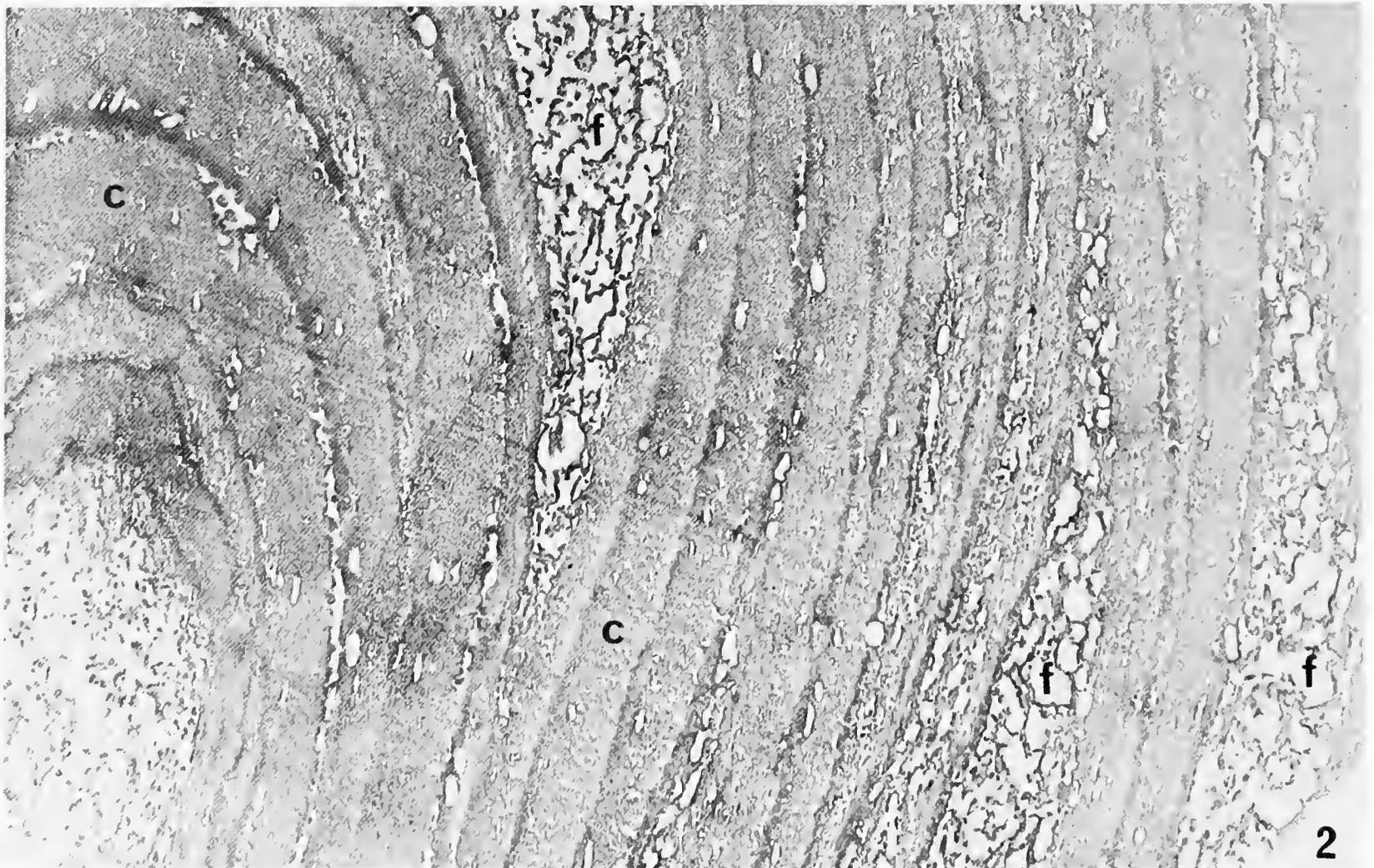
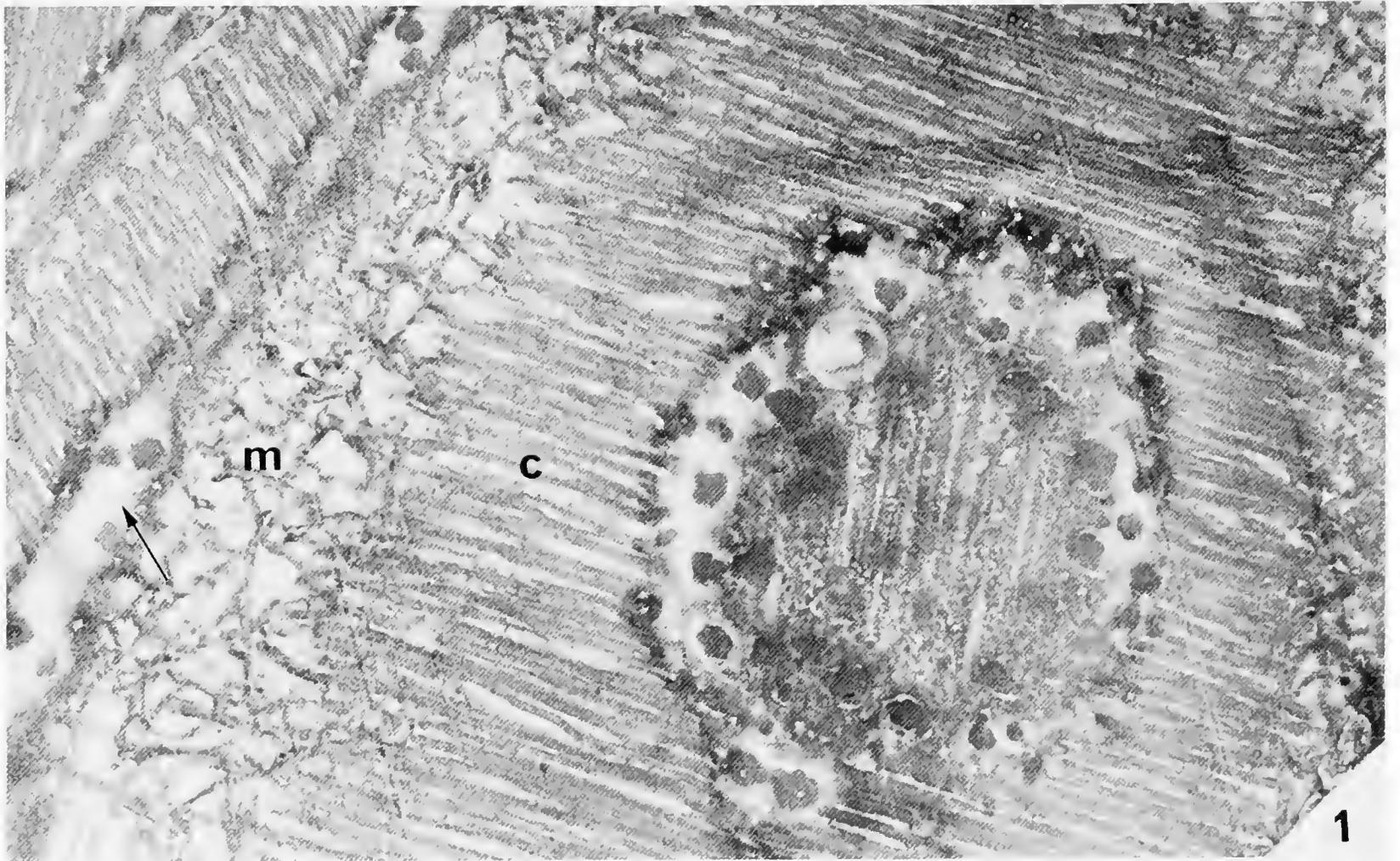


PLATE 20.—*Pristiograptus dubius* (Suess), ultrastructure of the cortical fabric: 1, as seen on tangential section ( $\times 25,300$ ); 2, a variety of peridermal material recognized in an internal outgrowth inside the first theca ( $\times 14,000$ ) (c = cortical fibrils (in 1) or cortical fabric (in 2); f = fusellar fabric (in 2), m = mesh, arrow indicates an intersheet space).

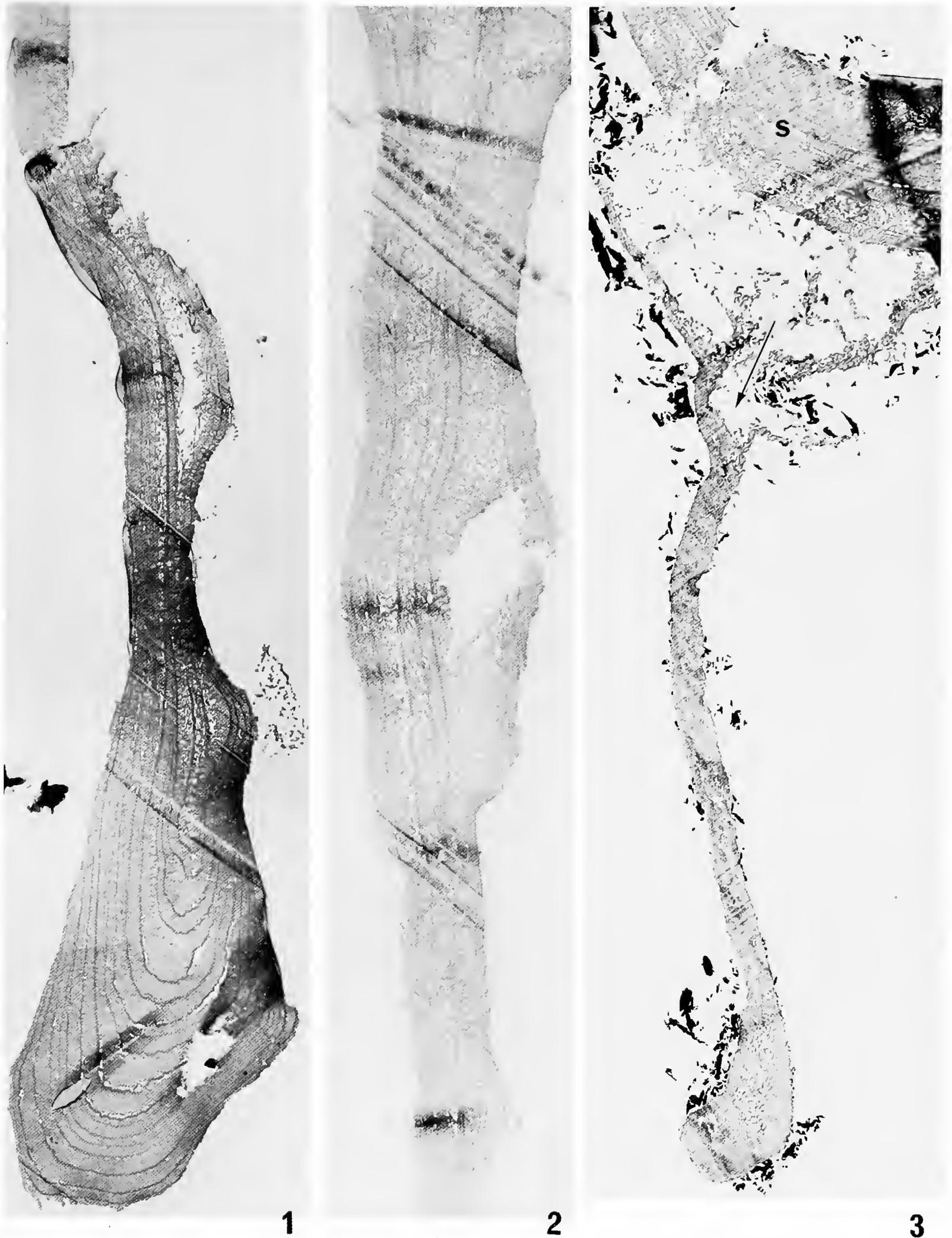


PLATE 21.—*Pristiograptus dubius* (Suess), ultrastructure of an intrathecal septum as seen on longitudinal sections: 1, shows thickening of its margin ( $\times 4,300$ ); 2, shows multilayered middle portion ( $\times 6,400$ ); 3, shows mode of junction of theca 2 to the sicula as seen on transverse section ( $\times 8,300$ ) (arrows indicate a bifurcation of fusellus near the junction, s = sicula).

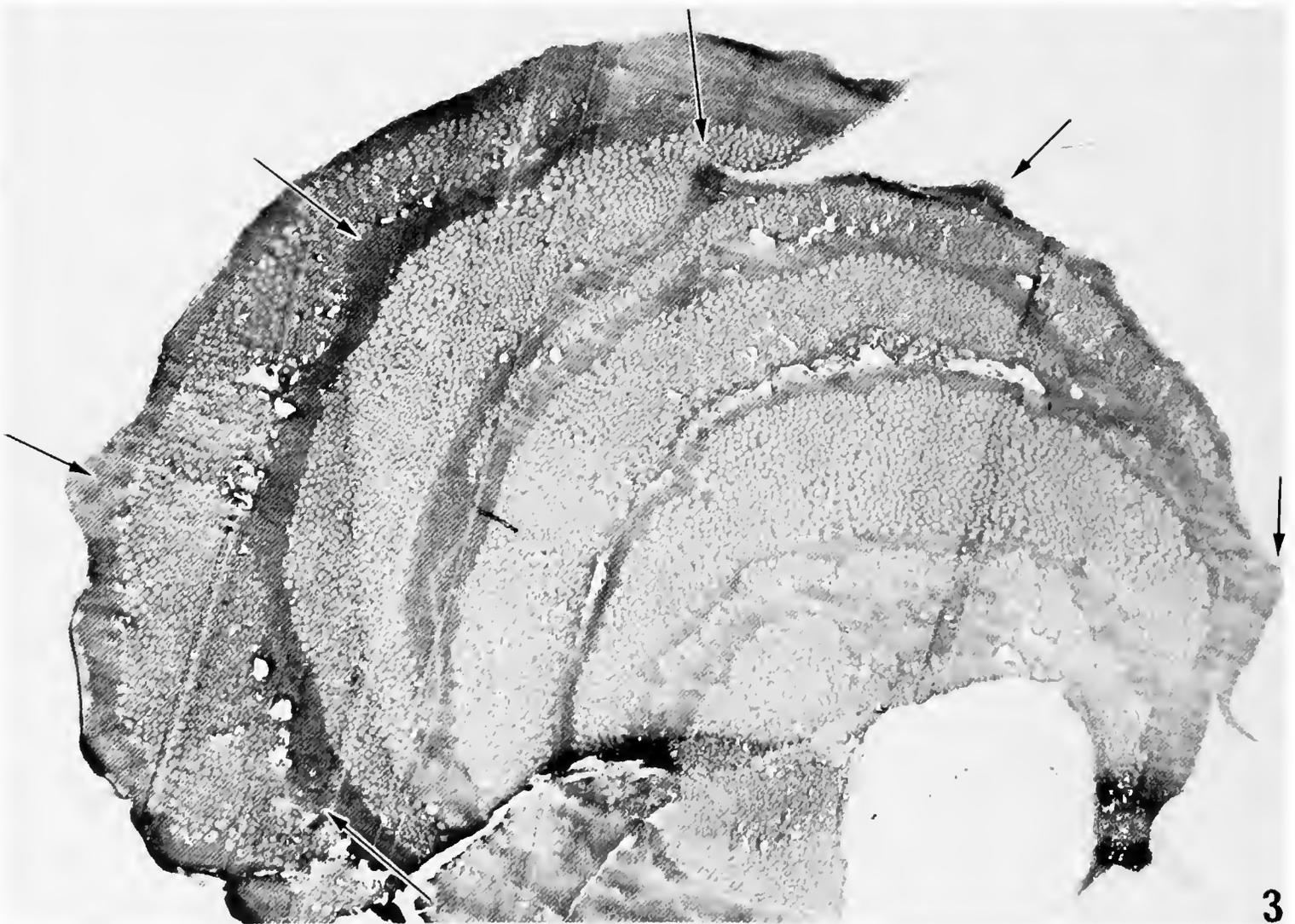
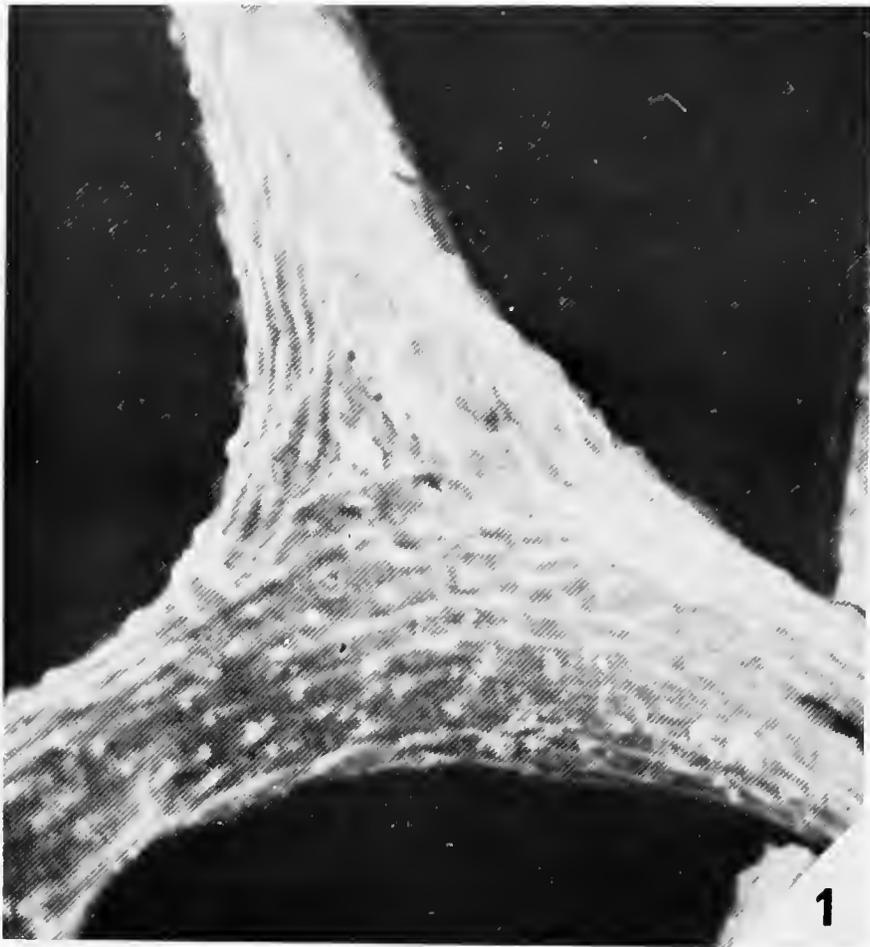


PLATE 22.—*Holoretiolites mancki* (Münch): 1, 2, Spinose outgrowths on the surface of the lists of the clathrium as seen in scanning electron microscope ( $\times 850$ ;  $\times 1,800$ ); 3, ultrastructure of a ventral list examined with transmission electron microscope on transverse section ( $\times 9,000$ ) (arrows indicate spines).

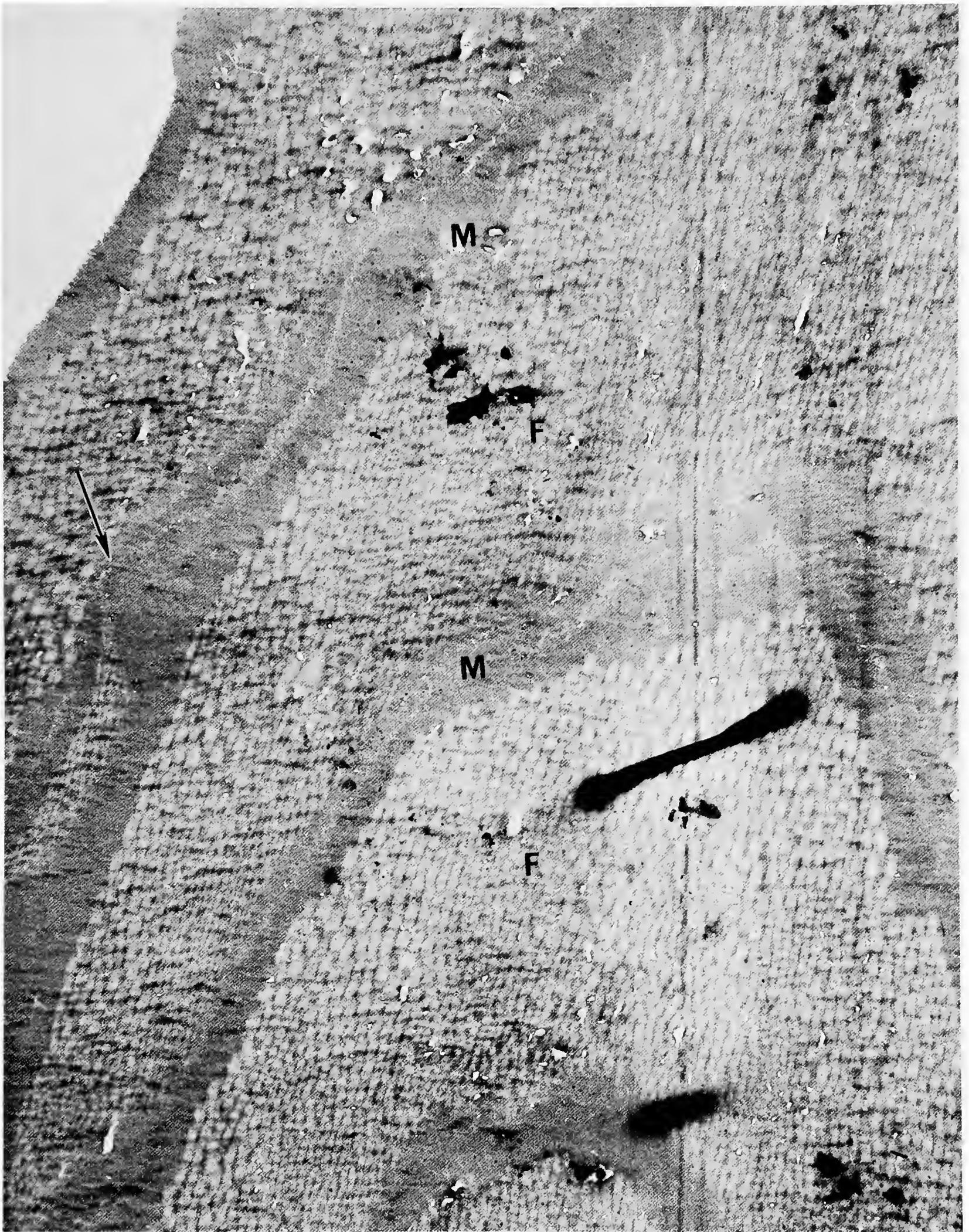


PLATE 23.—*Holoretiolites mancki* (Münch), a longitudinal section through an apertural loop ( $\times 14,000$ ) F = fibrous component, M = matrix component; arrow points to a spine).

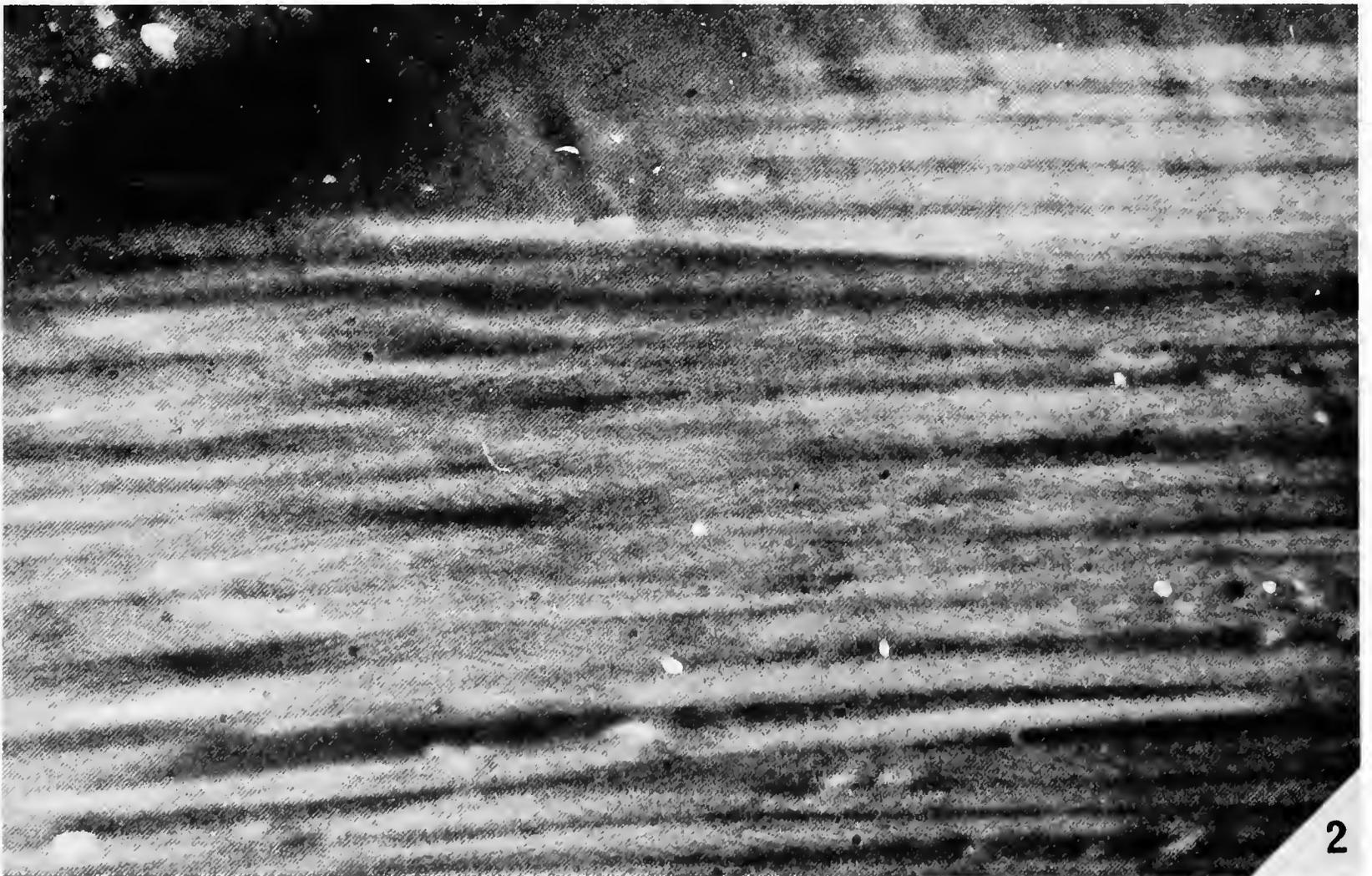
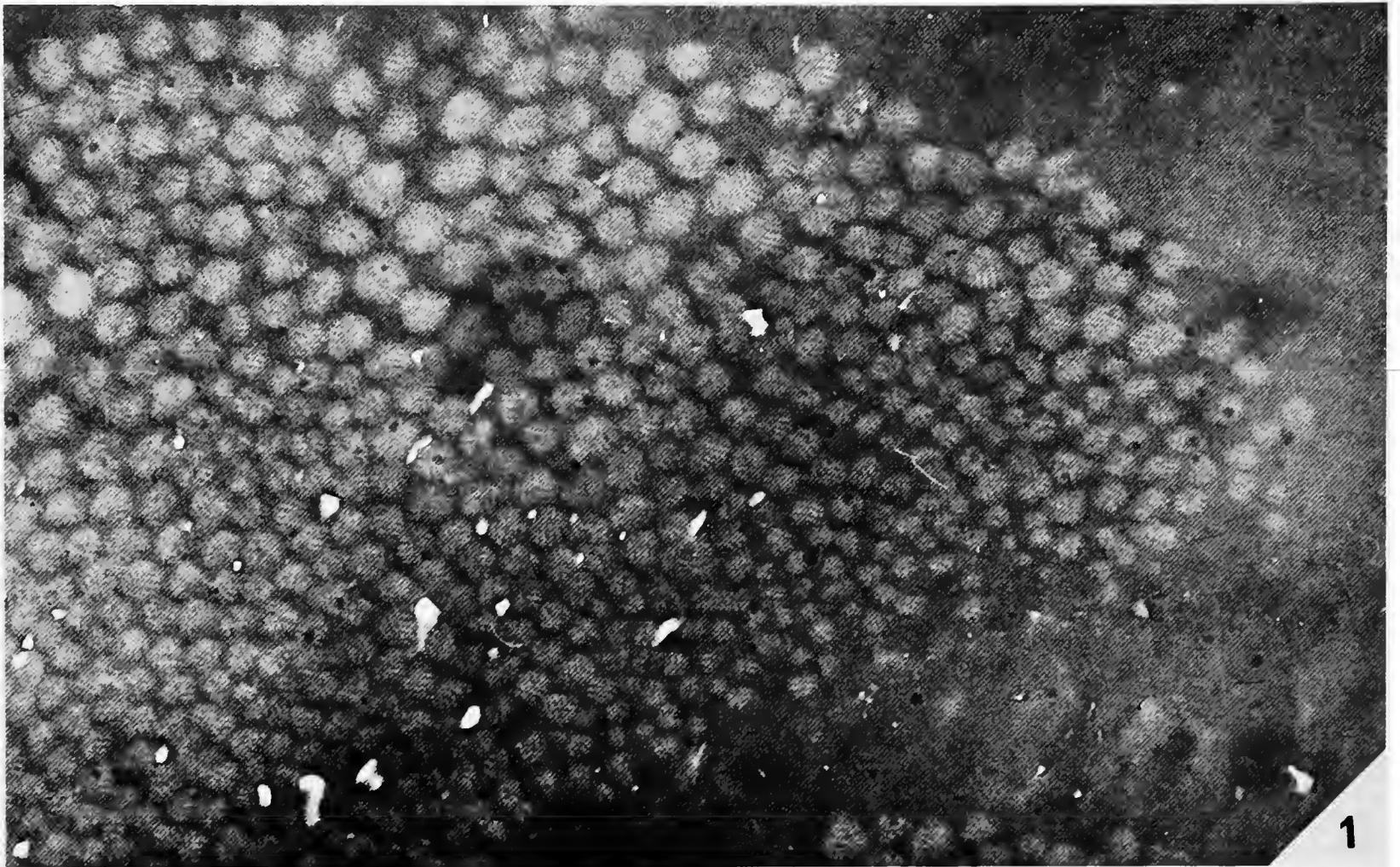


PLATE 24.—*Holoretiolites mancki* (Münch): 1, 2, Ultrastructure of the fibrous component of the virgular fabric as seen on transverse ( $\times 43,000$ ) and longitudinal ( $\times 43,000$ ) sections of the rods of the clathrium.

## Publication in *Smithsonian Contributions to Paleobiology*

*Manuscripts* for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy.

*Copy* must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margin, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Ammonoidea: Goniatitidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index*, if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys*, number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy*, use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text*, use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

*Illustrations* (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9b." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates*, and individual components should be lettered (Plate 9b) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.

