

A MONOGRAPHIC STUDY OF THE WEST INDIAN
SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With twelve plates

LEAF

Lamina.

The leaf-blade in *Phyllanthus* (and in the other genera of Phyllanthaceae as well) is invariably simple and entire, but there are many variations of size, shape, and texture. In a few species such as *P. urinaria* and *P. carnosulus* there may appear to be a minutely serrate or crenate margin, but this appearance actually is due to projections of individual or associated epidermal cells which belong in the category of trichomes; true vascularized teeth never occur.

The leaf of *Phyllanthus* varies in size from minute, as in *P. imbricatus* where it may be only 1.5 mm. long, to large as in *P. grandifolius* where it may attain 15 cm. in length and almost as much in width. It is not surprising that the leaves of *P. grandifolius*, which are borne on permanent branches, are large and persistent; but a few species, such as *P. juglandifolius* and *P. cornifolius* with the foliage leaves only on deciduous branchlets also have leaves 15 cm. long, although never as broad. On the whole, the leaves of *Phyllanthus* are medium-sized or small, and the median for the genus would perhaps fall at about 3 cm.

Most species of *Phyllanthus* have elliptic to oblong leaves, but as might be expected in so large a genus, there are some striking deviations. In some New Caledonian and South American species (e.g., *P. bupleuroides* and *P. duidae*) the lamina is prominently basally lobed and has the outline of a *Cercis* leaf-blade. A few xerophytic species such as *P. comosus* and *P. formosus* (sect. *Orbicularia*) have leaves with a pronounced spatulate outline. The apex of the blade varies from retuse to acuminate among various species, and in some of the Cuban species of sect. *Orbicularia* there is a long attenuate scarious tip, which however is differentiated from the rest of the leaf-blade. A pronounced "drip-tip" such as characterizes the leaves of many Lauraceae in the tropical rain forest is scarcely developed in any species of *Phyllanthus*.

Leaf texture within the genus runs the gamut from extremely tenuous and delicate as in *P. tenuifolius* (sect. *Cyclanthera*) to rigidly coriaceous in species of several sections (e.g., *Orbicularia*). The leaf surface is usually smooth, although many species have a papillate lower epidermis. *Phyllanthus acuminatus* is exceptional in having definitely scabrid leaf-surfaces.

* Continued from volume XXXVII, page 122.

Rothdauscher (1896: 8) regarded the monotony of anatomical features of the leaf as virtually a tribal character of the Phyllanthaeae. However, while it is doubtless true that a greater diversity exists in other tribes such as the Crotonaeae, the various histological characters within *Phyllanthus* provide data of considerable classificatory and evolutionary interest. Froembling (1896) indeed concurred with Rothdauscher in remarking on the great uniformity of leaf structure in the subtribe "Euphyllanthaeae". But although he studied over sixty species of *Phyllanthus* (s. str.) he did not investigate a single species of sects. *Elutanthos*, *Williamia*, *Orbicularia*, or *Epistylum*, which together make up the great majority of the woody West Indian species. It is not surprising, therefore, that his observations require some modifications on the basis of various features of the species in those groups. In the following account the remarks apply particularly to the West Indian species, although they often are relevant for the entire genus as well.

In the woody species of *Phyllanthus* the upper epidermis, overlaid by a cuticle which may attain considerable thickness, is made up of more or less vertically elongated cells with outer tangential walls that are polygonal in outline. The cells of the lower epidermis are usually much smaller in surface area, inclined to be more undulate in outline (or at least less sharply polygonal), and are tangentially elongated. In the herbaceous species with thin leaves, however, the cells of the upper epidermis are not sharply polygonal in outline, and in some species the perimeter of both upper and lower epidermal cells is undulate.

Froembling (1896: 69) was content to characterize the stomata of *Phyllanthus* as extremely variable with regard to the number of subsidiary cells. However, in the leaves of the woody species the stomata are clearly the "rubiaceous" type as defined by Metcalfe and Chalk (1950: xv); there are either two — or apparently by one redivision — three subsidiary cells with their long axes parallel to the opening between the guard cells (PLATE-FIG. 18). But in leaves of herbaceous species this arrangement may become obscured due to the more irregular cell outlines. Often the guard cells are surrounded by three subsidiary cells, two parallel to the long axis of the stoma and one more or less perpendicular; such a stoma might be considered to belong to the "cruciferous" type (PLATE-FIGS. 19 & 20). In some herbaceous species such as *P. polygonoides* the arrangement is still more obscure because here there may be a number of subsidiary cells which scarcely differ in outline from the rest of the epidermal cells, and in this case the stoma would have to be classified as "ranunculaceous". Or, in the case of a number of species such as *P. niruri* there may be more than one type on the same leaf (PLATE-FIG. 21). The herbaceous species often show a significant difference in distribution of the stomata, as they often have them on both surfaces of the leaf, whereas in the woody species they are always confined to the lower epidermis. Taking the genus as a whole, there is no doubt that the basic stomatal type is the "rubiaceous", which Rothdauscher observed to be the prevailing type in the other genera of Phyllanthaeae.

The mesophyll in those species of *Phyllanthus* investigated thus far is composed of typical palisade and spongy parenchyma of "bifacial" leaves. The three species of "Phyllanthus" in which a foliar hypoderm was reported by Froembling (1896: 69) prove to belong to other genera. Among the West Indian species of *Phyllanthus* a definite hypoderm has been observed only in *P. myriophyllus*, although it perhaps may be discovered in other species. The palisade tissue is usually made up of a single layer of very slender cells; in coriaceous leaves with a large volume it is the spongy rather than the palisade parenchyma which is increased in bulk. Froembling reported unusual palisade cells only in the species of the Old World section *Eriococcus*. In *P. elegans* (the only species of the section which has been introduced in the West Indies) Froembling found that the portion of the cell bordering the epidermis is enlarged so that the entire cell has a clavate shape; and in *P. roxburghii* this enlarged portion is lobed so as to have the outline of a mitten. No such unusual palisade cells have been detected in any of the native West Indian species. The spongy mesophyll in the leaf of *Phyllanthus* is composed of parenchyma cells which may be arranged compactly to loosely; in some of the species of sect. *Hemiphyllanthus* the spongy layer has a striking areolate appearance due to the regular organization of the cells around circular lacunae.

Froembling reported that the veins in the *Phyllanthus* leaf are all of the embedded type, as opposed to the veins of other Phyllantheae which Rothdauscher designated as "durchgehende"; in the latter the sclerenchyma or collenchyma associated with a vein is expanded into wings which abut on the upper and lower epidermis ("vertically transcurrent" veins of Metcalfe and Chalk, 1950; xvi). During the present study of the West Indian species of *Phyllanthus*, however, both types were observed. In *P. discolor* (sect. *Williamia*) there are vertically transcurrent veins with bundle sheath extensions (Esau, 1953: 430) of collenchyma cells interrupting the palisade layer and reaching both epidermises. But within the single sect. *Orbicularia* both types have been observed. *Phyllanthus orbicularis* has rigidly coriaceous leaves with conspicuous sclerenchymatous bundle sheath extensions which tend to become uniseriate above and multiseriate beneath, as in *P. discolor*. But in the related *P. scopulorum*, which has flexibly coriaceous leaves, the veins—though armed with sclerenchyma—are clearly embedded (PLATE-FIG. 22). Some of the species with coriaceous leaves in other West Indian sections (e.g., *Thamnocharis*) resemble *P. scopulorum* in having embedded veins with massive sclerenchymatous but extensionless sheaths. In these species the rigidity of the leaf-blade is enhanced by the very massive bundle of fibers which is associated with the marginal vein and which is responsible for the prominent rim-like margin of the leaf (PLATE-FIG. 23).

The veins of the *Phyllanthus* leaf are pinnately branched, and the laterals ordinarily ramify considerably and then unite near the margin to produce an arcuate marginal vein. The foliar vascular systems of individual species differ widely from one another in such details as branching pattern, massiveness, development of parenchyma vs. sclerenchyma in

bundle sheaths, and vein endings; consequently, despite the great variation in some of these characters, leaf vascular tissue appears to be a promising source of systematically valuable criteria. In species with membranous or chartaceous leaves, only the midrib and larger veins are jacketed with sclerenchyma; and the ultimate veinlet tips lying free in the mesophyll are bordered (if at all) only by parenchyma sheath cells. The veins of many species end with one or two essentially unmodified tracheids (PLATE-FIGS. 28, 30); but in other species one or more of the terminal tracheids are modified into swollen "storage tracheids" ("Speichertracheiden"; PLATE-FIG. 29). In some species with coriaceous leaves, however, the fibers of the bundle sheath extend out even to the ends of the minor veins; and in several species, such as *P. microdictyus*, the sclerenchymatous elements flare beyond the tips of the last tracheid (PLATE-FIG. 24).

The designation of these sclerenchymatous elements presents a rather difficult problem in terminology. In the following discussion these elements which project into the mesophyllar spaces of the leaf will be called "foliar sclereids", following the usage of Foster (1946). The sclereids of *Phyllanthus* would mostly belong to either Type III or Type IV of Foster's classification, for they are always elongated and not highly branched. In fact, except for their position and occasional branching the sclereids of *Phyllanthus* could just as well be called fibers. However, in a few species (e.g., *P. chryseus* and *P. comptus*) the sclerification of the veinlet-ends is due to peculiar, sometimes deformed, sclerenchymatous elements which are more or less intermediate between sclereids and tracheids (PLATE-FIG. 31).

Within the evolutionary series formed by the three related sections *Williamia*, *Williamiandra*, and *Orbicularia*, a trend of increasing sclerification is strikingly apparent. In the most primitive species of the complex, *P. discolor*, the ultimate veinlets are naked. The other species of sect. *Williamia*, *P. microdictyus*, exhibits sclereids which project beyond the veinlet-tips, as mentioned above. In sects. *Williamiandra* and *Orbicularia* the exertion of the sclereids has become far more pronounced, and the massive veins and free-lying portions of the sclereids occupy a very appreciable portion of the volume of the leaf (PLATE-FIGS. 25-27). In sect. *Williamiandra* (and sometimes in *Orbicularia*) many of these elongated sclereids extend vertically through the leaf as columns which abut against the upper and lower epidermis in the manner of the Type III sclereids illustrated by Foster for *Mouriri pusa* (1946: fig. 16). It is furthermore very interesting that sclereids of this kind have arisen independently in *P. duidae*, a species of the unrelated South American sect. *Microglochidion*.

On the basis of the observations made so far it can be said that the foliar sclereids of *Phyllanthus* appear to be terminal in origin and to have been derived from the fiber-like sclerenchymatous cells of the bundle sheath. Diffuse sclereids or stone cells have not been observed in the leaf of any species of *Phyllanthus*. Furthermore, foliar sclereids have thus far been detected only in the New World species. However, since they have originated independently in the West Indian and South American species,

there is no reason why they could not occur in some of the Old World species; further investigation of the leaves of the latter is therefore desirable.

As Froembling reported, almost all species of *Phyllanthus* which have been examined prove to have crystals, most often druses, in the mesophyll. In a smaller but still considerable number of species rhombic or prismatic crystals are produced as well. There is a definite tendency for the druses to occur in the layers of cells directly adjacent to the upper and lower epidermis, but occasional ones may also be found scattered in the mesophyll, and both druses and rhombic crystals may occur along the veins. The use of crystals as a taxonomic character is attended with the disadvantage that their expression may vary within a single species and that they may change form in cleared mounts which have been treated with caustic soda, as reported by Heintzelman and Howard (1948). It appears doubtful that the study of crystals will afford much assistance in distinguishing closely related species; but it is possible that a sufficiently broad survey might provide useful evidence on the supraspecific level. For example, the species of sect. *Orbicularia* appear to differ from most of the related sections such as *Williamia*, *Epistylum*, and *Thamnocharis* in having both rhombic crystals and druses, while the latter have druses alone.

Petiole.

The petiole of all species of *Phyllanthus* is quite short and never approaches the length of the blade. Ordinarily it has an uncomplicated form, being plane adaxially and more or less convex abaxially, sometimes with a flange of green tissue decurrent from the blade. In sect. *Asterandra* this flange is very distinctively modified by transverse pleating into an accordion-like shape, so that isolated leaves of this group are always easy to identify.

Anatomically, the structure of the petiole conforms to the simplicity of the external form. The epidermis consists of small squarish cells, and stomata have not been observed. The vascular tissue as seen in cross-section (PLATE-FIG. 5) assumes the form of a slightly adaxially concave arc, with no conspicuous wings, flanges, or exclaves of vascular tissue such as have been reported in the petioles of many Euphorbiaceae (Dehay, 1935). In *P. urinaria*, however, the usual situation is modified by the presence of a curious reticulum of many fine inter-connected tracheids which form a mesh on all sides of the central vascular core. This accessory tracheary tissue is probably correlated with the pulvinar nature of the petiole; the leaves of *P. urinaria* have been reported to be "sensitive" to touch.

Crystals are usually more abundant in the petiole than in the blade, and the proportion of druses to rhombic crystals may be different. Sclerenchyma often forms a conspicuous jacket around the vascular tissue, but no free sclereids or stone cells have been observed.

Stipules.

The leaves of *Phyllanthus* are always stipulate, although in some species the stipules are evanescent and thus at first sight may appear to be absent. Most commonly the stipules are triangular to lanceolate with an acute or acuminate, sometimes reflexed, tip. The margins and tip are usually scarious at maturity and are differently colored from the herbaceous basal area. The scarious portion of the stipule is composed of tabular cells without stomata and is often denticulate at the margin. The basal herbaceous portion, which may have stomata, is often thickened and persistent after the fall of the scarious tip.

Although the stipules of *Phyllanthus* never become as large and foliaceous as in species of *Amanoa* or *Drypetes*, they do show extensive variations in duration, size, shape, color, development of auricles, marginal toothings, etc. For this reason they provide some of the most convenient characters for readily distinguishing species. Measuring the sizes of stipules has the slight inconvenience that those of the proximal portion of branch or branchlet are usually larger than the distal ones; and the two at the same axil may be unequal. In *P. formosus* the two members of each stipule-pair are extraordinarily unlike, one of them being broad and conspicuously lacerate-dentate while the other is narrow and quite entire. This approaches the extreme heteromorphy of the stipules in *Vicia monantha* as illustrated by Glück (1919: fig. 2).

The species other than *P. formosus* do not have such a dimorphism of stipules on the same branchlet. However, in most species with phyllanthoid branching the stipules on the deciduous branchlet are quite different from those on the permanent axis; the latter are usually larger, broader, and of a much firmer texture. In many woody species these permanent-branch stipules are clustered at the apex of the stem into a dense scaly cone which encloses the apical meristem and unexpanded leafy branchlets. In such woody species as *P. cinctus* these stipules are indurate and the numerous parallel veins are stoutly armed with sclereids. In most herbaceous and some woody species of *Phyllanthus* the stipules have only a single vein which is not jacketed with sclereids (PLATE-FIG. 5).

Cataphylls.

In the section on growth form one of the essential characters of phyllanthoid branching was shown to be the reduction of the leaves on the seedling stem (and all subsequent persistent axes) to cataphylls, the reduced leaf blade usually resembling the stipules in appearance and thus three stipules appearing to be at the same axil. Actually, although the reduced blade of the cataphyll is usually just like the stipules in texture and color, it is very often narrower and thus may be distinguished by its shape and position.

The spatial relationship of the cataphylls in *Phyllanthus* is rather peculiar. They do not correspond to conventional cataphylls as defined, for instance, by Gray (1879: 401) or Goebel (1905: 384). As Goebel pointed

out, the term was originally coined by Schimper to refer to the scale leaves on rhizomes or the basal parts of aerial stems. Goebel added:

“To these leaf formations, both in their construction and function, all those epigeous parts which have been called bud scales (tegmenta) conform, and so closely that they have received the same name. This is not altogether wrong, inasmuch as these leaf formations upon an upright growing shoot stand upon the “lower” region of the shoot and are followed by foliage leaves.”

The cataphylls of *Phyllanthus*, however, do not correspond either to rhizome scales or bud scales, for they definitely appear on the upper portions of stems and branches and are *preceded* by typical leaves. Their position on the axis therefore appears to be the reverse of that of typical cataphylls. Jackson (1905: 131), would have called the scale-leaf of *Phyllanthus* a “hypsophyll”, which is defined by him as “a bract of the inflorescence, a reduced or modified leaf towards the upper end of the shoot.” As Goebel (1905: 390–391) remarked, however, it appears best to retain the word “hypsophyll” for those leaves directly associated with flowers. In form and evidently in function the scale-leaves of *Phyllanthus* resemble typical cataphylls, and their different position does not appear to be of fundamental importance. The main difference between the cataphylls of *Phyllanthus* and most bud-scales is that the latter are associated with seasonal growth.

Majumdar and Arshad Ali (1956) have studied the vascular anatomy of the cataphylls in *Phyllanthus amarus* (“*niruri*”) and *P. reticulatus*. They report that in *P. reticulatus* (which has trilacunar nodes) the traces from the lateral leaf-gaps of the node run into the stipules; the median trace gives off two branches which turn back and join the stipular traces. This observation has been personally verified as far as the branchlet of *P. reticulatus* is concerned. In *P. amarus*, on the other hand, they report that the main axis has unilacunar nodes (although the nodes of the deciduous branchlet are trilacunar) and that the two lateral branches of the median trace (midrib) pass directly into the stipules. Because of this difference they call the appendages of the *P. amarus* cataphyll “leaf lobes” and those of *P. reticulatus* “stipules”; but then they qualify this by adding that the difference between basal lobes and stipules in this case “is one of degree [rather] than of kind”. It is difficult as yet to evaluate these very interesting observations on the basis of the nodal anatomy of only two species of a genus as large as *Phyllanthus*. Despite the behavior of the traces, there is no difference in the cataphyllar stipules of *P. amarus* and *P. reticulatus* which would warrant giving them different names. Furthermore, the fact that the leaf-blade of *Phyllanthus* is always simple and entire quite precludes the possibility of *P. amarus* having three-lobed leaves. What the researches of Majumdar and Arshad Ali do show is that, as might be expected, the foliar traces of the advanced herbaceous species *P. amarus* have undergone considerable modification and reduction as compared to the more primitive *P. reticulatus*.

Anatomically the blade of the cataphyll in *Phyllanthus* is completely

different from the foliage leaf and closely resembles the accompanying two stipules. Stomata, palisade cells, and spongy parenchyma are lacking (at least in the expanded scarious portion), the epidermal cells are tabular and thick-walled, and the veins (if more than one) are parallel. In some of the herbaceous species of sect. *Phyllanthus* transitional forms between foliage leaf and cataphyll occur, particularly at the proximal nodes of permanent branches. These have a green foliose proximal part which distally is abruptly contracted into a brownish scarious tip. The cataphyll of some of the species of sect. *Orbicularia* (e.g., *P. scopulorum*) is especially interesting because the blade closely resembles the long scarious deciduous tip of the foliage leaf. This suggests that in some species of *Phyllanthus*, at least, the cataphylls would belong to the category of those derived mainly from leaf apex (cf. Schulze, 1934). However, drawing a strict homology between leaf apex and cataphyll blade would scarcely be justified until comparative developmental studies have been made.

Dingler (1885: 139) found in studying the seedling of *P. niruri* that the reduction of the foliage leaf to cataphyll occurs at the node where the first deciduous branchlet is attached; he therefore concluded that there is a direct causal relationship at work. It might be supposed, consequently, that it is the precocious expansion of the branchlet which inhibits the lamina of the cataphyll. However, the correlation between reduction of cataphyll blade and development of deciduous branchlet does not appear to be as exact as Dingler suggested. Examination of seedlings of *P. abnormis*, *P. amarus*, and *P. tenellus* has shown that the abrupt change from foliage leaf to cataphyll by no means takes place at precisely the same node where the first deciduous branchlet appears. Furthermore, there are a number of species (e.g., *P. formosus*, *P. berterioanus*, and *P. sellowianus*) with undoubted phyllanthoid branching in which the reduction of foliage leaf to cataphyll takes place considerably later in ontogeny or not at all. Nevertheless, there is in a general way an undoubted inverse correlation between development of deciduous branchlets and the blades of the leaves on the permanent axes.

Trichomes.

The great majority of the species of *Phyllanthus* may be described as completely glabrous, but many of them have a papillate lower epidermis, and in a few species papillae may occur on the upper leaf-surface as well. As Froembling pointed out, there are some species (e.g., *P. praetervisus*) in which all manner of transitions may be observed between epidermal cells which have merely a convex outer wall to those in which the cell is drawn out into a long hair. The hairs are uniseriate, composed of one to several cells, thin-walled, and usually obtuse at the ends. Foliar glands or capitate hairs of the sort found in the Crotonaeae are unknown in the Phyllanthinae. Froembling's report that unicellular hairs of *Phyllanthus* often assume a nearly unciniate form probably applies to species now included in *Glochidion*; in both genera, however, the hairs are never as long, sharp-pointed, and pronouncedly unciniate as those in the Andrachninae.

Among the native West Indies species well-developed trichomes occur in only a few groups. In sect. *Elutanthos* multicellular hairs occur on both stem and leaf, but their expression is quite variable, and *P. botryanthus* is completely glabrous. In sect. *Hemiphyllanthus* trichomes occur only on the axes, where they are clustered on peculiar longitudinal plates or ridges of cells. The result is an incrustate appearance which recalls that of the twigs in sect. *Williamiandra*, which have incrustate masses of cells that are derived from proliferation of lenticellar tissue.

INFLORESCENCE

The best general treatment of the inflorescence of the Euphorbiaceae (excluding the Euphorbiae!), despite its age, is that of Baillon (1858). He clearly stated that the cymose pattern is the most widespread and fundamental both in the Euphorbiaceae and the angiosperms as a whole. The study of the inflorescence of *Phyllanthus* agrees well with this and with the hypothesis of Rickett (1944) that the *dichasium*, or "complete cyme" of Gray (1879) is the basic type of which all other angiospermous inflorescences represent modifications. In many Euphorbiaceae the flower arrangement has become so highly modified that its fundamentally cymose nature is apparent only on careful inspection. In *Phyllanthus*, however, there is little doubt except for those few species with solitary flowers; and there is furthermore a broad spectrum of inflorescence types which can be related to one another.

The individual cyme in *Phyllanthus* is of course a determinate structure with a terminal female flower (if it is bisexual). But in those species with cymes aggregated into a compound inflorescence, the latter is indeterminate; there is never a single flower terminating the main axis as in *Jatropha* or *Euphorbia*. Since it appears that the phylogenetic trend of inflorescence modification in *Phyllanthus* has been one of reduction, the more elaborate types will be considered first.

The species of sect. *Elutanthos* have the least modified kind of inflorescence among the West Indian species and — except for the Australasian sect. *Nymanina* — the genus as a whole. Of the species of sect. *Elutanthos* the Mexican *P. grandifolius* has the most elaborate aggregations of flowers. The proximal portion of the floriferous branch (i.e., the branch of the current year) bears normal foliage leaves, some of which subtend thyrses of male flowers. Each male thyrses is composed of a number of cymules arranged alternately on the flexuous axis. The male cymules are dichasial only at the very base and monochasial thereafter, so that two or three "pseudo-racemes" of flowers appear fascicled together at one node. The distal portion of the floriferous branch is itself modified into a thyrses which only differs from the male inflorescence in that the individual cymules have fewer flowers and thus are more fascicle-like than raceme-like.

Phyllanthus grandifolius is interesting not only because of its elaborate aggregations of flowers, but also because it shows in an unspecialized condition the tendencies which lead toward the inflorescences of other

species. For example, two trends occurring in *P. grandifolius* and in many other species are: monochasial development of cymules and production of male flowers proximally relative to the female flowers (on the entire branchlet or thyrses). In *P. grandifolius* the sexes are more or less completely segregated, the male flowers being borne on axes in the axils of normal foliage leaves and the female directly in the axils of the distal leaves, which are usually reduced to bracts. There is thus in this species a striking (though not invariable) correlation between the terminalization of the female flowers and the reduction of the subtending leaves to bracts. This reduction phenomenon may not be taken as a general rule, however, because in other species it is the proximal leaves subtending the male flowers which are reduced. The terminalization of the female flowers, on the other hand, occurs almost invariably whenever the plant is monoecious and the cymules unisexual; only in the few species of sect. *Urinaria* is the order definitely reverse.

The West Indian species of sect. *Elutanthos* differ from *P. grandifolius* in having mostly bisexual cymules and less elaborate inflorescences. The flower arrangement in these, and all the other species with non-phyllanthoid branching, is so variable and dependent on the vigor of the shoot that it is very difficult to write a good taxonomic description of it. In *P. nutans*, for example, the female flowers tend to be clustered in the axils of reduced leaves on a flexuous "semi-naked" axis (more exactly, a racemiform thyrses), while the male flowers are borne either in clusters axillary to foliage leaves or at the lower nodes of the thyrses. In this, as in all the species of sect. *Elutanthos*, the boundary between the vegetative and fertile zones of the plant is not well defined.

In the herbaceous or subshrubby species of sect. *Paraphyllanthus*, (none of which occur in the West Indies), the cymules are reduced to dense clusters that are always axillary to foliage leaves. The flower-clusters are extremely variable, at least in the widespread *P. polygonoides*, which may be either monoecious or dioecious and which may have both unisexual and bisexual cymules on the same individual. Furthermore, branch buds may be produced at the same axil as a flower cluster.

The three West Indian species of sect. *Loxopodium* have a similar sort of floral arrangement, and branch-buds may similarly be produced at the same axils with the flowers; but usually the arrangement of the sexes is much more definite as to number and position. The cymules may contain from one to five female flowers and as many male, but the inflorescence axis is always so greatly contracted that it is not evident to casual inspection. There thus appears to be no fundamental difference between the pattern of flower production in the various sections with non-phyllanthoid branching; flowers may be produced (at least potentially) at any node on any axis (except possibly for the lowermost nodes on the seedling axis).

In the remainder of the West Indian species, however, as well as in the majority of those in the entire genus, the flowers are borne only on deciduous branchlets and never on the main axis or on permanent branches. Among these West Indian species with phyllanthoid branching, *P. juglandi-*

folius displays relatively unspecialized inflorescences. The cymules are mostly bisexual, and those of the proximal axils of a branchlet often have three or four female flowers accompanied by several males; the number of female flowers decreases distally until the cymules at the tip of the branchlet are entirely male. In a few other species such as *P. discolor* there may be two or three female flowers per cymule, but in most species there is only a single female flower and the cymules are often unisexual. *Phyllanthus juglandifolius* is exceptional not only in its relatively elaborate inflorescences, but more especially in its tendency toward proximal production of female flowers, which is exactly the reverse of the trend in most other species.

Perhaps the most striking evolutionary trend is apparent among the herbaceous species with phyllanthoid branching, in which there is a very evident shift from bisexual to unisexual inflorescences. With the exception of the anomalous *P. elsiæ* there are no woody American species of *Phyllanthus* which are dioecious; but in a number of the herbaceous species of sect. *Phyllanthus* entire plants, as well as individual cymules, may be unisexual. However, even in these species the dioecious condition is not absolute, for male branchlets will occasionally produce one or two female flowers at the tip, and while female branchlets never produce any male flowers (at least in the West Indian species) a female plant may produce a few male branchlets. In contrast to this imperfect dioeciousness in *Phyllanthus*, the West Indian representatives of the related genera *Astrocasia*, *Flueggea*, *Savia*, and *Securinega* appear to be completely dioecious.

In most of the herbaceous species of sect. *Phyllanthus* the combination of the trends toward unisexuality of cymule and terminalization of female flower has resulted in branchlets with proximal cymules of several male flowers and distal cymules each of a solitary female flower. The common weedy species *P. amarus* is exceptional in that it has bisexual cymules, each with one male and one female flower.

In a few species the reduction of the cymule has proceeded to the point where it is composed only of a solitary flower. This situation prevails in the herbaceous species of sects. *Callitrichoides* and *Cyclanthera* and in several shrubby species of sect. *Orbicularia*. Among the latter, however, the condition is not as strongly fixed, for occasionally paired flowers may be produced on a branchlet which otherwise has only solitary ones.

The West Indian species with bipinnatifid branchlets have a special sort of distribution of flowers. In *P. subglomeratus* and many of the South American representatives of sect. *Nothoclema* cymules are produced at all the nodes of both the ultimate and penultimate axes. In the other West Indian species of *Nothoclema*, *P. acuminatus*, flowers are likewise produced at all the nodes of the ultimate axes; but on the penultimate axis there are cymules only at the proximal nodes which do not subtend ultimate axes, and sometimes there are no floriferous nodes on the penultimate axis. In the species of sect. *Hemiphyllanthus* this "sterilization" is complete and flowers are produced only on the ultimate axes.

In the section on growth form the origin of cauliflory in *Phyllanthus* has been ascribed to the modification of floriferous branchlets to "naked" thyrses with the leaves reduced to scales and to the production of these modified branchlets in fascicles at nodes of the previous year's growth. It is probable that among the species represented in the West Indies, cauliflory has arisen independently at least twice: in sect. *Cicca* and in sect. *Epistylum*. The basic prerequisite for cauliflory is of course the reduction of the leaves subtending the cymules; but in *Phyllanthus* there is evidently not a very strong trend in that direction. It is true that in a great many species the proximal leaves of a branchlet are often smaller than the distal ones and subtend male cymules; this suggests that there may be some nutritional effect on both the expression of leaf size and sex of flowers. But on the other hand there are a number of species in which the correlation is reversed and it is the distal leaves subtending the female cymules which are reduced. This diversity in sex expression and leaf modification raises some interesting physiological problems. The species with phyllanthoid branching would seem to be promising experimental plants for research in sex determination such as that carried out by Nitsch et al. (1952) on the Cucurbitaceae. These authors showed that sex expression in the cucumber may be controlled by varying temperature and light, at least to the extent of modifying the number of nodes bearing a particular kind of flower. Similar experiments carried out with the view of comparing the response of a species of sect. *Urinaria* (with female flowers proximal on the branchlet) and a species of sect. *Phyllanthus* (with the female flowers distal) might yield significant results.

Croizat (1943, 1944) has discussed the morphology and evolution of inflorescence in *Phyllanthus* and has suggested a different interpretation from that adopted here. In his first paper he asserted:

"In certain groups of *Phyllanthus* true leaves are present, the floriferous axes being often reduced, bracteate, and, strictly speaking, leafless branchlets (see *P. laxiflorus* [*P. grandifolius*]). In other groups of the same genus the true leaves are represented only by scales, the aspect and function of foliage being assumed by the bracts of the floriferous axes (see *P. mexiae*)."

In his fuller account the following year it is evident that Croizat's view of the evolution of inflorescence in *Phyllanthus* is based on two main assumptions: first, that the solitary axillary flower represents the primitive type of inflorescence, and second, that the foliage leaves of species with phyllanthoid branching represent bracts which have presumably been "de-differentiated" into leaves. Majumdar and Arshad Ali (1956: 158), on the basis of their studies of *P. amarus* and *P. reticulatus*, have come to a similar conclusion as regards the latter point. Because the buds in the axils of the leaves of the branchlet produce only flowers, they suggest that the branchlets of these two species should be called inflorescences and the leaves should be called bracts.

The term *anthocladium* has been applied by Goebel (1931) to a branch in which the determinate (i.e. cymose) branching pattern of the inflores-

cence is superimposed on the indeterminate pattern of the vegetative shoot. In *Phyllanthus*, as specifically pointed out by Goebel (1931: 22), the floriferous axis is monopodial and thus cannot strictly be termed an anthocladium. Nevertheless, it is very evident that in *Phyllanthus* the fate of the deciduous branchlet is intimately related to flower production.* But to call either the anthocladium of *Euphorbia* subg. *Chamaesyce* or the deciduous branchlet of *Phyllanthus* an "inflorescence" is not only unwarranted but holds the danger of introducing confusion in terms. In all the species of *Phyllanthus* investigated, the leaves subtending the cymules are typical foliage leaves indistinguishable (except sometimes by a minor difference in shape) from those on the seedling axis. If one were to follow Croizat and Majumdar in calling the branchlet leaves "bracts", this would contradict the classical definition of the latter term (cf. Gray, 1879: 118), which definitely requires a bract to show a difference in form. Furthermore, neither in *Phyllanthus* nor in *Euphorbia* subg. *Chamaesyce* is there any evidence that the leaves associated with the flowers or cyathia have metamorphosed back from bracts.

FLOWER

Few other genera of angiosperms display a range of variation in flower structure comparable to *Phyllanthus*, even when such divergent groups as *Astrocasia* and *Margaritaria* have been removed from it. It is not surprising, therefore, that during the first half of the nineteenth century many small genera justified by "technical" floral characters were erected on various species now included in *Phyllanthus*. One of Mueller's greatest accomplishments was his perception of the essential similarity between these many small "genera", and his synthesis of these fragments into a unified and — on the whole — natural generic concept. In placing *Glochidion* within the confines of *Phyllanthus*, Mueller emphasized the relationship of these two groups in floral morphology, and Hooker implicitly recognized this when he had to justify the resurrection of *Glochidion* chiefly on the grounds of convenience.

Floral diversity is enhanced in *Phyllanthus*, as in other genera of the Euphorbiaceae, by virtue of the fact that the male and female flowers have often evolved in different ways. But at the same time there has been in both sexes a trend towards reduction of number of parts, accompanied by a decrease in variability. The structural differences between the male and female flowers in the various species may be ascribed to the interaction of two factors: the duration of the flower (the male being relatively fugacious) and the difference in the number of sporophylls. It appears that in some instances the number of calyx-lobes developed in the mature flower is affected by the shape of the androecium or gynoecium primordium during development. Thus in an appreciable number of the species which

* From a dynamic point of view it might be worth while to broaden the definition of "anthocladium" to include highly specialized monopodial branches which behave as inflorescence-units.

have male flowers with only two stamens the calyx-lobes of the male flower are reduced from five to four, whereas the female flowers still have five calyx-lobes.

The flowers of *Phyllanthus* are exclusively unisexual, and ordinarily there is no trace of the organs of the missing sex. Section *Cicca* is the only group in which definite staminodes occur; and these may even produce a few pollen grains, though it is not known if any of these "female" pollen grains are fertile. From time to time various authors have described species of *Phyllanthus* with a "pistillode" in the male flower, but on close examination this structure has always proved to be the apiculate tip of the staminal column, which may represent either an abortive stamen or one or more prolonged anther connectives. Any "Phyllanthus-like" plant which does have a pistillode may confidently be referred to some other genus.

The floral biology of *Phyllanthus* remains an almost uncharted area, partly because so many of the species grow in localities where protracted field observation is difficult. The great diversity in flower structure suggests specialization for different types of insect visitors, but almost nothing is known of how any of the species are pollinated. Personal observation in Cuba of the pollination of *P. dimorphus* by chrysomelid beetles (unfortunately not further identified) and of *P. orbicularis* by bees has given the merest glimpse into the pollination relationships of the genus.

Pedicle and Torus.

The pedicel of the male flower is terete, usually slender, and is about as long as or longer than that of the female flower. This proves to be a good, albeit superficial, character for distinguishing *Phyllanthus* from related genera such as *Savia* and *Securinega*, where the male flowers are mostly sessile and the female flowers long-stalked. In a few species of *Phyllanthus* (e.g., *P. tenellus*) the pedicel of the female flower is much longer than that of the male, but usually it is shorter and in some species such as *P. urinaria* is shortened to scarcely more than a broad platform beneath the calyx.

Histologically, the pedicel is usually rather simple. The epidermis (in the proximal portion, at least) lacks stomata and is composed of cells with rectangular outlines. A "hypodermis" may sometimes be distinguished, at least in the base of the pedicel, by the tannin content of the subepidermal layer. In all of the male flowers examined, sclereids are completely absent, the axis of the pedicel being occupied only by a few slender tracheids. The female flowers of many species likewise have only tracheids, but the pedicel of *P. niruri* shows a very characteristic sclerification. Towards the base of the pedicel slightly elongated "brachysclereids" occur around the outside of the vascular bundle; these become progressively longer distally but stop about halfway up the pedicel. Beneath the brachysclereid layer, however, is a layer of fibers which run to the very top of the pedicel

and end in the receptacular region. It is very curious that some of the woody species examined, although having much larger fruit than *P. niruri*, entirely lack fibers or sclereids in the pedicel. Crystals are typically much less numerous in the pedicel proper than in the receptacle or ovary.

The top (distal) portion of the pedicel is expanded (sometimes abruptly) into a receptacle which merges with the basally fused calyx lobes so that it is neither conspicuous nor clearly defined. In the female flower the upper portion of the pedicel may gradually (as compared with the male) enlarge up to the toral region, and in some of the species of sect. *Hemiphyllanthus* this dilated portion may become large and fleshy. The enlargement reaches such grotesque proportions in the female flower of *P. megapodus* that the expanded pedicel-receptacle is larger than the rest of the flower. In *P. subcarnosus* the expanded portion of the pedicel contains chlorenchyma.

The pedicel characteristically hangs so that the male and female flowers project below the plane of the leaves on the branchlet. After the fertilization period the pedicel of the male flower disarticulates, but that of the female flower remains relatively unchanged. During the development of the fruit the pedicel may elongate slightly, but (at least in the West Indian species) the increase in length is never very great.

Calyx.

The flowers of *Phyllanthus*, in common with those of most of the Euphorbiaceae, are apetalous with a gamophyllous calyx. The union of the calyx-lobes at the base is sometimes slight but almost always noticeable on close inspection, and except in very rare instances (e.g., *P. subcarnosus*) they never disarticulate separately from the receptacle. In many species the calyx, as if in compensation for the lack of petals, is petaloid and conspicuous, red or pink (and more rarely purplish) being the prevailing hues; and the disk is often of a contrasting color. In other species, particularly the herbaceous ones, the calyx is yellowish or whitish, and in a few the female calyx is green and foliose.

As suggested by Michaelis (1924) for the Euphorbiaceae as a whole, the basic arrangement of the calyx-parts in *Phyllanthus* appears to be five lobes in imbricate aestivation; four lobes in decussate pairs or six in two whorls represent derived conditions. The number of lobes may vary within the same species, and does not necessarily correspond between the male and female flowers. Although the male and female calyces of some species are very similar, the female calyx is very often larger, stouter, and composed of a greater number of lobes.

Usually each calyx-lobe of the male flower has a single unbranched or sparsely branched vein; in the latter case, the branch-tips, of more or less enlarged tracheids, occur flabellately near the tip of the lobe. In species with fairly massive male flowers, such as those of sect. *Thamnocharis*, there may be three parallel sparsely branching veins. The calyx of the female flower usually has more elaborate venation than that of

the male. In sect. *Paraphyllanthus* (which is not represented in the West Indies) the female calyx-lobes are quite green and foliaceous; the mid-vein branches much as in the leaf to form a reticulate pattern, and the interior of the lobe is occupied by chlorenchyma. The calyx-lobes of the species in this section are more leaf-like than those of any of the West Indian species, which have no well-defined chlorenchyma. However, stomata occur on the epidermis of the female flowers of many species and rarely even on the epidermis of the male (e.g., *P. ekmanii*). Reticulate venation is not well-developed in the calyx-lobes of any of the West Indian species, but in the lobes of species with massive female flowers (such as in sect. *Thamnocharis*) there are instead a number of parallel veins conspicuously jacketed with fibers.

The texture of the calyx varies from thinly herbaceous to coriaceous among different species; the margins even of the coriaceous lobes are thin, and sometimes are denticulate or lacerate. At anthesis the calyx-lobes of both male and female flowers are usually more or less spreading, but in some species the lobes of the female calyx remain erect and imbricate around the ovary. The female calyx remains relatively unchanged during maturation of the fruit except that sometimes the lobes become reflexed. *Phyllanthus subcarnosus* (sect. *Omphacodes*) is exceptional in that the female calyx-lobes are very early deciduous from the receptacle.

Disk.

The term *disk* as used here refers to the more or less glandular mass of tissue arising from the receptacle between the calyx and the androecium or gynoecium. In *Phyllanthus* the disk is invariably outside the stamens; but the situation is reversed in some other genera of Phyllanthaceae such as *Drypetes* and *Reverchonia*. In the male flower the disk is ordinarily divided into segments isomerous and alternating with the calyx-lobes. The disk-segments are often closely contiguous and they may be united in pairs or all united into a continuous saucer- or cup-shaded disk. A few species such as *P. emblica* have male flowers with the disk reduced or absent, and in *P. elsiae* the disk is absent in both sexes; the latter situation prevails in other genera of the Phyllanthinae such as *Glochidion* and *Breynia*. In the female flower of *Phyllanthus* the disk is most commonly continuous, and only in a rather small number of species is it divided into segments like the disk in the male flower.

The term *disk-segment* as used here is synonymous with the "disk-gland" of most authors. The latter term is unwieldy because there are some species of *Phyllanthus* in which the disk-segment is itself provided with glands. The disk-segment is more or less equivalent to the "nectary," but the latter term suffers from the ambiguity that it is sometimes applied to the entire disk of a flower and sometimes to the individual disk-segments. It must be kept in mind that the disk-segment is a topographical designation and is not intended to convey any developmental implications. The disk does not necessarily begin development as an entire structure and then break up into segments, either in ontogeny or phylogeny.

The disk may be greenish, yellowish, pink, or even deep red or purple when fresh, but on drying it usually loses its distinctive color and becomes brownish. In many species the disk-segments are crenulate or lobed and appear pitted under high magnification. Microtome sections show that in *P. reticulatus*, for instance, there is a stoma at the bottom of each of the well-like pits, and that the cells making up the disk are smaller and have denser cytoplasm than those in most of the other floral parts (PLATE-FIG. 46). Stomatal pits have been observed in the disk of most of the species studied from paraffin sections, and in some species (e.g., *P. ekmanii*) they can be easily seen in cleared whole mounts. This histological evidence leaves little doubt that the disk of *Phyllanthus* is a true nectary in function. The amount of nectar secreted by the disk is evidently small in most species, since the disk of flowers examined in the field usually appears merely moist. A considerable quantity of nectar has been observed only in *P. polygonoides*, an extra-Caribbean species. The flowers of most species appear to be quite odorless, but it has been reported that the common *P. epiphyllanthus* has flowers which give off an evil smell at night.

Many species have flowers with a relatively massive disk in one or both sexes. The Indonesian species *P. ceramanthus*,* with both the androecium and gynoecium almost completely enclosed in an urceolate disk, represents the extreme in vertical extension. *Phyllanthus emblica* has the most disparate disk structure in the two sexes of any species examined; the female disk is a cup like that of *P. ceramanthus* and with a lacerate rim, but the male is reduced or absent. The West Indian *P. chryseus* is of especial interest, not only because it has the relatively largest disk of any species examined, but also because of the vascular supply to it (PLATE-FIG. 45). In species such as *P. reticulatus*, which have a much smaller floral disk, there is no sign of a special vascular supply. This suggests that in *Phyllanthus*, at least, vascularization of the disk is a function of size and can have no particular significance for purposes of homologizing different parts of the flower.

The question of the morphological nature of the disk in the Euphorbiaceae is of some theoretical interest and has been discussed by a number of workers. Baillon (1858) clearly distinguished between staminode and disk; he regarded the latter as an expansion of the torus on the basis of his ontogenetic studies. His view is clearly shown in his discussion of the hypogynous glands of *Cluytia pulchella*:

“Quant aux cinq glandes bilobées de la fleur femelle, elles constituent un vrai disque, et l'on peut suivre facilement . . . son développement ultérieur a celui du pistil. Si c'étaient des staminodes, elles apparaîtraient avant lui.”

Baillon's assumption that there is a perfect correlation between the morphological nature of floral organs and the time of their initiation in development is bound to be suspect in this sceptical age. Michaelis (1924: 113), on the basis of his own studies on the Euphorbiaceae, does not con-

* *Phyllanthus ceramanthus* nom. nov.; *Ceramanthus gracilis* Hassk. Cat. Hort. Bogor. Alt. 240. 1844; non *Phyllanthus gracilis* Roxb. Fl. Ind. 3: 655. 1832.

sider the delayed appearance of the disk a proof against its staminodial origin. He found that in *Croton* and *Codiaeum* rudimentary calyx- and corolla-parts were delayed in ontogeny, and concluded therefore that the late appearance of the disk may likewise be only an indication of its rudimentary nature. The entire problem appears to need reinvestigation; but in any event, ontogenetic studies of *Phyllanthus* — in which the disk always appears very late — do not seem likely to provide decisive evidence.

Eichler, in his "Blütendiagramme" (1875: 4, 48–49) regarded the disk in most angiosperms as representing an emergence of the axis (specifically, the receptacle). In addition to remarking on the belated development of the disk, he added the important generality that the disk structures do not alter the arrangement of whorls in the flower and therefore cannot represent an independent cycle. Bentham and Hooker (1880: 239), Pax (1890: 1) and Pax and Hoffmann (1931: 13) followed Eichler's conception in interpreting the disk in the Euphorbiaceae.

A different interpretation has been presented by Michaelis (1924), who in a vigorous refutation of the "emergence" theory has suggested that the disk-structures of the Euphorbiaceae are mostly derived from reduced stamens. His argument is based on a number of his observations: (1) the regularity of position of the "Diskusdrüsen," which occupy the positions of the outer staminal whorl; (2) the resemblance of the disk-segments of *Chiropetalum*, *Cluytia*, et al., to immature stamens; (3) the development of "archesporial tissue" in the disk-segments of *Erythrococca*; (4) the occasional replacement of "disk-glands" by stamens; and (5) the lack of appreciable nectar or sugar content in the disk.

In the present study Michaelis's viewpoint has been considered only as it relates to the Phyllanthaceae, and no attempt has been made to check his observations on members of the Crotonoideae. A detailed reading of his work shows that he depended heavily on evidence from the polyandrous species of *Croton*, in which the disk-segments alternate with the petals and thus occupy the position of an outer staminal whorl. However, at least in the more primitive genera of Phyllanthaceae the disk-segments (where separate) are definitely opposite the petals and can scarcely represent an abortive outer staminal whorl. Furthermore, in the occasional hermaphroditic flowers of *Phyllanthus acidus*, the staminodes appear in addition to the normal hypogynous disk; in this species, therefore, there can hardly be any doubt that the disk is not staminodial in origin.

It is difficult to understand Michaelis's contention that the disk does not play a rôle as a nectary. It is true that, as he asserts, there is no evident amount of free nectar in the flowers of many Euphorbiaceae. But in *Phyllanthus*, at any rate, the anatomical structure of the disk shows that there can be little doubt of its secretory nature. The pendent male flowers of most species of *Phyllanthus* are furthermore hardly capable of holding any sizeable quantity of nectar.

Evidently Michaelis, in drawing up his "staminodial" theory of the disk, has leaned too strongly on evidence from the Crotonoideae. Baillon's ex-

PLICIT statement (1858: 127) that there are never any staminodes in the female flower of the Phyllanthoideae appears to be essentially correct (excepting *Phyllanthus acidus*). If Michaelis's observations of the Crotonoideae are correct, then it would appear that the disk in that subfamily is by and large not homologous with that in the Phyllanthoideae. Further research must be done in the Crotonoideae to reconcile the conflicting accounts of Michaelis and Baillon.

If the possibility of staminodial origin of the disk in *Phyllanthus* is rejected, the "emergence" theory remains to be examined. It is quite possible, as Baillon and Eichler suggested, that the disk is purely an expansion of the torus, as it appears to be in such families as the Cruciferae. However, the striking topographical arrangement of the disk-segments suggests another possibility. In the genera of Phyllantheae in which a corolla is developed (e.g., *Andrachne*, *Astrocasia*) the disk-segments are opposite the petals, not alternate as they would be if they represented the outer staminal whorl. In *Phyllanthus*, where the corolla is absent, the disk-segments (if free) occupy the same relative position as the missing petals (i.e., alternate with the calyx-lobes). This suggests that the disk may belong to the corolline whorl. In *Andrachne* and some of the primitive species of *Phyllanthus* (e.g., *P. polygonoides*) the disk-segments are more or less bifid (cf. Michaelis, pl. 1, fig. 1). Their appearance and antepetalous position suggests that the disk-segments in these plants may be "ligular" appendages of the petals corresponding to the "Nebenkrone" of the Caryophyllaceae. The production of glandular appendages by the floral leaves can hardly be considered remarkable in a family such as the Euphorbiaceae, where glandular structures are commonly associated with the basal portions of foliage leaves and bracts. Nor can the usual lack of vascular supply to the disk be considered surprising when it is recalled that the suppressed petals have left no rudimentary vascular traces either. However, at present it is really not possible to decide whether the disk-segments should be considered toral expansions or corollar appendages; the simple structure of the disk does not offer any clues definite enough to choose between the two alternatives.

Androecium.

According to Michaelis (1924: 121) the primitive androecium in the Euphorbiaceae is one of many stamens in several whorls; he found no evidence of phylogenetic increase in stamen number except in a few anomalous cases such as *Ricinus*. In *Phyllanthus* reduction from a polymerous androecium to one with few stamens may be traced in at least two phylogenetic lines, one of which is in the West Indies. *Phyllanthus discolor* (sect. *Williamia*) has ten to fifteen stamens with the filaments connate and the anthers spirally disposed or in three whorls; this is the highest stamen number found in any New World species. *Phyllanthus microdictyus*, the other species of sect. *Williamia*, has six to ten stamens in two or three whorls (the filaments being connate in all these related species). In sects. *Williamiandra* and *Orbicularia*, which are clearly derived from sect.

Williamia, the stamen number is mostly six, but in *P. phlebocarpus* of the latter section it is reduced to three. There can be little doubt that these species are related and that there has been a progressive reduction in stamen number during the evolution of the group. However, sect. *Williamia*, because of its phyllanthoid branching and areolate pollen grains, cannot be one of the most primitive groups in the genus. Furthermore, in sect. *Elutanthos*, which appears to be the progenitor of *Williamia*, the stamens are never more than three; and this small number also characterizes the vegetatively primitive species of sect. *Paraphyllanthus*.

Section *Polyandroglochidion* of New Caledonia, with up to fourteen stamens, is the only other group with over ten. In this group the pollen grains are colpate and the stamens free, but vegetatively the representatives have the specialized phyllanthoid branching. On the basis of the existing species of *Phyllanthus*, therefore, it would appear necessary to postulate an increase in stamen number from the three to five of primitive sections like *Paraphyllanthus* and *Menarda* to the ten or more of *Williamia* and *Polyandroglochidion*. That this is not impossible is apparent from the fact an undoubted increase in carpel number has occurred in a few cases. However, another and perhaps more likely possibility is that the various groups of *Phyllanthus* are descended from an ancestor — now extinct — which had a polymerous androecium combined with unspecialized branching. Evolution of the living representatives of *Phyllanthus* from such an ancestor would render unnecessary any hypothesis of increase in stamen number.

In the vast majority of the species of *Phyllanthus* the stamen number is six or less. Androecia of two, three, or four stamens have doubtless evolved by reduction from hexamerous and pentamerous ones such as those of sects. *Chorizandra* and *Anisonema*, respectively. More or less concomitant with reduction in stamen number are the two tendencies toward: (1) coalescence of stamens, at first by the filaments and then by the anthers; and (2) displacement of the line of anther dehiscence from vertical to horizontal.

Among the West Indian species, the introduced *P. tenellus* has the least-modified androecium, of five free stamens. In sect. *Cicca* there are four free stamens, and in sect. *Loxopodium* three. In the rest of the sections (except in relatives or descendants of sect. *Williamia*) there are either two or three stamens which are usually connate. In the most highly evolved androecia the anthers are oriented so that the line of dehiscence is horizontal and in sect. *Epistylium* they are deflexed so as to appear upside down.

Mueller depended heavily on these differences in stamen number and direction of anther-slits in distinguishing sections of the genus. Bentham (1878) rightly criticised this as leading to an unnatural classification; but Mueller was not unaware of the artificiality of the dehiscence character. The use of anther characters appears to have been largely a matter of expediency on the part of Mueller. Unfortunately for those who have subsequently had occasion to consider the subgeneric classification of

Phyllanthus, this character has proved to be a poor choice not only because of the violence it does to relationships but also because of its ambiguousness. Baillon (1858: 112) had already observed: "Je ne connais pas chez les Euphorbiacées, quoi qu'en disent quelques descriptions, d'exemples positifs de dehiscence transversale." As Baillon realized, the anthers in *Phyllanthus*, as in other Euphorbiaceae, nearly always open longitudinally with respect to their own axes; most "transversely dehiscent" anthers merely have been bent onto the horizontal plane without the line of dehiscence changing relatively to the long axis of the anther. Nevertheless, there is in some species at least a partial displacement of the dehiscence-plane; the slits of the anther sacs, instead of being perfectly parallel, come together on the abaxial face and are confluent in a single arc. This type of dehiscence may be truly "oblique" but in practice the distinction is excessively subtle. The reader of the descriptions in this work may assume that the anthers open by slits that are longitudinal or nearly so, and that the stated direction of dehiscence will apply in relation to the long axis of the flower rather than to the anther itself.

The final product of the trend towards reduction and coalescence of the stamens has been reached in those species of *Phyllanthus* in which the stamens with horizontally dehiscing anthers are completely fused, so that the androecium presents the appearance of a single stamen with a peltate anther that dehisces all the way around the circumference. This remarkable compound structure, or *synandrium*, characterizes all the species of the West Indian sect. *Cyclanthera* and occurs also in the Cuban *P. dimorphus* and in two species of Madagascar (Leandri, 1938). Personal examination of the Madagascarian *P. ivohibeus* has shown that this species, like *P. dimorphus*, belongs to sect. *Phyllanthus*. Possibly these two species are related so that the synandrium evolved only once within sect. *Phyllanthus*. But in any event the synandrium must have developed independently in the very different sect. *Cyclanthera*. Since many species of *Phyllanthus* have an androecium of three stamens with the anthers sessile atop a column, the independent origin of the synandrium can actually be accounted for rather easily on mechanical grounds; all that is required is fusion of the connectives and coalescence of the anther-slits.

The study of the androecium for taxonomic purposes, i.e., with the intention of finding "key" characters, is attended with the difficulty that the filaments are very late in developing. The conspicuous staminal column of the mature male flower may be scarcely evident in the bud, and stamens which actually are connate by the filaments may be interpreted mistakenly as free. This rapid expansion during anthesis also characterizes the styles of many species and should be kept in mind by anyone who is drawing up or attempting to use a description.

Anatomically the stamens of *Phyllanthus* offer little of interest, at least in the forms which have been investigated. Each stamen is supplied with a single trace of slender tracheids which in the connective may bifurcate or end entire. The traces of the individual stamens remain separate in the staminal column. The anthers, unlike those of many other Euphorbi-

aceae, have no special vesture or glandular development. The connective undergoes a number of modifications, being enlarged and emarginate between the anthers in some South American species and apiculate in several Old World species; but in our West Indian representatives it is unspecialized.

Pollen grains.

One of the most striking discoveries made during the study of the West Indian species of *Phyllanthus* was the extraordinary diversity of pollen morphology within the genus. Erdtman (1952) reported for the first time the characteristic pollen grain of subg. *Xylophylla*; but by a curious circumstance, all of the four species he reported on happened to have areolate grains, and he apparently was unaware of the great intrageneric variability. During the present study the pollen of about one-third of the species in the genus has been examined, including many Old World species and at least one species from all except one or two sections. Although a number of phylogenetically critical species have so far not been investigated (due to lack of material), the general lines of pollen morphology within *Phyllanthus* are now apparent.

Erdtman's general discussion of pollen morphology and his special treatment of the Euphorbiaceae have provided much assistance and stimulation during examination of the pollen of *Phyllanthus*. However, his very complex terminology appears not only unwieldy but also needlessly complicated as far as the needs of systematists, rather than palynologists, are concerned. Much of the terminology in the following discussion has consequently been adopted from that proposed by Faegri and Iversen (1950).

The small size of the microspores of *Phyllanthus* is doubtless partly responsible for their being so poorly known. They average around 20μ in diameter, and grains over 30μ broad are rare. Observation under an oil immersion lens is usually necessary to determine the ornamentation pattern of the exine. The use of pollen characters is therefore not practicable for routine determinations; but it is an invaluable aid in assigning species to their place within the genus.

The commonest and probably the basic type of pollen grain in the Phyllanthoideae and some of the tribes of Crotonoideae much resembles those in such families as the Flacourtiaceae, Sapindaceae, and Celastraceae. It is subglobose or broadly ellipsoidal and thin-walled, with a reticulate exine. In most cases the reticulum is sharply defined and raised, so that the ornamentation of the exine falls into the "OL" pattern of Erdtman (1952: 22), i.e., the spaces between the walls (muri) of the reticulum are dark at the outermost focus and bright at the inner focus. In the grains of many species of *Phyllanthus* the reticulum is so fine that it can scarcely be resolved even under oil immersion. The exine is provided with three longitudinal furrows (colpi) which usually have median round or elliptic germ-pores (ora). Both Erdtman and Faegri and Iversen have applied the term "tricolporate" to grains of this type.

Tricolporate pollen grains are characteristic of the presumably primitive petaliferous genera of Phyllanthaceae such as *Andrachne* and *Savia*, and of the apetalous genera more closely related to *Phyllanthus* such as *Securigena* and *Flueggea*. In *Phyllanthus* such grains occur in a number of groups, including sects. *Paraphyllanthus* and *Phyllanthus* (PLATE-FIG. 35). In several species, including those of sects. *Loxopodium*, *Urinaria*, and part of sect. *Phyllanthus*, the microspore is very similar except that there are four colpi instead of three. *Phyllanthus niruri* (PLATE-FIG. 34) has unusually large prolate grains which (like some other species of sect. *Phyllanthus*) have a "heterobrochate" exine, the reticulum being much coarser midway between the colpi than along their margins. In most species, however, there is no such striking difference in the fineness of different parts of the reticulum.

The majority of the species native to the West Indies have a type of pollen grain very different from that just discussed. It was illustrated by Erdtman (1952: fig. 97a) and described by him as "synrugoidorate," i.e., "provided with rugoid streaks surrounding angular (usually 5-angular) areoles." In the present work these grains will be referred to as "areolate" (PLATE-FIGS. 41 & 42). All such grains are spherical and quite similar in ornamentation, differing mainly in size and in the number of areoles. At each corner of the areole, where three furrows come together, is a circular germ-pore. There is a distinct and continuous exinous ridge which bounds the perimeter of the areole and at the same time defines the edge of the furrow; it is formed by the amalgamation of the minute club-shaped sculptural elements of the exine ("pila" of Erdtman, "clavae" of Faegri and Iversen). Within the areole, the clavae form a reticulum which is very much like that of ordinary colporate grains.

Areolate pollen grains of the kind just described are known only from New World species of *Phyllanthus*. However, areolate grains that superficially are very similar occur in the Old World species of sect. *Macraea*; Erdtman, in fact, noted no essential difference between the grain of the West Indian *P. mimosoides* and the Hawaiian *P. sandwicensis* [= *P. distichus*]. But close examination shows that in the latter the ora are located midway between the angles of the areoles and thus in the middle of one furrow rather than at the intersection of three of them (PLATE-FIG. 43). A similar kind of pollen grain occurs in the Indo-Chinese species *P. ruber*, whose affinities are rather doubtful. From various lines of evidence it is clear that the Old World species with areolate grains are not closely related to the New World species; apparently the areolate ornamentation has evolved quite independently in the two groups.

A third kind of areolate microspore occurs in the West Indian sect. *Cyclanthera*. It resembles the other two except for the fact that the reticulum within the areole is reduced to a single brochus. The areole therefore appears to have a median pore (or plug, depending on the plane of focus) and may be referred to as "foveolate" (PLATE-FIG. 40). It is evident from various considerations that sect. *Cyclanthera* is derived from

sect. *Callitrichoides*, and that its foveolate grain must be derived from the grain of the latter, which has ribbon-shaped areoles that give the exine a striate appearance (PLATE-FIG. 39). It is at present impossible to be sure if the "banded" grain of sect. *Callitrichoides* is derived from the areolate grain of other West Indian species. It might have evolved independently; but the relationships of sects. *Cyclanthera* and *Callitrichoides* are too obscure to decide the matter.

There are a number of other kinds of pollen in *Phyllanthus* which fall into neither the areolate nor the ordinary colporate type. In sect. *Nothoclema*, for instance, the colpi are greatly shortened to dumbbell-shaped furrows with a germ-pore at each end, and the exine is markedly echinulose ("pilate" in Erdtman's terminology) (PLATE-FIG. 36). The spherical grain of the introduced *P. pulcher* (sect. *Eriococcus*) has no evident furrows, or areoles, and the reticulum is broken only by equidistantly placed pores (PLATE-FIG. 44).

The diversity of pollen types in *Phyllanthus* is thus so great that it becomes difficult to interpret the possible evolutionary relationships between the different kinds. Erdtman has designated as "breynioid" the pollen occurring in the "subtribes" Glochidiinae, Phyllanthinae, and Sauropodiinae. As found in *Breynia* the pollen grain is more or less oblate with several (7 to 10) furrows, each having two ora, and a prominent reticulum set off from the furrow by a definite border. Well-marked breynioid grains have been observed in *Phyllanthus* only in the South American species of sect. *Microglochidion* (PLATE-FIG. 38). However, there is no sharp dividing line between breynioid and ordinary tricolporate grains; in *Glochidion*, for instance, the few species investigated have four-colporate grains which hardly differ from those of many species of *Phyllanthus*.

Erdtman (op. cit. 174) has attempted to relate the breynioid grains of *Breynia* and *Sauropus* to the 4-colporate grains of *Glochidion* on the one hand and to the "synrugoidorate" grains of *Phyllanthus* on the other. This idea has been confirmed, in a general way, in the present study. In sect. *Anisonema* (e.g., *P. reticulatus*) and several Old World groups, the microspore has three colpi which are conspicuously margined and confluent at the poles. If the number of colpi should be increased to five or six and their intersection at the poles be precluded by spatial conditions, the colpi might terminate instead at the margins of the two polar areoles thus formed. The result might be a pollen grain with relatively few large areoles, such as that of *P. subcarnosus* (PLATE-FIG. 41). Further specialization might lead on the one hand, by multiplication of the number of areoles, to the "poly-areolate" grains of many West Indian species, and on the other hand, by suppression of the furrows, to the porate grains of sect. *Eriococcus*. The areolate grain is thus nothing more than a breynioid grain with lateral connections at the ends of the furrows.

Erdtman's suggestions as to the morphological relationships of the pollen grains within the Phyllanthinae thus appear to be sound; but his speculations as to the origin of the "crotonoid" grain are less fortunate. He suggests that the polygonal pattern underlying the "crotonoid" ornamentation

of the grains of *Suregada zanzibarensis* indicates derivation from phyllanthoid pollen. According to this view, the grain of *Suregada* represents a transitional stage between that of *Phyllanthus* and that of *Croton* or *Jatropha*. It is very hazardous, however, to attempt to relate the microspores of genera as far removed as *Phyllanthus* and *Croton*; there is scarcely the slightest possibility that the latter genus is descended from the Phyllanthinae. It appears far more likely that crotonoid pollen grains have been derived from tricolporate types within the Crotonoideae. It is plain from the results of the present study that since very different pollen types may exist within closely related groups, comparisons between widely separated genera in a family such as the Euphorbiaceae are very liable to be unsafe.

Gynoecium.

The majority of the species of *Phyllanthus* have the typical euphorbiaceous gynoecium of three united carpels, and in common with all the Phyllanthoideae have a pair of collateral ovules in each locule of the ovary. In a few species, none of them native to the New World, the number of carpels is higher. The commonly cultivated *P. acidus* has a variable carpel number, fruits with three and with four locules being almost equally common. In sect. *Anisonema* the number fluctuates from three to ten, and Mueller (1866: 344) reported up to twelve locules in *P. reticulatus* (PLATE-FIG. 47). Otherwise, gynoecia with more than three carpels have been reported only in *P. ruber* (sect. *Nymphanthus*) and *P. buxifolius* (sect. *Scepasma*). It seems significant that the greatest variability in carpel number is concentrated in the single section *Anisonema*. Since the flowers in this section are otherwise basically pentamerous, it appears that in sect. *Anisonema* and groups derived from it evolution has proceeded from a five-carpellate gynoecium by reduction to three, and by multiplication to several carpels. Michaelis (1924: 120) recognized that the gynoecium has undergone both multiplication (e.g., *Hura*) and reduction (e.g., *Antidesma*) in sporophyll number, whereas he found no evidence of multiplication of sporophylls in the androecium.

During the preparation of the present study, a number of difficulties in the terminology of the gynoecium have been encountered; these are mostly due to the conflicting definitions in the literature. Hanf (1934) has proposed a new classification of terms which contains some drastic changes of concept; his system has been explained in translation by Just (1939). According to Hanf's view, each carpel of the angiospermous flower is terminated by a *stylodium*; the term "style" is restricted to apply to the elongated portion of a "coenocarpous" ovary (i.e., one with united carpels). The application of this concept gives the corollary that a single flower can have no more than one style; and in such families as the Ranunculaceae and Caryophyllaceae styles are considered to be absent, flowers of these groups having stylodia only.

Hanf's study of styler morphology has the great merit of clarifying the relationships between various styler apparatuses that have become ob-

scured through careless use of terms. However, his definitions are directly contradictory to those current in most systematic works. It seems worth while, therefore, to examine the propriety of adopting such a radically different terminology.

The word "stylodium" was apparently coined by Grisebach in his textbook "Grundriss der systematischen Botanik" (1854). His discussion (in translation) is as follows:

"The boundary between style and stigma is actually established morphologically by the stylar canal, but the designation style and style-arm (rami styli) is applied in systematics to all cylindrical carpel apices, and the [term] stigma is restricted to the glandular part of them. It is therefore appropriate to distinguish the style-like stigmas as stylodes (stylodium) from the true stigmas which are physiologically characterized by their reaction to the pollen grains. According to this definition, for example, the monocarpic pistil of the grasses has one style, two stylodia, and [two] stigmas."

Grisebach (op. cit.) described the gynoeceum of *Euphorbia* as having "stylo tripartito, stylodiis bifidis." In his description of *Cicca antillana* (1857) he still used the term stylodium, but by 1859, in the "Flora of the British West Indian Islands," he had abandoned it. Since the term has not been recently used in systematic literature, the force of custom and usage would appear to weigh against its adoption unless there should be compelling reasons for doing so.

It must be admitted that the word "style" has not always been used with precision. Gray ("Structural Botany," 1879) defined it as the "usually attenuated portion of a pistil or carpel between the ovary and stigma." In the sense of Gray, therefore, the word is a topographical designation and does not imply specific morphological value. The definition given by Fernald (1950): "the usually attenuated portion of the pistil connecting the stigma and ovary" breaks down when applied to a gynoeceum with united carpels but free styles.

Baillon (1858) held a similar concept during his studies on the Euphorbiaceae, for he described the stigma-bearing structures in terms of the style and its branches. Mueller Argoviensis, in his work for the "Prodromus," at first (1863) described the style of the Euphorbiaceae as ". . . varius, saepius brevius et in tot ramos divisus quot loculi ovarii." But in his generic description of *Phyllanthus* in the finished monograph (1866) he stated: ". . . styli loculis ovariorum isomeri." Mueller thus came to regard the style as the prolongation of the individual carpel rather than of the entire pistil, as he had at first. Pax and Hoffmann (1931) followed the same concept in describing the styles of the Euphorbiaceae as "frei oder verwachsen, wenn frei, dann meist 2-, seltener vielspaltig."

It appears that at least in the Euphorbiaceae the usage of Mueller is perfectly clear and accurate. The style may be defined as the attenuate portion of the carpel (not the pistil) between the ovary and stigma. When the styles are united, as they often are in the Euphorbiaceae, the compound structure may be termed the *stylar column*. The result of this

definition is that the stylar column, not the style, of *Phyllanthus* is the morphological equivalent of the style of the Labiatae. Any possible confusion may be obviated, however, by qualifying the latter organ as the "compound style."

The styles of *Phyllanthus* exhibit a remarkable latitude of variation in form, but they may be classified roughly into two types which become distinct at an early stage of development in the bud. In all species investigated the carpel at first is cupuliform with a horseshoe-shaped margin. In one case the adaxial portion of the rim early takes on the form of a "Y" and the carpel apex (i.e., the style) grows out more or less bifid. In the other case the rim retains its original shape longer, and the style is either entire or dilated into an adaxially channelled crenulate or lacerate expansion, the stigma. Since the stigma is not always well-defined, particularly in styles of the first type where the stigmatic surface is discontinuous, the *style-branch* is often the most convenient term.

The great variations in the mature stylar apparatus in different species are the result of the interactions of three growth processes: (1) the differentiation of the embryonic carpel apex into "bifid" or "entire" styles; (2) the relative amount of longitudinal vs. transverse growth; and (3) the degree of union between the styles. Many different recombinations of these three processes occur. The styles may be completely united into a column as in *P. ovatus* (sect. *Hemiphyllanthus*) or almost completely free as in sect. *Paraphyllanthus*; the stigmas may be scarcely defined in many species with slender bifid styles, or greatly dilated to form a calyptra as in *P. mirificus*. In species with dilated style-tips, the original adaxial margins of the hippocrepiform embryonic carpel are represented by a pair of adaxial auricles. Usually these are small and sometimes even obsolete, but in some species (e.g., *P. excisus*) they may be quite prominent. In a general way the auricles mark the point at which the stylar column ends (when the styles are connate) and the stigmatic surface begins. Below the auricles the stigmatic tissue is usually embedded in the center of the style or stylar column and is represented externally only by a slender adaxial suture. Internally, the loose conducting tissue of each style becomes confluent at the point where the tops of the ovarian parts of the three carpels are fused. In most species of *Phyllanthus* a prolongation of this tissue runs into the top of each locule and forms a cap-like structure, the *obturator*, which is closely appressed to the micropylar ends of the ovules (PLATE-FIGS. 48 & 49). Baillon (1858), who first applied the name obturator to this prolongation of the stylar tissue, recognized within the present limits of *Phyllanthus* two types of obturators: a single one over both ovules of a locule in *P. salviaefolius* (sect. *Oxalystylis*) and an obturator for each ovule in "*P. grandiflorus*" (identity uncertain). Examination of material in the present study has disclosed in every case a common obturator for both ovules, but its relative development and orientation appear to vary a good deal from species to species. It conspicuously overtops the ovules in *P. subcarnosus* but is nearly vertical in *P. polygonoides* (PLATE-FIG. 49). Unlike *Ricinus*, in which Baillon

reported traces of the obturator in the mature seed, the organ is transient in *Phyllanthus* and atrophies during maturation of the fruit.

The vascular supply of the carpel is quite similar in most of the species of sect. *Phyllanthus* investigated, but needs to be studied in other groups. At the base of the ovary the carpellar bundle divides into one dorsal and two ventral traces. The dorsal trace ramifies into a reticulum on the dorsal surface of the carpel, while the two ventral traces run vertically. The latter first give off the ovular traces and then abruptly bend abaxially and run obliquely across the lateral face of the carpel to join the dorsal reticulum near the base of the stylar column. The resulting compound bundle then enters the stylar column and bifurcates, each branch forking or remaining unbranched, depending on the character of the style-tips. The point at which the ventral traces leave the axis of the ovary and bend outwards is well-marked by a sharp discontinuity in the tissue, and the upper third of the axis is without vascular supply. The courses taken by the vascular bundles determine to a great extent the configurations of the carpels in the dehisced fruit. The portion of the axis beneath the "bending-point" of the ventral traces becomes the *columella*, which remains after dehiscence of the fruit as a column projecting from the center of the calyx. The obliquely ascending ventral traces on the lateral faces of the carpels determine the upper line of dehiscence of the cocci, which split on the lateral faces along lines curving away from the ventral traces.

Baillon (1858: 139-140), partly on the basis of his ontogenetic studies, considered the ovules of the Euphorbiaceae to be borne by the axis. From a merely topographic point of view it is correct to say the ovules are "axile," but this need not imply that they are inserted on a structure of "stem" or "branch" nature. The columella, which looks so much like a prolongation of the torus, has no vascular supply independent of the ventral traces, and its extent is exactly determined by the distance these travel vertically before turning outward. The columella is therefore a compound structure derived from the basal parts of the fused ventral margins of the carpels, and is morphologically equivalent to the central placental column of the Caryophyllaceae of the "free-central" placenta of the Primulaceae. There is no evidence to support the assertion of Lam (1948) that the Euphorbiaceae are a "stachyosporous" family (i.e., with sporangia borne on modified branches); the gynoecium of *Phyllanthus* is not fundamentally different from that of families admitted by Lam to be "phylloporous."

In *Phyllanthus* each locule of the ovary contains a pair of usually collateral anatropous pendent ovules. The funicle of the ovule is sharply deflected downward from the top of the columellar part of the axis (i.e., about one-third of the way down from the top of the locule), and the hilum is on the side of the ovule toward the center of the ovary. The ovule is more or less barrel-shaped with two integuments, the outer of two cell-layers, the inner of three. The nucellus in all species examined is at least slightly prolonged beyond the exostome of the micropyle as a more or less clavate beak which fills up the space between the micropyle and

the obturator (PLATE-FIG. 49). In species with a relatively massive obturator such as *P. subcarnosus* the nucellar beak, though well-developed, does not project very far beyond the micropyle, but where the obturator is short the tip of the nucellus may be strikingly elongated. In all observed cases there is an intimate contact between obturator and nucellus. The embryo sac, according to Maheshwari and Chowdry (1937), is the normal eight-nucleate type.

Baillon (1858: 613) pointed out that in sect. *Anisonema* the ovules, thought at first collateral, later become obliquely superposed as in *Glochidion*. This change of ovular position is probably due to spatial conditions, since the large number of locules results in a diminished average volume of each one (PLATE-FIG. 47). In all of the three-carpellate gynoecia examined, the ovules are collateral without exception.

Fruit.

In the great majority of the species of *Phyllanthus* the fruit is a dry thin-walled capsule which often dehisces explosively at maturity. The wall of the fruit is ordinarily composed of two distinct layers which are distinguishable from a rather early stage of the ovary (PLATE-FIGS. 48 & 49). The exocarp, which contains all the vascular supply, is usually thin, scarious, and greenish or reddish at maturity of the fruit; it covers only the outer tangential (abaxial) wall of each coccus. The yellowish endocarp, which lacks vascularization, has a heavily sclerified thick dorsal (tangential) wall and much thinner lateral (radial) walls (PLATE-FIG. 50). When the capsule dehisces, the carpels (now cocci) first separate from one another and from the columella; then the lateral walls split open along an arc as described previously. Often the endocarp also splits vertically along the middle of the dorsal valve, so that the coccus has the form of an irregularly four-valved box loosely enclosing the pair of seeds.

There are a number of species, however, in which the exocarp of the fruit remains fleshy until rather late in ontogeny (e.g., *P. juglandifolius*). In others the exocarp never dries up, and the fruit is either baccate or drupaceous, depending on the degree of sclerification of the endocarp. In *P. reticulatus* (sect. *Anisonema*), which has a baccate fruit, the endocarp is not only tenuous but is not clearly differentiated from the exocarp (PLATE-FIG. 47). In *P. emblica* the ripe fruit is drupe-like with a fleshy exocarp and bony endocarp, but when the fruit eventually dries up the endocarp separates into three massive cocci. The fruit of *P. elsiae* is at first fleshy but on drying the exocarp becomes pithy, while the endocarp is sclerified but thin. In the related *P. acidus* the massive endocarp is bony and indehiscent while the exocarp remains fleshy, so that in this species the fruit is a true drupe with a three- or four-celled putamen. Mueller's description (1886: 413) of the fruit of sect. *Cicca* as capsule-like with two-valved cocci was due to his mistaken inclusion of the very different genus *Margaritaria* in the same section with *Cicca*.

In a general way the type of fruit (i.e., whether dry, baccate, or drupaceous) is definitely related to the habit of particular species. The her-

baceous annual species all have an explosively dehiscent capsule which falls away from a persistent calyx. The shrubby species tend to have a more tardily dehiscent capsule which may fall with the pedicel and columella still attached, and in *P. reticulatus* and *P. subcarnosus* the fruit is fleshy. Finally, in *P. acidus*, *P. elsiae*, and *P. emblica*, all of which are trees, the fruit is drupaceous or "woody." This unmistakable correlation between relative explosiveness of fruit and life-span of plant nicely illustrates adaptation in dispersal capacity which must have a basis in natural selection. It also indicates that fleshiness of fruit *per se* may not always be a reliable mark of affinity, and is consequently of little value as a generic character.

Seed.

Usually there is a pair of seeds in each cell of the fruit of *Phyllanthus*, each of which has a trigonous outline due to compression against one another and the locule walls. Sometimes, however, only one of the seeds will attain full size, and the other will be under-developed. In sect. *Cicca* the relative development of the pair of seeds is most variable, for there may be either two equal seeds, one large and one small, or one large one only; and locules in which these three types occur may be found in a single fruit. In *P. emblica* the seeds of a pair are unequal, but both appear viable. Swartz (1800) characterized the seeds in the fruits of the West Indian sect. *Epistylum* as "subsolitaria"; this may be correct, but in the other native West Indian species there are nearly always two equal seeds in each locule. The tendency towards abortion of one of the ovules, which is also noticeable in the genus *Savia*, indicates the existence of a reduction trend toward the uniovulate condition of the Crotonoideae. However, in all of the Phyllantheae so far investigated the suppression of the second ovule takes place late in ontogeny, probably after anthesis; even though a locule of the mature fruit may have only one seed, examination of the ovary at an early stage has always shown two ovules in each cell.

The development of the seed-coat from the integuments appears to be somewhat variable and requires further investigation. The epidermal layer of the outer integument usually becomes variously modified during maturation of the seed; the resulting diversity in ornamentation of the testa provides convenient taxonomic characters for recognizing or distinguishing many species. Only rarely is the seed-coat quite smooth and uniformly colored as it is in *P. hyssopifolius* (PLATE-FIG. 57). In *P. juglandifolius* the seed-coat, although smooth, has a mottled appearance somewhat like that of *Ricinus* (PLATE-FIG. 64). Many different species have the seed-coat covered with raised dots, or points, which may be regularly or irregularly arranged; seeds of this type may be termed verruculose (PLATE-FIGS. 51, 52, 59). A great number of other species have seeds which though nearly smooth are seen under a lens to be covered with fine lines or ridges, on close inspection. Often the epidermal cells, which usually have their long axes transverse to the long axis of the seed, are so translucent that the cells of the subepidermal layer (which run

parallel to the long axis) show through. This gives the effect of longitudinal striae crossed by very fine striolae (PLATE-FIG. 55). In some of the herbaceous species of sect. *Phyllanthus* the seed-coat is very highly specialized. When the seeds of *P. junceus*, *P. echinospermus*, or related species, are placed in water they change from finely ridged or striate to "hispid" in appearance. Microscopic examination shows that this reaction is due to peculiar hygroscopic epidermal cells which are heteropolar: one end has conspicuously uneven wall-thickenings which give the lumen a scalloped outline, while the other is smoothly and less massively thickened. Slightly excentric toward the "smooth" end is a median peg of cellulose which runs through the lumen between the tangential walls. When the seed is wetted the longer unevenly thickened cell-ends swell out on the adaxial side and assume the form of concave arcs, while the shorter ends remain appressed to the surface of the seed; the projecting ends thus give the appearance of trichomes projecting from the seed-coat. This behavior presumably allows greater penetration of water into the seed-coat and consequently earlier germination of the seed. Such an adaptation, combined with the explosively dehiscent capsule, affords these herbaceous species a highly efficient mechanism for rapid dispersal and ecesis.

The seed of *P. urinaria* has a curious and unique kind of seed ornamentation (PLATE-FIGS. 53 and 54). The seed-coat is not only provided with sharp transverse ridges, but it has in addition deep pits on the sides; this combination of characters makes the seeds of *P. urinaria* unmistakable among those of the West Indian species. The deep pits on the radial walls perhaps represent a different sort of adaptation for permitting rapid penetration of water and faster germination.

In *P. orbicularis* developmental study has clearly shown that the heavily sclerified "palisade" layer of the seed-coat is developed from the outer layer of the inner integument (PLATE-FIG. 50); it is this layer which imparts to the seed most of its mechanical strength. In *P. orbicularis*, the middle layer of the inner integument is very inconspicuous in the seed, but the inner layer, though not enlarged, stands out because the cells are all filled with tannin. It will be noted that in this species, the two layers of the outer integument are relatively unimportant and not noticeably specialized. Too few species have been studied to know if the ontogeny of the seed is similar in every species; it is possible that in some species the sclerified layer is derived from the inner layer of the outer integument, but this remains to be demonstrated.

The mature embryo, which is embedded in rather copious whitish cartilaginous endosperm, ordinarily has a slender terete radicle and broad foliaceous cotyledons (e.g., in *P. juglandifolius*). In some of the herbaceous species (e.g., *P. amarus*), however, the cotyledons are narrowly oblong and only slightly broader than the radicle. Sometimes the embryo is slightly curved; Gaertner (1791: 125, pl. 108) described and illustrated the seed of *P. maderaspatensis* as having a "subspiral" embryo. Gaertner (op. cit. 127, pl. 109) clearly distinguished *Glochidion* on the basis of its very distinctive seeds, in which the seed-coat is fleshy and the hilar cavity

so enormously enlarged that the embryo is deformed; unfortunately, he chose to describe the genus under Banks' manuscript name *Bradleja*. This seed character, so clearly pointed out by Gaertner, is one of the best features for distinguishing *Glochidion*. Unfortunately, it has been passed over in recent years, with the result that the boundary between *Glochidion* and *Phyllanthus* has appeared weaker than it actually is.

CYTOLOGY

The cytology of *Phyllanthus* remains one of the poorest known areas of the morphology of the genus. Perry (1943), in the only previous specific contribution to the cytology of the Phyllanthaceae, found a diploid number of 28 in *P. caroliniensis* and *P. emblica*; he suggested that the basic number is 7 and that these species are therefore tetraploids. On the basis of his finding a diploid number of 56 in *Breynia*, he concluded that the latter is closer to *Phyllanthus* than one would judge from the treatment of Pax and Hoffmann (1931); evidence from other fields tends to support his statement. On the other hand Perry observed a diploid number of 16 in *Securinega obovata* [= *Flueggea virosa*]. This apparent difference in base-number indicates that further investigations in the Phyllanthaceae should produce interesting data for purposes of determining evolutionary relationships.

The only additional species whose chromosome number has been investigated is *P. juglandifolius* (sect. *Asterandra*), root-tip preparations of which were made by Dr. E. G. Voss from material in the University of Michigan Botanical Gardens. The diploid number as seen in root-tip smears of this species is approximately 160; the number is so large that both of us could agree only that it lies between $20n$ and $24n$ (assuming 7 as the basic number), and is probably closer to 168 than to 140. Although one can scarcely draw any far-reaching conclusions on the basis of the chromosome complement in only three species out of 650, the very high chromosome number in *P. juglandifolius* is quite suggestive. It indicates that amphidiploidy might have occurred repeatedly during the evolution of the West Indian species related to sect. *Asterandra*, and raises the possibility that the difficulty in determining relationships within the genus may be due to ancient hybridizations between rather widely separated species. Cytological examination of additional species from tropical America can hardly fail to throw considerable light on the difficult problem of intrageneric relationships. Unfortunately all efforts to germinate seeds of the shrubby species of sects. *Elutanthos*, *Williamia*, *Orbicularia*, and *Thamnocharis* have been unsuccessful. Collection of cytological specimens in the field may be the only means of successfully attacking the problem.

Perry has concluded from his data that "it appears that the direction of evolution in this family has been from the annual to the perennial condition, as was found for the Crassulaceae, Leguminosae, Ranunculaceae." Apparently he was impressed by the fact that some of the herbaceous species have lower chromosome numbers than the woody ones. However,

on the basis of morphological evidence other than chromosomes there is no doubt that at least in *Phyllanthus* the annuals are definitely derived from shrubby or suffruticose ancestors; and this is surely true of the Euphorbiaceae as a whole. The higher chromosome number of woody species is itself not a reliable indicator of primitiveness; Stebbins (1950) and others have shown that the arboreal habit tends to favor polyploidy during the course of evolution.

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(To be continued)

EXPLANATION OF PLATES *

PLATE I. GROWTH FORM.

FIG. 1. *Phyllanthus platylepis* Small (grown from seed of *Webster 3651*, Levy Co., Fla.).

FIG. 2. *Phyllanthus pachystylus* Urb. (*Webster 3906*, Moa region, Cuba), 1/10 natural size.

FIG. 3. *Phyllanthus tenellus* Roxb. (cult. Univ. of Michigan Bot. Gardens), 1/4 natural size.

FIG. 4. *Phyllanthus juglandifolius* Willd. (cult. Univ. of Michigan Bot. Gardens).

PLATE II. BRANCHLET ANATOMY. (× 50)

FIG. 5. *Phyllanthus reticulatus* Poir. (*Webster 5237*, Jamaica); cross-section of branchlet slightly above the node. At the bottom of the picture is the petiole and the two stipules. FIG. 6. Section through nodal region, showing trilacunar node with lateral stipular traces.

FIG. 7. *Phyllanthus maleolens* Urb. & Ekm. (*Holdridge 1381*, Haiti [MICH]); cross-section of branchlet through nodal region, showing trilacunar node with large stipular traces.

* Voucher specimens are deposited at both the University of Michigan and Harvard University herbaria, except where another herbarium is specifically indicated.

FIG. 8. *Phyllanthus williamoides* Griseb. (Webster 4014, Cuba); cross-section of branchlet.

PLATE III. STEM ANATOMY. ($\times 50$)

FIG. 9. *Phyllanthus botryanthus* Muell. Arg. (Harvard slide 2922, probably from Curran & Haman 164, Curaçao); cross-section of mature stem. FIG. 10. Tangential section.

FIG. 11. *Phyllanthus emblica* L. (Harvard slide 2120, Cuba); tangential section. FIG. 12. Radial section.

FIG. 13. *Phyllanthus pachystylus* Urb. (Webster 3906, Cuba); vessel elements.

PLATE IV. PHYLLOCLADES.

FIG. 14. *Phyllanthus* \times *elongatus* (Jacq.) Steud. (Webster s.n., cult. Harvard greenhouse); cross-section of penultimate axis, $\times 25$. FIG. 15. Cross-section of ultimate axis, $\times 40$. Both axes are still so young that the sclereids in the cortex are not yet hardened.

FIG. 16. *Phyllanthus epiphyllanthus* L. (Jervis 1368, Cuba); cross-section of phylloclade, taken from dried specimen, $\times 72$. The dark brown masses represent the compacted remains of the tannin-filled cortical parenchyma cells. Note the concentric bundles.

FIG. 17. *Phyllanthus montanus* Sw. (Webster 5637, Jamaica); cross-section near tip of phylloclade, $\times 72$. The structure on the right is a scale-leaf. Note that at this level palisade tissue is developed only on one side.

PLATE V. STOMATA ($\times 175$)

FIG. 18. *Phyllanthus microdictyus* Urb. (Webster 3809, Cuba); in this, and the following figures, the upper epidermis is shown on the left-hand side of the figure and the lower epidermis on the right-hand side.

FIG. 19. *Phyllanthus heliotropus* Wright ex Griseb. (Shafer 10708, Cuba [US]).

FIG. 20. *Phyllanthus selbyi* Br. & Wils. (Britton et al. 14157, Isle of Pines).

FIG. 21. *Phyllanthus niruri* L. (Britton et al. 6438, Puerto Rico [NY]).

PLATE VI. LEAF ANATOMY.

FIG. 22. *Phyllanthus scopulorum* (Britton) Urb. (Webster 3849, Cuba); cross-section of nearly mature leaf, from specimen preserved in FAA, $\times 40$.

FIG. 23. *Phyllanthus ekmanii* Webster (Jervis 3650, Cuba); cross-section of mature leaf, from dried specimen, $\times 35$.

FIG. 24. *Phyllanthus microdictyus* Urb. (Webster 3809, Cuba); cleared leaf-blade, $\times 85$.

FIG. 25. *Phyllanthus incrustatus* Urb. (Shafer 4453, Cuba [NY]); cleared leaf at focus just beneath upper epidermis, showing arrangement of sclereids. $\times 85$.

FIG. 26. *Phyllanthus comosus* Urb. (Webster 3883, Cuba); marginal area of cleared leaf, $\times 85$.

FIG. 27. *Phyllanthus formosus* Urb. (Shafer 4102, Cuba [NY]); marginal area of cleared leaf, $\times 85$.

PLATE VII. LEAF VENATION. ($\times 50$).

- FIG. 28. *Phyllanthus emblica* L. (Jack 4246, Cuba).
 FIG. 29. *Phyllanthus botryanthus* Muell. Arg. (Triana 3664, Colombia).
 FIG. 30. *Phyllanthus reticulatus* Poir. (Britton 4067, Jamaica [NY]).
 FIG. 31. *Phyllanthus chryseus* Howard (Webster 3853, Cuba).
 FIG. 32. *Phyllanthus scopulorum* (Britton) Urb. (Webster 3849, Cuba).
 FIG. 33. *Phyllanthus spathulifolius* Griseb. (Webster 3896, Cuba).

PLATE VIII. POLLEN GRAINS.*

- FIG. 34. *Phyllanthus niruri* L. (Ekman H16515, Hispaniola [S]).
 FIG. 35. *Phyllanthus trigonus* Urb. (Ekman H2792, Hispaniola [S]); polar view, outer focus.
 FIG. 36. *Phyllanthus acuminatus* Vahl (Wright 1938, Cuba [S]); more or less equatorial view, outer focus.
 FIG. 37. *Phyllanthus heliotropus* Wr. ex Griseb. (Ekman 10735, Cuba [S]).
 FIG. 38. *Phyllanthus vaciniifolius* (Muell. Arg.) Muell. Arg. (Sandwith 1315, Br. Guiana [S]).

PLATE IX. POLLEN GRAINS.

- FIG. 39. *Phyllanthus carnosulus* Muell. Arg. (Wright "714", Cuba [GOET]).
 FIG. 40. *Phyllanthus berterioanus* Muell. Arg. (Leonard 8826, Hispaniola [NY]); upper right-hand quadrant shows the appearance at outer focus.
 FIG. 41. *Phyllanthus subcarnosus* Wr. ex Muell. Arg. (Wright 1946, Cuba [S]); insert shows the appearance of the grooves at outer focus (i.e., very narrow).
 FIG. 42. *Phyllanthus maleolens* Urb. & Ekm. (Ekman H6849, Hispaniola [S]).
 FIG. 43. *Phyllanthus distichus* Hook. & Arn. (Degener 11645, Hawaiian Islands).
 FIG. 44. *Phyllanthus pulcher* Wall. ex Muell. Arg. (Broadway 5459, Trinidad [S]).

PLATE X. FLORAL ANATOMY.

- FIG. 45. *Phyllanthus chryseus* Howard (Webster 3853, Cuba); longitudinal section of male flower bud, $\times 30$.
 FIG. 46. *Phyllanthus reticulatus* Poir. (Webster 5237, Jamaica); longitudinal section of male flower, showing stomatal pits in disk, $\times 30$. FIG. 47. Cross-section of female flower, $\times 30$.
 FIG. 48. *Phyllanthus* \times *elongatus* (Jacq.) Steud. (Webster s.n., cult. Univ. of Michigan greenhouse); cross-section of ovary at the level of the obturators, $\times 45$.
 FIG. 49. *Phyllanthus polygonoides* Nutt. ex Spr. (Webster & Wilbur 2965, Texas); longitudinal section of ovary showing association of obturator and nucellar beak, $\times 100$.

* The drawings in plates VIII and IX are semi-diagrammatic and (except for figs. 35, 36, and 40) indicate the appearance of the exine at roughly the level of the base of the individual sculptural elements (muri or pilae). All drawings are on the scale of 1 cm. = 5.9 μ .

FIG. 50. *Phyllanthus orbicularis* HBK. (Webster 3867, Cuba); longitudinal section of immature fruit, $\times 100$. Above, ovary wall; in the center, two seeds showing the two cell-layers of the outer integument and the three of the inner.

PLATE XI. SEEDS.

FIG. 51. *Phyllanthus pudens* L. C. Wheeler (Bush 906, Texas [GH]); verruculose ornamentation, $\times 22$.

FIG. 52. Ventral and radial view, $\times 7$.

FIG. 53. *Phyllanthus urinaria* L. (Cory 49975, Texas [GH]); transversely barred ornamentation, $\times 45$.

FIG. 54. Ventral and radial view, $\times 14$.

FIG. 55. *Phyllanthus amarus* Schum. & Thon. (Small & Small 6818, Florida [GH]); finely (longitudinally) ribbed ornamentation, $\times 45$.

FIG. 56. Ventral and radial view, $\times 14$.

PLATE XII. SEEDS.

FIG. 57. *Phyllanthus hyssopifolius* HBK. (Ekman H15612, Hispaniola [S]), $\times 12$.

FIG. 58. *Phyllanthus emblica* L. (Jack 4246, Cuba [NY]), $\times 6$.

FIG. 59. *Phyllanthus niruri* L. (Parks 14595, Texas [GH]), $\times 12$.

FIG. 60. *Phyllanthus williamoides* Griseb. (Webster 4014, Cuba), $\times 6$.

FIG. 61. *Phyllanthus pachystylus* Urb. (Webster 3906, Cuba); mature carpel, or coccus, showing two seeds in position, $\times 6$. Note the crescent-shaped split in the radial walls of the carpel, and the separation of the two layers of the tangential wall. FIG. 62. Seeds, $\times 6$.

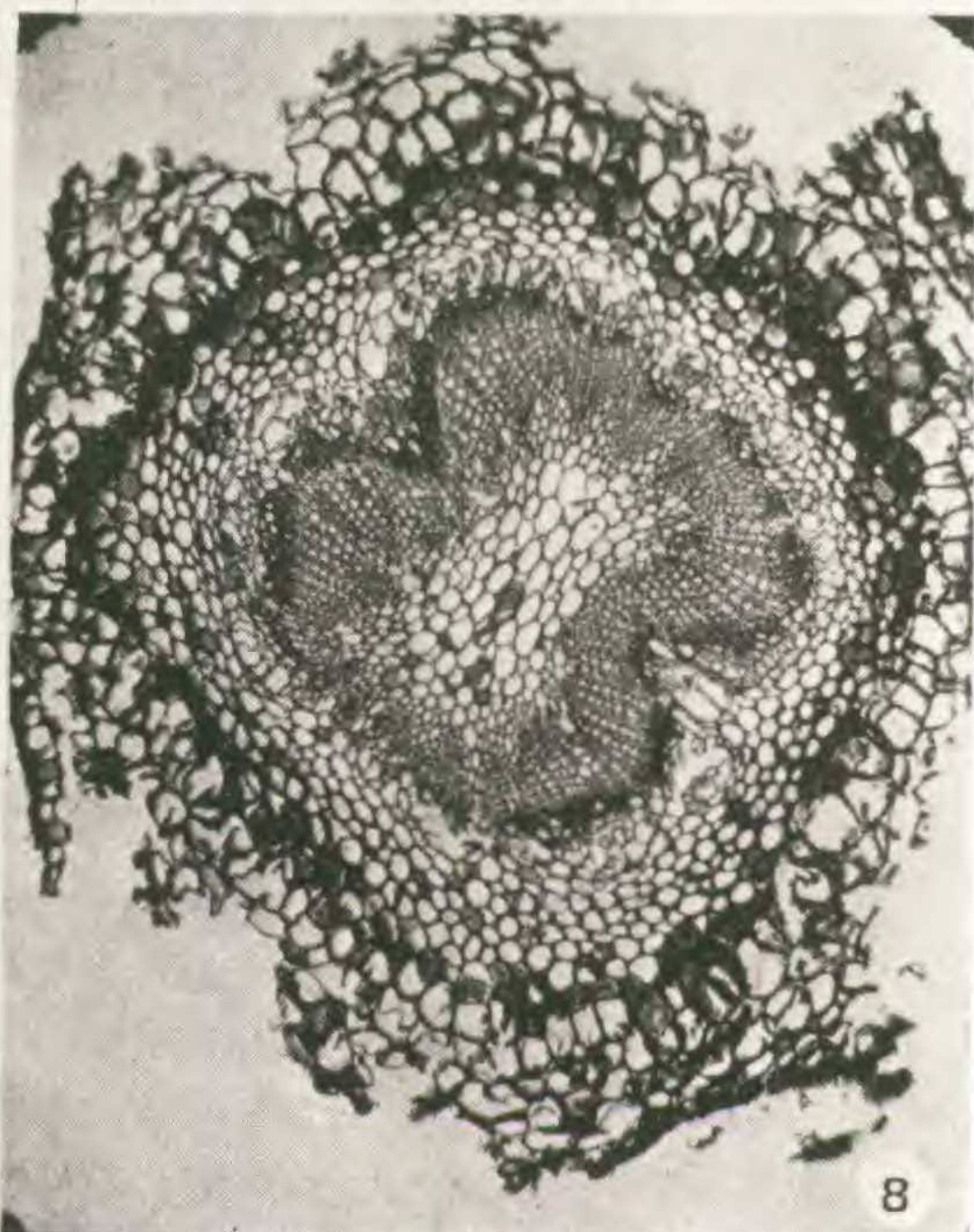
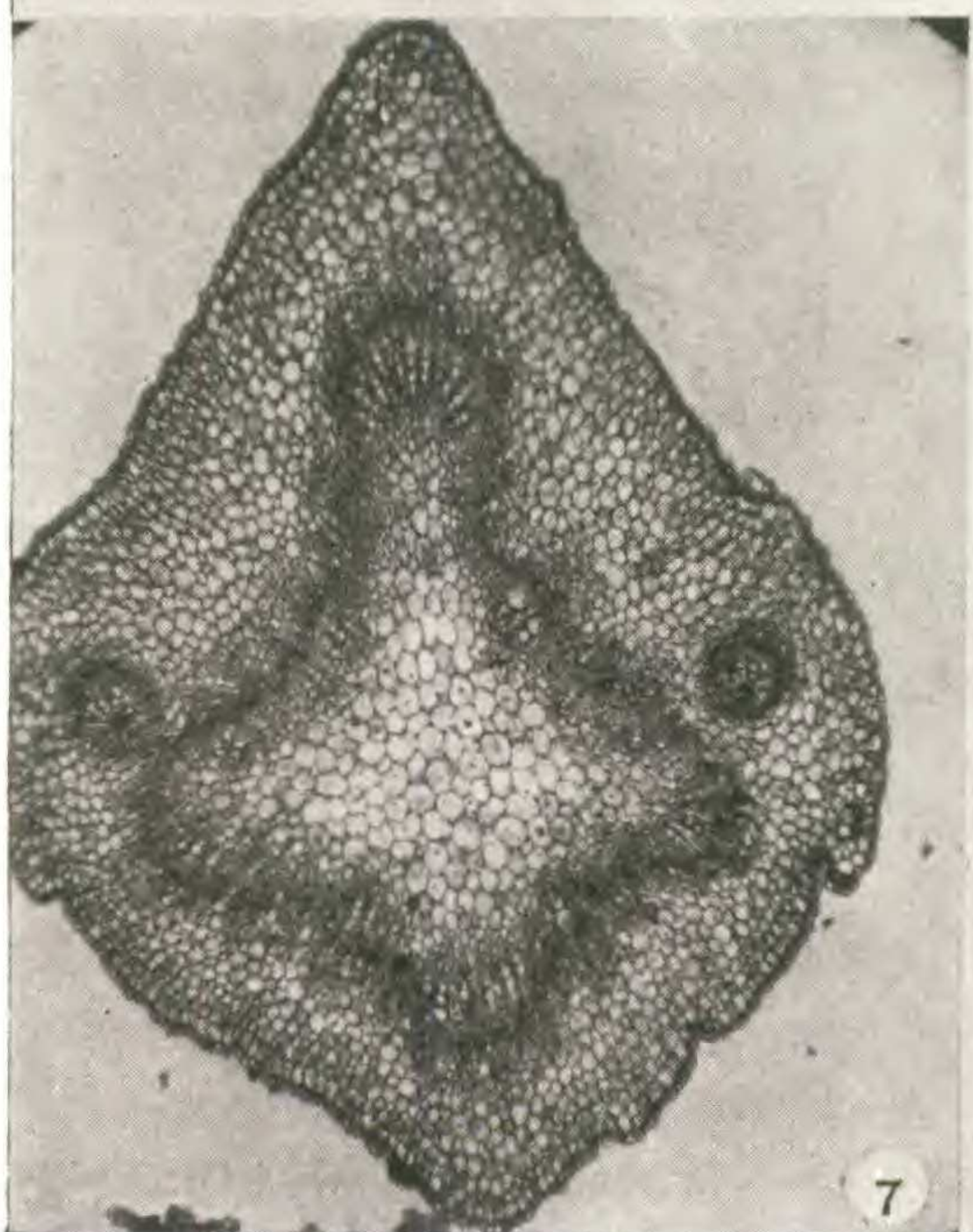
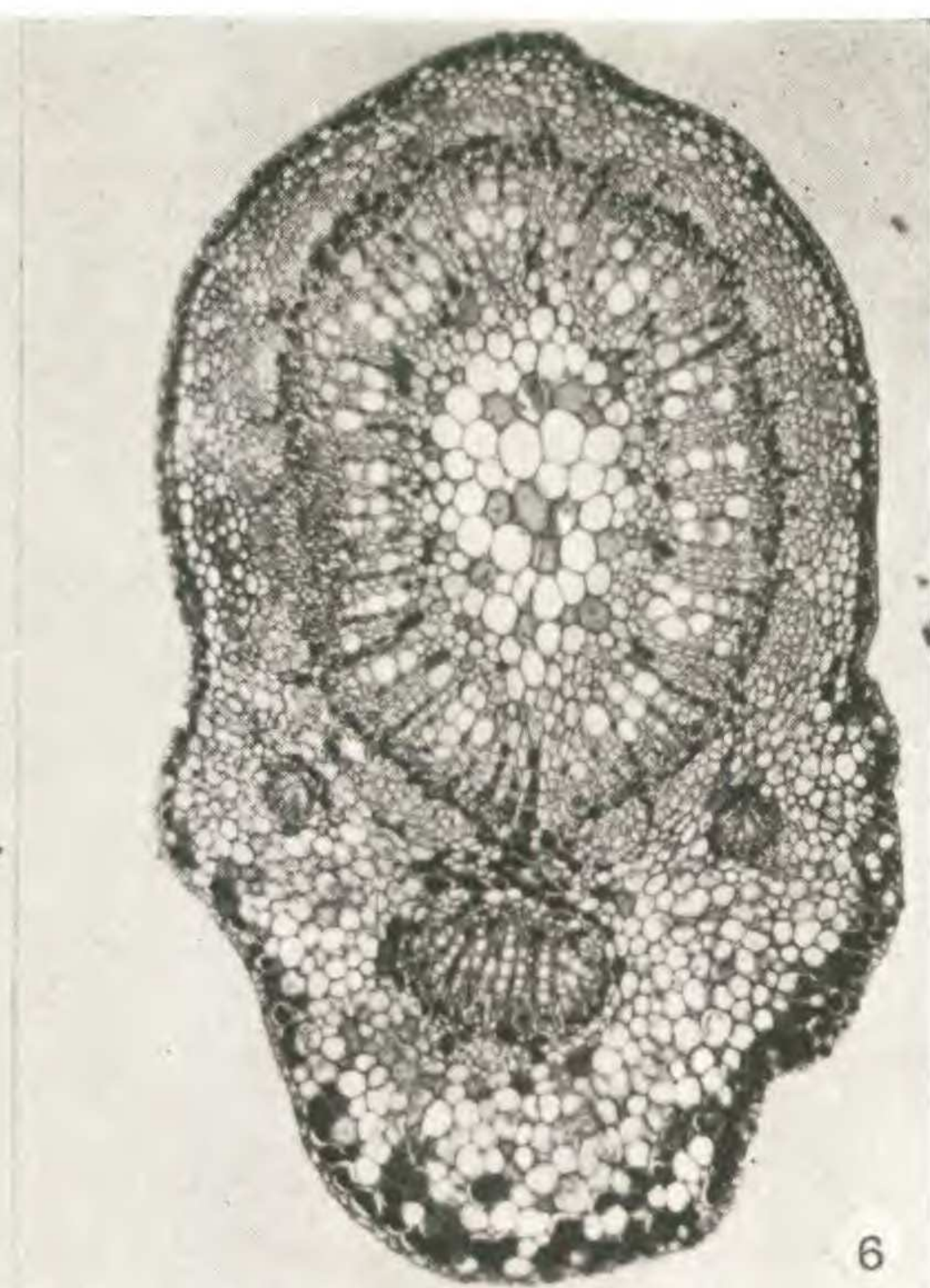
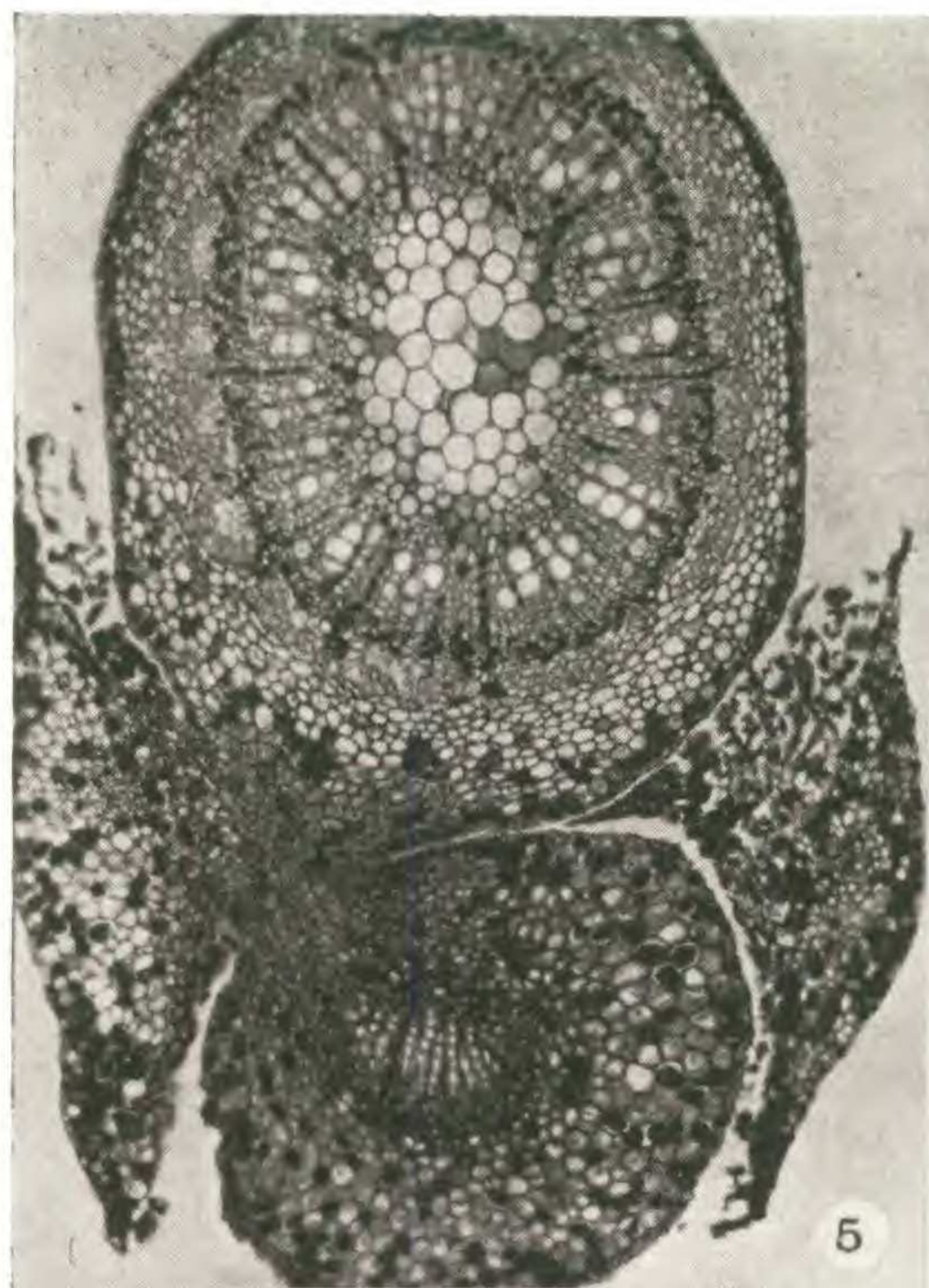
FIG. 63. *Phyllanthus nutans* Sw. (Britton 929, Jamaica [NY]), $\times 6$.

FIG. 64. *Phyllanthus juglandifolius* Willd. (Webster 4028, Cuba), $\times 6$.

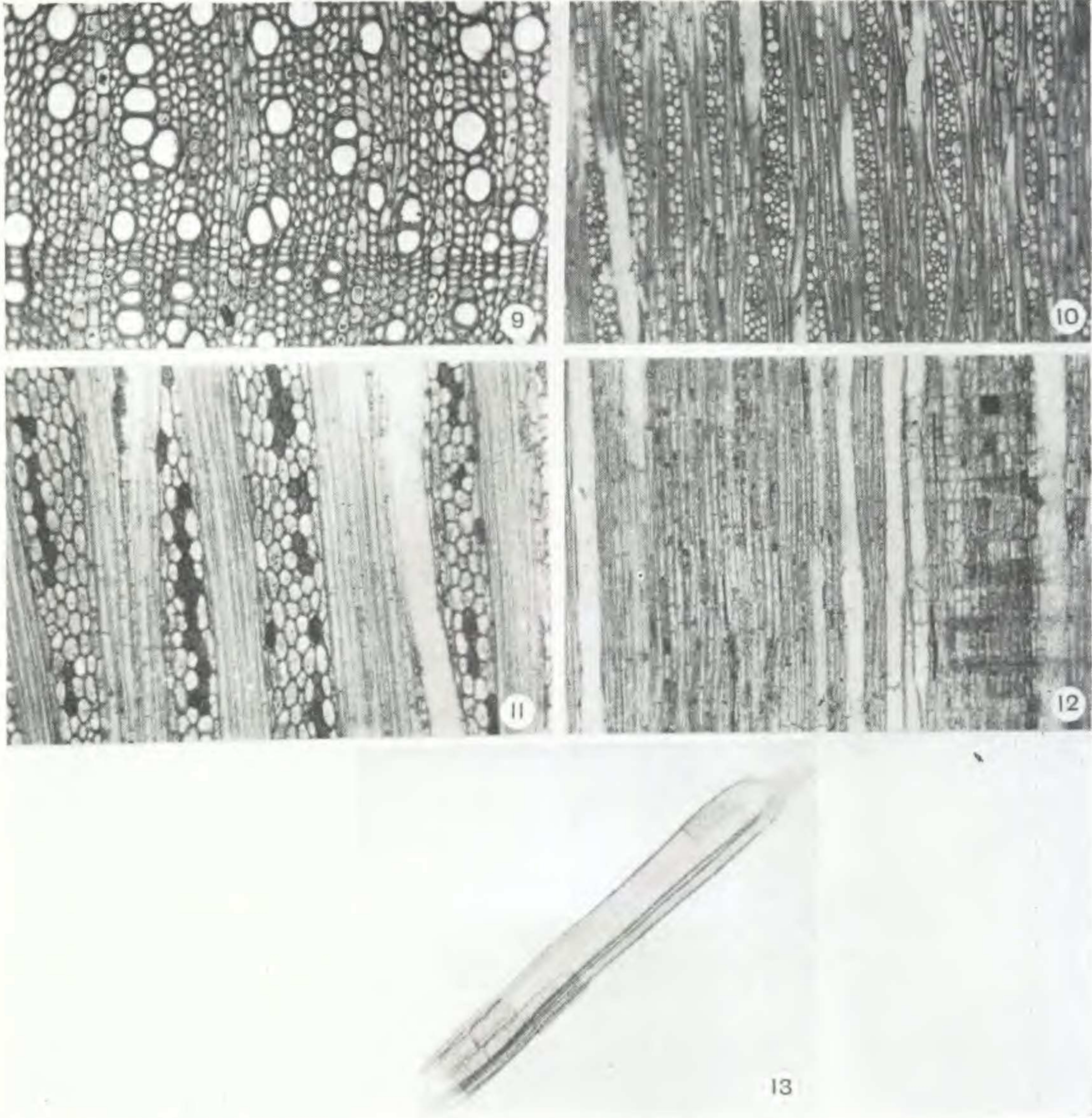
FIG. 65. *Phyllanthus ekmanii* Webster (Ekman 6206, Cuba [S]), $\times 6$.



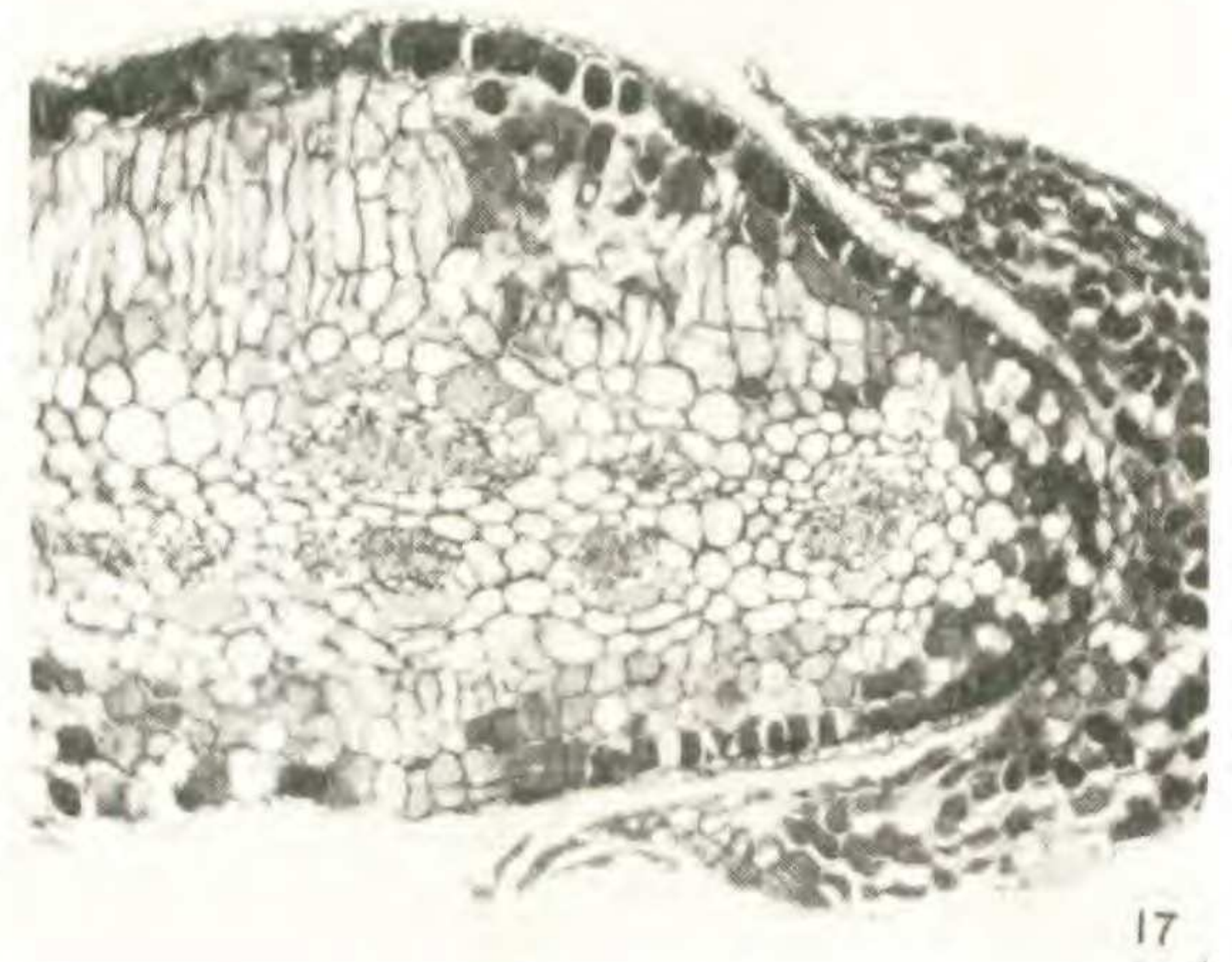
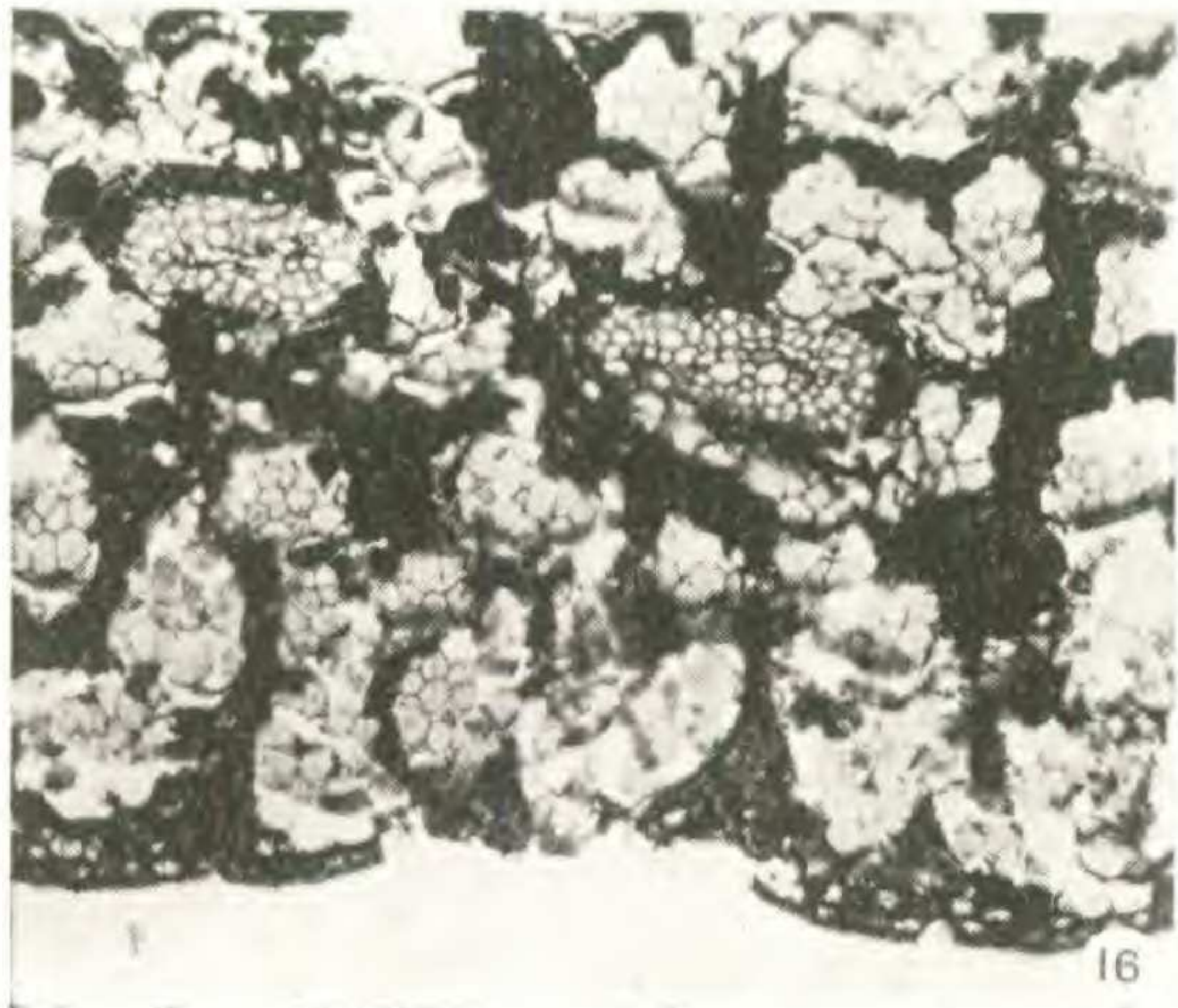
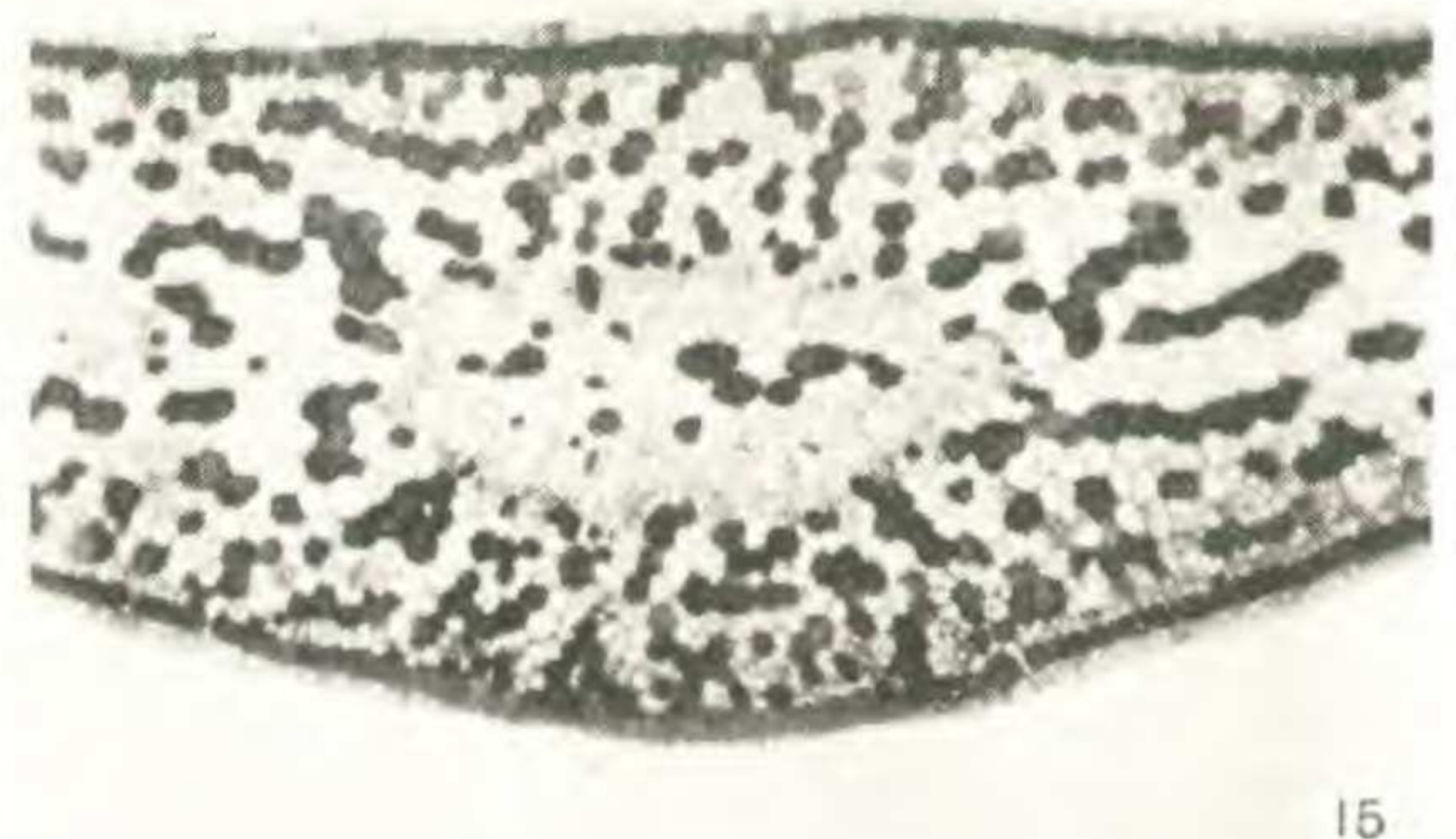
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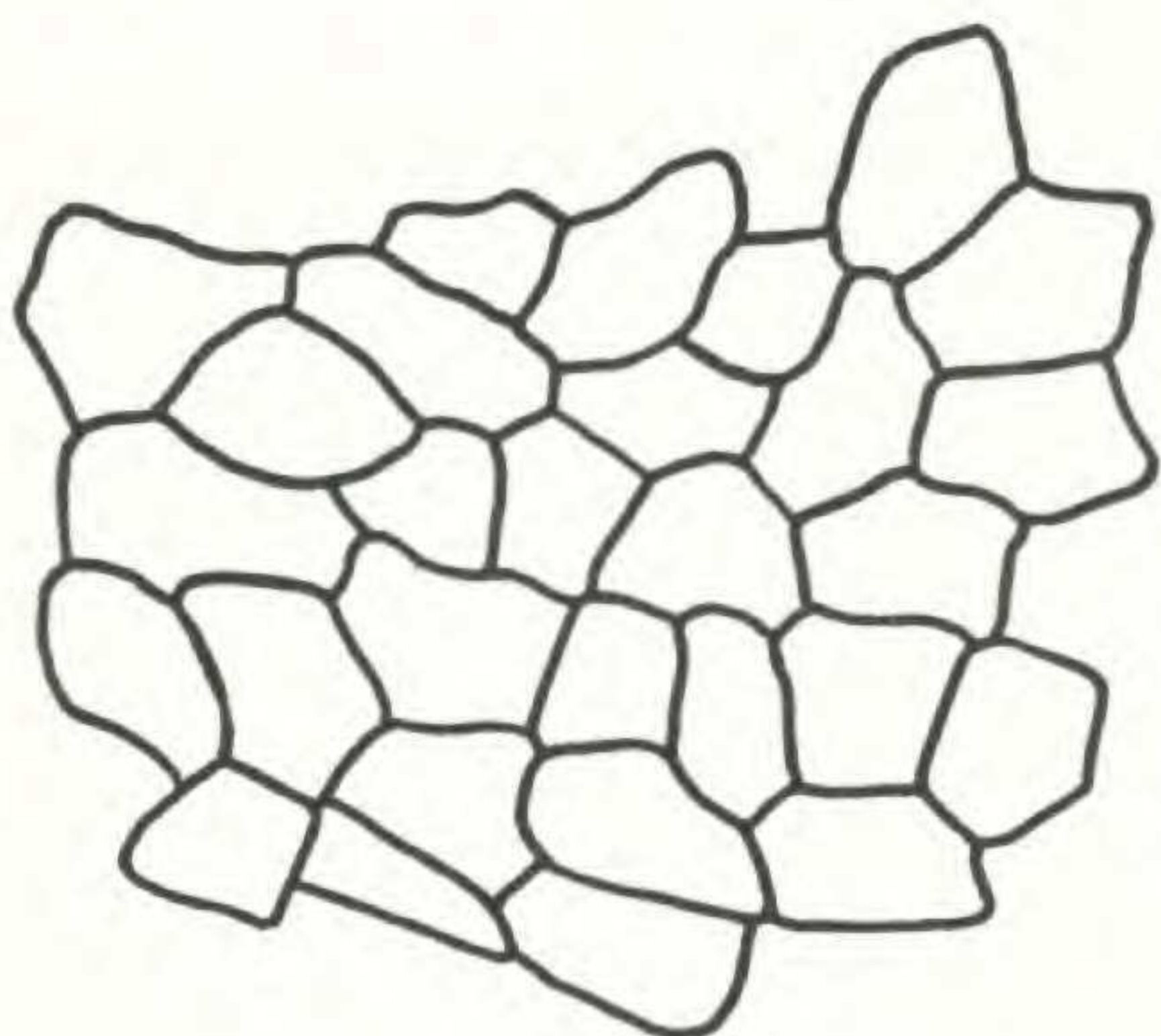
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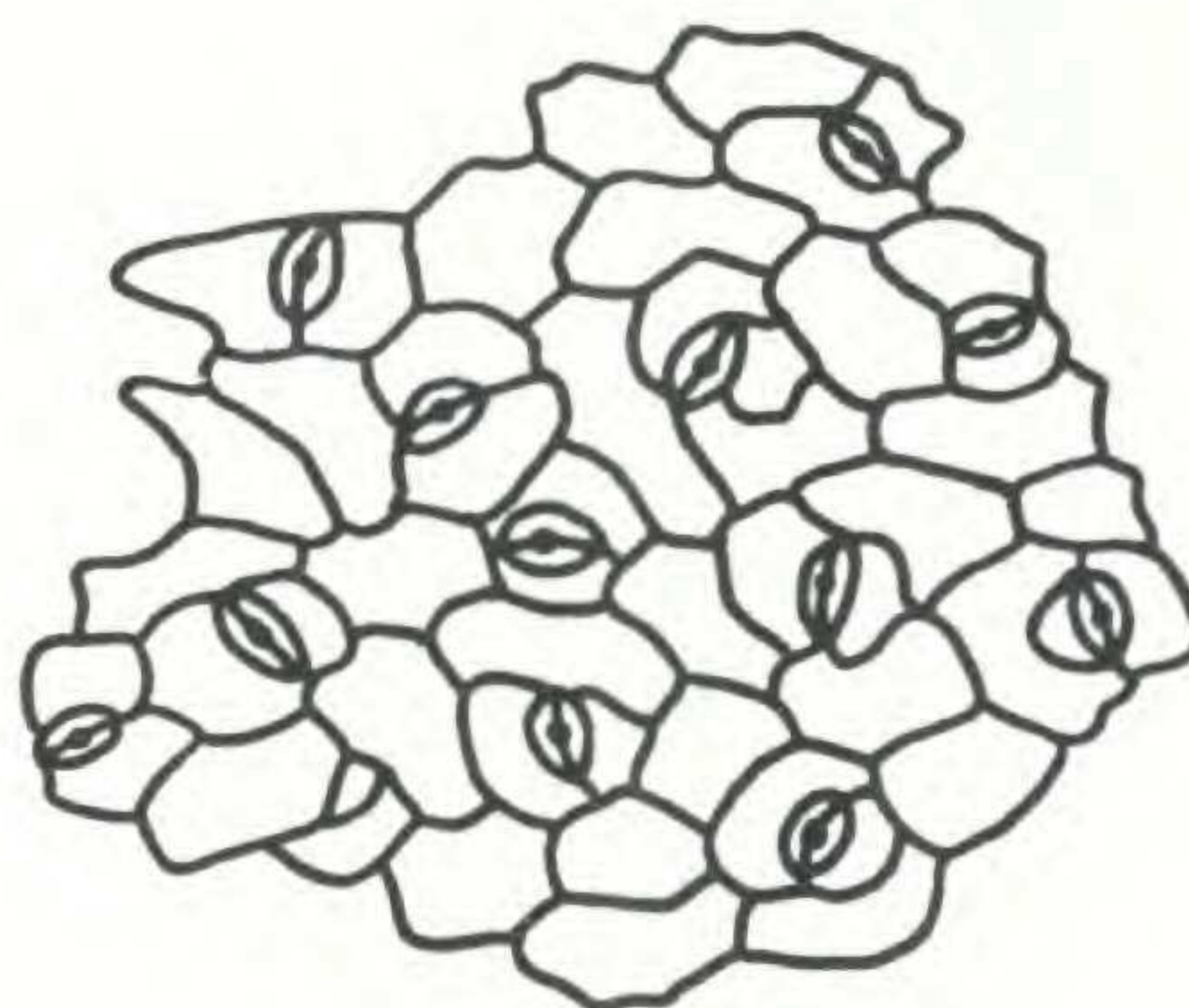
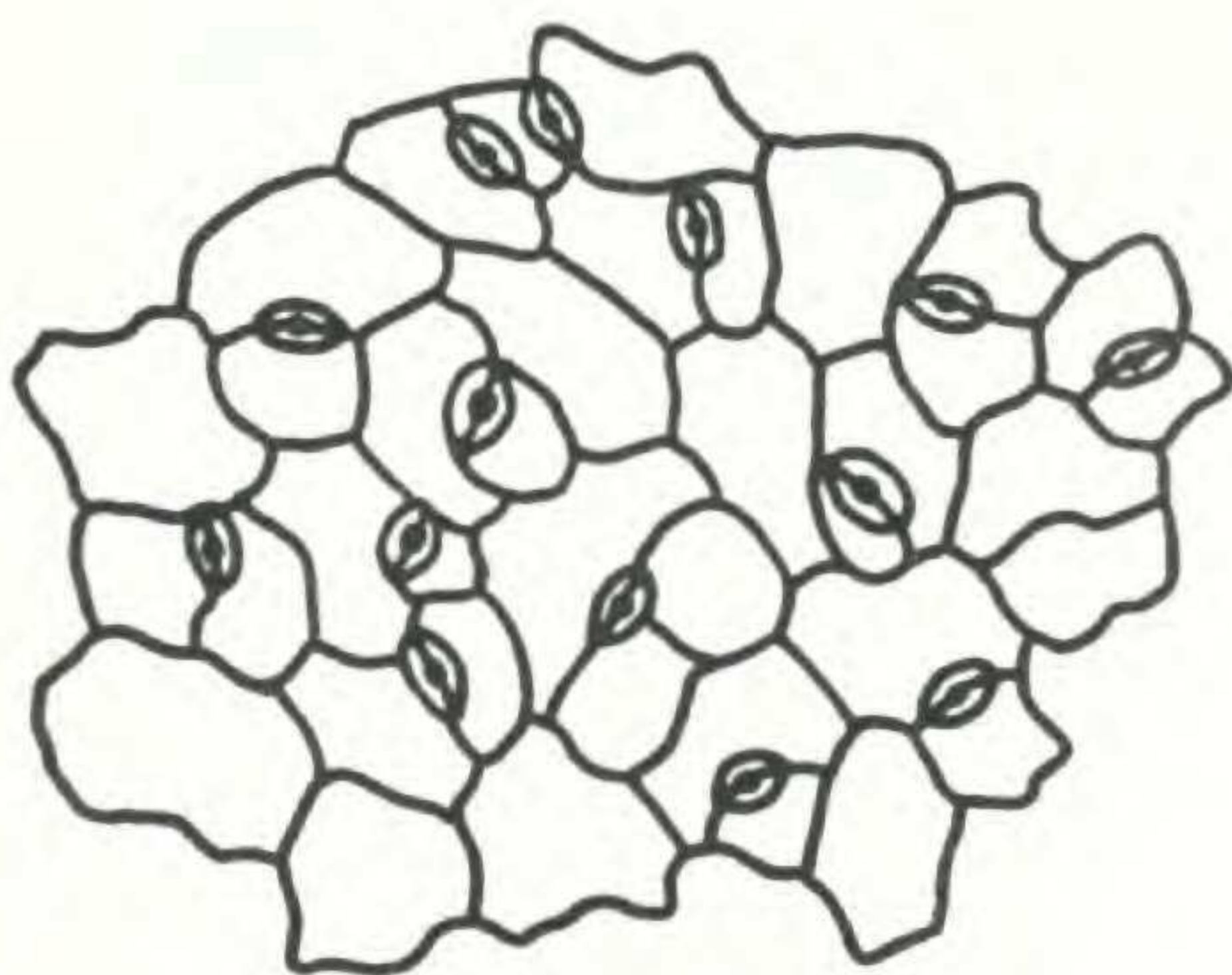
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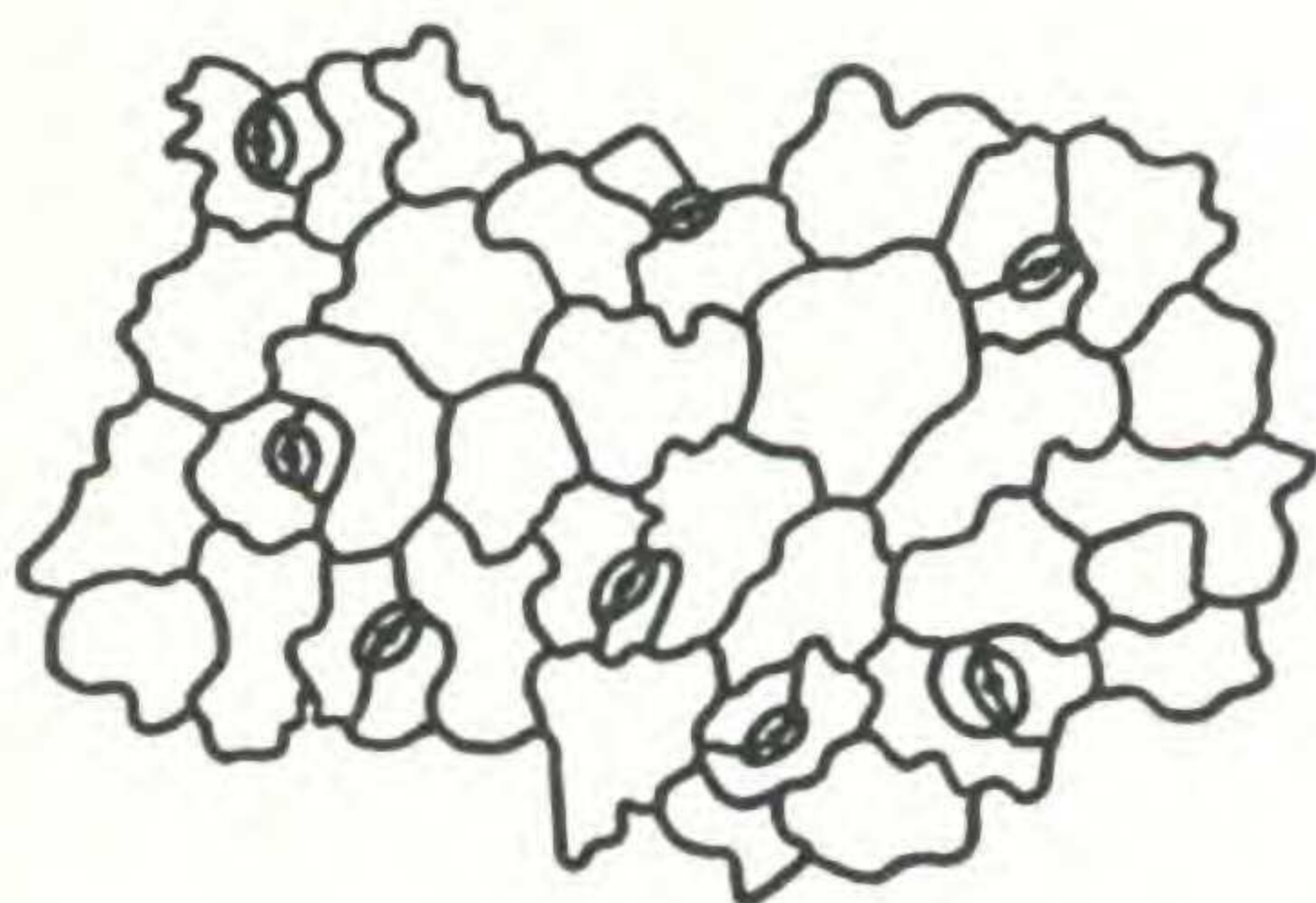
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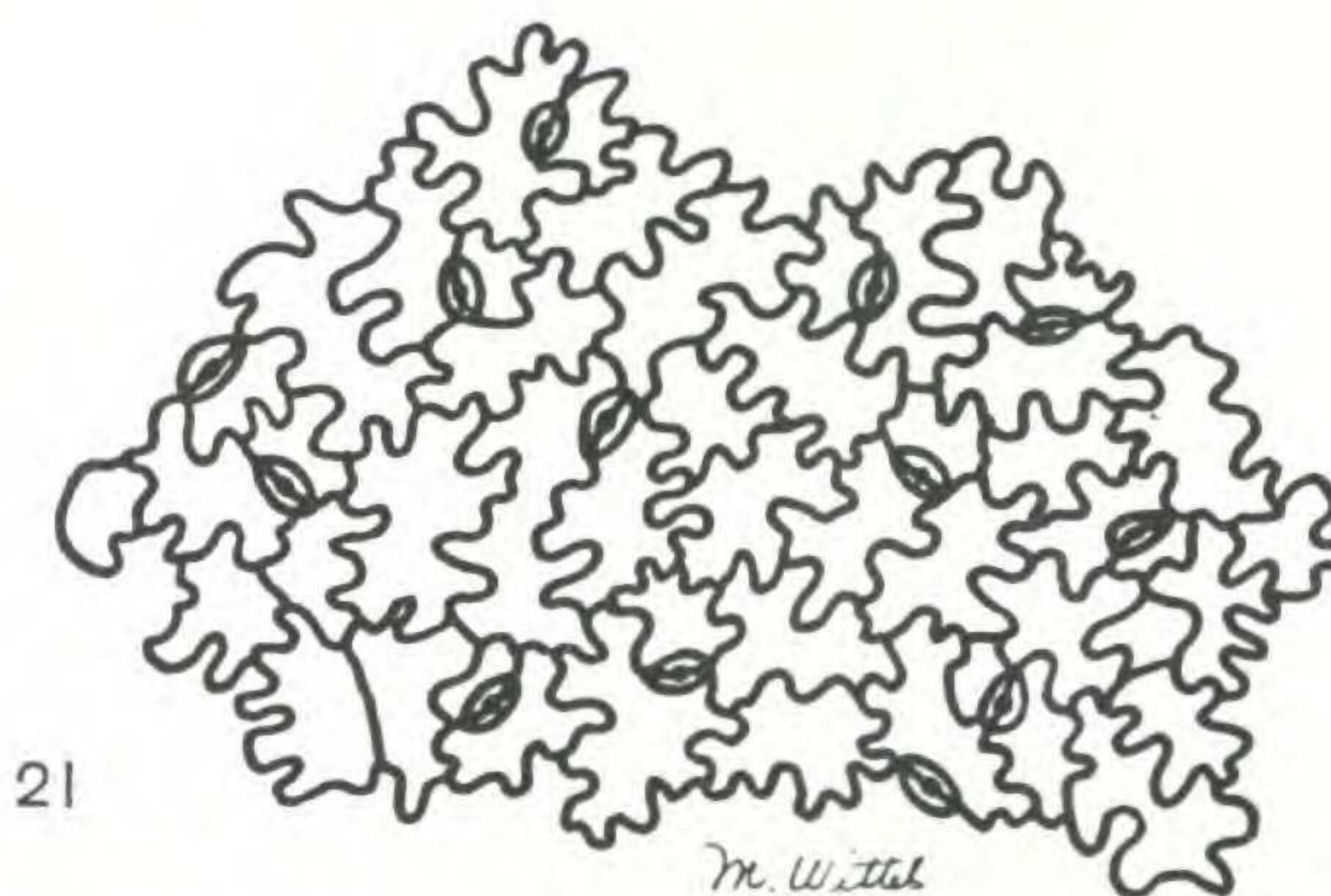
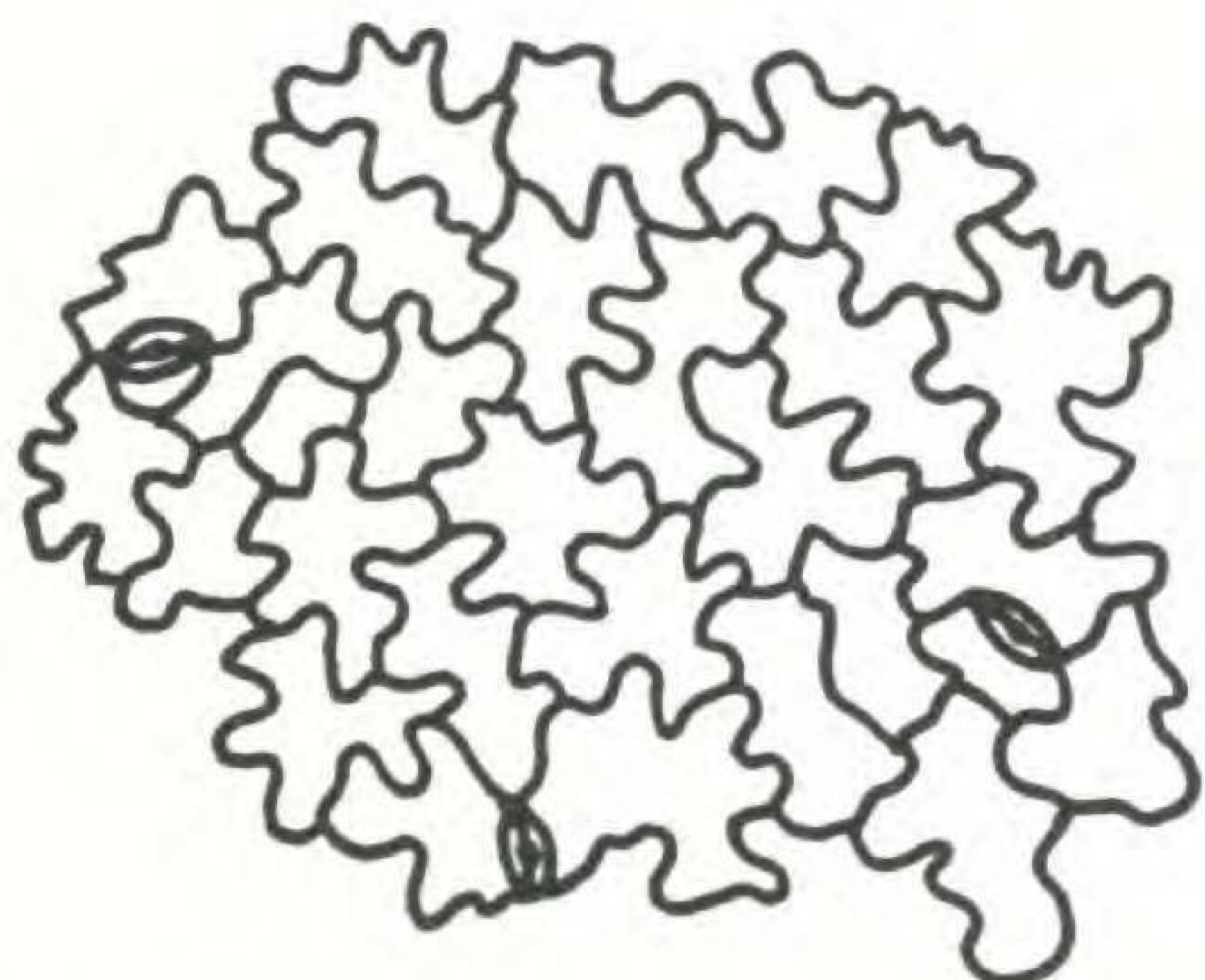
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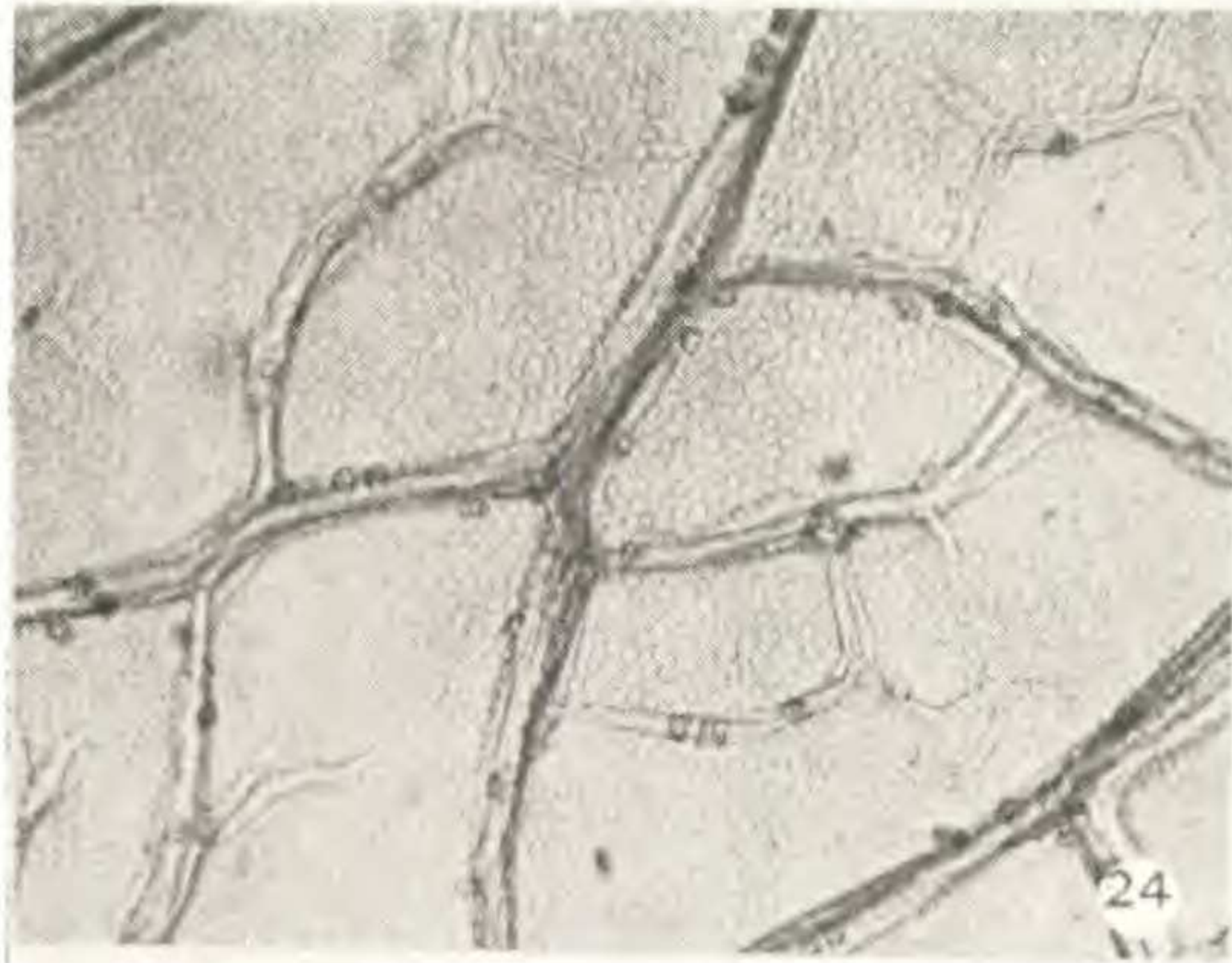
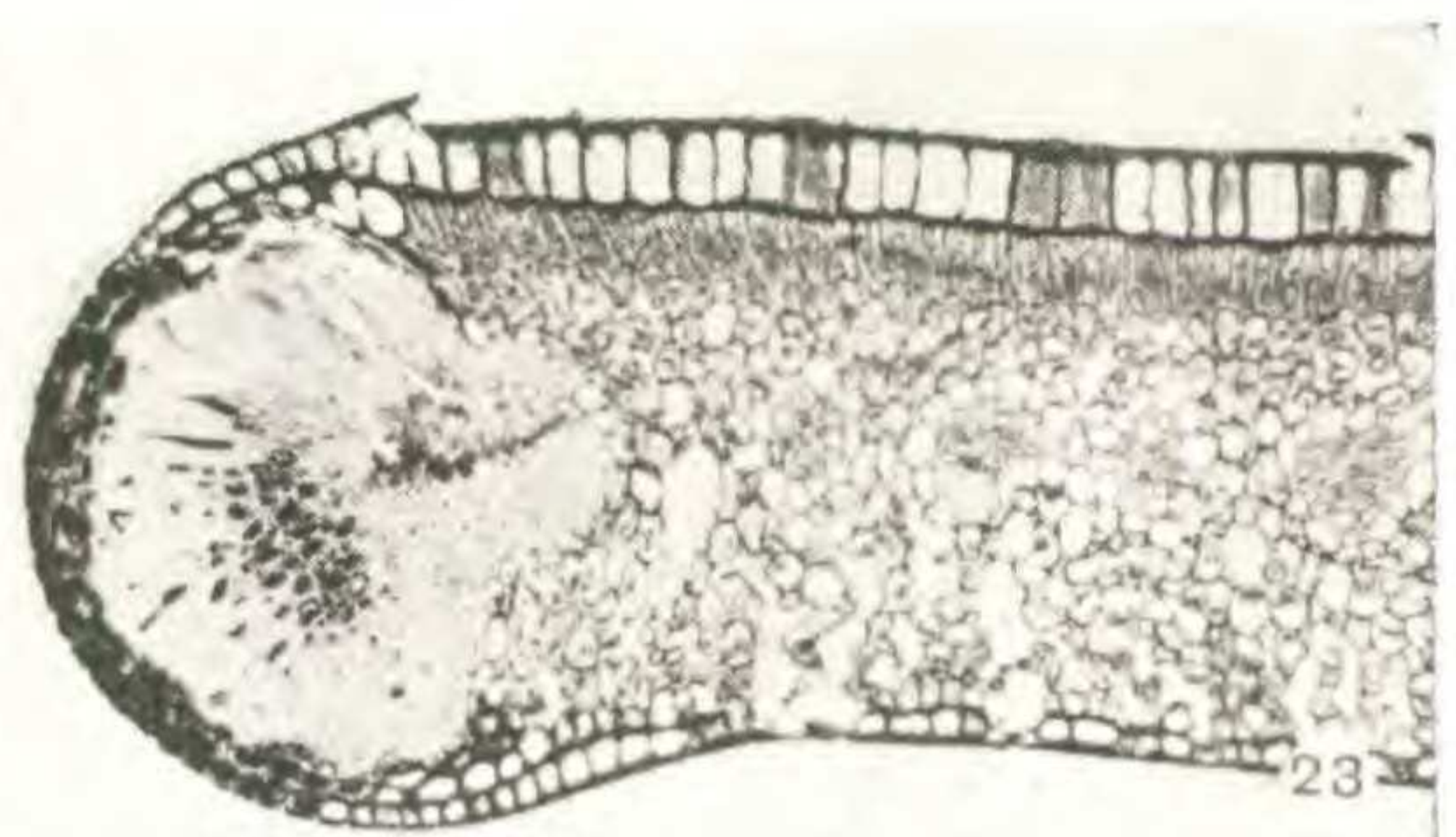
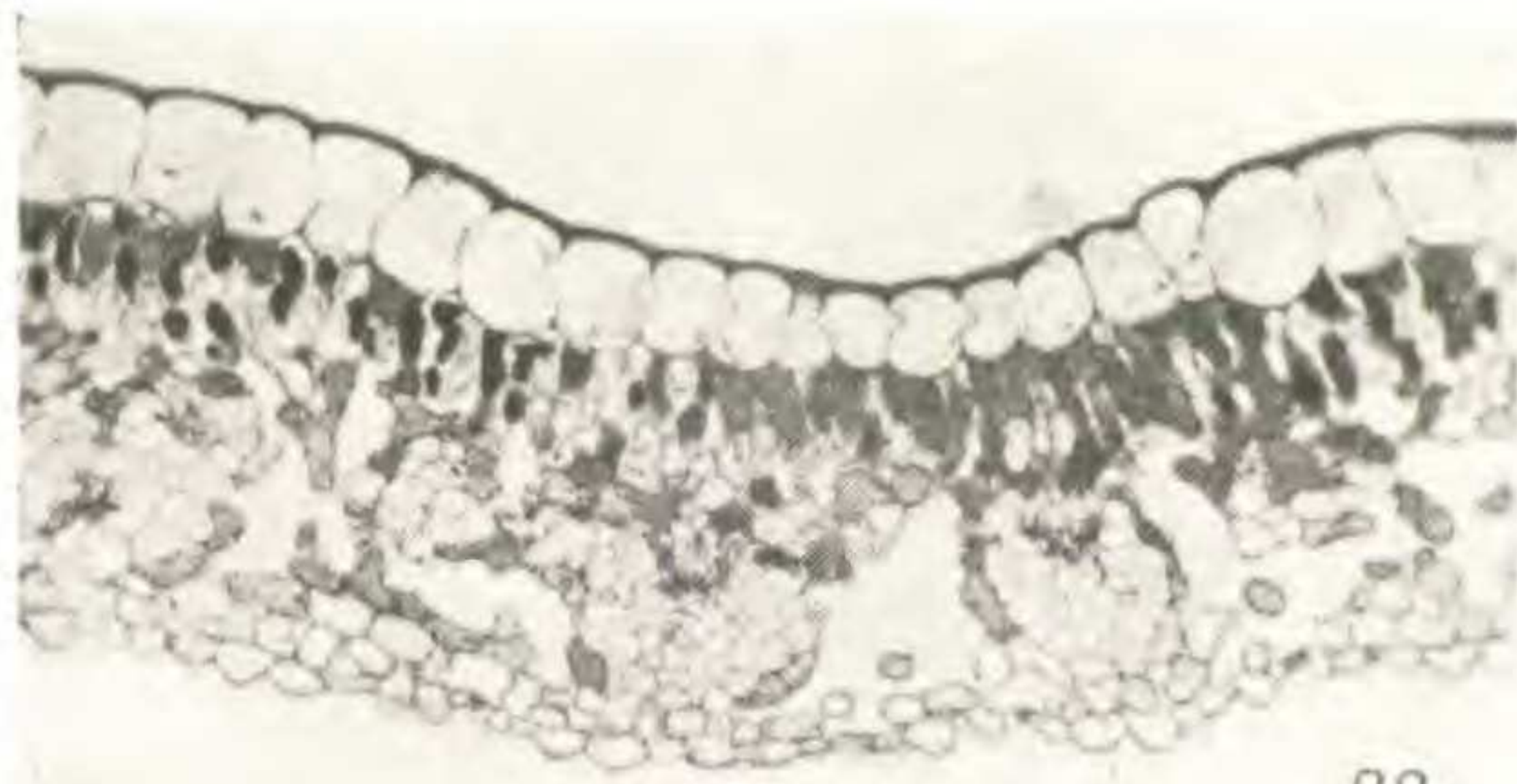


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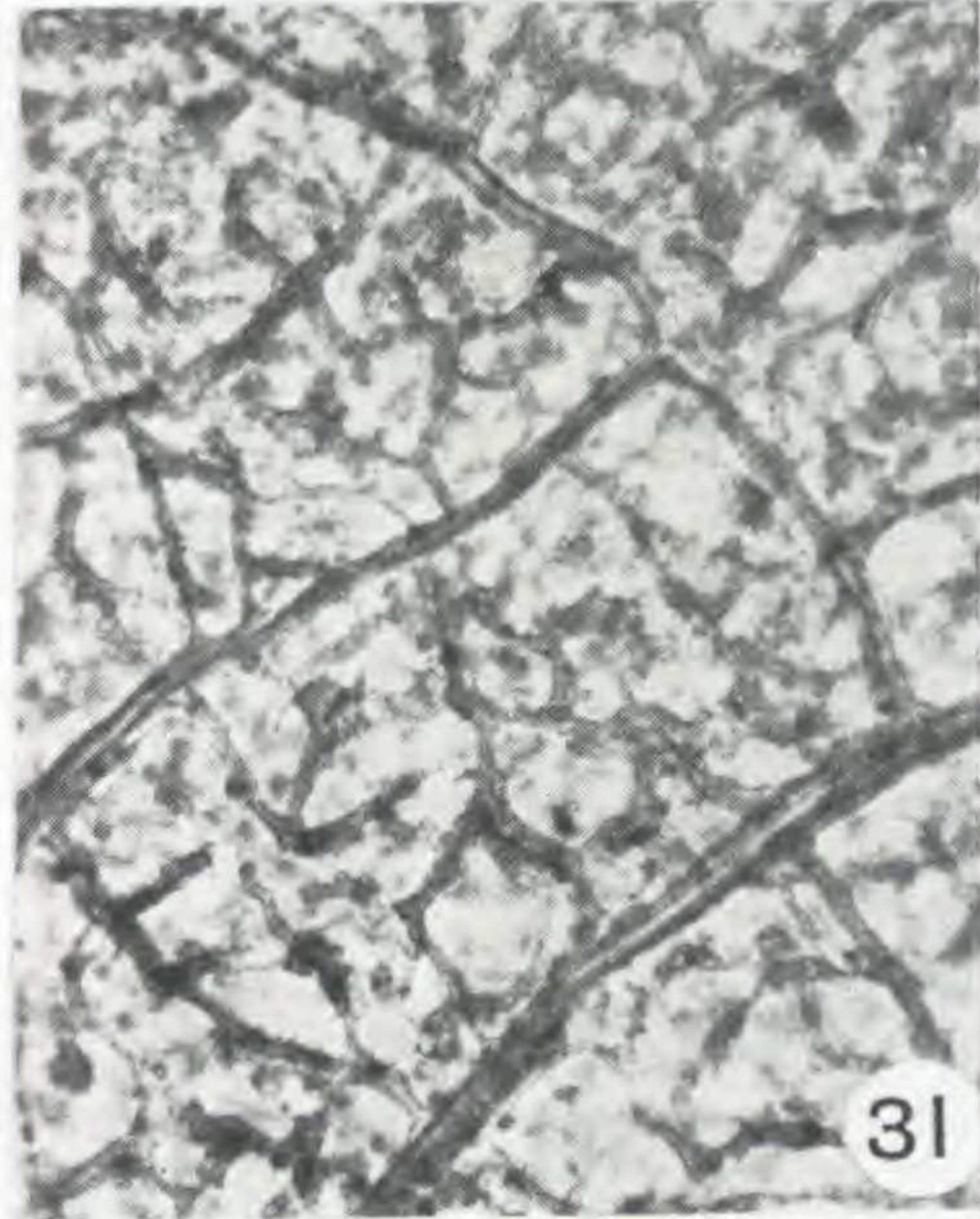
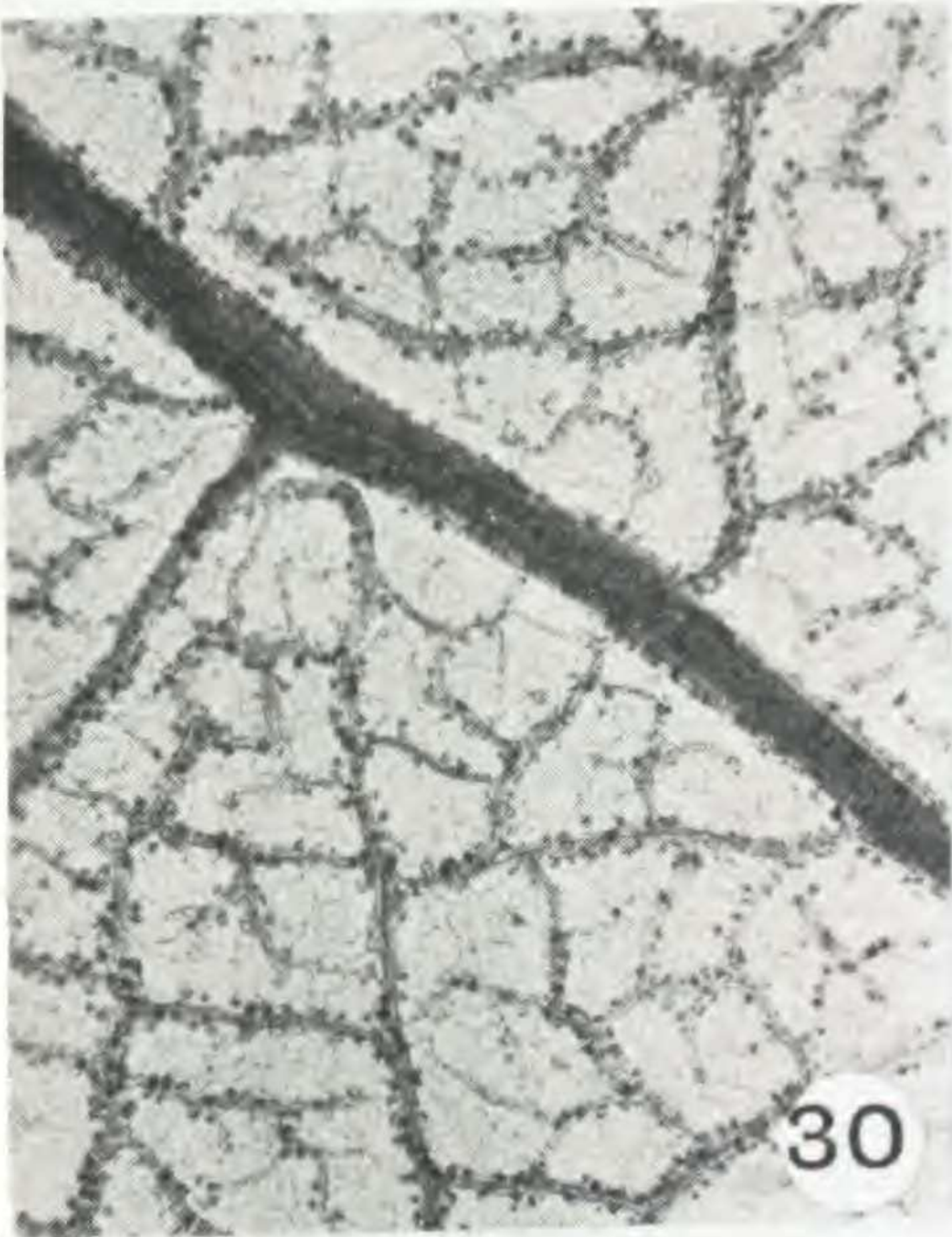
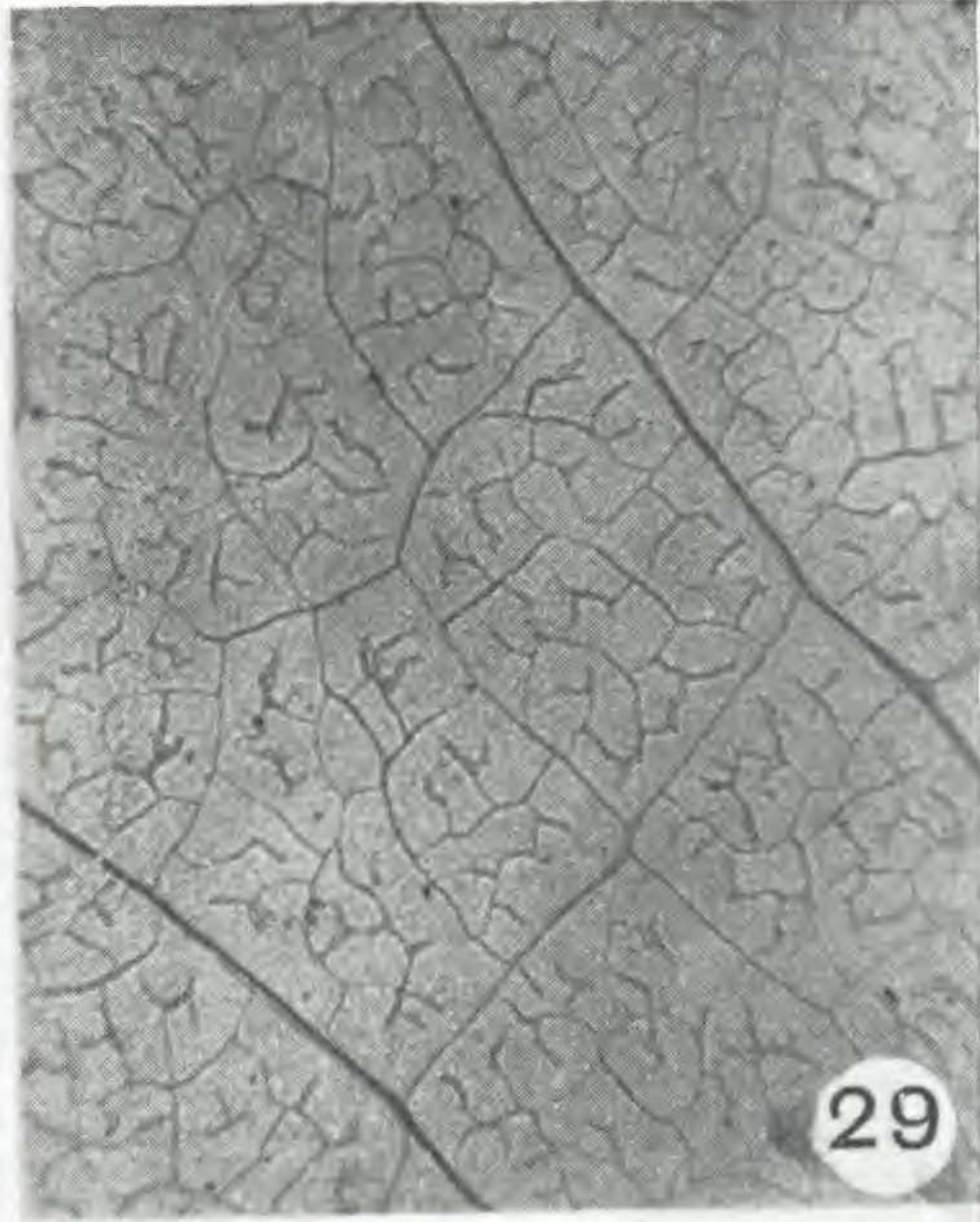
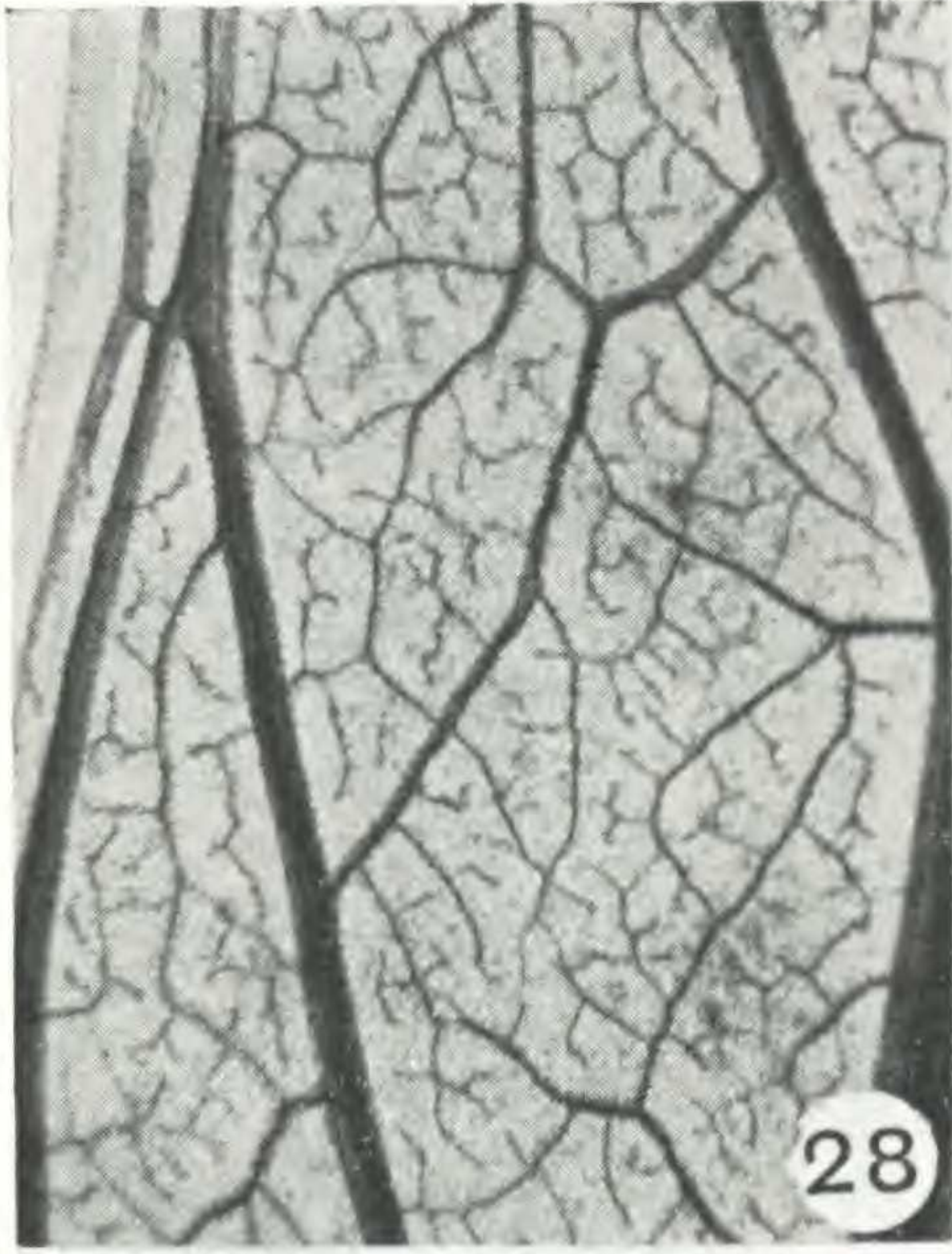


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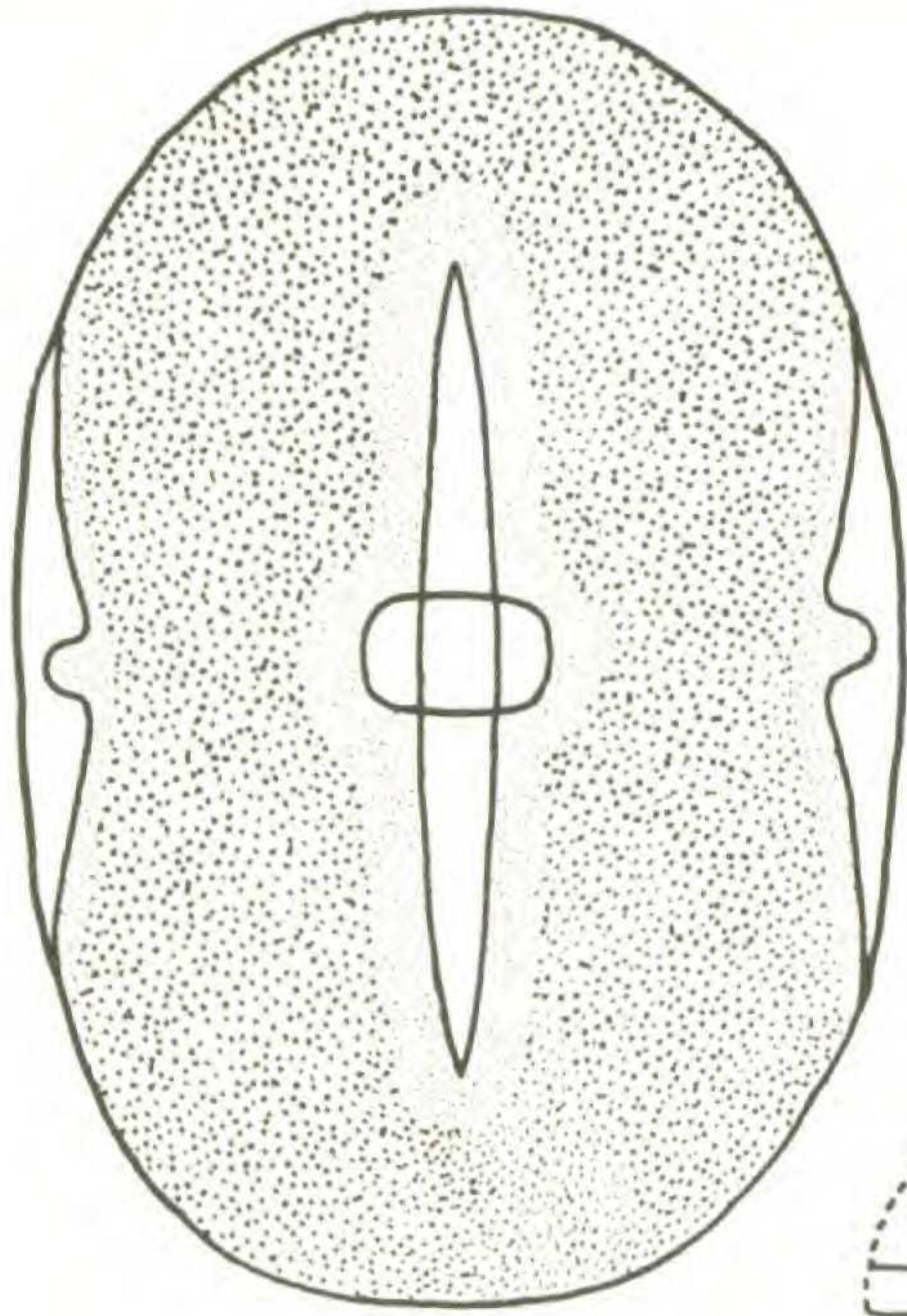
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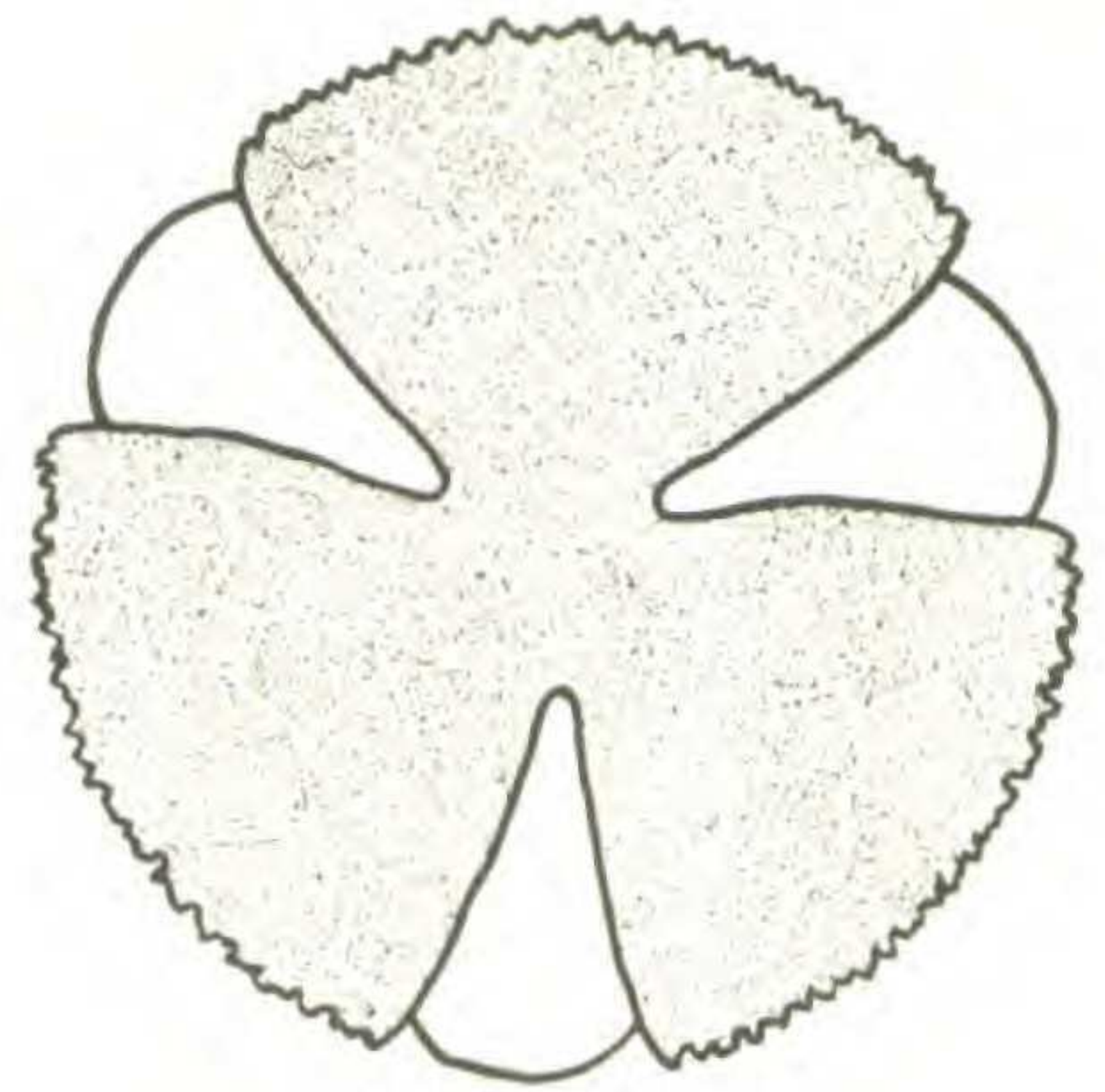
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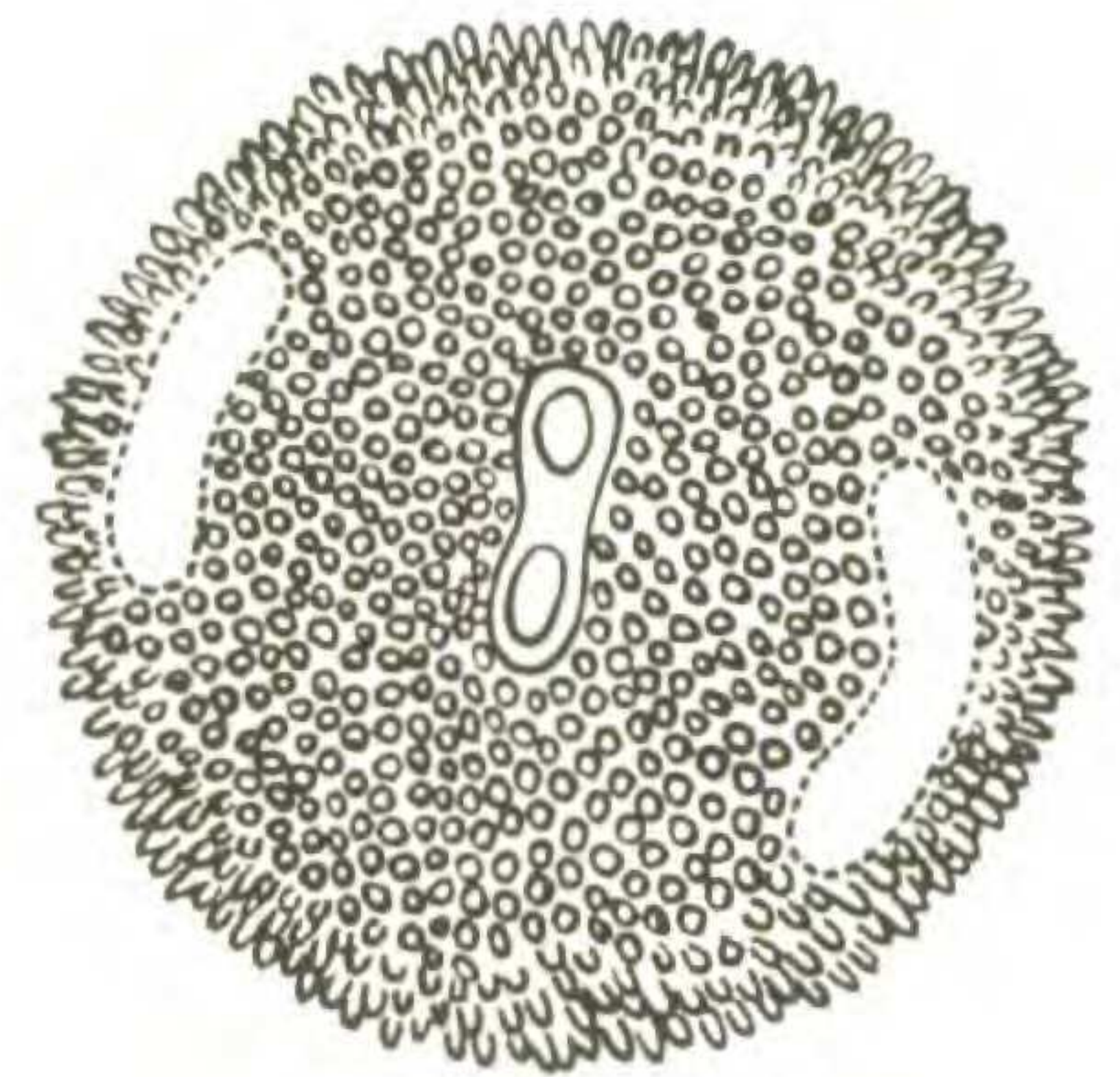
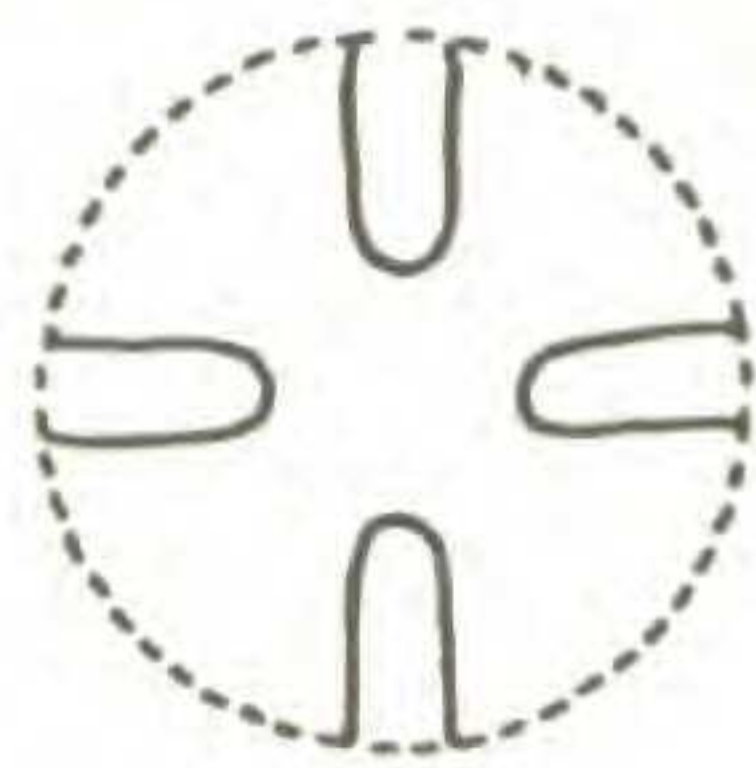
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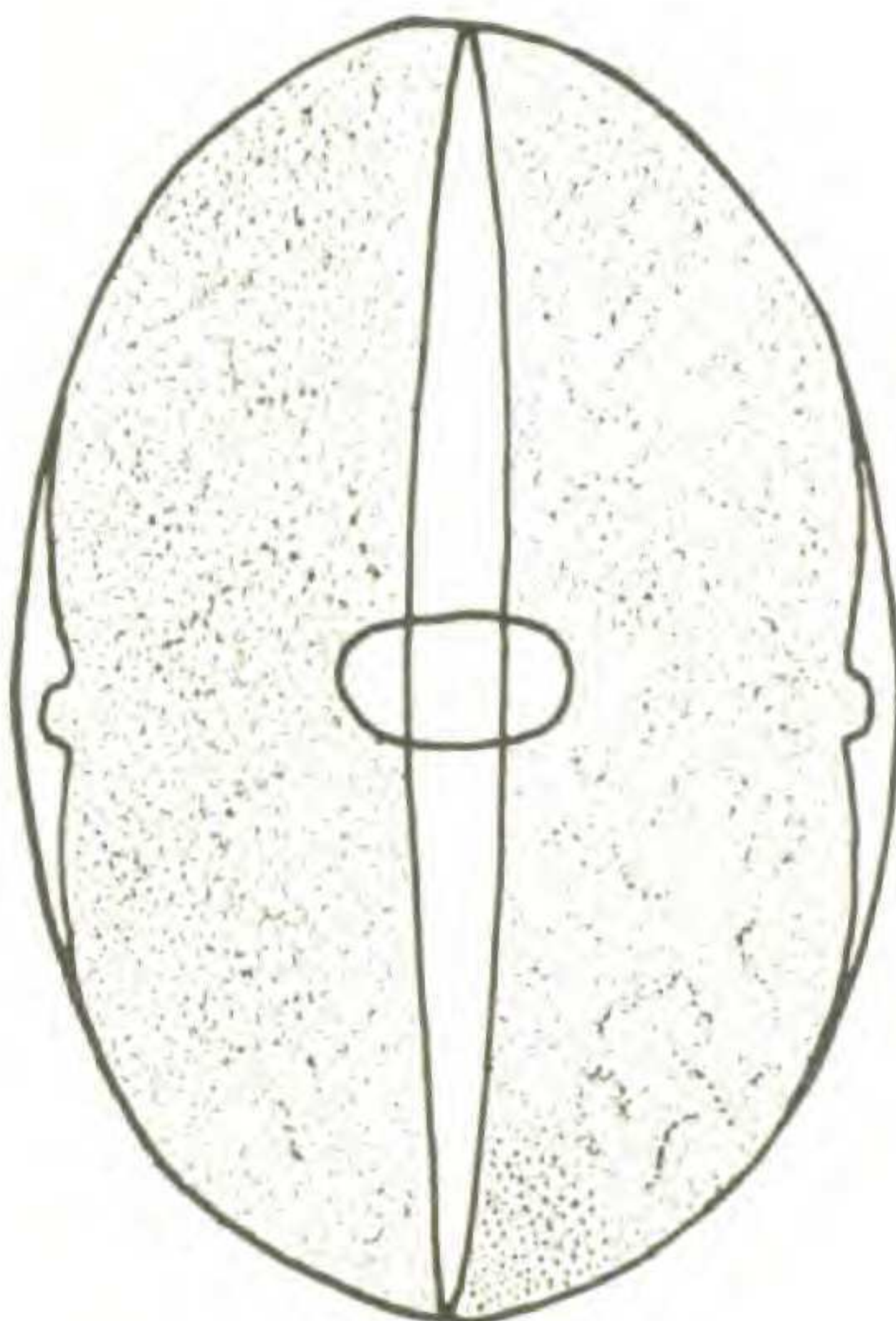
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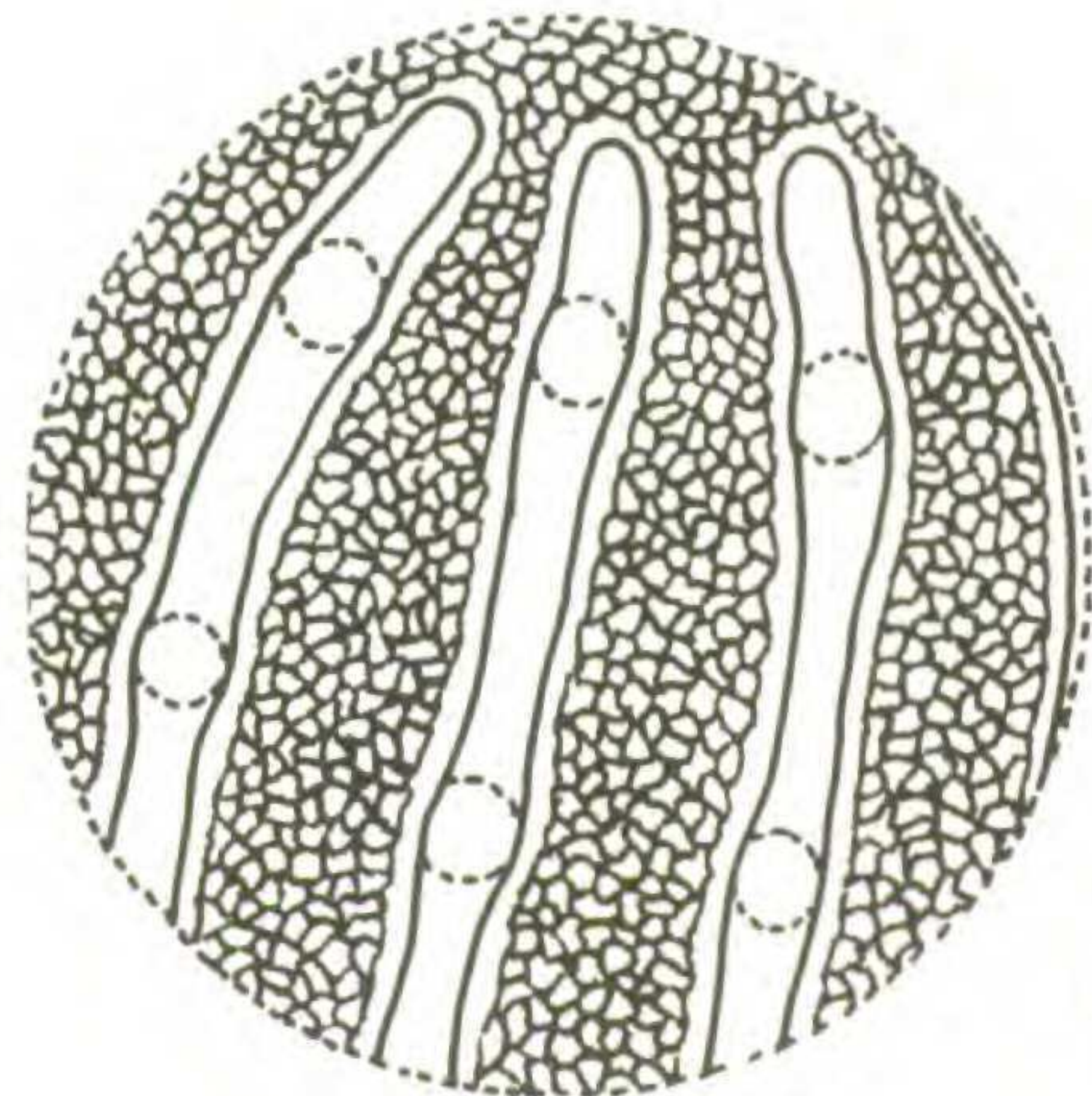
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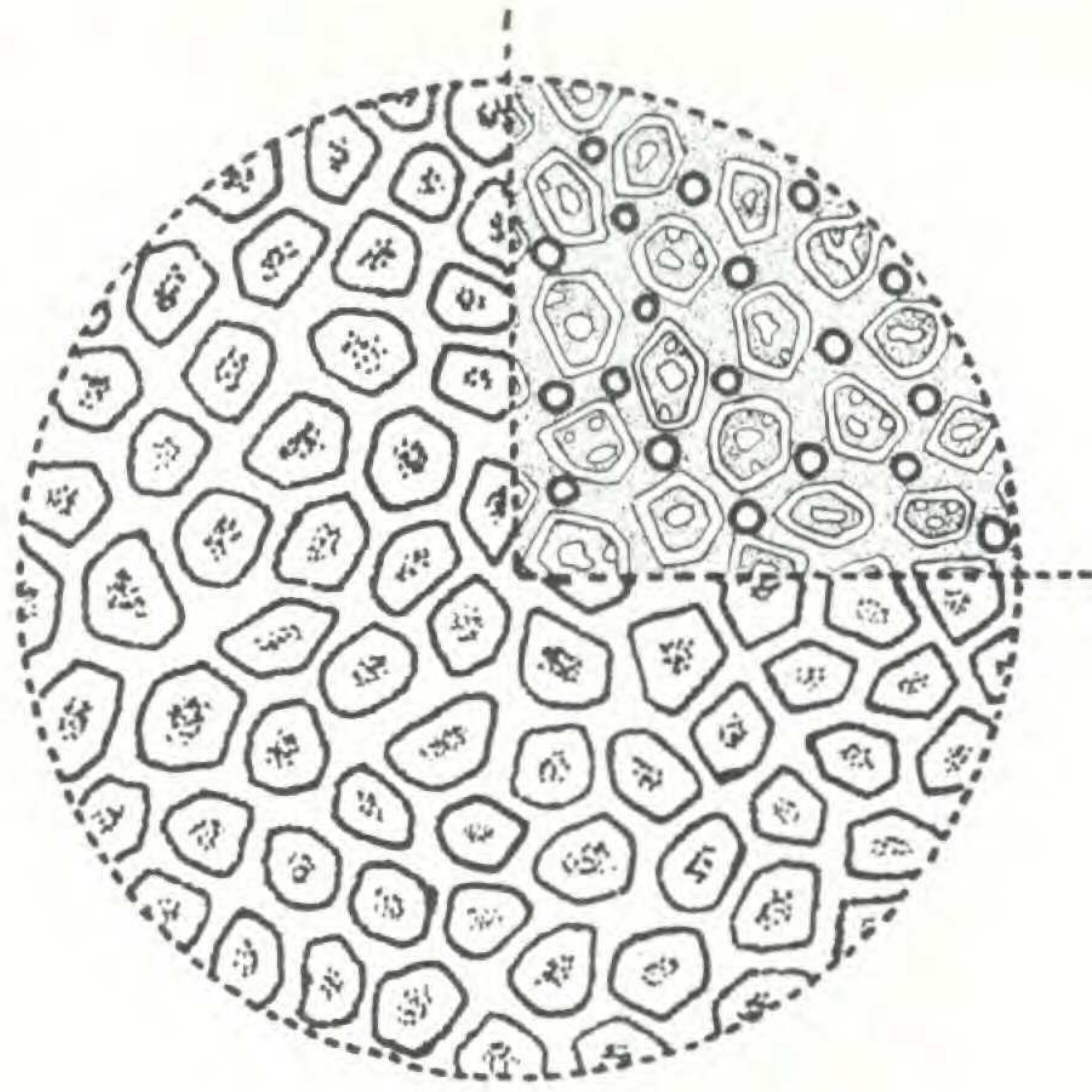
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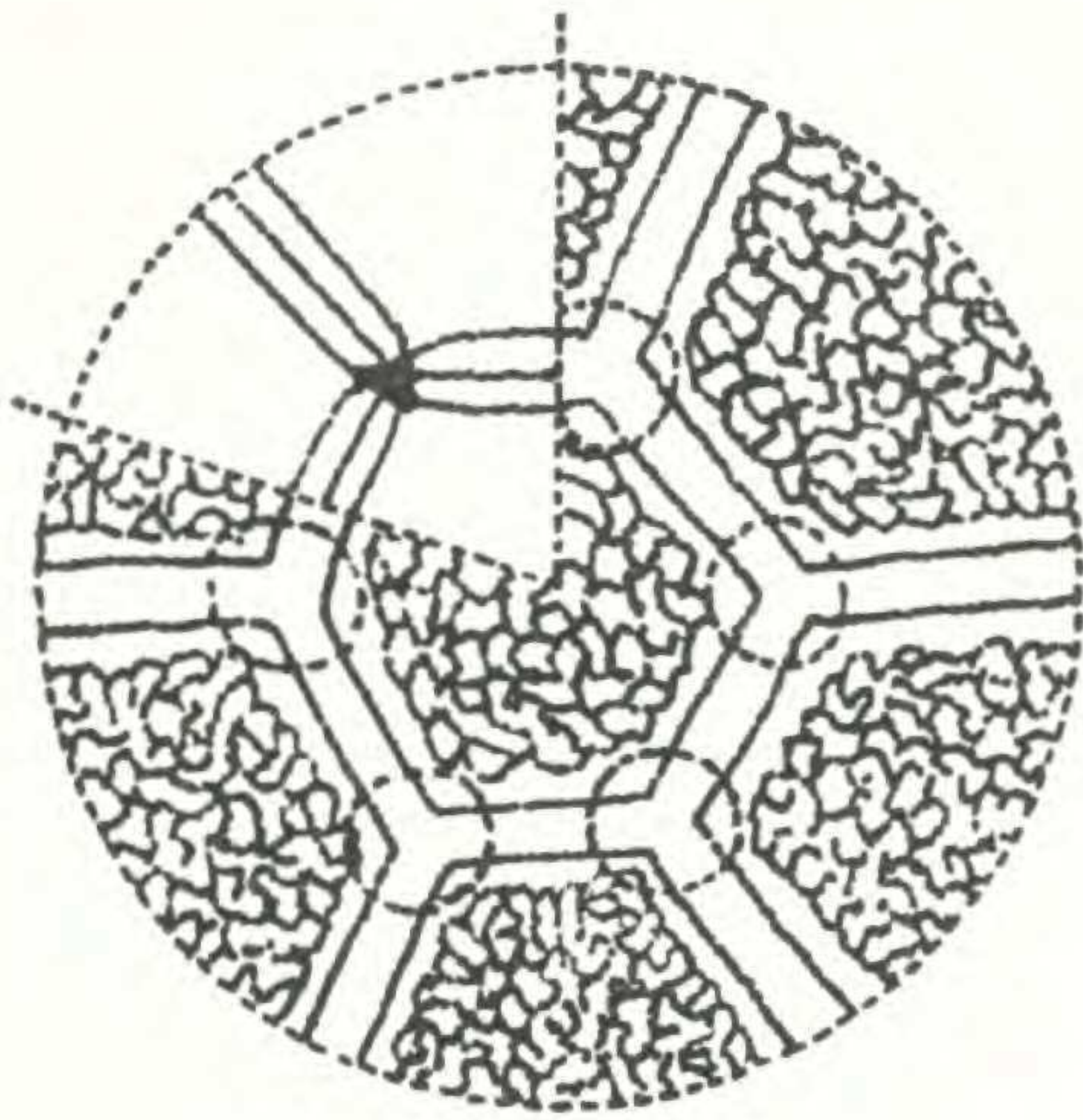
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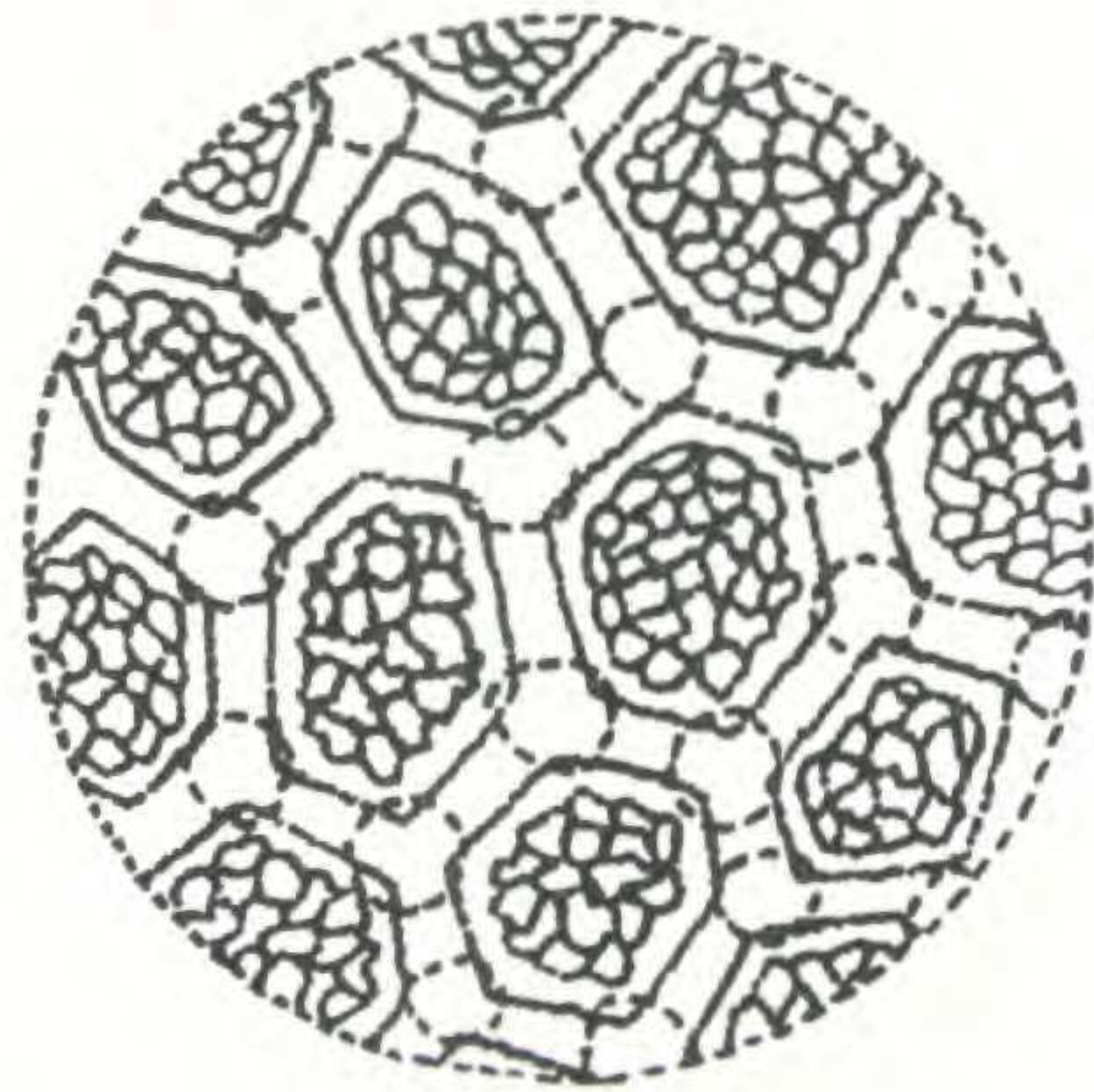
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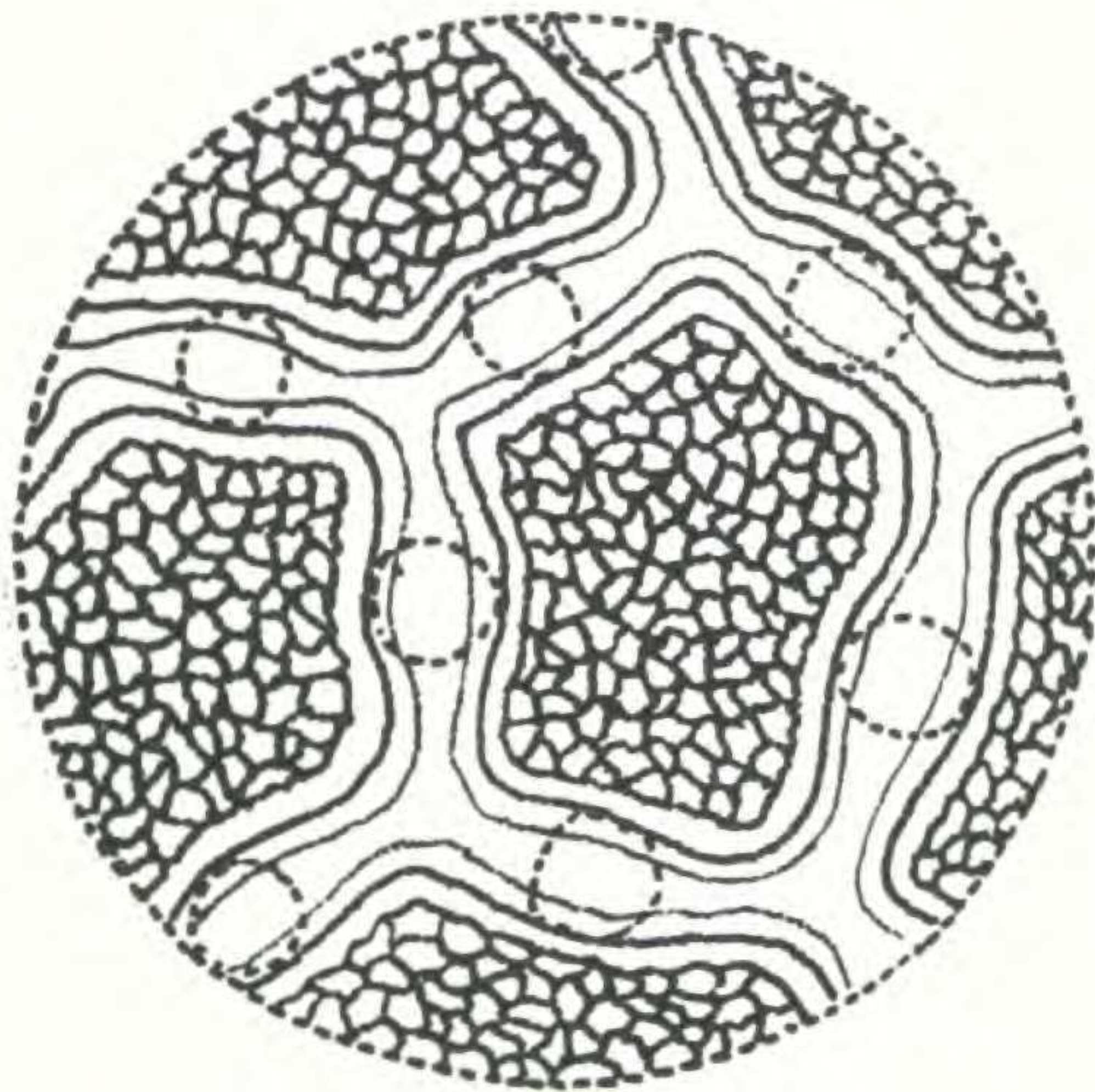
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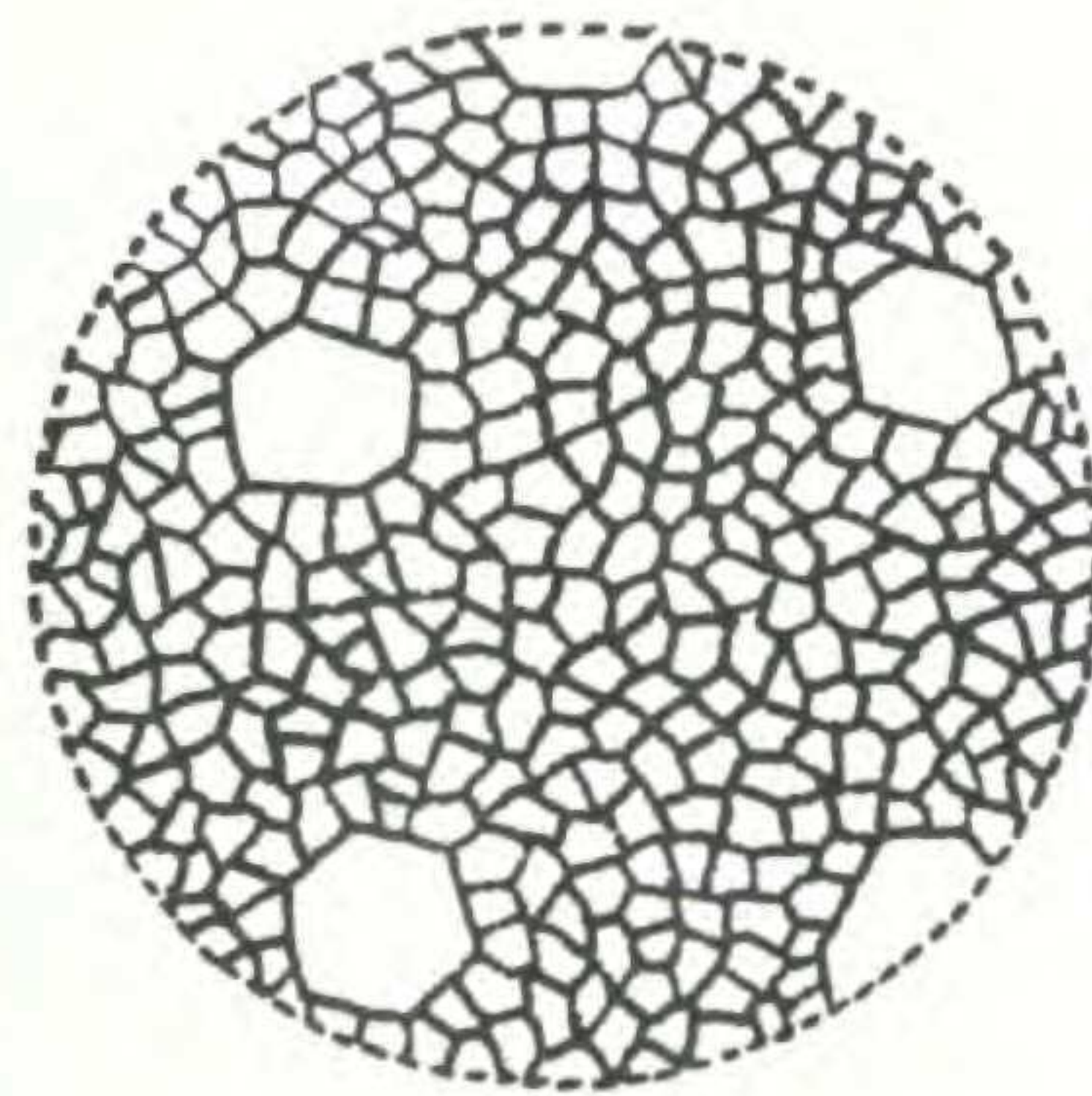
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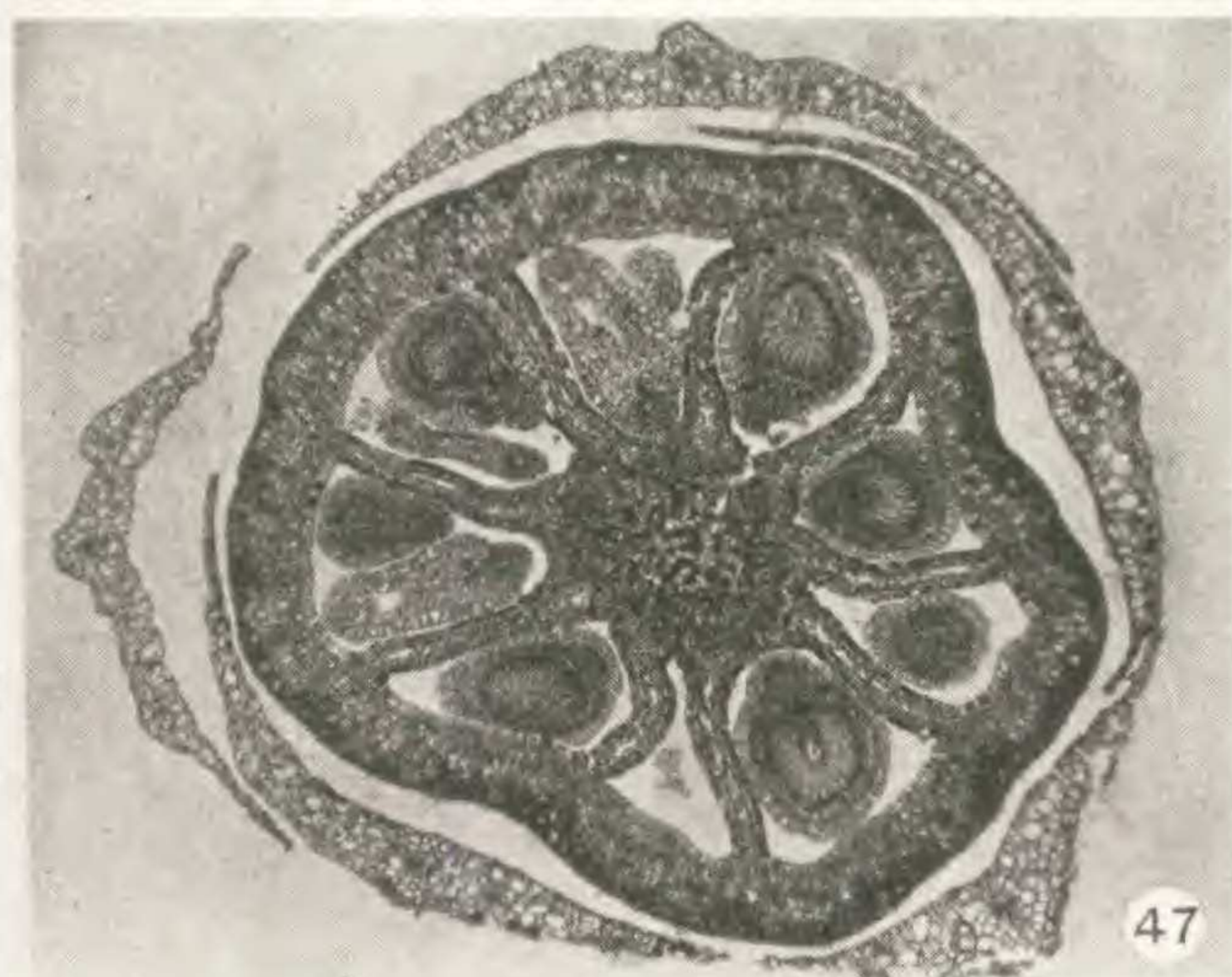
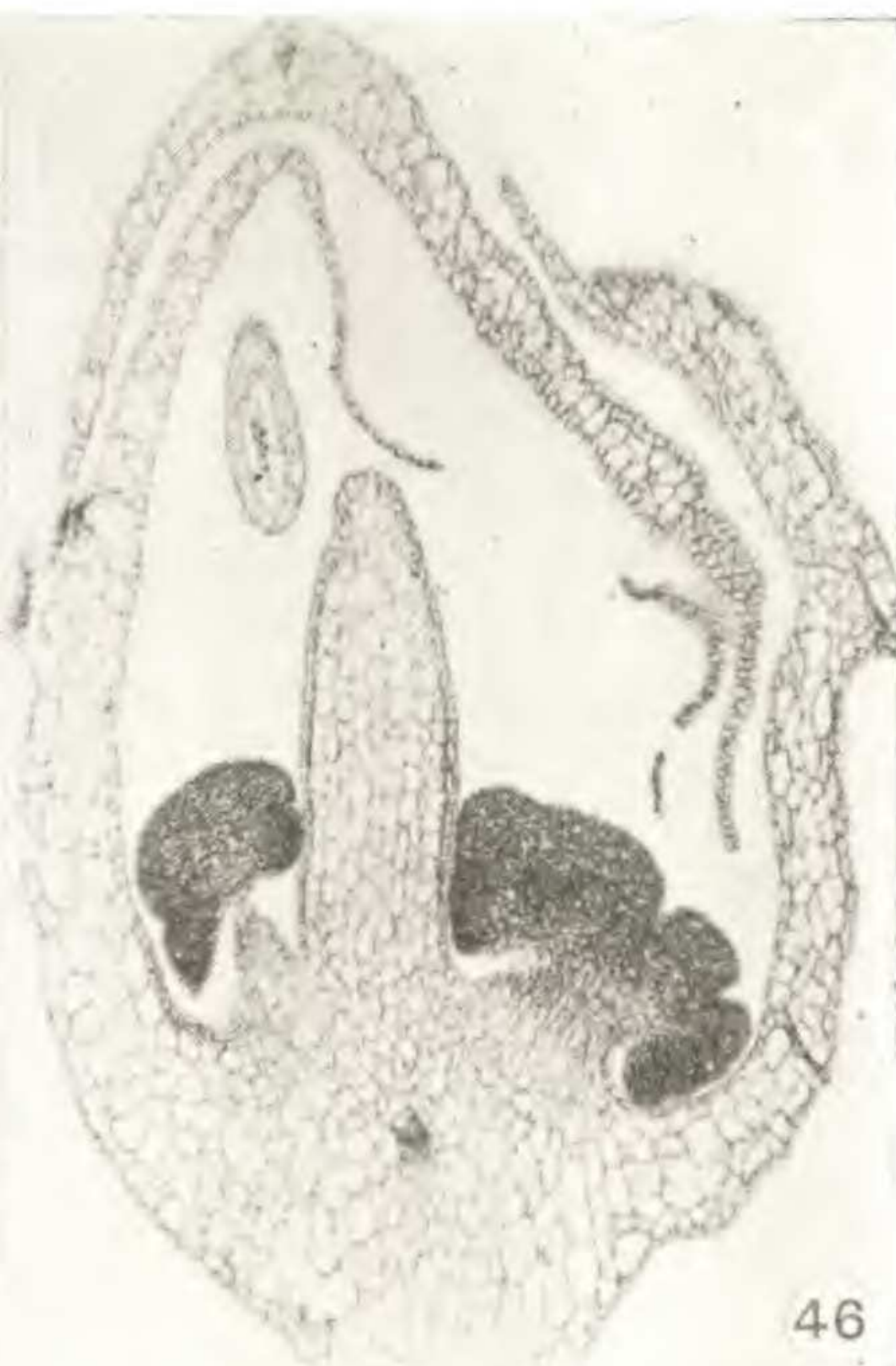
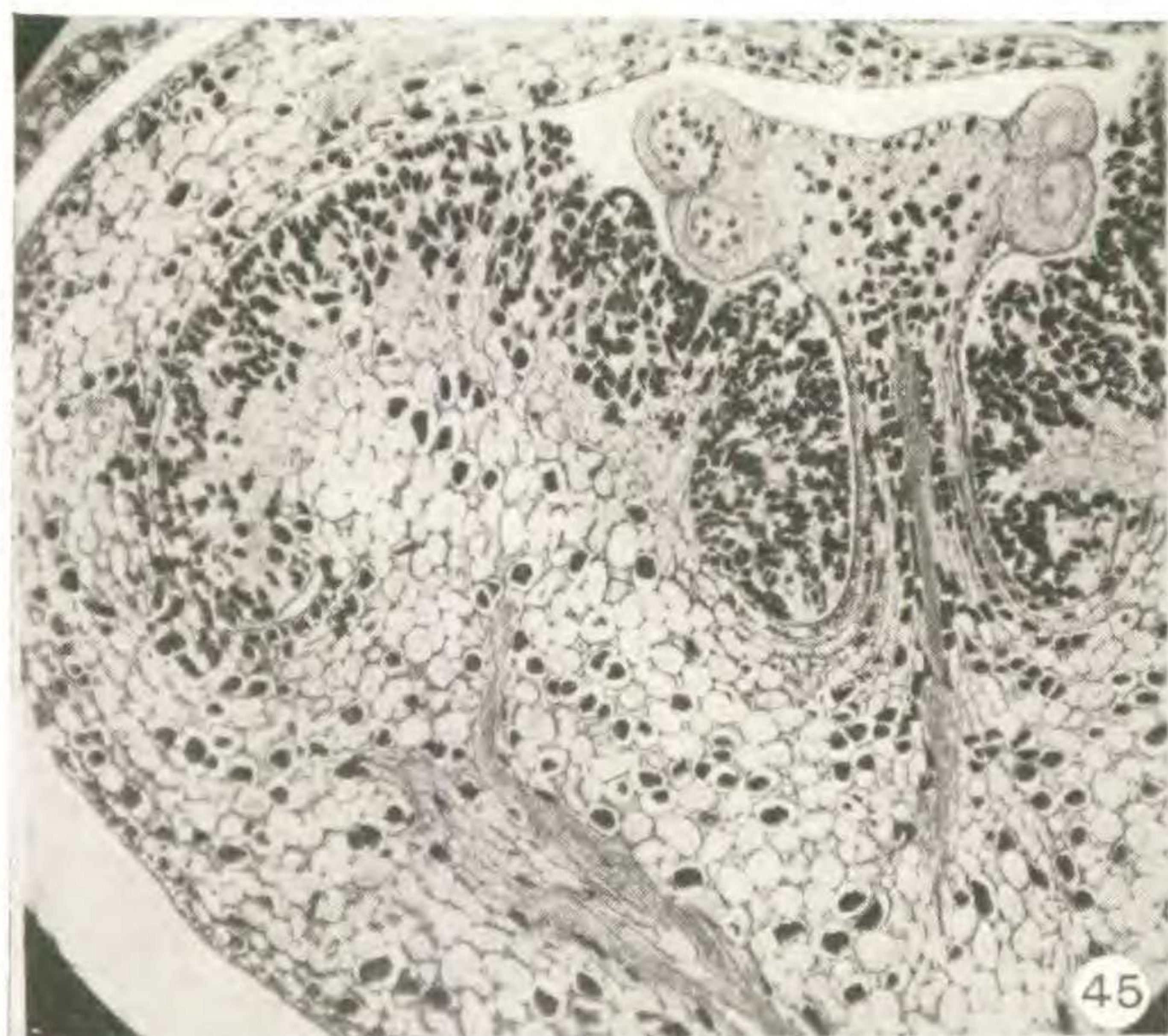
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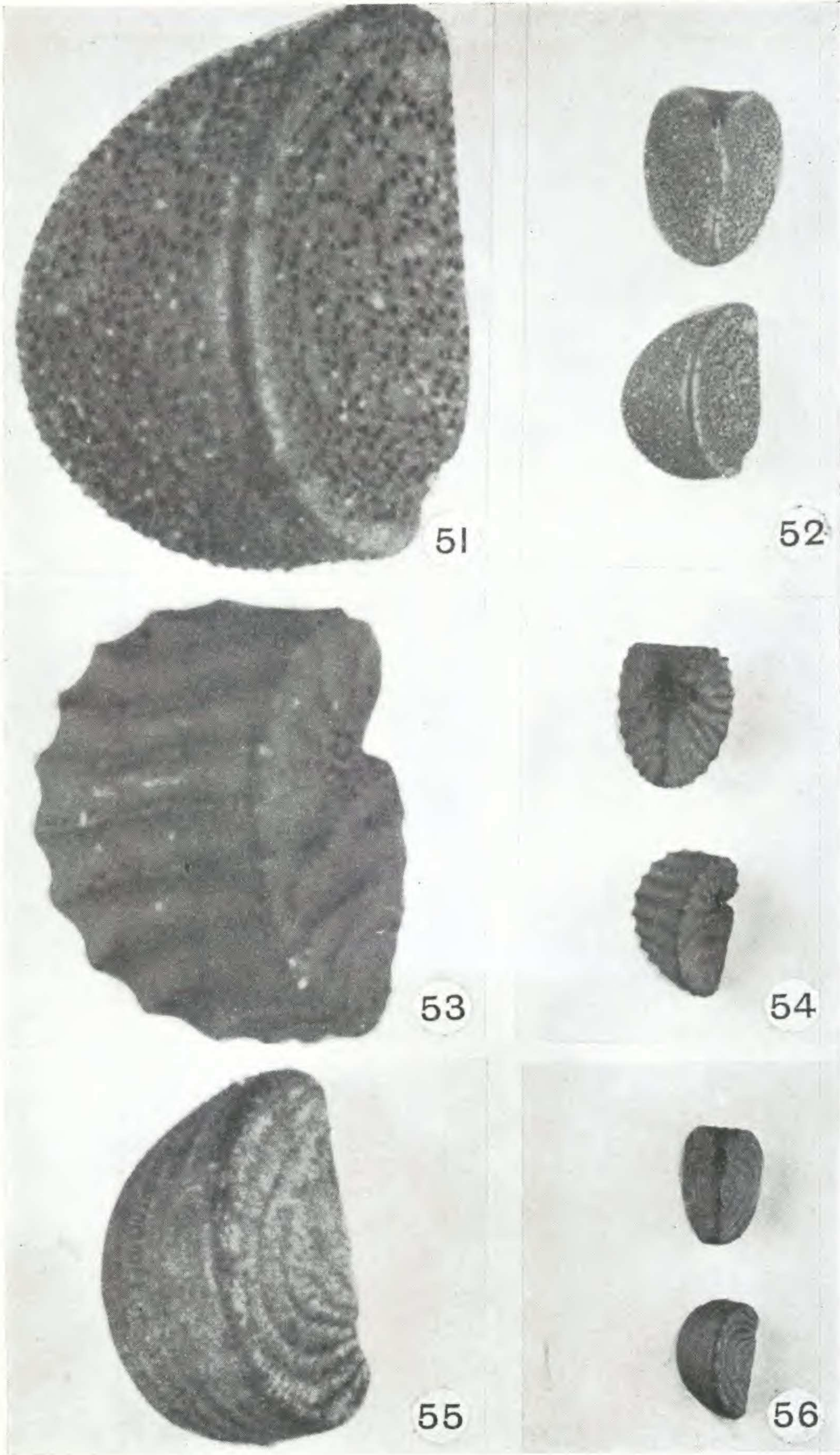
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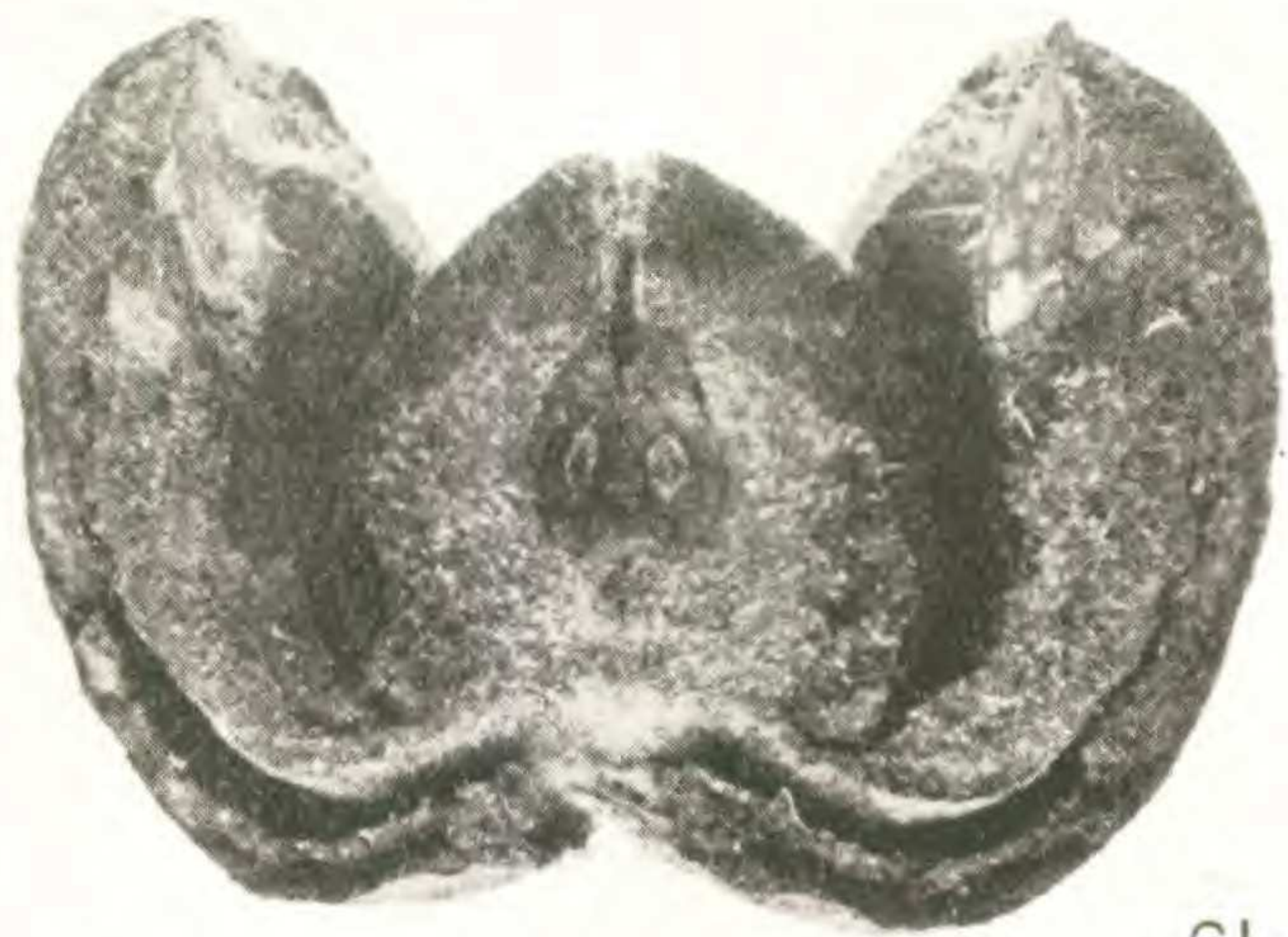
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