

THE FLORAL MORPHOLOGY OF SECAMONE AND THE EVOLUTION OF THE POLLINATING APPARATUS IN ASCLEPIADACEAE*

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ABSTRACT

The floral anatomy and morphology of several species of *Secamone* is discussed. Ontogenetic studies reveal that the anthers are 4-locular. In this respect *Secamone* differs from other members of the subfamily Cynanchoideae of Asclepiadaceae. The bilocular anthers of other Cynanchoideae are a result of phylogenetic suppression of the two outer locules of each anther, as shown by ontogenetic studies and by the origin and nature of the tapetal tissue. Ontogeny of the pollinium sacs is followed in *Secamone*. Pollen mother cells undergo considerable elongation before the formation of the tetrads. The two meiotic divisions are simultaneous, contrasting in this respect with the successive divisions of other Cynanchoideae and agreeing with the Periplocoideae and Apocynaceae. The resulting tetrads have different configurations depending on the direction of the second meiotic spindle; they are rhomboidal or T-shaped. This is in sharp contrast to the linear tetrads characteristic of all other members of Cynanchoideae, but similar to Periplocoideae and Apocynaceae. The ontogeny of the stigma head is followed, which reveals that at maturity the entire stigma head of *Secamone* is glandular, contrasting sharply with the five restricted glandular regions of this structure in other Asclepiadaceae and agreeing with similar structures of the Apocynaceae. The five glandular furrows of *Secamone* in which the simple translators are secreted are not well defined. Each translator consists of a more or less solid portion which is pushed upward and slightly outward by another more or less fluid substance. Thus the whole translator of *Secamone* is comparable to the stalk-adhesive disc of Periplocoideae and the corpusculum of higher Cynanchoideae. *Secamone* thus presents several primitive characters shared with Periplocoideae and Apocynaceae but not with other Cynanchoideae (where it has been placed by taxonomists). It shares with other Cynanchoideae, however, the presence of pollinium sacs and a primitive development of the translators. It is difficult to draw a sharp line between members of Apocynaceae and Asclepiadaceae since they apparently represent closely consecutive levels of floral evolution. FUAD M. SAFWAT, Department of Botany, college of Agriculture, University of Baghdad, Baghdad, Iraq.

INTRODUCTION

One of the most significant families of flowering plants from the evolutionary point of view is the Asclepiadaceae. The interest of this group is derived from the floral structure of its members, which exhibit extreme adaptation to insect pollination.

As early as 1809, Robert Brown separated the Asclepiadaceae from the Apocynaceae. The basis for both the separation of the families and the currently accepted subdivision of subfamilies within them has been designed to reflect increasing adaptation to entomophily. The Apocynaceae, generally speaking, have pollinating habits scarcely more elaborate than those of the average entomophilous angiosperm; the Asclepiadaceae, on the other hand, are distinguished by cross-pollinating devices equalled in complexity only by the orchids. But impressive intergradation is apparent among the two constituent subfamilies of each.

According to Schumann (1895) the Apocynaceae are divisible into two subfamilies: (1) the Plumerioideae, in which the stamens are free or loosely gathered around the "stigma head," the anthers with a small connective and the four anther

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sacs full of pollen, which is granular (tetradinous in *Condylocarpon*), with no translating apparatus developed; (2) the Echitoideae (or Apocynoideae), in which the stamens are connivent about the stigma head, with a greatly enlarged connective and four anther locules empty at the base and with granular pollen (except in a few genera, as *Apocynum*, where the pollen grains remain in tetrads). In some genera of the latter subfamily a primitive pollen-translating apparatus is developed through agglutination of excess secretions of the stigma head.

Similarly, the Asclepiadaceae are divided into two subfamilies: (1) the Periplocoideae, in which the anthers are connivent with the stigma head, with four locules full of pollen which remains in tetrads, and a rather elaborate pollinating translator apparatus in many genera; (2) the Cynanchoideae (or Asclepioideae), in which the stamens usually are adnate to the stigma head, each anther lobe having but one pollinium sac completely enclosing the pollen (two sacs in the tribe Secamoneae), and the pollinating apparatus is most highly specialized. In Periplocoideae a translator consists usually of an open shovel- or cornucopia-like receptacle to receive pollen tetrads shed at maturity and a lower stalk-adhesive disc combination which becomes glued to the body of the pollinator; in Cynanchoideae the translator is a yoke-like structure consisting of a solid body, the corpusculum or "gland," and two lateral cartilaginous straps, the translator arms, to which the pollinium sacs become glued at maturity—the corpusculum bears a longitudinal fissure upon its outer face, within which the pollinating insect's appendage becomes clamped mechanically.

Although over 300 genera have been described in this family, morphological and anatomical studies have been restricted to a very small number of them, notably *Asclepias*. The floral structure of the African and Asian asclepiads has scarcely been touched from this standpoint although those two great continents are centers of the most primitive genera of the family. It is almost axiomatic that the primitive groups within a given family may furnish more evolutionary information than the more advanced ones.

Secamone, of the subfamily Cynanchoideae, is one of many neglected genera of Asclepiadaceae which await extensive morphological and anatomical investigation, and which further merits attention since it is one of the few genera of the family indigenous to both Asia and Africa. Species of *Secamone* are twining or prostrate, frequently branched shrubs or undershrubs with leathery or herbaceous, often small leaves. The terminal or lateral inflorescences are cymes or panicles with white or yellowish flowers. The flowers are very minute and in describing them R. Brown wrote

"From the extreme minuteness of the parts, no genus has been more difficult to determine than this"

One of the problems which faced earlier asclepiad morphologists concerned the number of anther locules in this genus, in which the pollinium bears paired, instead of the customary solitary, pollen sacs at either end of the translator. In describing this situation authors almost always have stated merely that the complimentary pairs of pollinia "adhere closely at maturity." When it is recalled that

in all members of the subfamily Cynanchoideae previously investigated the anthers are bilocular, the case of *Secamone* becomes most interesting.

Demeter (1922) is the only recent morphologist to deal in detail with evolutionary trends in the closely related families Apocynaceae and Asclepiadaceae. One of the points he raised was the problem of the derivation of the bilocular anther of the subfamily Cynanchoideae from the basic 4-locular type shared by other Apocynales. Demeter, unfortunately, was unable to obtain either fresh or preserved material of the critically important genus *Secamone* to complete his studies; consequently, no developmental studies of the floral parts was possible. This led him to purely tentative conclusions. He advanced two explanations for the paired pollinia of *Secamone* anthers and wrote

“Es ist fraglich, ob dies ein Zeichen für Primitivität ist, insofern, als es hier noch zu keiner Reduktion gekommen ist, oder ob sich hier die pollinien, frühe rauch einfach, nun sekundär wieder, etwa durch eine, falsche Scheidewand.”

(It is questionable whether this is an indication of primitiveness, insofar as here it has still arrived at no reduction, or whether the pollinia, still simple in early development have perhaps become doubled secondarily by a false secondary wall.)

Demeter apparently favored the second hypothesis. He mentioned the case of *Thevetia nereiiifolia*, an apocynaceous plant. Here, he observed, the whole contents of the pollen sac do not develop into pollen but, in the formation of pollen mother cells, patches of tissue remain sterile and grow in bridge-like manner from one wall to the other of the pollen sac, just as in certain Onagraceae. Demeter continued with his conjecture and maintained that, perhaps in the same manner, the pollinia of *Secamone* could have become doubled by a false partition (as in certain ovaries), the polliniferous plates assuming a complanate position.

Such a purely hypothetical conclusion cannot be accepted unless it is supported by anatomical evidence. With this in mind an attempt was made to secure buds and flowers of species of the genus *Secamone*. Alcoholic preserves of flowers and floral buds were sent from the Royal Botanic Gardens, Kew, by the Director, Sir George Taylor, to whom I am particularly grateful. My thanks are also due Dr. H. Wild, of the Southern Rhodesia Government Herbarium, for preserved buds and flowers of *S. frutescens*, and Dr. R. A. Dyer, Director of the Botanical Survey of the Union of South Africa, for preserved material of *S. alpinii*.

Special attention was paid to the ontogeny of the anther, pollinia and the stigma head. The study then was extended to cover vascular anatomy and general morphology of the flower. The results obtained revealed interesting evolutionary information which was then applied to certain other groups in the Apocynaceae and Asclepiadaceae as well. From the comparative morphology and ontogeny of these groups certain new approaches to the problems of anther locule suppression, translator specialization, pollen formation and coronal evolution were possible.

MATERIALS AND METHODS

Serial transverse and longitudinal sections of flowers and floral buds of the species studied were prepared from material preserved in formalin-aceto-alcohol. The preserved material was embedded in paraffin either by the standard alcohol-

xylene method or through the tertiary butyl-ethyl alcohol procedure. Microtome sections were 6-10 μ ; aqueous crystal violet and erythrosin in clove oil produced satisfactory staining, rendering vascular tissue quite distinct. Fast green in clove oil and safranin (Johansen's methyl cellosolve formula) gave satisfactory results with the pollinium sacs and the translators. Harris' haematoxylin was also employed.

The species which were studied are listed below together with their sources and collectors, with their numbers whenever available.

SPECIES	SOURCE	COLLECTOR & NUMBER
<i>Secamone alpinii</i> Schult.	Botanical Survey of the Union of South Africa	
<i>S. frutescens</i> Decne.	The Southern Rhodesia Government Herbarium.	
<i>S. afzelii</i> (R. & S.) K. Schum.	Royal Botanic Gardens, Kew.	Onochie, F. H. I. 33276
<i>S. myrtifolia</i> Benth.	Royal Botanic Gardens, Kew.	Milne-Redhead 5116
<i>S. platystigma</i> K. Schum.	Royal Botanic Gardens, Kew.	Dawkins 610
<i>S. punctifolia</i> Decne.	Royal Botanic Gardens, Kew.	Drummond & Hensley 3617
<i>S. stenophylla</i> K. Schum.	Royal Botanic Gardens, Kew.	Drummond & Hensley 2769
<i>S. stenophylla</i> K. Schum.	Royal Botanic Gardens, Kew.	Faulkner 1718
<i>S. stuhlmannii</i> K. Schum.	Royal Botanic Gardens, Kew.	Milne-Redhead & Taylor 7597
<i>S. zambesiaca</i> Schult.	Royal Botanic Gardens, Kew.	Wild, S. R. G. H. 22621
<i>S. sp.</i>	Royal Botanic Gardens, Kew.	Drummond & Hensley 2794
<i>Periploca graeca</i> L.	Cornell University	H. E. Moore, Jr.
<i>Hemidesmus indicus</i> R. Br.	Poona, India	U. R. Desphande 60963
<i>Gonolobus barbatus</i> H. B. & K.	Nayarit, Mexico	Dressler & Wirth 2719
<i>Matelea quirosii</i> (Standl.) Woods.	Michoacán, Mexico	Dressler & Wirth 2747
<i>M. carolinensis</i> (Jacq.) Woods.	Gray Summit, Missouri	Safwat
<i>Cynanchum laeve</i> (Michx) Pers.	Washington University, St. Louis, Missouri	Safwat
<i>C. laxum</i> Bartl.	Missouri Botanical Garden, St. Louis, Missouri	Safwat
<i>Sarcostemma clausum</i> (Jacq.) Roem. & Schult.	San Luis Potosí, Mexico	Hewitson & Hunter 85
<i>Asclepias curassavica</i> L.	Missouri Botanical Garden, St. Louis, Missouri	Safwat
<i>Apocynum cannabinum</i> L.	Gray Summit, Missouri	Safwat
<i>Vinca rosea</i> L.	Florida	Woodson

FLORAL MORPHOLOGY AND ANATOMY OF SECAMONE

The calyx lobes are small, almost free and imbricate. Within them at the base a number of small glands are found. The corolla is gamopetalous, 5-parted, rotate or campanulate and contorted in aestivation. Frequently below the sinus

of the lobes one finds protuberances from the corolla tube, giving the appearance in serial sections of a corolline corona, as is well seen in *S. stenophylla* and certain other species.

The stamens are epipetalous with very short filaments which are free from one another or united for a very short distance. The anthers have very short lateral wings and are usually terminated by a small hyaline appendage which becomes inflexed upon the stigma head; the dehiscence is longitudinal. The staminal corona segments, rather simple filaments, are free from one another and attached to the staminal column or higher up the stamens, frequently bent inward and sickle-like, or are represented by a small hump on the dorsal side of the stamens.

Although the anthers of practically all species of *Secamone* have a thin hyaline apical appendage, that of *S. frutescens* differs in that the cells are glandular; it is not difficult to observe the secretion since it fixes in FAA and stains with safranin.

The two carpels usually are more or less subinferior and united only at their styler regions, where, together, they form the stigma head. The stigma head consists of a lower trapezoid structure of various configuration; above this it is sharply constricted and may be cylindrical-fusiform, as in *S. zambesiaca* (plate 2, fig. 1), *S. afzelii* and *S. myrtifolia*, or abruptly enlarged and broadly 2-lobed, as in *S. frutescens*, *S. platystigma*, *S. punctifolia*, and *S. stenophylla*. Within the ovaries the ovules are anatropous and borne on submarginal placentas.

In all the species studied the relative position of the stamens to the stigma head is the same, the anthers being slightly above the trapezoid body and forming jointly the well-known gynostegium of the milkweeds.

Vascular Anatomy—Two different patterns of vasculature were observed in the flowers of *Secamone* with many intermediate types in between. These two extremes are represented by *S. frutescens* and *S. stenophylla*. In the former the vascular supply to the calyx lobes is the 3-trace 3-lacunar type while in the latter it approaches the 1-trace 1-lacunar condition. The anatomy of these species will be discussed separately since they show other significant differences in their floral organization.

Secamone frutescens—The pedicel of a flower of *S. frutescens* is terete and has an amphiphloic siphonostele corresponding to that of a young stem of the plant, the xylem being embedded in a cylinder of protophloem parenchyma. The vascular cylinder superficially appears dissected and not continuous due to the fact that certain provascular cells have not been differentiated into xylem elements. Outside the vascular cylinder there are patches of laticiferous tissue.

The pedicellar wood consists chiefly of protoxylem with relatively scant development of metaxylem, no vessels being observed and the secondary walls of the tracheids being either spirial or annular.

The pedicellar stele expands and abruptly becomes increasingly lobed with five distinct and five alternate and less distinct salients becoming increasingly prominent. At this level the pedicel further expands together with the stele, and the traces begin to diverge; thus transition of the pedicel into the receptacle becomes clear.

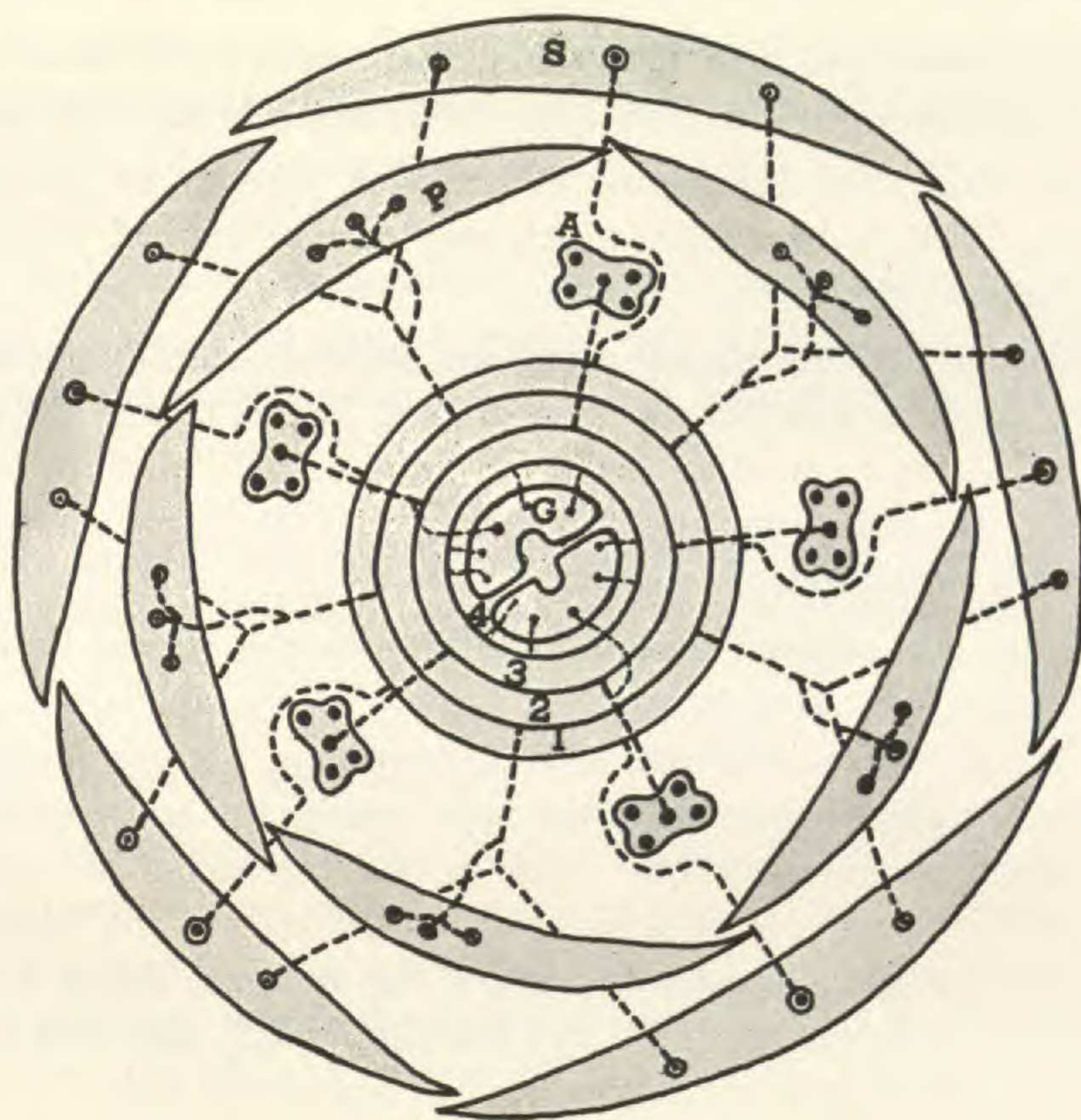
Five traces will form the midribs of the calyx lobes (text-fig. 1) and almost immediately above them five other traces leave the stele and traverse the receptacle for a short distance. Then each gives rise to two lateral traces, one of which will form the lateral bundle of one of the calyx lobes while the second will form the lateral bundle of the adjacent lobe. Thus, the calyx laterals are adnate to the corolla midribs, as also has been reported for certain Apocynaceae by Woodson and Moore (1938). Upon the departure of the calycine traces, phloem strands can be seen leaving the inner faces of the stelar phloem and invading the pith where they branch and anastomose as was also reported by Scott and Brebner (1891) in the stems and roots of certain Gentianaceae, Apocynaceae, Solanaceae and Plumbaginaceae. Woodson and Moore have observed the same in the pedicel and receptacle of certain genera of Apocynaceae.

After the departure of the calycine traces there appear 10 bundles, five large, which are destined to supply the stamens and five alternate and small, which will furnish the five corolline traces (text-fig. 1). At this level also a residual stele can be seen, in the center of the receptacle, which will supply the walls of the carpels and the ventral traces of the ovules. This is substantiated by the fact that the constitution of the residual stele is soon followed by the appearance of the two ovarian cavities. Soon the anatropous ovules make their appearance in the section.

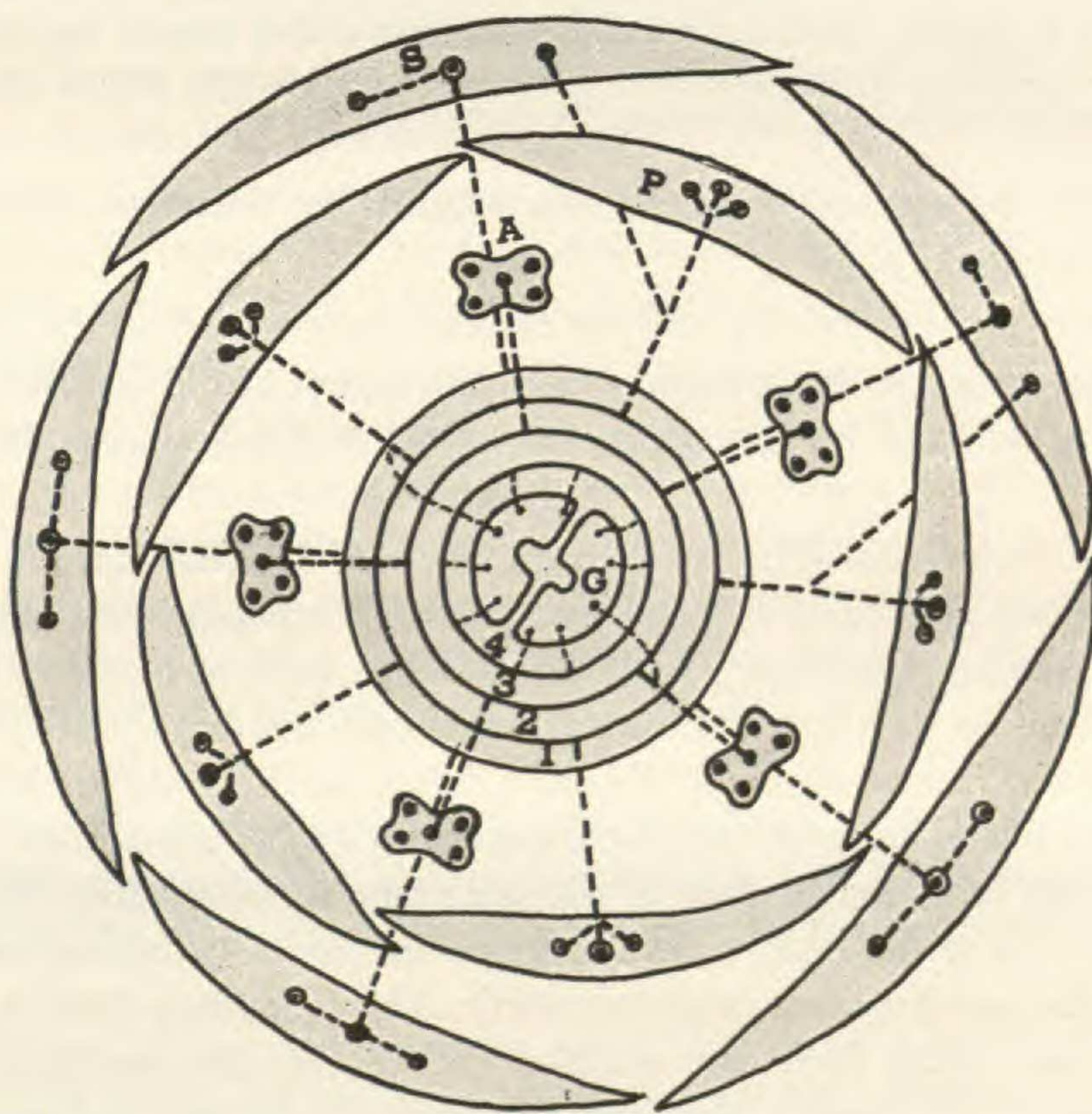
It is interesting to note that the placentas, although described in the Asclepiadaceae as well as in Apocynaceae as marginal, are in reality submarginal. The ovules are not borne on the whole surface of the placentas but rather on the inner side only (plate 2, fig. 2). Thus, there can be seen in serial sections that two small margins of each placenta are devoid of ovules. It is worth mentioning here that the sterile margins of the placentas are directed upwards instead of in the usual downward direction seen in Asclepiadaceae and Apocynaceae. This is also found in *Mandevilla*, an apocynaceous plant (see Woodson and Moore, plate 5). Baum (1949) by means of growth studies on younger stages of *Cynanchum vincetoxicum*, *Asclepias syriaca*, and *Erythraea centaurium*, showed that placentas of these plants are not inwardly folded carpel margins but arise from the submarginal upper face of the carpel; hence the placentas should be called submarginal.

While the two stamen bundles are giving rise to the two carpel dorsals, the calyx lobes begin to separate from the receptacle. This separation is continued while the two carpel walls are still united with the surrounding tissue. It is clear that the carpels are more or less subinferior, a character not found in other Asclepiadaceae but usual in Apocynaceae (Woodson, 1935). Soon the two apocarpous carpels start separating from the corolla-staminal tissue; at the same time the calyx lobes are completely freed from the corolline ring.

On the inner surfaces of the calyx lobes a number of small glands called "squamellae" are found. In this species, as in several others in the genus *Secamone*, the calycine squamellae are usually on three of the five calyx lobes; the outer are devoid of them. Each gland consists of a central core surrounded by a palisade layer of glandular epidermal cells. No vascular tissue was observed in these small



1



2

Text-fig. 1. Diagram of the floral vasculature of *Secamone frutescens*.
 Text-fig. 2. Diagram of the floral vasculature of *Secamone stenophylla*. S: calyx lobes,
 P: corolla lobes, A: stamens, G: carpels, 1-4 consecutive residual steles.

bodies. Similar glands have been reported in Apocynaceae (Woodson and Moore 1938), and Asclepiadaceae (Woodson 1933, 1941, 1954; Holm 1950 and others).

Squamellae have been interpreted as modified stipules in Apocynaceae by Woodson (1930, 1938), a hypothesis which may also be applied to the obviously homologous glands of *Secamone*.

When separation of the carpels from the staminal-corolline tissue is completed, the five corolline bundles give rise to their lateral traces. Soon the styles of the two carpels unite to produce the stigma head, and the stamens become freed from the corolla. It can be seen in serial sections that the stamens are close to the stigma head with no adnation apparent.

The wings of the adjacent anthers, jointly with the stigma head, form the stigmatic alar chambers. Five interrupted patches of the epidermal cells of the stigma head in all species sectioned, save *S. frutescens*, become protuberant and project into the five alar chambers. In the latter species the entire epidermal layer of the stigma head becomes papillate. And, as one approaches the regions of the stigma head which bear the translators, not only the cells of the stigma head become protuberant but also the adjacent cells of the stamens; this is a well-known character in many Apocynaceae. Frye and Blodgett (1905) described the relationship between the anthers and the stigma head of *Apocynum* thus

“Immediately beneath the anther locules is a beard of epidermal hairs extending transversely across the faces of the anthers, forming a ring around the stigmatic head (figs. 1, 2, b). These hairs meet similar ones from a ring around the head, thus preventing pollen from falling into the base of the flower.”

This situation is another primitive feature retained in *Secamone* although in a reduced, nonfunctional state.

At a slightly higher level the stamens become appressed about the stigma head but not adnate—thus, the gynostegium. Soon the region of the translators appears in the sections followed by the appearance of 20 pollinium sacs, two in each anther lobe.

Secamone stenophylla—The pedicel of a flower of *S. stenophylla* is an amphiphloic siphonostele like that of *S. frutescens*. The stele expands below the receptacle and becomes 5-lobed, contrasting with the 10-lobed stele of *S. frutescens*. From the five angles of the stele five traces leave and supply the calyx lobes (text-fig. 2). The origin of the lateral traces of the calyx lobes, however, differs from that of *S. frutescens*; a lateral trace of one of the outer calyx lobes arises from a corolline bundle while the other lateral trace of the same lobe is derived from its own midrib. Similarly, one of the inner calyx lobes receives one of its lateral traces from a corolline bundle and the other from its midrib. The remaining three lobes receive their lateral traces from their own midribs. When the calycine traces leave the stele, there remain 10 bundles, five large, and five alternating and smaller; these are the staminal and corolline bundles respectively.

The ovarian cavities make their appearance rather high in serial sections and their walls are supplied by many slightly lignified bundles. The origin of the

dorsal bundles of the two carpels is different. One of the carpels receives its dorsal trace from a staminal bundle, while the other receives its dorsal trace from a corolline bundle. The apocarpous carpels are united with the staminal filaments slightly above the receptacle.

As the carpels free themselves from the staminal filaments, the corolline bundles give rise to their lateral traces, and the epipetalous stamens become separated from the corolla tube; at this level the carpels become close to one another and finally fuse to form the stigma head. The stamens soon become appressed to the stigma head, unlike those of *S. frutescens*, but still there is no adnation. The areas of the stigma head between the adjacent anther wings show marked protuberances, and these project into the alar chambers. At this level, also, the five corona lobes become separated from the stamens. The corolla tube is provided with about 15 more or less conspicuous vertical ridges which are considered as a corolline corona by some authors.

Calycine Vasculature of Other Species—Several intermediate types of vasculature occur between the two extremes just mentioned. For example, in *S. myrtifolia* one of the outermost calyx lobe traces gives rise to a lateral trace of the adjacent lobe; in *S. zambesiaca* one of the lateral traces of the calyx lobes arises independently from the stele while the dorsal bundles of these lobes give rise to the other lateral trace of each lobe; an innermost lobe, however, receives a single trace which in turn forms its own laterals. In the few examples of calycine vasculature mentioned, one can follow a gradual trend from the strictly 3-trace 3-lacunar type to a condition which approaches the 1-trace 1-lacunar condition. Woodson and Moore have classified an assemblage of genera and species of Apocynaceae with a combination of different types of calyx vasculature under their type IV; they would consider the type represented by *S. frutescens* as more primitive than the types which approach the 1-trace 1-lacunar condition predominant amongst the majority of Gamopetalae.

Ontogeny of the Pollinium Sacs—In a cross section of a very young anther of *S. frutescens* no differentiation of the sporogenous tissue is apparent (text-fig. 3). In a later stage, however, four plates of hypodermal cells become apparent at the four angles of the anther, each 3-4 cells long (text-fig. 4). These are the arche-sporial cells; and, hence, a 4-locular condition is evident from the beginning. These hypodermal cells undergo a tangential division to produce a primary parietal layer outward and a primary sporogenous tissue inward (text-fig. 5). The cells of the outer layer divide both tangentially and anticlinally to produce from 3-4 layers, the innermost of which is the uninucleate tapetum (text-fig. 6 and plate 3, fig. 1). A few cells on the inner side of the primary sporogenous tissue undergo division to produce the inner tapetum, which is frequently 1-2 layers thick. Thus the tapetum has two different origins and evidently serves, through differing secretions, both for nutrition of the developing pollen cells and as a binding substance for the resulting tetrads to group them into the pollinium sacs.

The primary sporogenous cells act directly as pollen mother cells without giving rise to daughter cells. There are from 3-4 pollen mother cells within each

anther locus and these are radially elongated (plate 3, fig. 2). However, unlike other members of the Cynanchoideae, the two ends of the pollen mother cells are not always the same in width and the shapes of the cells are complementary one to another. The two outer cells are more or less similar in width at both their upper and lower ends, while the middle cell has one end narrow and the other, wide.

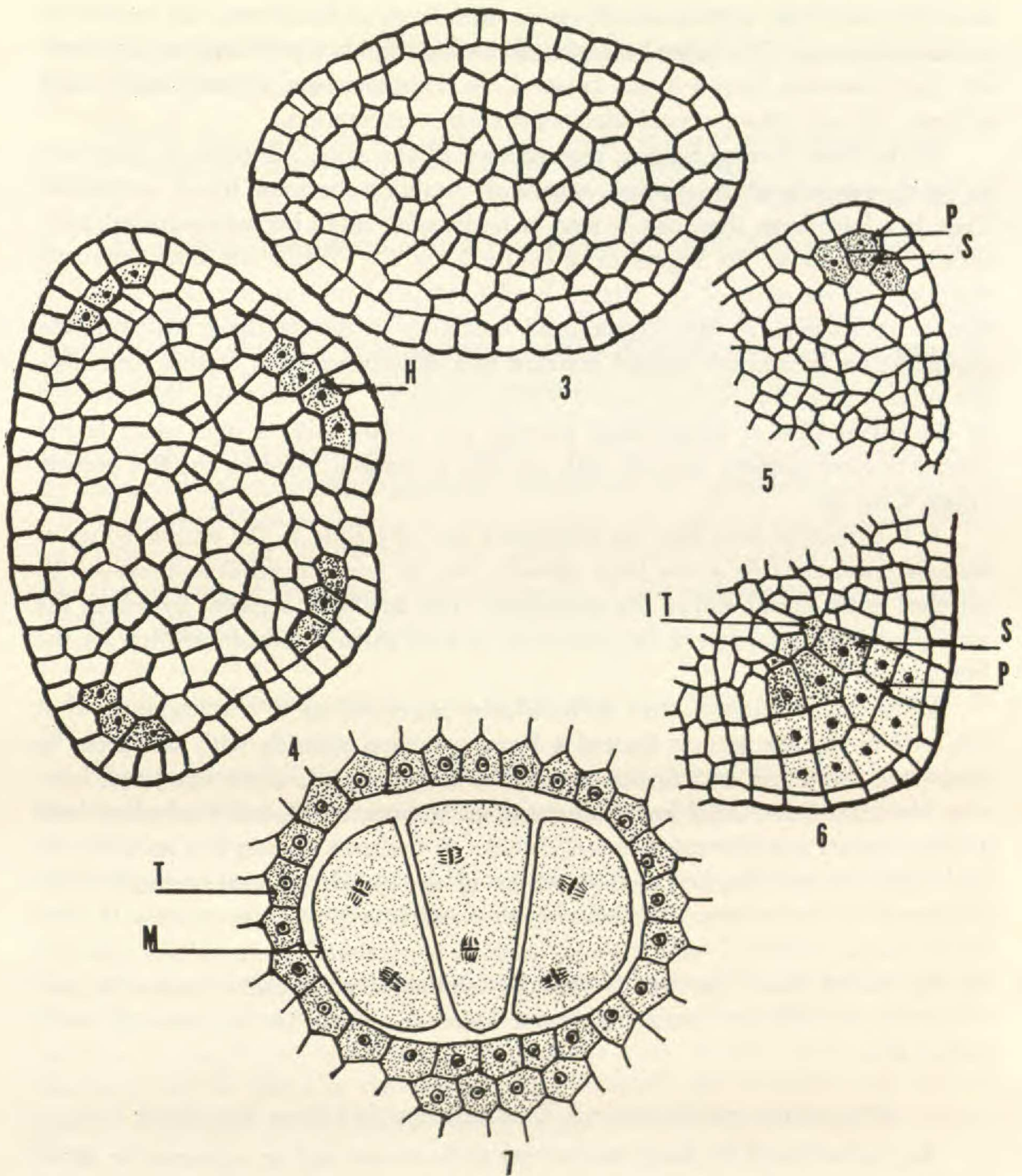
The nuclei of the pollen mother cells undergo two simultaneous meiotic divisions as seen in text-fig. 7; cell wall formation between the four daughter nuclei is slightly delayed. The ultimate configuration of the resulting tetrads depends upon the direction of the second meiotic spindle. Accordingly, the two lateral pollen cells form a rhomboidal tetrad while the middle result in a T-shaped tetrad (plate 3, figs. 3-4).

The tapetum persists for some time after the formation of the tetrads, which are not separated from one another but continue to lie in a solid mass. The thin walls of the pollen mother cells stain with fast green in the early stages of their maturation; but, as the tapetum becomes disorganized, the outer walls of the pollen mass, as well as the walls within, become thickened and show strong affinity for safranin. At maturity, each tetrad of pollen is enclosed within its compartment of thickened walls. Besides these common walls, each individual pollen grain has its own thin intine. When the pollinium sacs are mature, the anthers dehisce longitudinally by means of hypodermal mechanical cells as in the Apocynaceae and the subfamily Periplocoideae of Asclepiadaceae, in contrast to the apical pores of the majority of Cynanchoideae of the latter family.

The pollinium sacs of most of the species are more or less globular, each translator carrying four sacs belonging to two adjacent anther halves; but in *S. alpinii* and *S. myrtifolia* they are elongated. In serial transverse sections of the anthers with globular pollinia the four anther locules appear all at the same level; where pollinia are elongated, the locules appear in serial transverse sections at two different levels. The inner locules (the ones closest to the stigma head) are vertical and the pollinium sacs are erect within them, but the outer locules and their included pollinium sacs are obliquely horizontal. Upon attachment to the translator, however, both inner and outer pollinium sacs become horizontal due to inflexion of the anthers.

Ontogeny of the Translators—The development of the translators was followed in *S. frutescens* and *S. alpinii*. In a young bud of the latter (slightly less than 1 mm. in diameter), the stigma head shows a roughly circular contour surrounded by closely packed glandular epidermal cells slightly below the level of the anther locules. The anthers are closely appressed to the stigma head, but there is no adnation. At such a level, the stigma head is provided with five vertical protuberances between the adjacent anther wings. As the two lobes of the stamens become clear in serial sections, the stamens become appressed to the stigma head at only 10 points of the anther lobes. The five grooves of the stigma head between the adjacent anthers, so customary in mature flowers, are not differentiated until the time at which the pollen is fully mature.

At the time of pollen development the five grooves of the stigma head are lined with closely-packed glandular cells (plate 5, fig. 2). These cells stain darker



Text-fig. 3. Transverse section of an undifferentiated anther (X 700).

Text-fig. 4. Transverse section of a young anther showing the four hypodermal plates (H), (X 700).

Text-fig. 5. Transverse section of an anther showing the first periclinal division of a hypodermal plate. Primary parietal cell (P). Primary sporogenous cell (S), (X 710).

Text-fig. 6. Further development of the anther. Origin of the inner tapetum (IT), (X 600).

Text-fig. 7. Pollen mother cells (M) undergoing two simultaneous meiotic divisions and surrounded by the tapetum (T), (X 800).

than the rest of the epidermal cells in *S. alpinii*; in *S. frutescens*, the contrast is not so pronounced. The lateral margins of the five stigmatic grooves show a yellowish lipoid secretion in two bands (plate 4, fig. 1); these bars, stained lightly with safranin, did not take a crystal violet-erythrosin combination.

As the buds develop further, the secretion of the same substance is continued by the deeper cells of the grooves, apparently secreting the same lipoid compound. Thus, in a later stage, there can be seen in sections five small horseshoe-shaped, non-cellular bodies near the stigma head (plate 4, fig. 2). While the buds approach maturity the secretion of the stigma head continues, but the secretion is not as firm as previously. As the stigma head continues to secrete the translators, the products thus formed are pushed outward and slightly upward; at this time also, the areas opposite the anthers secrete similar material. The substance thus secreted by the stigma head is accumulated between the anther lobes as five small bodies similar in their staining reaction with safranin to those secreted by the five grooves (plate 4, fig. 4).

It is curious to note that the translators are very close to the anther wings at maturity, and the tips of the latter actually can be seen—in serial sections—to be attached to the dorsal slits of the translators. This might be a means by which the anthers give some support to the translators to keep them in proper position for the insect visitors.

When mature flowers were sectioned, the entire surface of the stigma head at the level of the five grooves showed a foamy secretion staining with fast green in contrast to the firmer safranin-staining bodies first produced; above this level, however, the horseshoe-shaped bodies appeared in sections which previously had been pushed upward and outward (plate 4, fig. 3). At the time of complete maturity the pollinium sacs are attached to the portions of the translators nearest them at the dehiscence of the anthers. This attachment is either vertical, as is the case in most of the species sectioned, or horizontal as in *S. alpinii* and *S. myrtifolia* (plate 2, fig. 4). In the latter, the four horizontally-elongated pollinium sacs can be seen occupying two different levels and appear in serial sections one at a time in either anther lobe.

POLLINIUM AND TRANSLATOR DEVELOPMENT IN OTHER ASCLEPIADS

An evaluation of the floral mechanism of *Secamone* and an appreciation of the floral evolution of the Asclepiadaceae must be based upon comparative studies of both more primitive and more advanced genera. For this purpose I have selected *Periploca graeca*, of the Periplocoideae, and *Asclepias curassavica* and *Cynanchum laeve*, of Cynanchoideae.

Periploca graeca—The ontogeny of the anthers of *P. graeca* is essentially as it is in *Secamone*, except that the four archesporial plates are each from 10-12 cells long and that in the formation of the inner tapetum many cell divisions take place. The entire tissue embraced by the concavity of the sporangia acts as inner tapetum (plate 6, fig. 4). This conclusion is supported by the fact that the nuclei of these cells are paired, as are those of the 1-layered outer tapetum; and, at a later stage of development, the cell walls of this tissue become extremely delicate and difficult

to distinguish. Similar observations have been made by Rao and Rao (1954) on *Cryptostegia grandiflora* of the same subfamily. In *Vinca rosea*, an apocynaceous plant, Boke (1949) observed that

“Within the sporogenous cells, deeper cell layers contribute to the tapetum and in this region it is frequently more than one layer in thickness,”

which I have corroborated (plate 6, fig. 3).

The primary sporogenous cells may undergo periclinal division to form elongate daughter cells which serve as pollen mother cells; or, more often, they themselves act directly as pollen mother cells. In either event they undergo two simultaneous meiotic divisions, as in *Secamone*, various Apocynaceae, and other members of the subfamily Periplocoideae of Asclepiadaceae. The resulting pollen tetrads are tetrahedral and isobilateral together with some intermediate types depending on the direction of the second meiotic spindle. Similar observations have been made by Rao and Rao (1954) on *Cryptostegia grandiflora*, and by Nirulla and Richharia (1945) on *Hemidesmus indicus* of Periplocoideae and by Sax and Husted (1936) on *Periploca sepium*. In the latter two species, however, the authors have reported also the presence of linear and T-shaped tetrads in one and the same anther locule.

The ontogeny of the translators of *P. graeca* was extensively and correctly studied by Demeter (1922). I have nothing to add to his basic findings, although a few additional details which lend significance to a later discussion should be added here.

The translators of the Periplocoideae are rather unique in both structure and development. A translator almost always consists of an open cartilagenous shovel- or cornucopia-like structure which is lined with a foamy secretion and, at maturity, receives pollen tetrads from adjacent anther halves. Below this is a stalk which ends in a basal adhesive disc (plate 5, fig. 4). Both the stalk and the disc aid the process of pollination through the insect visitors. Delpino (1867) has described this process and found that, when an insect visits a flower of *Periploca*, the adhesive disc may become attached to its tongue or other parts of its body by the sticky surface. As the insect removes a translator the stalk becomes bent; and, when another flower is visited by the same insect, the shovel and its pollen may become inserted between any two adjacent anthers upon the receptive surface of the stigma head.

Ontogenetic studies of the translators reveal that the secretion of the translators is restricted to five vertical grooves of the stigma head (plate 5, fig. 3). The side walls of each groove commence secretion at only four isolated marginal points—two at the upper end of a groove, and two at the lower. Later, two patches of deeper glandular cells at both ends within the grooves begin to secrete similar material; thus bring together the previously secreted pairs of plates. An essential difference between the order of secretion of upper and lower parts of a translator is that in the former the first-secreted substance of the stigma head is a foamy-alveolar type and stains with fast green. This substance is important because it lines the shovel of the translators and thus aids in keeping the pollen tetrads adhering to its surface. This frothy substance is then followed by another secretion from the

same glandular cells of the stigma head, except that this new secretion is a more or less solid substance which stains with safranin. From the two substances, and in the order of secretion just mentioned, the shovel is produced. The lower portions of the five grooves of the stigma head also are lined with glandular cells; but the order of secretions is reversed—first hard, then foamy. The first solid compound is pushed outward and slightly upward by a more alveolar substance secreted by the same cells. The lower portion of the translators consists of the stalk and an adhesive disc. At maturity, the shovel and the stalk are joined and the process of translator formation is completed.

Asclepias curassavica—Woodson (1954) studied the ontogeny of the pollinium sacs of four species of *Asclepias*. He pointed out for the first time that the tapetum on the dorsal side of each locule is massive while that on the ventral side is uniseriate or at most biseriate, and that there are two distinct functions reflected in this differentiation. Woodson's observations agree with the organization mentioned above for *Periploca graeca* and *Cryptostegia grandiflora*. I have observed the same in species of *Cynanchum* and *Matelea* as well as in *Asclepias curassavica*.

The ontogeny of the anthers of *A. curassavica* is essentially as that in *Secamone* except that only two archesporial plates are developed, which anticipates the presence of but two locules (plate 6, fig. 1).

The tapetum of the dorsal half of each anther locule, which is derived from the plate of cells dorsal to the primary sporogenous tissue, becomes massive and multiseriate (plate 6, fig. 2). As the tapetal cells develop further, they become vacuolate and contain certain lipoid bodies which stain very prominently with safranin. This was first observed by Woodson (1954) in *Asclepias*. I have observed the same in species of *Cynanchum* and *Matelea* as well as in *Asclepias*. At maturity, both the ventral and the dorsal tapetum become disorganized but the latter persists for some time after the disappearance of the former—as in *Periploca*. The cells become 1- to 3-nucleate at maturity and the cell walls become increasingly delicate. The tapetum of the milkweeds as well as of the apocynads is the secretory type and in *Asclepias*, as in *Secamone*, it is highly evolved, certainly performing a dual function; thus it seems that the ventral tapetum serves as a nutritive source for the development of the pollen, whereas the dorsal contributes to the formation of the pollinium sac membrane and in binding the pollen tetrads together.

The primary sporogenous cells act directly as pollen mother cells without giving rise to daughter cells. These cells undergo striking radial elongation. Each mother cell undergoes two meiotic divisions which are successive. Thus, after the first division, a cell wall is formed between the resulting diads (plate 6, fig. 2); the other division takes place to produce the tetrads. The tetrads in *Asclepias*, as well as in other genera of the subfamily Cynanchoideae except *Secamone*, are linear in their composition, the two meiotic spindles being parallel to the long axis of the pollen mother cells. Further details of development of the pollinium sacs are found in Woodson's work (1954) as well as in that of others.

Cynanchum laeve—The ontogeny of the translators of *C. laeve* is quite similar to those of *Asclepias cornuti* (= *A. syriaca*) studied by Corry (1883) and of *A. curassavica* by Woodson (1954).

In very young buds of *C. laeve* the stigma head consists, in cross section, of a roughly circular structure with no trace of the system of grooves so characteristic of this organ in mature buds; at this time it does not seem to be different from that of Apocynaceae and other Asclepiadaceae. Soon, however, five primary vertical grooves become differentiated and from either side of each there develops secondarily a less-pronounced, obliquely descending furrow (text-fig. 15). The primary grooves as well as the secondary furrows are lined with many narrow, compactly-arranged cells which stain prominently with safranin.

The first indication of the translator apparatus is initiated as two lines of lipoid substance secreted by the margins of the five grooves. This is continued until finally the inner cells of the grooves join in the secretion as well. This structure, which is the corpusculum or "gland," is 2-parted in early stages of development and, consequently, has a dorsal slit at maturity. The dorsal slit aids in the withdrawal of the pollinium by becoming the organ of attachment to the body of insect visitors. At maturity the corpusculum becomes dark brown and is very hard, with vertical striations corresponding to the cells of the grooves which have secreted them. The cells of the lateral secondary furrows secrete a less rigid substance to produce the translator arms. (text-fig. 14).

DISCUSSION

Except for the small tribe Secamoneae, the anthers of all members of the subfamily Cynanchoideae of Asclepiadaceae have but two locules. In this tribe, however, as well as in the subfamily Periplocoideae and in all Apocynaceae, the anthers are 4-locular. The question arises whether there is any evidence of suppression or fusion of microsporangia in early stages of development of the anthers of Cynanchoideae.

Several morphologists have investigated this problem—Frye (1901), Gager (1902), Richharia (1934) and others—but almost all agree that there is no evidence provided by ontogenetic studies of several genera. Engler (1876) came to the empiric conclusion that only the anterior locules are developed and believed that the posterior locules become diverted to the formation of the hyaline appendage of the anthers. Demeter (1922) came to the conclusion that the outer locules have been transformed into the lateral anther wings of the Cynanchoideae which he calls "Leitschienen." Both assumptions seem wholly gratuitous in the complete absence of evidence of such transition.

Demeter (1922) attacked the problem of suppression of anther locules through the study of the closely-related family Apocynaceae, finding that, in the Plumerioideae, the four locules are filled with pollen whereas, in the more advanced subfamily Echitoideae, the posterior locules are partially empty while the anterior are more fully developed. From such observations he concluded that, perhaps in the same way, the bilocular anthers of the Cynanchoideae may have been derived.

My own studies tend to confirm the view that the 2-locular anthers of Cynanchoideae have been derived from a primitive 4-locular condition, but from other considerations. First, the two hypodermal archesporial plates appear in exactly the same position as do the ventral pair of locules in the Periplocoideae, *Secamone*, and Apocynaceae. It seems that suppression of the two locules of the anthers of Cynanchoideae is due simply to the failure of the corresponding hypodermal plates to differentiate in the early ontogeny of the anthers. It is not necessarily true—as Engler and Demeter assumed—that a lost plant organ must be transformed to perform another function. Second, the staminal bundle of all bilocular anthers of Cynanchoideae occupies a position very close to the dorsal epidermis of each anther and dorsal to the locules, while the same bundle occupies a position nearly between the dorsal and the ventral anther locules in the 4-locular anthers. The most interesting evidence to support the assumption of a suppression of the dorsal locules is derived from the origin of the complementary layers of tapetum in the anthers of both Asclepiadaceae and Apocynaceae.

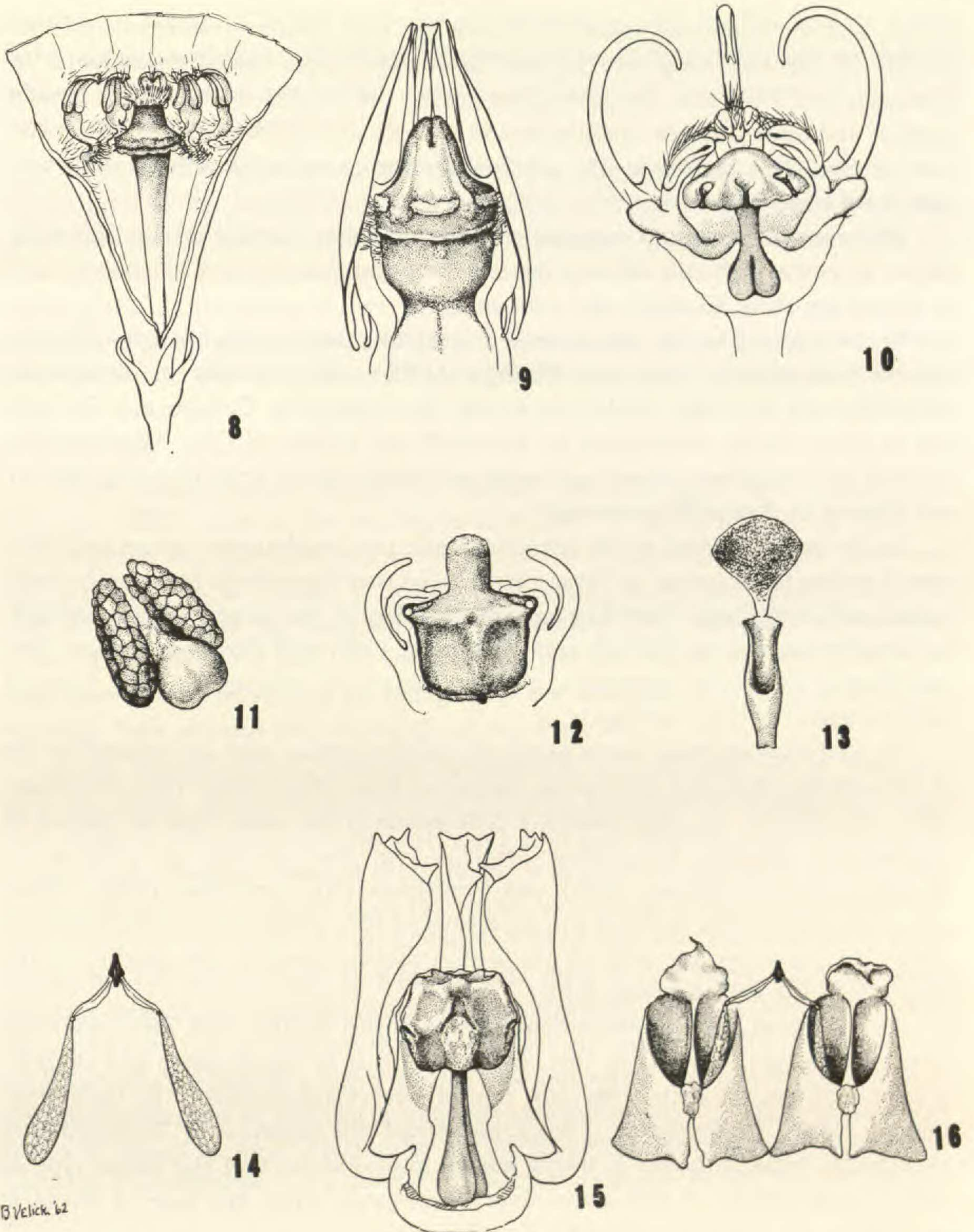
The dual origin of tapetum in many families of flowering plants is a well-established fact which is best expressed by Macré and Thomas (1930), who wrote

“Les tapis externe tire son origine, comme les cellules mères primordiales du cloisonnement de l'assise staminale sousépidermique Les cellules qui constituent ce que nous appelons le tapis interne, elles, tirent leur origine de cellules banales du connectif. Malgré cette diversité d'origine, elles évolueront exactement de la même manière que les cellules du tapis externe; souvent même (*Solanum Dulcamara* L., par exemple), ces caractères spéciaux appaissent d'abord dans les cellules du tapis interne.”

Frequently the inner tapetum of the Asclepiadaceae and Apocynaceae is more than one layer thick. In certain genera as *Asclepias*, *Periploca*, and *Cryptostegia*, the inner tapetum of the anther locules is very massive. In *Asclepias*, the inner tapetum of the two locules is oriented toward the vascular trace (i.e., dorsally), creating the impression that they represent the ventral locules of primitive 4-locular anthers, with the two dorsal locules having disappeared without a trace. This conclusion is based on a comparative study of *Periploca* where there are four anther locules with the tapetum in all cases oriented toward the vascular bundle.

An interesting aspect of the ontogeny of the anthers of *Secamone* is the development of the pollinium sacs. A pollinium, in a general sense, consists of a body of tetrads which are transferred en masse in pollination. This structure so characteristic of the Cynanchoideae is not restricted to this group, however.

In the Apocynaceae the pollen at maturity is usually granular but remains in tetrads in certain genera of both Plumierioideae and Echitoideae (e.g., *Condylocarpon* and *Apocynum*, respectively). In Periplocoideae of Asclepiadaceae, the pollen grains are in tetrads but not enclosed within sacs, while in Cynanchoideae they are enclosed within definite chambered sacs. In Orchidaceae close parallelism may be found. Swamy (1949) has reported in some genera of Orchidaceae, as *Cypripedium* and *Vanilla*, that the pollen grains separate from one another and become free. In *Pogonia* the four cells of a tetrad adhere to form a “compound grain.” In the tribe Orchideae (Ophrydeae) and Neottiae this tendency is carried



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Text-fig. 8. Flower of *Vinca minor* longitudinally opened to show the relationship of the anthers and the stigma head (X 4).

Text-fig. 9. Flower of *Apocynum cannabinum* with two stamens removed to show the plates secreted by the stigma head (X 10).

Text-fig. 10. Flower of *Periploca graeca* with two stamens and one pollinium removed; two pollinia are in position within the grooves (X 5).

Text-fig. 11. Pollinium of *Secamone alpinii* (X 140).

Text-fig. 12. Flower of *S. alpinii* with two stamens removed, as in fig. 10 (X 14).

Text-fig. 13. Pollinium of *P. graeca* showing the shovel, stalk and adhesive disc (X 30).

Text-fig. 14. Pollinium of *Asclepias subulata* (X 16).

Text-fig. 15. Flower of *A. subulata* with two stamens removed to show the primary and two secondary furrows above the receptive surface of the stigma head (X 4).

Text-fig. 16. Two adjacent anthers of *A. subulata* to show their relationship to a pollinium (X 10).

farther, and the compound grains are themselves held together into mealy pollinia (which in the Orchideae are divided into small units called massulae). In *Coelogyne* and *Pholidota*, the microspore mother cells and their derivatives remain together and continue their development as a single unit; in more advanced genera, such as *Oncidium* or *Vanda*, the pollinia develop as coherent units and become quite hard in texture.

Pollinium formation is reported to occur in other families of the flowering plants, as in the subfamily Mimosoideae of the Leguminosae, in Chlaenaceae, and in several genera of Ericaceae and Juncaceae.

In the majority of the Apocynaceae the simultaneous pollen mother cell division is predominant. Frye and Blodgett (1905) observed this in *Apocynum*, Täckholm and Söderberg (1918) in *Vinca*, Rau (1940) in *Cerbera* and *Vallaris* and in many species investigated by Schürhoff and Müller (1937). Meyer (1938) reported the occurrence of both successive and simultaneous types of pollen mother cell division in *Rauwolfia canescens*.

In the Periplocoideae of the Asclepiadaceae, the simultaneous pollen cell division is predominant just as in Apocynaceae. The resulting tetrads are usually tetrahedral and isobilateral depending on the direction of the second meiotic spindle. In *Hemidesmus indicus* (Nirulla and Richharia, 1945) and *Periploca sepium* (Sax and Husted, 1936), the occurrence of linear tetrads in addition to other types of pollen tetrads has been reported.

In all Cynanchoideae investigated, the pollen mother cells are reported to be of the radially elongated type, as in *Asclepias* (Frye 1901; Gager, 1902; Woodson, 1954, and others). In other genera I have observed the same type in species of *Cynanchum*, *Matelea*, *Gonolobus*, *Stapelia*, and *Sarcostemma*, as well as in *Asclepias*, *Daemia* (Biswas, 1957) and *Caralluma* (Rao and Rao, 1954). These elongated mother cells undergo two successive meiotic divisions to produce tetrads, which are linear because both of the second meiotic spindles are parallel to the long axis of the pollen mother cells.

In *Secamone* of the Cynanchoideae, the pollen mother cell division is the simultaneous type, agreeing in this respect with that of Apocynaceae and *Periplocoideae*, and sharply contrasting with that of other Cynanchoideae. In the formation of tetrads in *Secamone*, I have mentioned the presence of T-shaped and rhomboidal types, although it might not be impossible to find the linear type as well if more species of this genus were investigated, since this type of tetrad is reported in the primitive subfamily Periplocoideae.

Formation of pollinium sacs in the Cynanchoideae does not necessarily require linear tetrads, although Richharia (1934) postulated

“that for the organization of pollinium the presence of linear tetrads as has been already said above is necessary and mechanical principles also demand this, hence with some variation here and there, as in *Hemidesmus indicus*, all members belonging to this group, Cynanchoideae, where pollinia are well organized, will exhibit linear tetrads, irrespective of their number of sporangia in each stamen.”

In the Apocynaceae the entire surface of the stigma head secretes a more or less sticky substance which in *Apocynum* reaches its maximum organization as five

amorphous bodies ("Teller" of Demeter) alternating with the five anthers (plate 5, fig. 1, and text-fig. 9). In all Asclepiadaceae so far investigated, there are definite regions of the stigma head which actually participate in the secretion of the more highly evolved translators.

In all species of *Secamone* investigated, the entire surface of the stigma head at the level of the translators becomes secretory, although the five grooves within which secretion is limited in more advanced genera are also present (plate 5, fig. 2). The areas of the stigma head opposite the anthers secrete a similar substance which accumulates in the form of five plates between the lobes of each anther. The secretion of the grooves alone is utilized in forming the translators; the superfluous secretion would appear to be solely vestigial. One can hardly avoid the reflection that this situation is reminiscent of an ancestral type which is more like the Apocynaceae.

From morphological studies of certain Asclepiadaceae and Apocynaceae, Demeter (1922) came to the conclusion that from the five-plate type of translator of *Apocynum* the most advanced translators of the Asclepiadaceae might have been derived simply by a "process of folding." In applying this principle, he believed that the shovel and the stalk-adhesive disc portion of a translator of *Periploca graeca* are homologous with the corpusculum and the translator arms of *Asclepias* respectively. Had he studied the ontogeny of the translator of *Secamone*, he would probably have avoided this homology, as we shall see.

In the Apocynaceae, a primitive development of translators can be seen in a very few genera. In the Plumierioideae, generally, the pollen is granular and there is no definite translator formation, although a viscous substance is secreted by the stigma head. Delpino observed in *Lochnera*, a member of this subfamily, that the pollen falls from the anthers upon the upper, non-receptive part of the ring of the stigma head in five heaps. In the subfamily Echitoideae the viscous secretion of the stigma head is retained and in a few genera, such as *Apocynum*, specialization is attained through the secretion of five plates alternating with the five anthers. It is curious to note that in *Apocynum* the pollen tetrads remain together at the time of shedding, due perhaps to a more evolved and specialized tapetum which functions through its secretion as a source of nutrition and perhaps aids in keeping the pollen grains in tetrads as well. To transfer the pollen tetrads by insect pollinators there has been a development of a simple pollinating apparatus in the form of the five plates.

In the Asclepiadaceae one can observe both elaboration and reduction of the pollinating apparatus in different groups. In the most primitive subfamily Periplocoideae, as in *Apocynum*, a tendency of the translators to form a pollen-receiving "shovel" is reached in *Periploca*. Within the same subfamily, the genus *Cryptolepis* is considered to be rather primitive because of the poorly developed translators, a fact which led R. Brown to include it within the Apocynaceae. Falconer (1845) more convincingly separated *Cryptolepis* from the latter and included it within the Asclepiadaceae. In describing the stigma head and the primitive translators Falconer wrote of

"five straight, shallow, narrow converging furrows, along which are laid as many very delicate, narrow-oblong or linear, bronze-coloured, horny-looking, transparent, membranaceous straps or appendiculae."

He observed that, although the flowers show the characteristics of Apocynaceae

"yet it is very evident that the plant described above has the whole accessory stigmatic apparatus of the Asclepiadeae . . . although in a less considerable degree of evolution . . ."

Evidently this type of translator is primitive insofar as the more elaborate shovel or pollen-receiving structure is not yet effected. The pollen tetrads fall onto the sticky ligular part from the adjacent anther lobes at maturity. From this type the more elaborate translator of *Periploca*, perhaps, has been derived through the development of the pollen-receiving structure—a condition which seems to be parallel to the development of similar structures—the five plates of *Apocynum*.

From ontogenetic studies of *Periploca graeca* Demeter (1922), and as I also observed, found that the secretion of a translator follows two different patterns. Thus, in the secretion of the shovel, the substance first produced by the glandular cells of the stigma at that level is a sticky, more or less alveolar substance; this, in a later stage, is followed by another more or less solid secretion. This order of secretion is reversed in the development of the stalk-adhesive disc region.

In *Secamone*, there is nothing equivalent to the shovel of *Periploca*, and the first indication of reduction is evident. It is not surprising to find this structure missing here, since the pollen tetrads are held together in definite pollinium sacs. The pollinium membrane is formed through the secretion of the highly specialized tapetum so characteristic of all Cynanchoideae. This condition certainly does not require a stigmatic adhesive—as in the case of Periplocoideae—to keep the tetrads together.

The secretion of the translators of *Secamone* in reality corresponds to that of *Periploca graeca* and is homologous to the stalk-adhesive disc composition of the latter. The conclusion is based on the ontogenetic studies discussed earlier. In the secretion of the translators of *Secamone*, there is greater emphasis on the solid portion which is larger, relative to the more fluid alveolar part than in the stalk-adhesive disc of *Periploca*, where the reverse is true. In the evolution of the translators, it seems that there has been a greater emphasis on the more solid portion than on the less rigid parts and that this condition has reached its maximum state in the most highly evolved asclepiads.

After having considered the ontogeny of the translators of Periplocoideae and *Secamone*, it is not difficult to correlate similar structures, but on a higher level of evolution, in Cynanchoideae. It is quite clear that the basic parts of a translator in the flowers of the highly evolved asclepiads are the same as in *Secamone*, i.e., a portion which clamps the pollination to insect visitors—the "gland" or more accurately the corpusculum—and a pair of appendages of less rigid substance to which the pollinium sacs are attached—the translator arms. In *Secamone* and members of the Periplocoideae, where only the five vertical, or primary grooves, of the stigma head exist, such a distinction between the translator arms and the corpusculum is not as clear as in *Asclepias*, for example. In the latter, as in other highly evolved

members of Cynanchoideae, one can distinguish two types of secretion of the stigma head: the corpusculum which is secreted by the glandular cells of the vertical grooves, and the two translator arms secreted by two lateral, obliquely descending furrows. Thus, the five areas of the stigma head of *Asclepias* correspond to the secretion of the translators and have the appearance of inverted Y-shaped templates (text-fig. 15). Since the oblique furrows are missing in *Secamone* it would seem that the entire translator apparatus is homologous with the corpusculum of the Cynanchoideae.

The term "corona" has been used variously by asclepiad taxonomists and, in many cases, genera within this family have been differentiated on the basis of the nature of such structures. Woodson (1941) has pointed out the danger in using this term in a very loose sense in the classification of the family. The terminology which he adopted to delimit what is meant by "corona" has the approval of recent authors (Lawrence, 1951); he recognizes three types of corona in the Asclepiadaceae: (1) a faucal annulus derived from the corolla tube, (2) a fleshy radial structure consisting of "various elaborations or enations of the staminal filaments only," (3) sterile appendages of the anthers.

In *Secamone* one may find a combination of all these coronas. In *S. stenophylla*, for example, there are both a staminal and a corolline corona; on the other hand, while in *S. alpinii* the staminal corona is highly developed and there is no corolline corona. In *S. frutescens* the staminal corona is poorly developed—almost lacking—but the apical appendage of the anthers is glandular. The only other species of *Secamone* reported without a staminal corona is *S. astephana*. In describing the latter Choux (1926) writes

"Les anthères présentent sur leur face dorsale dans le moitié inférieure deux côtes saillantes formant un triangle à sommet dirigé vers le haut. Mais il n'a sur le dos de ces anthères aucune trace de couronne. Cet organe fait donc ici entièrement défaut."

The corona of the Apocynaceae is usually of the faucal annulus type; in certain asclepiads this type has been retained; but certain others have been added. It is not impossible that the evolution of corona has followed several lines to produce the most specialized forms met in the Asclepiadaceae. The case of *S. frutescens* might represent a transitional step in the shift of the corona from the corolla tube, which is so predominant in the apocynads, to the stamens, so customary in the majority of the Asclepiadaceae.

Fahn (1953), after an extensive study of many species belonging to 52 families of flowering plants, came to the conclusion that

"the main phylogenetical trend of the location of the nectary in the flower is acrocentripetal, i.e., a migration of nectariferous tissue from the outer to the inner flower organs"

Similar conclusions have been drawn by Bonnier (1879), Daumann (1931) and W. Brown (1938).

If one accepts Fahn's notion, one is led to assume, in the case of *S. frutescens*, that the glandular apical appendage of the anthers is a secondarily acquired character and that the staminal corona is vestigial. The lack of a staminal corona in certain highly evolved Asclepiadaceae might support the view that such is a derived

condition. On the other hand, one might argue that the glandular nature of these appendages is a primary character and that the minute corona of *S. frutescens* is not a vestige of a once well-developed organ but rather represents the beginning of evolution of such a structure; the hyaline appendage commonly present in Cynanchoideae would then be construed as derived. In a very few cases, however, these appendages are fleshy, as was reported by Woodson (1941) in *Gonolobus* and *Fischeria*.

SUMMARY

Now that we have discussed several morphological problems in the Asclepiadaceae it may not be amiss to make a few phylogenetic comments. The two closely related families, Apocynaceae and Asclepiadaceae, have been distinguished from one another on the basis of the more specialized pollinia and translators of the latter. Several voices have been raised against this separation: A.-L. de Jussieu, Adanson, and Giseke in the early nineteenth century, Demeter (1922) and others. A. de Candolle (1844) and most contemporary botanists have retained Brown's original separation, while de Candolle hinted that he retained the separation fully aware that the only clear-cut distinction lies in the organization of the pollen. Baillon (1884), although accepting Brown's system, admitted that

“Les Asclepiadées ont tous les caractères des Apocynées, sauf de leur pollen qui est réuni en masse.”

Although there is a large gap between the highly-evolved asclepiads and the most primitive apocynads, the homologies of the most primitive members of the former and the most advanced forms of the latter are unmistakable. It is the degree of development of the pollinating apparatus which separates the two related families. However, this difference is not so striking when one carefully examines the process of pollination in both. One is led almost to believe that this is an orthogenetic evolution.

It has been frequently pointed out that the stigma head of the asclepiad flower differs from that of the apocynads in being more highly specialized and in having definite regions where the translators are secreted. This distinction does not hold true in *Secamone* where the entire surface of the stigma head secretes, although only five poorly-developed grooves contribute to the formation of the translators. Thus, in a member of the highly evolved subfamily Cynanchoideae, one finds a retention of a primitive trait so common in the Apocynaceae. In *Baisse*, an apocynaceous plant, MacFarlane (1933) describes a similar situation in which the five templates of the stigma head are present although the entire organ is glandular. It is quite obvious that the areas of the stigma head opposite the anthers in other Cynanchoideae have lost the ability to secrete during the course of evolution, due perhaps, to the adnation of those organs. In *Secamone* such interruption is avoided since the anthers and the stigma head are not adnate at the level of the translators.

Although the stigma head is not highly evolved in *Secamone*, the organization of pollen tetrads into definite pollinium sacs is a highly-evolved trait. This condition clearly demonstrates that not all of the floral organs advance or retrogress at the same rate or time in the course of evolution.

Although the presence of pollinium sacs in *Secamone* ties this genus with other Cynanchoideae, the type of tetrads and their formation differs markedly from other members of the subfamily. The pollen mother cells in *Secamone* have different configurations depending on their position relative to one another in an anther locule, unlike the elongate prismatic pollen mother cells of other Cynanchoideae. Each pollen mother cell in other Cynanchoideae undergoes two successive meiotic divisions to produce linear tetrads; this is not the case in *Secamone* where these cell divisions are simultaneous, in this respect agreeing with Periplocoideae and Apocynaceae.

The occurrence of the 4-locular anthers of Apocynaceae, Periplocoideae, and *Secamone* certainly presents a primitive character in contrast with the bilocular anthers of Cynanchoideae; *Secamone* does not present a false partition of the sporogenous tissue to simulate the customary 4-locular anthers as was postulated by Demeter (1922), but rather is archetypically 4-locular.

It is a common impression that in all Asclepiadaceae the two carpels are superior at maturity; in Apocynaceae on the other hand there are different degrees of ovary position from superior to essentially inferior (Woodson, 1935). In *Secamone* one frequently finds the carpels more or less subinferior, a situation not otherwise much different from the apocynads.

Phylogenetic classification essentially represents a continuous scale of measurement in which a hierarchy of quantification is as important as in the physical world. Emphasis of dissimilarity is no more important than emphasis on similarity in depicting the course of evolution. Unfortunately, otherwise very competent research would appear to upset the essential balance by the over-emphasis of differences; in other words, "splitting" all too frequently is not compensated by equally appropriate "lumping," with a resulting chaos that may well be more apparent than real. Whether to "lump" or to "split" is a question not to be decided upon the adequacy of our knowledge of a single population, or taxon, but rather upon the adequacy of our knowledge of related populations as well, in order to render both in better perspective as a whole.

In view of the present study, as well as from investigations of others, I am inclined to believe that phylogeny is better portrayed by combining Asclepiadaceae and Apocynaceae into a single family and re-subdividing the group into five subfamilies according to the degree and kind of specialization of the translator apparatus and the relationship between the pollen tetrads to one another at the time of maturity, thus: Plumerioideae, Echitoideae (or Apocynoideae), Periplocoideae, Secamonoideae and Asclepioideae.

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EXPLANATION OF PLATE

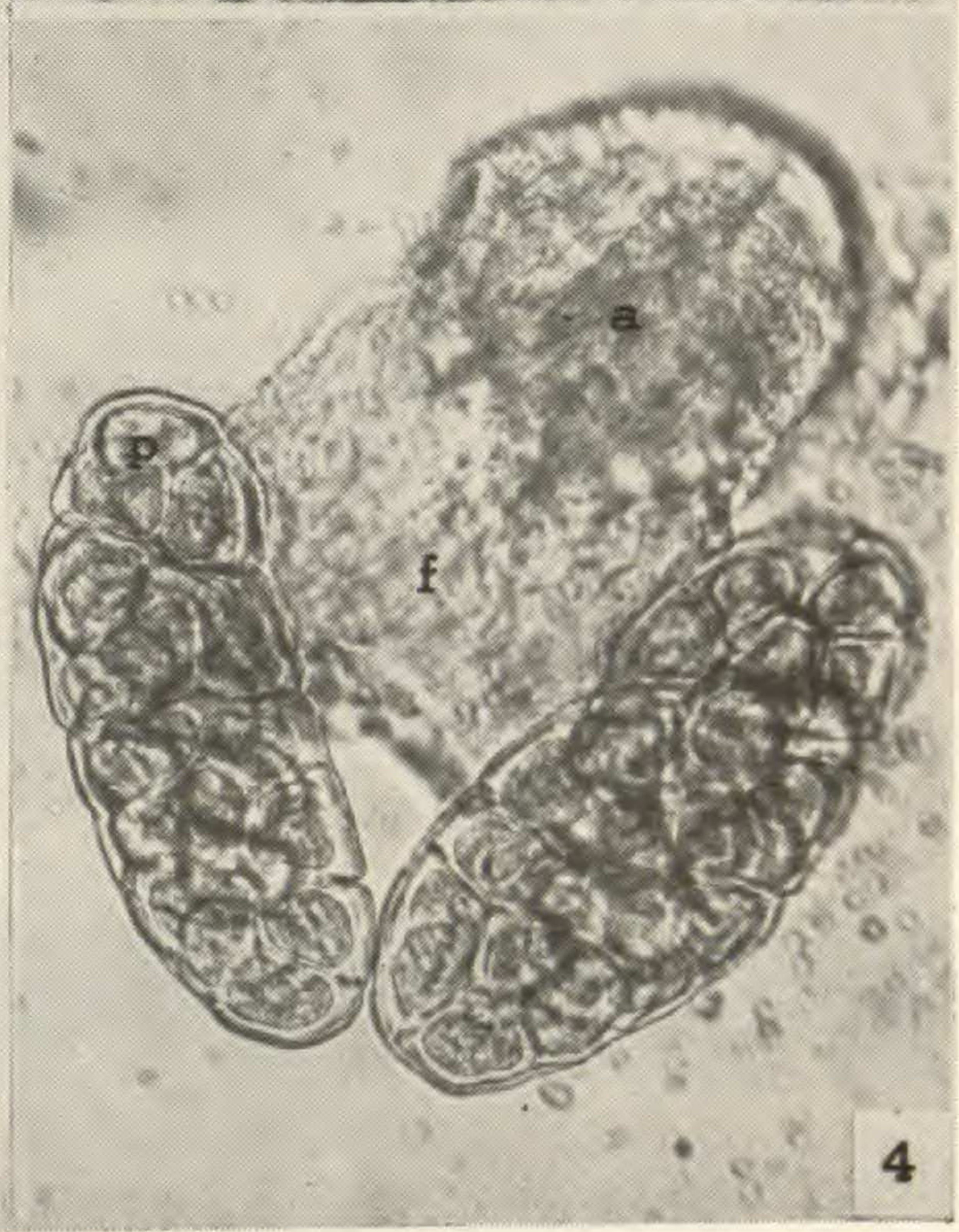
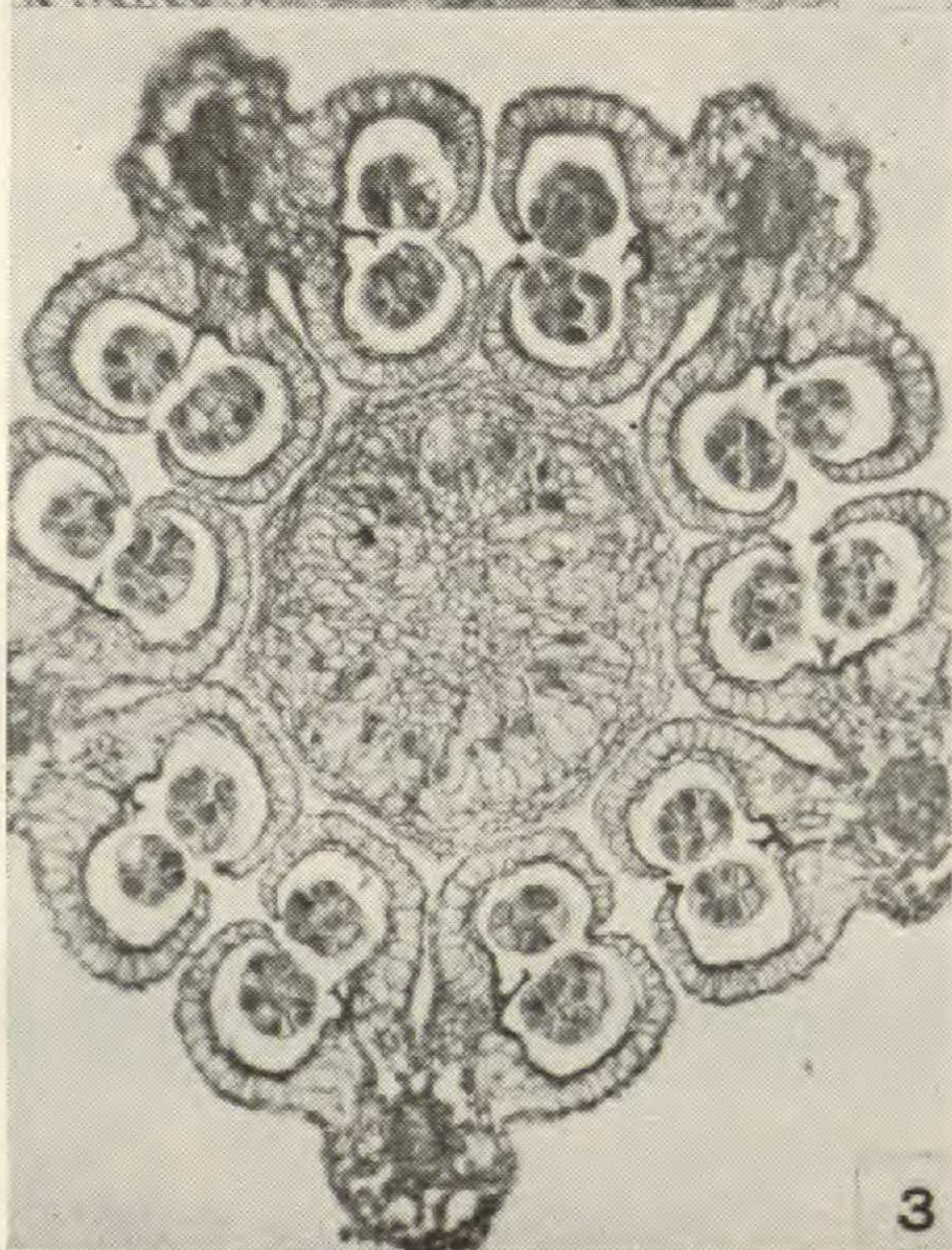
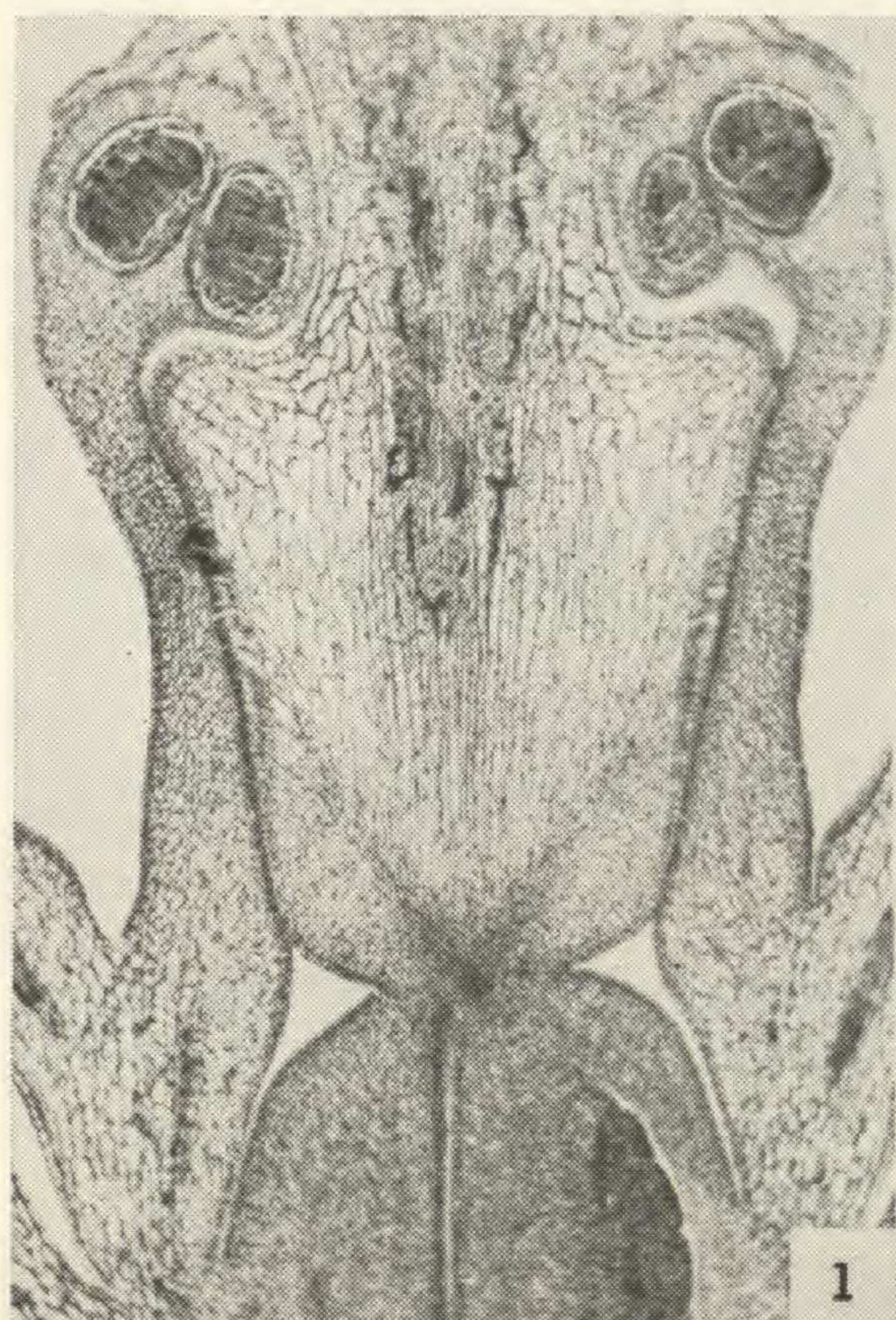
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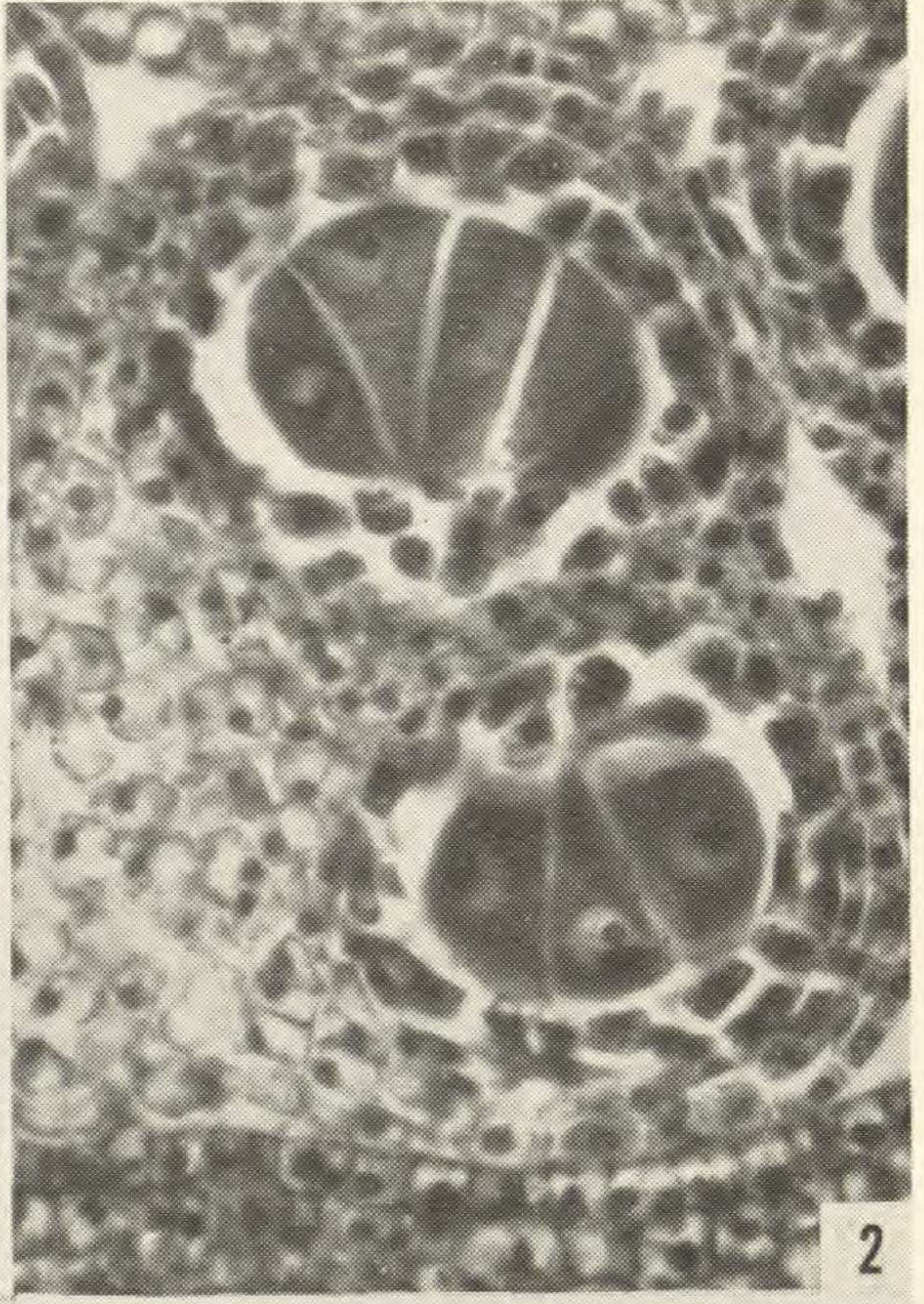
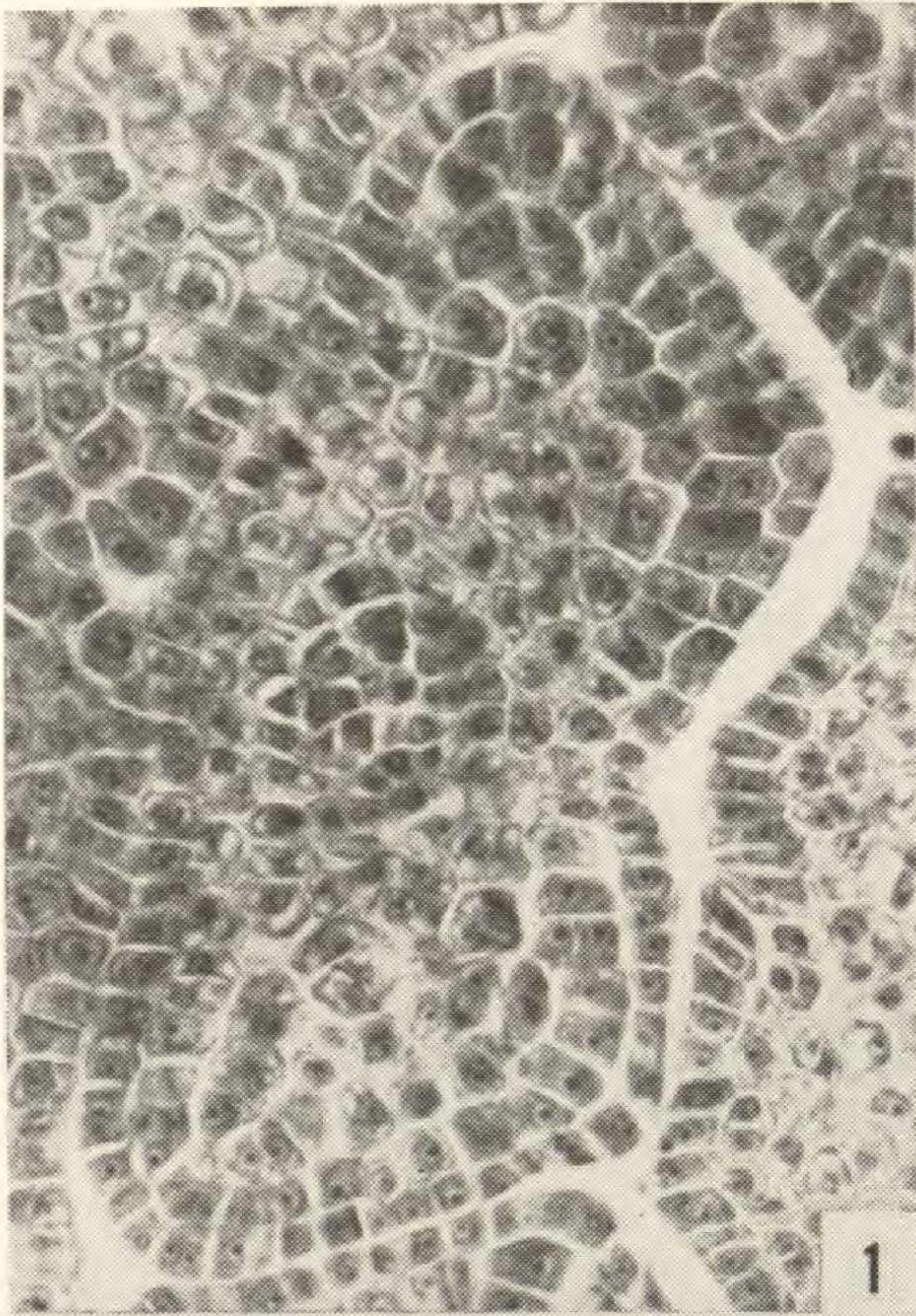
Fig. 1. Longitudinal section of a bud of *Secamone zambesiaca* (X 70).

Fig. 2. Transverse section of a carpel of *S. afzelii* showing the two sterile margins of the placenta (s) (X 300).

Fig. 3. Transverse section of a mature bud of *S. frutescens* showing the 4-locular anthers (X 75).

Fig. 4. Pollinium of *S. alpinii* (glycerin jelly mount) with translator and two of the four pollinium sacs: (X 500), horseshoe-shaped body (a), foamy substance (f), pollinium sac (p).





EXPLANATION OF PLATE

*Plate 3**Secamone frutescens*

Fig. 1. Transverse section of a young anther showing the division of the primary parietal cells (X 600).

Fig. 2. Transverse section of half an anther showing the pollen mother cells (X 500).

Fig. 3. Transverse section of half an anther shortly after the completion of the two simultaneous meiotic divisions (X 520).

Fig. 4. Transverse section of an anther locule showing the rhomboidal and T-shaped tetrads (X 570).

EXPLANATION OF PLATE

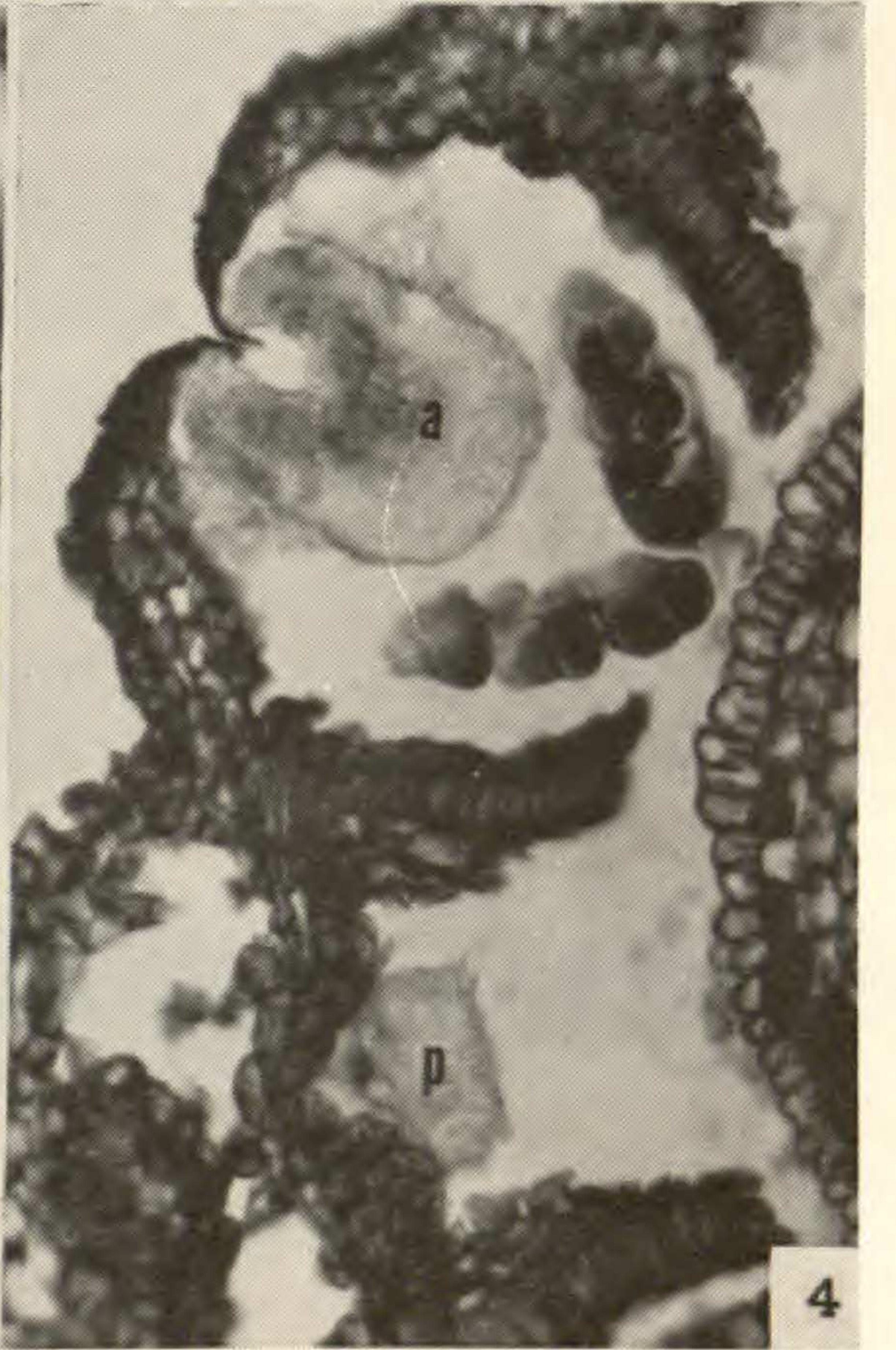
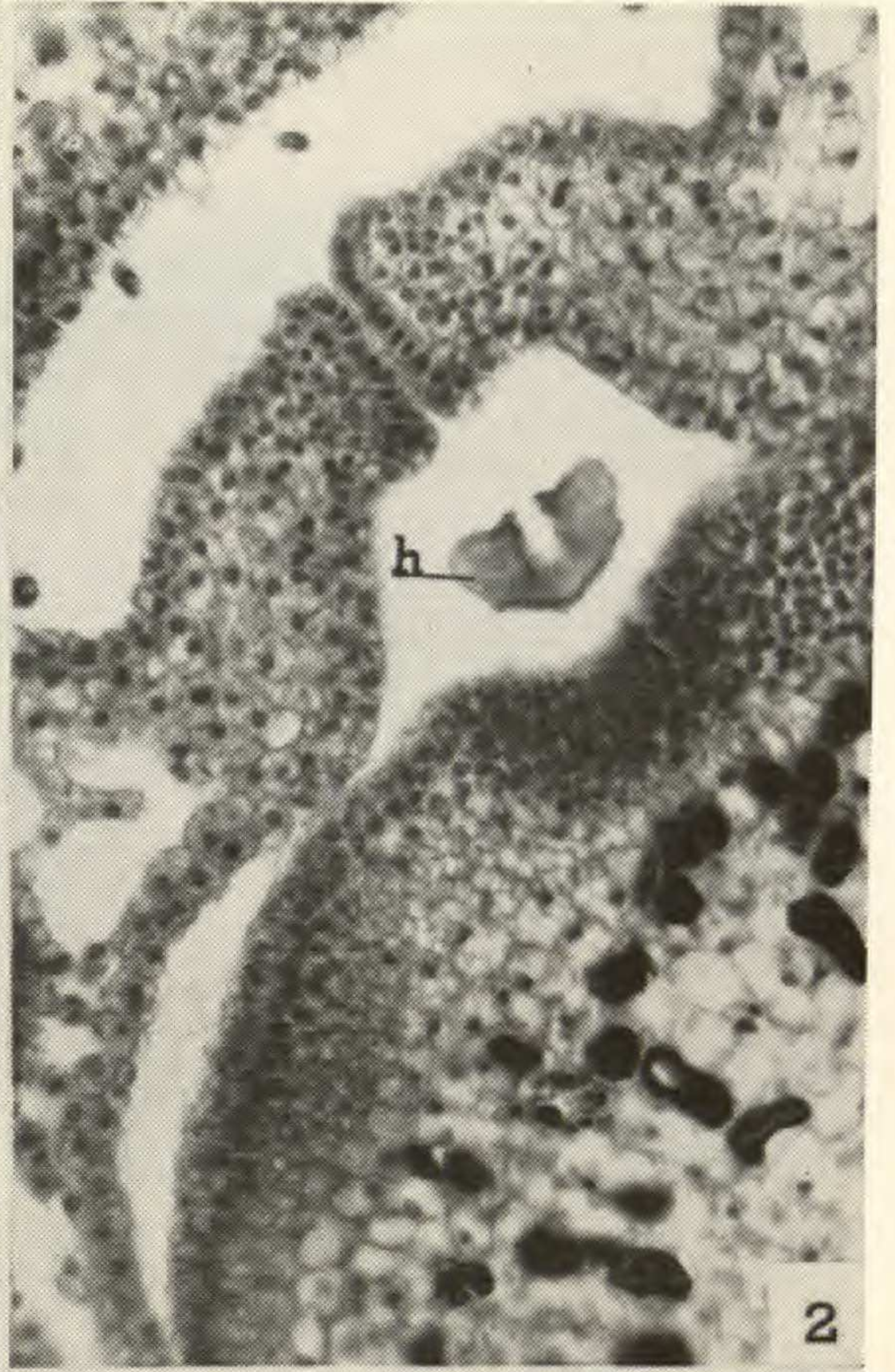
*Plate 4**Secamone alpinii*

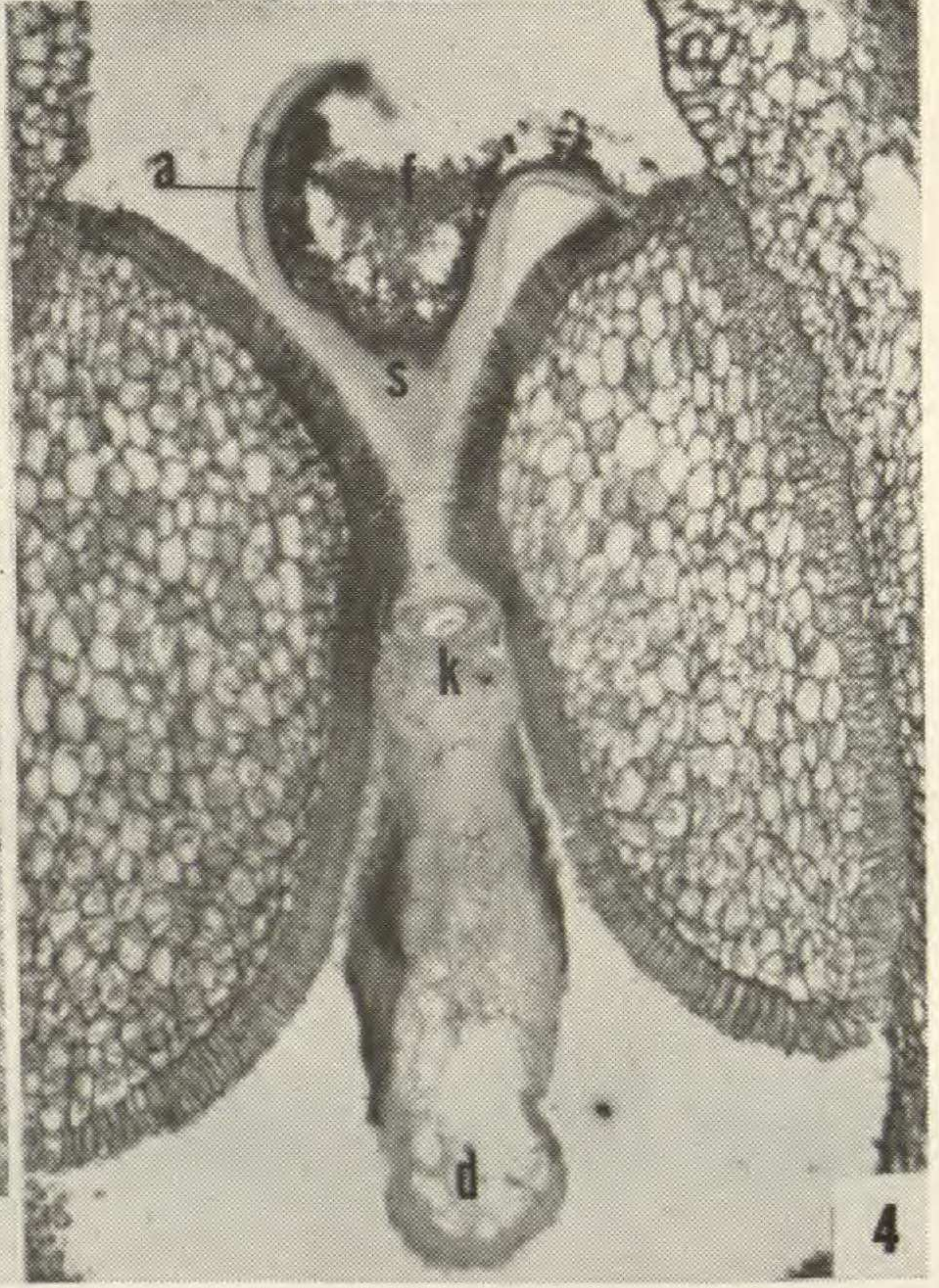
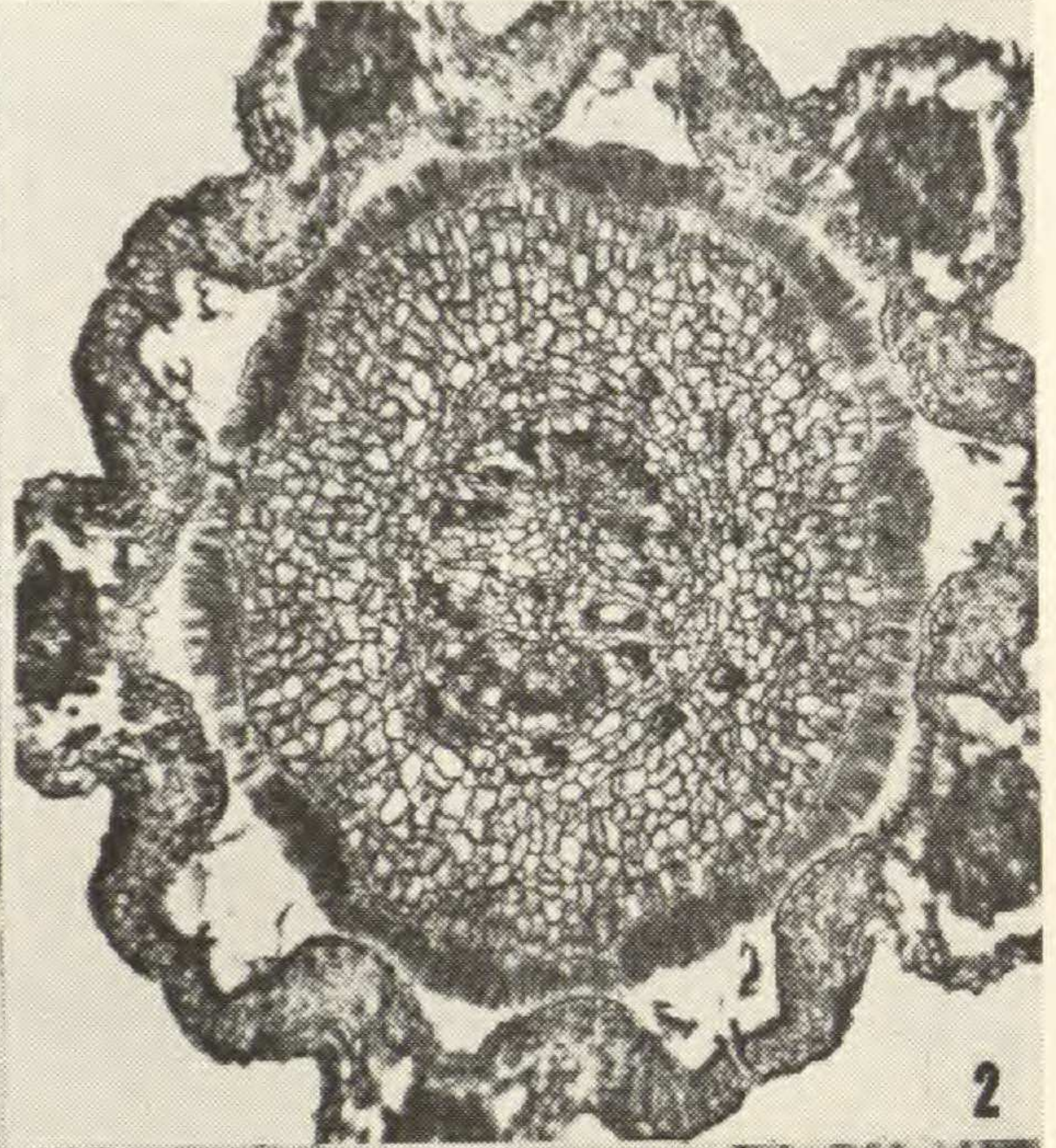
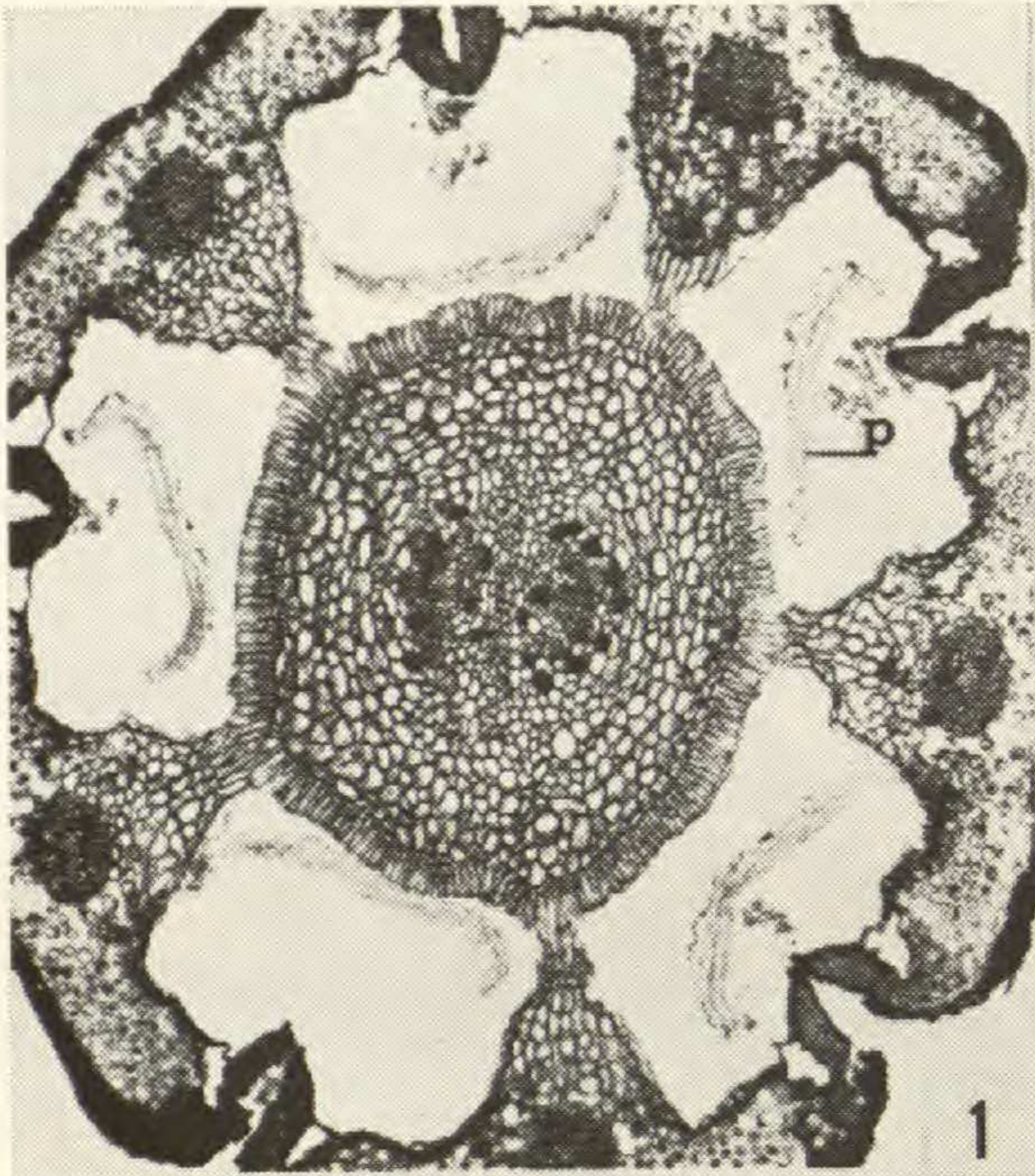
Fig. 1. Transverse section of gynostegium showing an early stage of the secretion of a translator by the stigma head (b), (X 350).

Fig. 2. Later stage in which the horseshoe-shaped body (h) is produced (X 230).

Fig. 3. Longitudinal section of a gynostegium showing the horseshoe-shaped body (a) and the foamy secretion (f), (X 480).

Fig. 4. Transverse section of a mature flower showing the horseshoe-shaped body (a) and a small additional body (p) secreted by the stigma head against an anther (X 350).





EXPLANATION OF PLATE

Plate 5

Fig. 1. Transverse section of a flower of *Apocynum cannabinum* showing the five small plates (p) alternating with as many stamens (X 85).

Fig. 2. Transverse section of a flower of *Secamone frutescens* showing the continuously glandular stigma head (x 85).

Fig. 3. Portion of the stigma head of *Periploca graeca* showing the interrupted glandular regions alternating with the anthers (X 75).

Fig. 4. Tangential section of a flower of *P. graeca* showing a pollinium with shovel (s), stalk (k), adhesive disc (d), solid substance (a), foamy secretion (f), (X 90).

EXPLANATION OF PLATE

Plate 6

Fig. 1. Transverse section of a young anther of *Matelea quirosii* showing the beginning of divisions within the two hypodermal plates and the origin of the bilocular anther (X 470).

Fig. 2. Transverse section of an anther of *Asclepias curassavica* showing the outer massive tapetum and the pollen mother cells after the first meiotic division (X 125).

Fig. 3. Transverse section of a young bud of *Vinca rosea* (X 85).

Fig. 4. Transverse section of a bud of *Periploca graeca* showing the massive inner tapetum of the two anther locules of half an anther (X 290).

