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A Biosystematic Study Of Taenidia and Pseudotaenidia (Umbelliferae)

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A BIOSYSTEMATIC STUDY OF TAENIDIA
AND PSEUDOTAENIDIA (UMBELLIFERAE)

DISSERTATION

Submitted to the Graduate School
of
West Virginia University
In Partial Fulfillment of the Requirements for
The Degree of Doctor of Philosophy

by

Roland Lee Guthrie, B.S.F., M.S.

Morgantown
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1968

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TABLE OF CONTENTS

LIST OF MAPS

LIST OF TABLES

LIST OF ILLUSTRATIONS

Plate Page

LIST OF ILLUSTRATIONS (Cont.)

Plate Page

LIST OF ILLUSTRATIONS (Cont.)

INTRODUCTION AND STATEMENT OF THE PROBLEM

The primary research objectives of this work are to investigate and to evaluate the phylogenetic relationship between two genera of the Umbelliferae and, by means of the study of these genera, to evaluate in general the principal characteristics that are used to classify the Umbelliferae along phylogenetic lines.

Because the criteria used for classification of the Umbelliferae is based almost entirely on fruit structure, the two genera that are the subjects of this investigation are, from a taxonomic viewpoint, structurally ideal for the study. In addition to being monotypic genera, they differ morphologically only in the structure that is considered by taxonomists to be of primary phylogenetic significance, i.e., the fruit. The cytological, morphological and anatomical portion of this research is therefore a study of the development of the basic fruit structure of the genera with the objective of determining their basic similarities or differences. Since the fruit is a matured ovary and has its beginning in the development of the flower, the study begins with the development of the flower primordia and follows its development to the basic flower structure and on to the development of the mature fruit. A study was made also of the chromosomes as to their numbers, sizes and shapes in order to assess their value as phylogenetic indicators.

In addition, the gross morphology of the entire plant in each genus was studied in the field and in the herbarium. To facilitate this work, specimens were borrowed from many of the principle herbaria of the United States and Canada. Data from field collections and from herbarium specimens were incorporated into range maps in order to compare the distribution of the genera. The literature pertaining to previous studies on the morphology and phylogeny of the Umbelliferae and to the ecology of the genera being investigated were reviewed and are herein referred to when pertinent to the research.

The subjects of the investigation are Taenidia integerrima (L.) Drude, commonly known as Yellow Pimpernel, and Pseudotaenidia montana Mackenzie, commonly known as Mountain Pimpernel. Since both genera are monotypic, they will be referred to by their generic names in most instances. From the time of the discovery of Pseudotaenidia in 1903, a question has existed as to the taxonomic relationship between Taenidia and Pseudotaenidia. The utilization of morphological features that have been considered as having great phylogenetic significance in the Umbelliferae has resulted in these two genera being placed relatively far removed form each other in the family in spite of the fact that these plants are virtually indistinguishable except when they are in the fruiting stage. The following paragraphs briefly trace the history of the taxonomy of the Umbelliferae and describe the present day criteria used in the classification of Taenidia and Pseudotaenidia.

The family Umbelliferae has long been considered by taxonomists to be a natural family, that is, a family with well defined characteristics and with few or no characteristics that grade into or may be confused with those of other families. Although the name Umbelliferae was not applied to this family until 1789 by A. L. de Jussieu in his Genera Plantarum, the members of this family had been recognized and grouped together on the basis of their umbellate inflorescence from very ancient times. The first person to make use of a second characteristic in delimiting the family was Andrea Cesalpino (1519-1603) who utilized the uniform presence of a two-celled ovary, each cell of which gives rise to a single "seed", i. e., mericarp.

Little attempt was made, however, to form any systematic classification within this large and phylogenetically confusing family until Paul Hermann (1646-1695) recognized that the fruits provide diagnostic characteristics which can be used as a basis for classification. Using fruit characteristics, Hermann divided the family into the following three groups: (1) plants with ovate fruits, (2) plants with large and flattened fruits, and (3) plants with hairy or spiny fruits. Later, Pierre Magnol (1638-1715) devised a different classification based on fruit characteristics. Magnol divided the family into four groups based on surface characteristics and size of the fruit as follows: (1) fruit ribbed, (2) fruit large, (3) fruit spiny, and (4) fruit long. With various modifications, the use of fruit characteristics as the principal diagnostic features in classifying the Umbelliferae has continued until the present day. This is true, not only in delimiting genera, but also in delimiting the larger grouping of tribes.

The tribe *Ammineae* of which *Taenidia* is a member, along with such genera as *Bupleurum*, *Apium*, *Carum*, *Pimpinella*, *Foeniculum*, *Oenanthe* and *Ligusticum*, is characterized by having the primary ribs on the fruit all alike and a mericarp which is semicircular in cross-section. The entire mericarp is subcylindrical in shape. The tribe *Peucedaneae* in which *Pseudotaenidia* has been placed, along with such genera as *Angelica*, *Ferula*, *Peucedanum* and *Pastinaca* differs from the *Ammineae* in having the lateral ribs much broader than the dorsal ribs and a mericarp that is long and narrow in cross-section. The entire mericarp is lenticular in shape. To summarize, *Taenidia* and *Pseudotaenidia* are placed in two different tribes on the bases of the size of the lateral ribs in relation to the size of the dorsal ribs and by the shape of the mericarp. Great phylogenetic importance has therefore been placed upon these two features.

The question as to the phylogenetic relationship of *Taenidia* and *Pseudotaenidia* to each other and to other members of the Umbelliferae is well illustrated by Fernald's (1950) keys to the family. His synoptic or natural key, which is based upon characteristics that are considered to be of phylogenetic importance, places *Taenidia* and *Pseudotaenidia* at nearly the opposite ends of the large subfamily Apioideae. In contrast, Fernald's artificial key based on what are considered to be superficial characteristics, places the genera adjacent to each other. The natural key makes an early separation on the bases of the laterally flattened (flattened at a right angle to the plane of the commissure) fruits of *Taenidia* and the dorsally flattened (flattened parallel to the plane of the commissure) fruits of *Pseudotaenidia*. Those umbelliferous genera with fruits that are round or nearly round in cross-section are included in the synoptic key with those that are dorsally flattened. The inclusion of genera with fruits round in cross-section with those that have dorsally flattened fruits appears to be a matter of convenience. If this is so, genera with round fruits should not be included with those having dorsally flattened fruits for it weakens the theory that the manner in which umbelliferous fruits are flattened is the primary diagnostic feature to be used in determining phylogenetic relationships.

Because of the great uniformity in gross flower structure throughout the Umbelliferae, flowers have been little used diagnostically except that in some cases they are used to differentiate between species and then only on the basis of flower color. Leaves are seldom used in generic description because of their extreme variations from species to species within so many genera.

On the basis of the above statements, two alternatives are presented: (1) that the direction in which the fruit is flattened and the relative size of the ribs are of primary phylogenetic importance and that all other characteristics are of secondary or little importance and (2) that the direction in which the fruit is flattened and the relative size of the ribs are not necessarily the primary diagnostic features and that other characteristics may be of equal or of greater value as indicators of relationship. Assuming that the first alternative is correct, then Taenidia and Pseudotaenidia are not very closely related but exhibit an outstanding example of parallel evolution in vegetative features. Assuming the second alternative to be true, then Taenidia and Pseudotaenidia are very closely related yet produce fruits that are about as different as any two umbelliferous fruits could be. It would follow then that perhaps one is a derivative of the other and that a remarkable example of divergent evolution has occurred in the characteristics of the fruits. An understanding of the phylogenetic relationship of Taenidia and Pseudotaenidia should therefore contribute additional information on which to base the phylogeny of the family Umbelliferae.

MATERIALS AND METHODS

Plant materials collected in the field for cytological and morphological study were fixed in Carnoy's 3/1 solution (Johansen, 1940) and then stored in 70% ethyl alcohol. Flowers and immature fruits were processed by standard methods for embedding and serial sectioning. Immature flowers for chromosome studies were mordanted with ferric ammonium sulphate for twenty-four hours and then the microsporangia were smeared and stained in acetocarmin.

Mature fruits were processed differently from immature ones. The oily nature of the endosperm makes infiltration difficult and the presence of schlerenchyma in the schizocarps may cause the sections to shatter when cut.

For serial sections of mature schizocarps the best results were obtained by double embedding: first in celloidin and then in tissuemat. The schedule that gave satisfactory results is as follows (adapted from Johansen, 1940):

(This schedule assumes that the material has already been fixed in Carnoy's 3/1 solution and stored in 70% ethyl alcohol.)

70% tertiary butyl alcohol	24 hrs.
85% tertiary butyl alcohol	1 hr.
95% tertiary butyl alcohol	1 hr.
100% tertiary butyl alcohol	1 hr.
Equal parts tertiary butyl alcohol, absolute ethyl alcohol and ether	1 hr.

Equal parts absolute ethyl alcohol and ether . . . . . 4 hrs.

(fresh solution after 2 hrs.)

2% celloidin . . . . 24 hrs.

(It was found that better infiltration of celloidin could be obtained by punching a very small hole in each mericarp with a sharpened needle before infiltration was attempted.)

4% celloidin . . . . 24 hrs.

6% celloidin . . . . 24 hrs.

8% celloidin . . . . 24 hrs.

10% celloidin . . . . 48 hrs.

(To hasten the infiltration of celloidin, the material was kept on a hot plate at a temperature of 48°C. A jar was inverted over the vials of material to prevent loss of heat.)

Remove fruits from celloidin and hold in chloroform vapor for a few moments to initiate hardening of the celloidin.

Immerse in chloroform . . . . 24 hrs.

1 part castor oil to 3 parts xylene . . . . 12 hrs.

Pure xylene . . . . 12 hrs.

Pure melted tissuemat (M.P. 60-63°C.) . . . . 24 to 48 hrs.

Fruits were sectioned 12 u. in thickness and then were stained with safranin and fast green following the schedule of Johansen (1940).

HISTORY AND NOMENCLATURE OF *TAENIDIA*

The type locality for *Taenidia integerrima* (L.) Drude is the state of Virginia, however the exact place in Virginia where the plant was first collected is unknown. A total of seven scientific names have been applied to this species. The following list contains a chronological account of the scientific names that have been given the species and the publication in which the names first appeared (Mathias and Constance, 1945).

Smyrnium integerrimum L., ...	*Species Plantarum*, 1753 (page 263).
Angelica integrifolia Walt., ...	*Flora Caroliniana*, 1788 (page 115).
Sison integerrimus Spreng., ...	*Systema*,1 : 887, 1825.
Zizia integerrima DC., ...	*Memoires de la Societe de Physique et D'histoire Naturell de Geneve*, 4 : 493, 1829.
Pimpinella integerrima A. Gray, ...	*Proceedings of the American Academy of Arts and Sciences*, 7 : 345, 1863.
Pimpinella integrifolia Wood, ...	*The American Botanist and Florist*, 1870 (page 139).
Taenidia integerrima (L.) Drude, ..	*Die Naturlichen Pflanzenfamilien*, 3^8: 195, 1898.

The presently used generic name *Taenidia* is derived from the Greek word *tainidion* which literally means *a little band* and which is used in reference to the small, scarcely prominent ribs on the fruit. Its specific epithet *integerrima* means *quite entire* and refers to the entire margin of the leaflets.

HISTORY AND NOMENCLATURE OF PSEUDOTAENIDIA

On August 29, 1903, Kenneth Kent Mackenzie, a New York attorney and amateur botanist, discovered a plant which was new to science. Although this particular species of plant had been collected in Maryland and Virginia prior to the time of Mackenzie's collection, it had not been regarded as different from the well known species Taenidia integerrima (L.) Drude. The reason for its going unrecognized is well explained by Mackenzie's own account of the discovery.

> "While botanizing last August on Kate's Mountain near White Sulphur Springs, West Virginia, I noticed a plant which I took to be Taenidia integerrima (L.) Drude. As this is a common plant, I did not take any specimens at the time. A few days later, however, on another part of the same mountain I saw another plant, which also seemed to be Taenidia integerrima but the fruit of which did not correspond to my recollection of the fruit of the first plant. This led me to investigate and get specimens of both plants. When put side by side the difference in the fruit was at once noticeable. In fact the fruits represent two very widely separated types of umbelliferous fruits, and are almost as distinct from one another as two umbelliferous fruits can well be, but outside of the fruits the two plants are apparently identical" (Mackenzie, 1903).

On the basis of fruit characteristics, Mackenzie placed his newly discovered plant in a new genus and named the plant Pseudotaenidia montana Mackenzie. The generic name Pseudotaenidia is derived from the Greek word pseudos which means false and from Taenidia, the genus to which it possesses a great habitual resemblance. Its specific epithet, montana means of the mountains. Kate's Mountain, Greenbrier County, West Virginia is the type locality for Pseudotaenidia. Type specimens are deposited in the herbarium of the New York Botanical Garden.

The similarity of the fruits of *Pseudotaenidia* to the fruits of species in the western North American genus *Peucedanum* led to its inclusion in this genus by Koso-Poljansky (Mathias and Constance, 1945). The new name that was proposed for *Pseudotaenidia* was published in the *Bulletin of the Imperial Society of Naturalists* in Moscow in 1916 as *Peucedanum montanum* K.-Pol. This name is however, a homonym for *Pseucedanum montanum* Blankenship, a plant now known as *Lomatium montanum*, Coult. & Rose (Mathias and Constance, 1945).

GEOGRAPHICAL RANGES

The geographical range of *Taenidia* was described in *Monograph of the North American Umbelliferae* as "from Canada to North Carolina, west to Minnesota and Arkansas" (Coulter and Rose, 1900). Subsequent research considerably enlarged the known range of this species. *Britton and Brown's Illustrated Flora* defines the range of *Taenidia* as "from Quebec to Minnesota, south to Georgia and Louisiana" (Gleason, 1952). An earlier description of its range and one which corresponds very closely to that determined in this research was given by M. L. Fernald (1950) as "from western Quebec to Minnesota, south to Georgia, Alabama, Mississippi, Louisiana, and Texas".

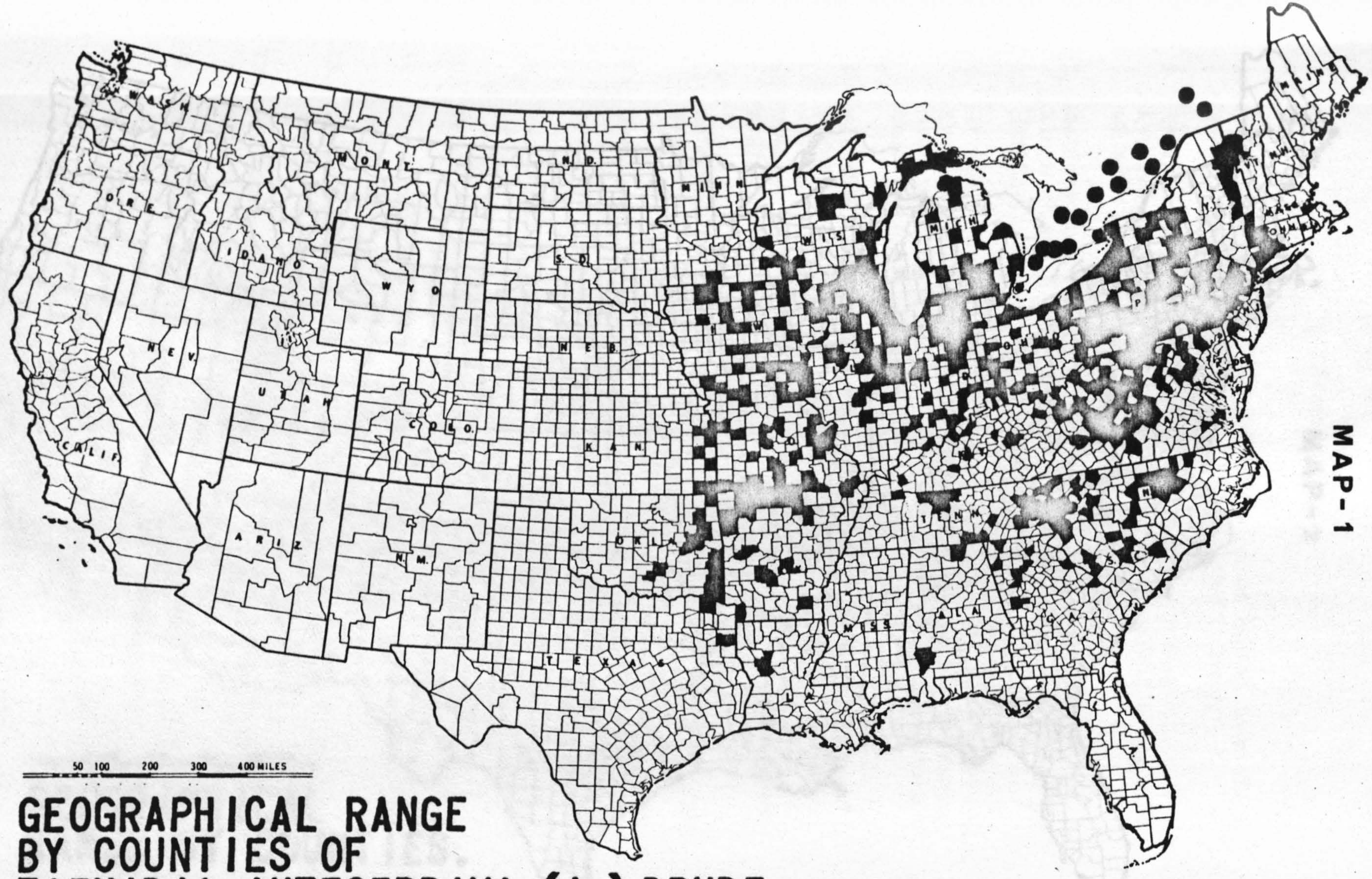
The present research work produced only a little change from Fernald's range description. Based on the study of 1,725 specimens from forty-nine herbaria, a more detailed range description is as follows: from southern Quebec and southeastern Onterio, south to Central Georgia and southern Alabama, west to northern Michigan, northern Wisconsin, southern Minnesota, to eastern Kansas, Oklahoma, and Texas. Map 1 illustrates the range of *Taenidia* by counties.

No specimens of *Taenidia* were found which had been collected in the state of Mississippi where it was reported by Fernald (1950). It is reasonable to assume that *Taenidia* grows in Mississippi as it grows in all the surrounding states.

The geographical range of *Pseudotaenidia* is accurately described in *Gray's Manual of Botany* as being "from southern Pennsylvania to West Virginia and western Virginia" (Fernald, 1950). Based on data obtained from 122 specimens, some borrowed from various herbaria and some collected for this study, the range of Pseudotaenidia is as follows: from Bedford County in southern Pennsylvania, south in the mountains of eastern West Virginia, western Maryland, and western Virginia. Map 2 is a range map by counties for Pseudotaenidia which, when compared with the Range Map by counties of Taenidia (Map 1), graphically illustrates the relatively restricted range of Pseudotaenidia.

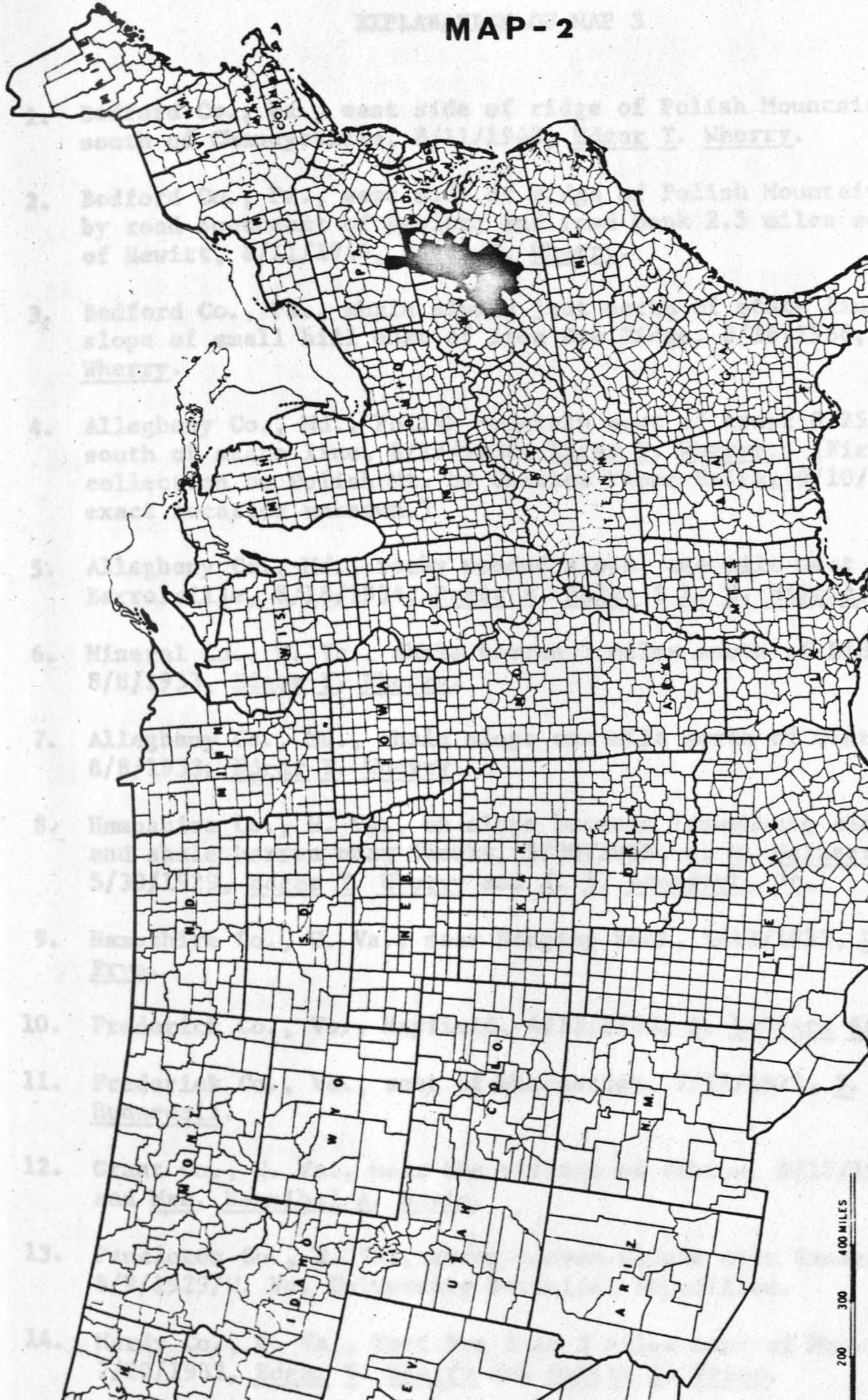
Since Pseudotaenidia has such a limited range and is a comparatively rare species, all the known collecting stations are listed in the Explanation to the Map of Collecting Stations for Pseudotaenidia. Map 3 of the collecting stations is of a much larger scale than the map of the ranges by counties and is meant to show more accurately the actual areas where collections have been made. Some of the 48 collecting stations as shown on Map 3 represent more than one collecting site. The combining of sites was done where two or more sites were in close proximity. The separate areas in the combined stations are, however, described in the Explanation to Map 3. A discussion of the range of Pseudotaenidia in relation to Brallier shale outcroppings as shown in Map 3 is given in the section on Ecological Considerations.

MAP-1



GEOGRAPHICAL RANGE
BY COUNTIES OF
TAENIDIA INTEGERRIMA (L.) DRUDE
COLLECTING STATIONS IN CANADA ----- ●

MAP-2



GEOGRAPHICAL
RANGE BY COUNTIES.

PSEUDOTAENIDIA <u>MONTANA</u> MACKENZ.

EXPLANATION OF MAP 3

1. Bedford Co., Pa., east side of ridge of Polish Mountain 6.5 mi. south of Chaneysville, 8/11/1940, Edgar T. Wherry.

2. Bedford Co., Pa., west side of ridge of Polish Mountain 1.5 mi. by road southeast of Hewitt; and road bank 2.5 miles southwest of Hewitt, 8/11/1940, Edgar T. Wherry.

3. Bedford Co., Pa., shale slopes just north of state line on west slope of small hill east of Iron Ore Ridge, 8/16/1936, Edgar T. Wherry.

4. Allegheny Co., Md., Polish Mountain west of crest 0.25 miles south of state line, 8/17/1936, Edgar T. Wherry. (First collection on Polish Mt. by Charles Piper Smith, 9/10/1918 exact location unknown.)

5. Allegheny Co., Md., rocky wooded slope, one mile west of Barrelville, 8/16/1954, Harry E. Ahles & R. H. Hilpin.

6. Mineral Co., W. Va., shale barren 3 miles south of Ridgley, 8/8/1933, Edgar T. Wherry.

7. Allegheny Co., Md., shale slope one mile north of Oldtown, 8/8/1933, Edgar T. Wherry.

8. Hampshire Co., W. Va., on slope between Frenchburg and Romney ~~and shale barren near Shanks, 5/30/1929,~~ E. H. Walker; 5/30/1929, Edgar T. Wherry and J. E. Benedict, Jr.

9. Hampshire Co., W. Va., near Hanging Rock, 5/13/1933, Wilbert Frye.

10. Frederick Co., Va., Hayfield, 4/12/1933, G. Ledyard Stebbins.

11. Frederick Co., Va., west of Winchester, 7/17/1928, F. W. Hunnewell.

12. Grant Co., W. Va., near the village of Cabins, 6/10/1937, Mr. and Mrs. Hannibal A. Davis.

13. Pendleton Co., W. Va., steep canyon slopes near Smoke Hole, 8/9/1929/W. Va. University Botanical Expedition.

14. Hardy Co., W. Va., Fort Run 2 to 3 miles east of Moorefield, 7/20/1933, Edgar T. Wherry and Ruskin S. Freer.

15. Hardy Co., W. Va., near Lost City, 8/18/1931, Earl L. Core.

16. Augusta Co., Va., 1 mile from highway through Buffalo Gap and vicinity of Stribling Springs, 5/31/1936, H. A. Allard; 8/29/1917, E. S. Steele.

17. Augusta Co., Va., Mt. Elliot, 5/24/1933, E. P. Killip.

18. Augusta Co., Va., North of Craigsville, 9/6/1913, E. S. Steele.

19. Bath Co., Va., Millboro Springs and south of Millboro Springs, 6/5/1938, E. P. Killip; 9/12/1946, Carroll E. Wood, Jr.

20. Bath, Co., Va., Hot Springs and 2.5 miles W.N.W. of Hot Springs, 5/14/1916, F. W. Hunnewell.

21. Pocahontas Co., W. Va., Laurel Run between Neola and W. Va. Rt. 39 on lower slopes of Meadow Creek Mountain, 8/8/1958, Roland L. Guthrie.

22. Greenbrier Co., W. Va., on slope 0.25 mile up Wade's Draft from road between Alvon and Neola, 8/3/1957, Roland L. Guthrie.

23. Allegheny Co., Va., shale barren along U. S. Rt. 220 3 and 5 miles north of Covington, 9/6/1936, Earl L. Core; 5/10/1930, Edgar T. Wherry.

24. Greenbrier Co., W. Va., Kate's Mountain near White Sulphur Springs (the type locality), along U. S. Rt. 60 on hill north of White Sulphur Springs airport, and south slopes of Brushy Mountain east of White Sulphur Springs, 8/29/1903, Kenneth Kent Mackenzie; 4/13/1945, Maurice G. Brooks; 5/28/1954, G. B. Rossbach.

25. Monroe Co., W. Va., Slaty Mountain near Sweet Springs and along Cove Creek near Sweet Springs, 8/12/1924, Edgar T. Wherry; 7/22/1929 W. Va. University Botanical Expedition.

26. Roanoke Co., Va., Hanging Rock, 6/30/1942, Carroll E. Wood, Jr.

27. Roanoke Co., Va., 2.1 miles north west of Dixie Caverns on Fort Lewis Mountain, 7/13/1942, Carroll E. Wood, Jr.

28. Washington Co., Md., along Potomac River just east of Harper's Ferry near Sandy Hook (formerly known as Keep Tryst), 9/4/1902, J. B. S. Norton.

29. Shenandoah Co., Va., Tom's Brook, 6/2/1929, F. W. Hunnewell.

30. Shenandoah Co., Va., Crest of Massanutten Mountain near Woodstock Observation Tower, 8/13/1951, F. W. Hunnewell.

31. Shenandoah Co., Va., rocky slopes between Mathias, W. Va. and Columbia Furnace, Va., 7/20/1933, *Ruskin S. Freer*.

32. Shenandoah Co., Va., Great North Mountain in the vicinity of Orkney Springs, 9/1/1911, *E. S. Steele*.

33. Shenandoah Co., Va., western slope of Three-Top Mountain and shale slopes southeast of Forest Camp near Elizabeth Furnace, 7/3/1932, *H. K. Svenson*; 7/21/1933, *Edgar T. Wherry*.

34. Shenandoah Co., Va., Upper Overall Run, 8/14/1938, *E. H. Walker*.

35. Rappahannock Co., Va., Gooney Run along Skyline Drive, 9/24/1945, *J. T. Baldwin, Jr*.

36. Page Co., Va., along Skyline Drive at the Neighbor (Neighbor Mountain), 7/30/1956, *F. W. Hunnewell*.

37. Rappahannock Co., Va., Skyline Drive below Mary's Rock in Shenandoah National Park, 6/19/1938, *F. R. Fosberg*; 6/19/1938 *Vera B. Taplinger*.

38. Page Co., Va., Stony Man Mountain near Luray and Little Stony Man Mountain, 8/20/1901, *E. S. Steele*.

39. Page Co., Va., near Knob Mountain, 6/24/1949, *F. W. Hunnewell*.

40. Green Co., Va., Appalachian Trail on Bear Fence Mountain, 7/28/1940, *E. H. Walker*.

41. Shenandoah Co., Va., four miles east of New Market, 7/26/1933, *Edgar T. Wherry*.

42. Rochingham Co., Va., foot of slopes of Blue Ridge Mountains in the vicinity of Elkton, 8/27/1918, (collector unkown).

43. Nelson Co., Va., vicinity of Afton, 9/4/1912, *E. S. Steele*.

44. Rockbridge Co., Va., slope of North Mountain near Lexington, 8/26/1924, *J. R. Churchill*.

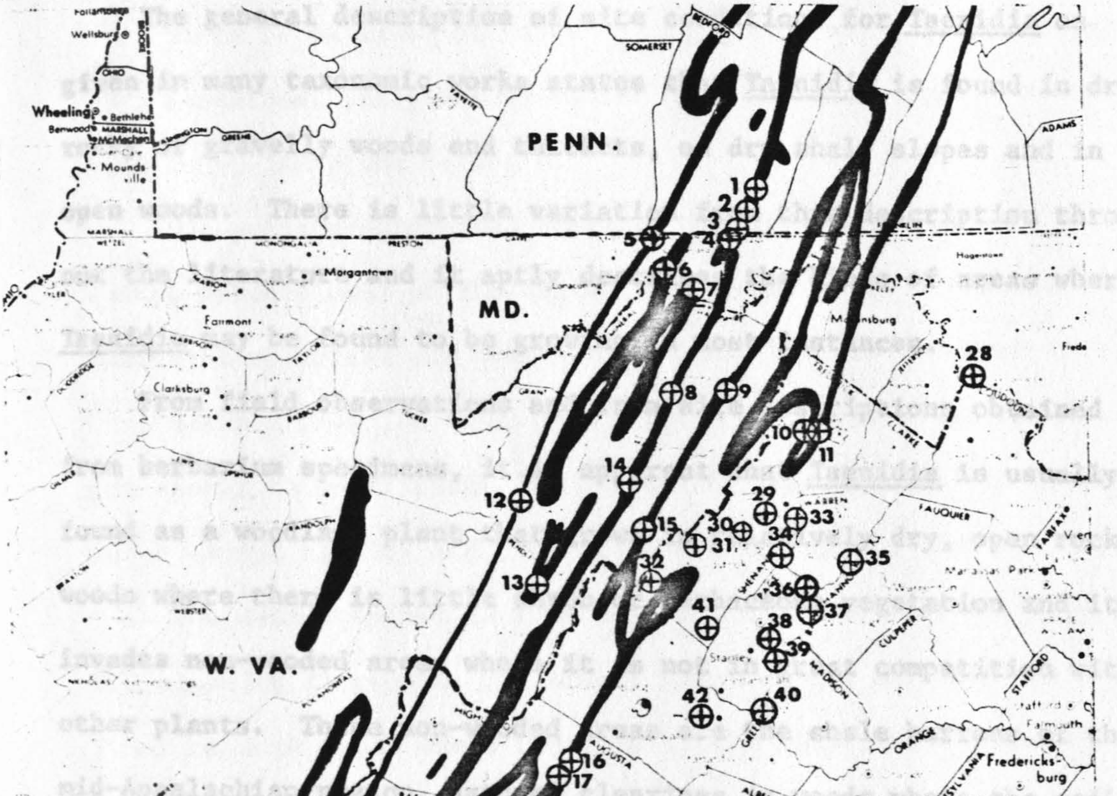
45. Amherst Co., Va., 0.5 mile north of Slaty Gap on Robinson's Gap Trail, 8/8/1933, *Ruskin S. Freer*.

46. Bedford Co., Va., Hickory Stand Mountain about 5.25 miles from James River and 1 mile from summit of mountain and Hickory Stand Mountain about 5.25 miles from Camp Concord, 8/2/1933, *Ruskin S. Freer*.

47. Rockbridge Co., Va., High Rock Knob between Petite's Gap and Marble Spring, 8/2/1933, Ruskin S. Freer.

48. Bedford Co., Va., Parker's Gap Trail on Apple Orchard Mountain, 8/2/1933, Ruskin S. Freer.

MAP - 3



COLLECTING STATIONS FOR PSEUDOTAENIDIA — ⊕

BRALLIER SHALE OUTCROPPINGS — ▬

ECOLOGICAL CONSIDERATIONS

The general description of site conditions for Taenidia as given in many taxonomic works states that Taenidia is found in dry, rocky or gravelly woods and thickets, on dry shaly slopes and in open woods. There is little variation from this description throughout the literature and it aptly describes the kinds of areas where Taenidia may be found to be growing in most instances.

From field observations and from site descriptions obtained from herbarium specimens, it is apparent that Taenidia is usually found as a woodland plant that grows in relatively dry, open rocky woods where there is little shrub or herbaceous vegetation and it invades non-wooded areas where it is not in great competition with other plants. These non-wooded areas are the shale barrens of the mid-Appalachian region, natural clearings in woods where the soil is too thin to support a luxuriant growth of plants, rocky bluffs and banks where the forest canopy is broken, on sandy beaches of rivers and lakes and on poor soil of artificially created open areas such as highway and railroad cuts. An indication of its restriction to a woodland habitat except where competition is reduced is also shown by the habitat that Taenidia occupies in states that are mostly in the Grassland Formation. It is very rarely a member of true open grassland communities or associations where grasses predominate. Taenidia occurs mostly on wooded slopes and rocky bluffs along river and creek valley courses, in open Bur Oak woods and in other dry site types of woodland. In other words, in the prairie states it usually grows in areas that are extensions of the Deciduous Forest Formation into the Grassland Formation.

There is no association of *Taenidia* with any particular type of rock formation. It grows where the underlying or exposed strata are sandstone, limestone or shale.

Since the geographical range of *Taenidia* covers nearly the entire eastern half of the United States and parts of southeastern Canada, temperature and the amount of rainfall it receives vary considerably over its extensive range. Temperature and rainfall do not appear to be critical factors in its distribution within its range except as they are interrelated with edaphic factors.

The data obtained in this research indicate that *Taenidia* has the capacity to grow in relatively poor and dry soil and that it is found on such areas where there is little competition from other plants (probably because of the poor growing conditions) and where ~~there is only little or no shading. As~~ compared to *Pseudotaenidia*, the wide geographical range of *Taenidia*, its local abundance and its ability to occupy more diverse habitats attest to its relative aggressiveness and greater environmental adaptability. No variation in phenotype was discovered in this research.

H. A. Allard (1946) states that, "*Taenidia integerrima* is one of the few persistent members on the shale barrens of the family Umbelliferae." This statement should include *Pseudotaenidia* as well. Along with *Pseudotaenidia*, *Taenidia* grows on shale barrens of the most extreme form. On some shale barrens where both occur, *Taenidia* exceeds *Pseudotaenidia* in abundance. On these shaley habitats, the two genera do not commonly intermingle but usually segregate into discrete scattered colonies. In transition zones (transitional from relatively open barren conditions to the dry woodlands of the region) Taenidia and Pseudotaenidia grow in discrete colonies but also as scattered plants with individual plants spaced several feet apart from each other.

The geographic and ecological ranges of Taenidia and Pseudotaenidia overlap only on the shale barrens and in dry woodland areas that are transitional to more mesic woodlands. The fact that they coexist on the shale barrens and dry site woodlands without genetic intermixing has taxonomic implications that will be discussed in a later section of this work. The following description of the region where the ranges overlap will be used as an aid in evaluating the relationship between these genera.

The term shale barren, first used by Steele (1911) aptly describes the shale rock talus slopes that support a very open type of vegetation characterized by scatterings of stunted trees, some shrubs and a limited number of herbaceous species. Although there are exceptions which will be noted later, many barrens occur on outcrops of Brallier shale of Upper Devonian strata. The name Portage is used in some of the older West Virginia geological publications (Woodward, 1943). In Maryland this shale has been called the Jennings formation (Platt, 1951). These names are synonomous and only the term Braillier will be used in this paper as this is the name that is now generally accepted.

Brallier shales that form barrens outcrop in a long narrow region from extreme south central Pennsylvania through western Maryland, eastern West Virginia and western Virginia to southwestern Virginia. Although Brallier shales occur both north and south of the extremes given above, the character of the shale changes from the hard form of the barren region to a softer more clayey form which is not as resistant to erosion and degredation and which as a consequence does not form barrens (Platt, 1951).

Shale barrens occur in the Ridge and Valley Province of the Appalachian Mountains, a region characterized by broad valleys separated by long ridges the main axis of which lies in a northeast-southwest direction. Sediments that form the various geologic strata of the Ridge and Valley Province were deposited in a narrow syncline during the Paleozoic Era, a period of time estimated to have lasted from 500,000,000 to 200,000,000 years ago, a span of 300,000,000 years. The stratum that forms many of the barrens, the Brallier, was deposited during the Devonian Period near the middle of the Paleozoic Era or about 260,000,000 years ago. Since deposition the strata of this geographic region have been tilted into various inclined attitudes and greatly eroded into the land form of the Ridge and Valley Province (Platt, 1951).

Although there are notable exceptions such as the outcrops on Kate's Mountain, in Greenbrier County, West Virginia, Brallier shales generally outcrop on the lower slopes of the mountains, often not much elevated above the valley floors at elevations commonly of 1,000 to 2,000 feet above sea level. According to Platt (1951) one of the most remarkable characteristics of the Brallier shales is a lithologic constancy that is matched by few other strata. Throughout its entire length from south central Pennsylvania to southwest Virginia, it maintains the same character and appearance.

Platt (1951) was the first person to make extensive detailed experimental studies and measurements of the ecological factors operating on the shale barren flora. Up to this time, many writers had speculated on the ecological factors through visual observation and limited environmental measurements.

Steele (1911) said, "The barrenness is perhaps largely due to the constant washing away of the fine particles of soil, but in some cases it seems as if it must be chargeable to chemical composition." Wherry (1930) ascribed the limitations of the barrens of the mid-Appalachian Mountains to changes in physical and chemical character exhibited by these Devonian strata along their strike. Allard (1946) noted the apparent xeric conditions and called it a counterpart of the great American deserts. In spite of the apparent xeric conditions of the shale barrens, Steele (1911) and others have noted that the vegetation does not reflect extreme drought.

The scattered vegetation then does give the overall appearance of extreme xeric conditions but individual plants of the indigenous shale barren flora do not exhibit symptoms of drought such as wilting on the hottest of days (Platt, 1951). The stunted nature of tree and some shrub species indicate growth is affected by lack of moisture but otherwise, the vegetation exhibits a healthy appearance. Platt (1951) has shown by tree ring count that the trees on the barrens, although stunted, live a normal life span.

Platt (1951) agrees with other writers that, "By appearances one has the impression of a skeletal soil, severely leached and thus low in nutrients, easily displaced by forces of heat and cold, rain, snow, hail and frost and subject to desert-like temperatures and moisture conditions."

Although the rock mantle is basically responsible for the scaracity of vegetational cover, Platt disagrees with earlier writers as to the extremity of drought conditions. He shows through several experiments that extreme drought conditions exist only in the rock mantle that overlays the C horizon of shale barren soils. Platt (1951) writes, "The excessive dryness of the barren surface throughout most of the growing season greatly reduces the availability of nutrients present." The principal effect of the lack of moisture and nutrients in the rock mantle is on surface rooted species and not on those rooted in the C horizon.

The limiting factor that controls the nature of the vegetation is the rock mantle and the mantle exerts this limitation principally in inhibiting the germination of seeds and the establishment of seedlings. Plants once rooted in the C horizon have sufficient moisture and nutrients available for growth (Platt, 1911). Wherry (1930) has written that, "The rock is made up of quartz and clay minerals, and exhibits a neutral reaction. The accumulation of humus in the heaps of loose fragments results in the development of considerable acidity, little mineral matter capable of neutralizing the organic acids formed being present." Core (1940) has written that, "Wherry's statement in regards to acidity requires slight modification. In certain locations the shale is very calcareous."

Platt's work indicates that most barrens are slightly acid. He states, "Some 50 pH determinations show the barrens to have a pH range of 4.5 to 5.5 and those of the north slope to be somewhat more acid with a range of 4.0 to 5.0. The deeper soil portions, more recently derived from the parent rock, are more acid than the upper ones which are older and have a higher organic content" (Platt, 1951).

The present writer has made pH tests of 4 areas on two barrens which closely coincide with Platt's determinations. Samples taken from extreme barren conditions on Kate's Mountain in Greenbrier County show a range in pH of 5.0 to 5.8. The same stratum above Wade's Draft in Greenbrier County in an open mixed dry site oak and hickory woods gave a pH range of 4.5 to 4.9. Evidently the hydrogen ion relationship of soils derived from the Brallier shale is very uniform.

The only significant difference obtained in Platt's investigation between the soil profiles of a typical shale barren and that of a more heavily vegetated slope is the substitution of a thin mantle of rock fragments for the A and A_0 horizons (Platt, 1951).

Because of the mountainous character of the shale barren region, local variations in the climate undoubtedly occur. In spite of this, the climate in general between the northern and southern extremities of the shale barren region is quite uniform. Isopleths of various meterological factors follow the same directional trend as do the ridges, i. e., in a northeast-southwest direction (Platt, 1951). The region is characterized as being warm, temperate, and rainy with no distinct dry period. Rainfall varies from locality to locality in the region from 21 to 40 inches in one year. Platt (1951) says that there is no evident relationship between rainfall and the degree of barreness occurring in various parts of the region.

That there is nothing peculiarly inherent in the chemical and physical nature of Brallier shales that permits the support of a shale barren flora is demonstrated by the production of shale barrens and the growth of the same endemic plants on other shales. On Massanutten Mountain, in Virginia, Hamilton shales of the Romney formation and also the Martinsburg shale of the upper Ordivician form the barrens (Platt, 1951).

Summary of Available Information on Ecological Factors of the Shale Barren and Near Shale Barren Environments (after Platt, 1951).

1. Most barrens are formed on south or southwest facing slopes.
2. The open nature of the vegetation and the direction of slope insure sunlight on all plants for 8-12 hours per day. (Transitional zones receive less direct sunlight.)
3. Except for a very few exceptions, shale barrens are formed by Brallier shale. (As noted above the Hamilton and Martinsburg shales form some barrens.)
4. Most barrens are located at elevations of from 1,000 to 2,000 feet above sea level.
5. The chemical and physical nature of the Brallier shales are remarkably uniform throughout the shale barren area.
6. The vast majority of the barrens are slightly acid with a pH

of 5.0 to 5.8. Transition areas may be slightly more acid with a pH range of 4.5 to 5.8. The hydrogen-ion relationships of soils derived from the Brallier are quite uniform on most barrens.

7. There are no unusual ions or unusual accumulations of minerals in shale barren soils.
8. No A or A_0 soil horizons develop on barrens.
9. Extreme drought conditions exist only in the rock mantle.
10. The apparent factor that limits the kind and number of plants able to grow on shale barrens is the dryness of the rock mantle which exerts its limitation on the germination of seeds and the establishment of seedlings.
11. Plants once rooted in the C horizon have sufficient moisture for growth and survival.
12. That local variations of ecological conditions occur on shale barrens is demonstrated by the presence of shale barrens with no endemic plants. The presence of non xerophytic species, and the fact that no one shale barren supports a growth of all the endemic species supports this conclusion.
13. Climatic factors throughout the shale barren region are generally uniform, recognizing that local variations occur because of mountainous nature and rough topography of the terrain.

Some investigators have written that <u>Pseudotaenidia</u> is <u>endemic</u> to the habitat just described, but Fernald (1950) did not classify it as endemic. This appears to be a matter of interpretation.

An endemic is a lower or higher taxon that is restricted to a relatively small geographic area or one that is very limited in its ecological tolerance. There is no full agreement among botanists that would define the criteria to be used in the classification of a plant as to whether it is an endemic or not. As a consequence of this lack of agreement, lists of endemic species growing on the Appalachian shale barrens vary considerably from author to author depending upon his own interpretation. This variation in opinion can be illustrated by comparing the work of Fernald (1950) who recognizes no endemics on the Appalachian shale barrens, to the works of Core (1940), who recognizes 12 endemics. Platt (1951) in his study of the shale barrens lists only eight strict endemic species and nine others which are native to the mid-Appalachians and occur most frequently on the shale barrens. From studying Platt's writings, one can see that he has restricted his list of endemics to those species which inhabit only those areas which conform to the definition of a shale barren in its strictest sense, that is slopes on which the A and A_0 soil horizons do not exist and where the C horizon is covered by a talus of shale. Pseudotaenidia does occur on these shale slopes of the most extreme type but also it occurs adjacent to the barrens in areas that are transitional between the shale barren and the more mesic woodland vegetation that is most abundant vegetational cover in the region. Platt (1951) calls the mesic woodlands the normal vegetation. The use of the term normal is perhaps inaccurate for the shale barren flora itself is a normal vegetation and is the climax vegetation so long as conditions on the shale barrens remain as they are. The fact that Pseudotaenidia does occur in these transitional areas is presumably the reason Platt did not include it in his list of endemics.

The area occupied by Pseudotaenidia on the shale barrens and on the transitional zones combined is an extremely limited one. To the present writer, Pseudotaenidia lies well within the usual definition of an endemic plant. Further support to this contention is furnished by the fact that Pseudotaenidia grows under extremely limited and quite uniform ecological conditions that are prevalent on the shale barrens and in the transitional zones on the periphery of the barrens.

Pseudotaenidia is not as exacting in its ecological requirements as those endemics that are restricted to the more open shale barrens. This is evidenced by its relative abundance in the transitional zones adjacent to the barrens and by its abundance on many areas of the same type as that of the transitional zone but relatively far removed from true barrens sometimes by as much as twenty to twenty-five miles. For the purpose of simplicity in this paper, both of these will be called transition zones whether located adjacent to barrens or not. These transition zones are usually on south facing slopes, as are most true barrens, but they support a moderately open forest of dry site tree species such as black, scarlet and chestnut oaks, mockernut hickory and sasafrass. Two species, red maple and white pine, which are capable of growing on relatively dry sites, but which usually occupy areas where moisture is more abundant, are common in some of the transitional areas. The most common shrub associates are Vaccinium Spp. and Kalmia latifolia L. These are not, however, abundant. It was noticed in several of the transitional areas examined that old chestnut stumps and sprouts, *Castanea dentata* (Marsh.) Borkh., are very much in evidence. American Chestnut must have been one of the dominant species before the chestnut was decimated by the blight.

The substrate on these transitional areas is characterized by a very thin A and A_0 horizon. An average depth of 1 inch for the A_0 was obtained by a number of measurements of several sites. The A_0 has an abundance of shaly flakes throughout, and the shale strata is exposed in small scattered spots.

On the barrens *Pseudotaenidia* occurs as scattered individuals as it does in transitional zones but it occurs more abundantly in the transition zone in small groups of from ten to twenty plants growing within a few feet of each other. This grouping occurs where the forest canopy is rather open. The areas of most intense sunlight in these relatively open woods produce the highest number of plants per unit area. Although not an obligate heliophyte as apparently are the open shale barren endemics, *Pseudotaenidia* does not grow in deep shade but does thrive in light shade. The size and color of the plants growing in light shade in the transition zone is quite different from the size and color of those on the open barren. Those growing in light shade average about half the height of those on the barrens and are much lighter green in color. Also those in moderate shade stand less erect, i. e., they are often somewhat drooping, are weaker more flimsy plants with less strengthening tissue. This appears to be a typical shade reaction. It was observed that the condition of moderate shade in no way inhibited the flowering and fruiting and as indicated by the numbers of plants observed does not inhibit reproduction in any way. The relatively larger number of plants in the transition zone as compared to barrens was observed on Kate's Mountain and near Wade's Draft in Greenbrier County, near Laurel Run in Pocahontas County and at Cabins in Grant County, in West Virginia. In these areas no other herbaceous plant was observed growing near Pseudotaenidia except for Taenidia.

The writer cannot agree with Edgar T. Wherry's (1953) statement that "Pseudotaenidia montana - few of the localities of this unique taxon are actually on Brallier (Portage) barrens, it being known on other shales, on sandstone, on limestone and even in Virginia, on granite." A thorough check of the collecting sites has shown Pseudotaenidia to grow on Brallier shales either on barren slopes or in transitional areas in about one-half of the forty-eight known collecting areas.

For the purpose of this investigation, the main points as brought out by the above discussion are listed below.

1. Pseudotaenidia grows on true shale barrens often of Brallier shales but just as often on barrens produced by other shale, or transitional areas underlain by other shales, sandstones, or limestones.
2. It grows more extensively and abundantly on transition zones of open dry site oak-hickory woods, underlain by shale.
3. Although fewer in number on true barrens, the individual plants are about twice as tall, sturdier, and darker green in color than those of the transition area.

4. Pseudotaenidia is not an obligate heliophyte as are those endemics restricted to open barrens.
5. Apparently the presence of an A and A_0 soil horizon in transition zone provides a more favorable medium for seed germination and seedling establishment of Pseudotaenidia and probably explains its relative abundance in this habitat.

The uniform and narrow range of ecological conditions which limit the range of shale barren endemics indicates very strongly that they have narrow environmental tolerances or requirements and perhaps consist of only one ecotype. Any species that is restricted to one ecotype is a rare plant unless the particular conditions to which it is adapted constitute a geographically extensive habitat (Stebbins, 1942). The shale barren habitat is an extremely limited one, with soil moisture constituting by far the most limiting factor.

That Pseudotaenidia must be richer in ecotypes than the strictest of the endemics is evidenced by its occupying a greater range of ecological conditions, that is from the true barrens to the transition zones as described previously. Since Pseudotaenidia is evidently richer in ecotypes than the more strict endemics, it follows that this is a result of a somewhat greater environmental tolerance. There is no variability in phenotype. Any genetic variation exhibited by Pseudotaenidia is a hidden one expressed only in its ability to occupy slightly different ecological niches. Pseudotaenidia therefore probably contains only one biotype and perhaps only two ecotypes. It is possible that Pseudotaenidia contains only one ecotype which is broad enough to permit all individuals to grow on true barrens or in transitional areas. Be it of one or two ecotypes, <u>Pseudotaenidia</u> is a very conservative taxon. According to Stebbins (1942), conservatism rather than aggressiveness is a general characteristic of rare plants.

REPRODUCTIVE ISOLATION

On the basis of the identical gross morphological features of _Taenidia_ and _Pseudotaenidia_ in vegetative and reproductive structures, one is led to suspect that the two genera may produce hybrid offspring that are intermediate in their fruit characteristics. No such intermediate forms have been found. During the course of this research, all specimens examined, borrowed herbarium specimens, collected specimens, and those studied in the field, were observed to be very distinct in the fruiting stage as being characteristic of one genus or the other. A very definite barrier apparently exists which prevents either the production or the survival of hybrid offspring.

Spatial separation is not a factor. Although _Pseudotaenidia_ has a very restricted range, _Taenidia_ occurs within the range of _Pseudotaenidia_ as a relatively common component of the flora, often growing within a very few feet of _Pseudotaenidia_.

The lack of production or survival of hybrids cannot be attributed to any difference in the flowering period or to a difference in the time of development of stamens or pistils. The flowering and early fruiting period of the two genera lasting from April to June occurs concurrently. The concurrent stages of development during this period are as follows: (1) umbels enclosed in the axils of the sheathing leaf bases, (2) newly emerged umbels with flowers in the bud stage, (3) umbels or umbellets with partially to fully opened flowers, (4) umbels or umbellets with some flowers in anthesis, and (5) umbels or umbellets having the beginning stages of fruit development. In both genera, the latter three stages often occur concurrently within a single umbel.

The flowers of Taenidia and Pseudotaenidia, in addition to being identical in basic structure, are also typical of the family and are essentially like those of many other Umbelliferae. They do not have a special pollinating structure that is adapted to pollination by any particular insect species. The lack of a specialized pollinating apparatus and the identical color, shape, size and structure of the flowers are characteristics which appear to eliminate the action of two different specialized pollinating agents as a factor in preventing the cross-pollination of Taenidia and Pseudotaenidia. Also, the possibility of there being different scents that are specific for attracting a different species of insect to each genus is unlikely. In his studies of the genus Sanicula, Bell (1954) states: "The flowers of Sanicula, like the flowers of most Umbelliferae, seem not to be modified to attract any single type of pollinating agent." They are termed promiscuous plants by Grant (1949) and are pollinated by numerous and varied types of insects. A situation such as this rules out the pollinating system as a possible isolating mechanism either in the evolution or maintenance of species in genera so pollinated.

On the basis of the preceding evidence presented, it seems very likely that cross-pollination between Taenidia and Pseudotaenidia is a very common occurrence. The barrier to the production or survival of hybrid offspring apparently exists after the stage of cross-pollination.

An isolating barrier resulting from an incompatibility of the genomes cannot be attributed to a difference in the number of chromosomes. As it will be shown later, both genera have a diploid chromosome number of 22. The size and shape of complementary chromosomes appear to be very similar. One should not conclude, however, on the basis of chromosome size, shape and number that the genomes are compatible.

The determination of the nature of the reproductive isolation between _Taenidia_ and _Pseudotaenidia_ is beyond the immediate scope of this present research. Such a study would involve the growing of these genera under suitable conditions in which controlled pollinations could be effected.

The probability of a reproductive barrier subsequent to pollination, however, suggests certain hypotheses regarding the taxonomic position of _Taenidia_ and _Pseudotaenidia_. These hypotheses will be discussed in the Summary and Conclusions.

GROSS MORPHOLOGY

Because of the taxonomic significance of the identical floral and vegetative characteristics of Taenidia and Pseudotaenidia, the following description of their morphology is presented. The gross morphology of the two genera was studied in the field, from herbarium specimens borrowed from various herbaria, and from a review of published taxonomic descriptions. Some minor characteristics which are different from those in descriptions published in the major taxonomic works will be noted.

Taenidia and Pseudotaenidia possess many morphological features that are, with few exceptions, typical and uniform throughout the family. They are erect, herbaceous perennials (Figs. 173, 174) having flowers which are individually small, borne in compound umbels, regular, perfect, epigynous, and 5-merous except for the pistil which is bicarpellate. The calyx is rudimentary and the petals are prolonged at the tip into an inflexed apex. The five stamens are alternate with the petals and apparently arise from an epigynous disk. Their anthers are versatile, two-celled, and they open lengthwise. There are two styles, but in contrast to most members of the Apiodeae, neither Taenidia nor Pseudotaenidia possess a stylopodium.

A fruit type, characteristic of the Umbelliferae, called a schizocarp or cremocarp is produced by both genera (Figs. 175, 176). In dehiscence at maturity the two fruit-halves, called mericarps, separate along a plane of division called the commissure. For a time after division, the mericarps remain attached to the plant by a slender stalk called the carpophore. The two carpophores supporting the two mericarps of the longitudinally divided fruit are produced by the longitudinal division of the ventral traces of the schizocarp. The alternate, compound leaves with sheathing bases are typical of the Umbelliferae.

As stated in the introduction, the fruits afford the only means of separating the genera. A detailed description of fruit characteristics will be covered in the section describing the morphology of the fruit. Following are detailed descriptions of characteristics shared by *Taenidia* and *Pseudotaenidia*. The descriptions follow those of Mathias and Constance (1945). Morphological features that were determined to be different from, or in addition to those given by Mathias and Constance are enclosed in parenthesis.

Height --- 3 - 8.5 dm.

Leaves --- Petiolate with wholly sheathing petiols, sheating base striped with purple, cauline leaves like the basal, membranaceous, two to three times ternately compound with the upper leaves progressively less compound.

Leaflets --- Entire or aberrant plants of *Taenidia* with serrate leaflets (none were found in this study) or occasionally with a basal lobe in *Pseudotaenidia* (leaflets of *Taenidia* occasionally occur with a basal lobe), variable in shape from ovate to elliptical, usually shortly mucronate at the apex, 1 to 3.5 cm, long, 5 to 24 mm, wide, glabrous or glaucous (frequently, near the tips of the leaves, the leaflets may remain unseparated at their bases).

Inflorescence --- Loose, compound umbels, peduncles terminal and axillary. Rays of umbel are few, varying from plant to plant and from umbel to umbel on the same plant from 7 to 15 rays with 11 being the most common number. Rays spreading to ascending, the rays with perfect flowers much exceeding the rays with staminate flowers in length. In both genera the centrally positioned flowers of the umbellets are normally staminate. (Pistillate flowers occur rarely in the outer whorl of rays.)

Involucel & Involucre --- Involucel wanting in both genera. An involucre composed of a single linear bract occurs rarely in *Pseudotaenidia*, (no involucre was found in this study).

Flowers --- Petals five, yellow in color, (no specimens found to support the creamy petal color for *Pseudotaenidia* as described by Fernald [1950]), reflexed; stamens five, reflexed, alternate with the petals; calyx teeth five, rudimentary; styles two, short, spreading; stylopodium lacking; ovary inferior and bicarpellate.

Carpophore --- 2-cleft to base.

Stems --- Minutely ribbed, greenish, usually purplish toward the base, hollow between the nodes at maturity, nodes enlarged.

Underground Stems --- Branched or unbranched, subfusiform tubers.

DEVELOPMENT OF THE FLOWER

The process of flower development in Taenidia and Pseudotaenidia from its primordial origin to the fully differentiated flower proceeds in order and structural development in a manner that is very similar to the type of development as reported for Daucus carota L. by Borthwick, Phillips, and Robbins (1931) and for Eryngium yuccifolium Michx. and Zizia aurea (L.) W. D. J. Koch by Jurica (1922) and for various European Umbelliferae as reported by Martel (1905). Some differences in interpretations from the above authors will be discussed.

The following account describes the process of flower development in Taenidia and Pseudotaenidia as observed in this research. The process of development and the resulting floral structure is so similar in the two genera, they will be described as a single flower representing both Taenidia and Pseudotaenidia.

The primordium that initiates the formation of the flower first appears as a protuberance of undifferentiated tissue on the apex of the umbellet ray (Fig. 1). In a slightly older stage of development, the flower primordium resembles an inverted cone with its greatest diameter at its apex from which point the primordium tapers gradually toward its base and point of attachment to the umbellet ray (Fig. 2). In a still older development, the enlarged apex of the conelike structure comes to resemble a flat disk supported by a relatively thick stalk (Figs. 1 and 45). For the remainder of this report, the term disk will be employed to all references to the flat upper region of this structure.

The primordia that produce the sepals, petals, and stamens, as well as those primordia that initiate carpel development, originate in sub-epidermal cells of the margin and upper surface of the disk. From the material observed, it appears that a very few cells just beneath the epidermis of the disk become actively meristematic in five discrete areas around the margin of the disk and initiate petal formation (Figs. 1, 3, 48, 77 and 83). Just how many cells initiate the growth of petals was not determined, however, it appears that several, perhaps four to six are involved in the organogenesis of each petal during the initial stages. That the epidermis of the disk remains actively meristematic is evidenced by the observation that with the growth of sepals, petals, stamens and carpels, the cells of the epidermis of the disk increase in size and in number by anticlinal division. The epidermis of the disk becomes the epidermis of the young floral structure.

The primordia of the petals and the quite rudimentary sepals arise in alternate fashion from the disk margin (Fig. 8). The five sepals develop into very inconspicuous teeth which persist as visible structures through the stages of fruit maturation, however, in Pseudotaenidia the sepals often become obscured by the lateral wing development of the schizocarp wall. The inflexed position of the petals, a characteristic that is quite prevalent throughout the Umbelliferae, is apparent in the very early stages of development (Figs. 1 and 48). The inflexed position of petals is a result of a relatively greater increase in size and number of cells in the upper epidermis of the petals than in that of the lower epidermis. The greater number of cells in the upper epidermis results from a higher rate of anticlinal division.

Stamen primordia are initiated a very short distance from the margin toward the center of the disk (Figs. 3, 48, 77, and 83) and appear as relatively thick mounds of undifferentiated tissue. Apparently a very few cells just beneath the epidermis initiate stamen development. Stamens arise alternately to the petals (Fig. 51) and mature in an inflexed position similar to that of the petals, a position which they continue to hold until anthesis when they straighten out and become free of the covering petals.

At the stage of development when the growth of sepals, petals, and stamens has been initiated, a relatively large, nearly flat, circular area of undifferentiated tissue occupies the greater part of the center of the disk (Figs. 77, 83). The three outer whorls of floral structures, i. e., sepals, petals, and stamens, are initiated so nearly simultaneously that it does not seem possible to say which of these appears first. The almost simultaneous initiation of these primordia in _Taenidia_ and _Pseudotaenidia_ is identical to the development reported for _Daucus carota_ (Borthwick et al. 1931).

The commissural plane, which is not in evidence at the above described stage of development, will ultimately divide the ovary in such a manner that there are on the anterior side next to the axis of the umbellet, two sepals, three petals, and two stamens. On the opposite, posterior side, there are three sepals, two petals, and three stamens.

Petals, stamens and the very rudimentary sepals develop to a recognizable form before the carpel primordia originate. The two carpel primordia begin as mounds of tissue developing on opposite sides of the relatively flat central area of the disk just inside the whorl of stamens (Figs. 78, 84). As more tissue of the disk lateral to the growing carpel primordia become meristematic, the mound-like primorida extend laterally and upward until they have the forms of two u-shaped ridges (Figs. 79, 80, 85). The two ridges, each representing the growth of a single carpel, lie at a 45° angle to the surface of the disk (Figs. 4, 46). Borthwick et al. (1931) named the structure in Daucus carota that corresponds to the above described carpel primordium in Taenidia and Pseudotaenidia the outer rim of the carpel primordium (Figs. 4, 46, 80, 86). Borthwick's terminology is continued in this paper. The outer rims of the carpel primordia extend laterally, as a result of additional cells just beneath the epidermis of the disk becoming actively meristematic. The development of the ridge is inward toward the center of the disk (Fig. 81). In vertical section a carpel primordium appears as two separate ridges (Figs. 4, 86). The inner portions of the two carpel primordia, are the last portions of the carpel primordia to be initiated and therefore are relatively small as compared to the outer rims at this stage of development (Figs. 4, 86). Following the terminology of Borthwick et al. (1931), the inner portions of the carpel primordia will be called the inner rims (Fig. 4, a and e).

The outer rims of the carpel primordia continue to be actively meristematic and develop as structures that arch over the central portion of the disk, until they meet (Figs. 5, 47, 88). The outer rims subsequently become closely adnate (Figs. 6, 7, 14, 47, 48). The closely adnate but not physically joined outer rims of the two carpel primordia form a cavity (Figs. 6, 47). The relatively large cavity is ultimately divided into two locules by the upward growth of the inner rims of the carpel primordia (Figs. 4, 5, 89). The inner rims of the two carpel primordia, give rise to one or occasionally to two ovules in each of the two locules (Figs. 9, 10). If two ovules are present, only one of the two anatropous ovules in each locule develops to maturity.

The adnation of the outer rims of the carpel primordia forms a notch at the apex of the ovary (Fig. 10). The notch or groove is persistent and becomes even more pronounced as the fruit matures, however lateral wing development obscures the presence of the notch in the mature fruit of *Pseudotaenidia*. The notch defines the upper edge of the plane of the commissure.

The sequence of stages as ennumberated above describes the development of the basic flower structure of *Taenidia* and *Pseudotaenidia*. Subsequent development is by means of enlargement and maturation of the floral structure.

The use of the term *acropetalous*, as was used by Peyer (1853) in describing the order of initiation of floral primordia in the Umbelliferae, is not accurately descriptive of the order of development in *Taenidia* and *Pseudotaenidia*. Neither would it seem appropriate for the type of development described by Jurica (1922) for *Eryngium* yuccifolium nor for the description as given by Borthwick et al. (1931) for Daucus carota. The primordia of the sepals, petals and stamens appear at nearly the same level on the surface of the disk, and therefore do not develop in the usual sense of acropetalous differentiation. They do develop toward the apical meristematic region of the center of the disk even if it is not elongated upward. In this sense, the order of initiation is acropetalous. To this writer, the term centripetal more accurately describes the type of primordial initiation as occurs in Taenidia and Pseudotaenidia.

Two styles, one on each side of the notch at the apex of the ovary develop near the central axis of the flower (Figs. 11, 49). The more or less swollen, glandular structure, the stylopodium, present in most Umbelliferae, and located at the base of the styles is absent in both Taenidia and Pseudotaenidia. The lack of a stylopodium is particularly noteworthy since it is a characteristic feature of the sub-family Apioideae to which both Taenidia and Pseudotaenidia are classified.

At the time when all the floral primordia have been initiated and locule formation is nearly complete, sepal, petal, stamen and carpel primordia all are attached at approximately the same level to the upper surface of the disk. The base of the locules are actually located slightly above or at the level at which the petals are attached (Figs. 14, 48).

The superior position of the ovary in the immature flower of the Umbelliferae was noted by Kadan and Tichomirov (1954).

> The question pertaining to the nature of the ovary and fruit of the Umbelliferae, notwithstanding the sesquicentennial age of the question itself, and truly a tremendous amount of work devoted to it, it cannot be considered definitely solved. In the course of this time many hypotheses on the origin of the inferior ovary within the family have been advanced, but after the discovery that in early stages of the flower the ovary appears as superior they were supplanted by the hypotheses that the ovary should be accessed as secondary-superior or semi-inferior.

The classification as secondary-superior or semi-inferior by Kaden and Tichomirov, however, does not describe the position of the ovary which is wholly inferior in the mature flowers. The position of the ovary should be based on its position at maturity and not on that of early developmental stages. In the mature flower, the bases of the locules are found considerably below the level of the attachment of petals and stamens (Fig. 10). The arches of tissue formed by the outer rims of the carpel primordia are positioned directly above the ovules. Between the two ovules two columns of tissue represent the matured inner rims of the carpel primordia which divided the cavity into two locules.

It is clearly evident that with maturation, the sepals, petals and stamens are carried upward, well above the level of the disk surface that is represented by the bases of the locules in the mature flower, and that the tissue in the region between the ovules, above the ovules and part of the schizocarp surrounding the ovules represent tissue formed by the carpel primordia. That portion of the schizocarp, however, which lies below the level of the locule bases and the outer portions of the schizocarp that supports the sepals, petals, and stamens is formed by the growth of tissue produced in the formation of the stalked, disk-like flower primordium previously discussed. The inferior position of the ovary is thus ontogenetically produced. The inferior position of the ovary has an origin attributable to upward growth of tissues formed by the phylogenetically fused bases of sepals, petals and stamens. The ontogenic growth of the region of fusion results in the elevation of the apparent bases of the sepals, petals, and stamens to a position that is nearly level with the apex of the ovary. This is perhaps an explanation of the conclusion of Payer (1853) that the inferior ovary is produced by the growth of a ring-like zone of the axis which raises all of the primordia except the carpels.

Because of the phylogenetic fusion of the floral parts, the use of the term carpel as related to *Taenidia* and *Pseudotaenidia* and perhaps to many Umbelliferae is ambiguous. The primordial growths in the flat central area of the disk that produces the walls of the two locules and ultimately gives rise to the ovule primordia are called the carpels by Jurica (1922) and by Borthwick et al. (1931). On the other hand, throughout most descriptive taxonomic literature the fruit of the Umbelliferae is described as splitting at maturity into two carpels or mericarps with the term carpel being used synonymously with the term mericarp. As has been discussed previously, the mericarp is partially constituted of tissues produced before the carpel primordia are initiated, i. e., the phylogenetically fused bases of sepals, petals, and stamens. Because a variety of tissues are involved in the development of the fruit-half, the term mericarp rather than the term carpel will be used in this work to refer to the fruit-half, although it is recognized that the carpel forms a large part of the mature mericarp.

The flowers of Taenidia and Pseudotaenidia develop from their primordial beginnings to the mature flower in an identical manner to that as described above. The resulting mature flowers are identical in form, structure, size, and color. The complete flowers of both genera have five rudimentary calyx teeth, five inflexed yellow petals that are alternate with the sepals, five inflexed stamens that are alternate with the petals. A two-celled inferior ovary of identical structure and shape is found in both genera. The structure of the ovary is described in the section on the morphology of the fruit. In neither genus is a stylopodium produced. No differences in the external appearances of the flowers of the two genera is evident.

MORPHOLOGY OF THE FRUIT

In Taenidia and Pseudotaenidia a number of umbellet rays, usually about one-half of the total number of the rays of an umbellet, bear flowers which produce fruit. The average length of the fruit producing rays is nearly twice that of the non fruit-producing ones. The shorter and fruitless umbellet rays are commonly referred to as sterile rays. The sterile rays, however, bear staminate flowers. The hundreds of flowers of both Taenidia and Pseudotaenidia examined in this research showed that each umbellet has about one-half of its rays, usually the outer ones, bearing complete fruit-producing flowers; and about one-half, usually the central rays, bearing staminate flowers. The literature does not report the occurrence of pistillate flowers in either genus. It was found in this work that pistillate flowers occasionally occur in the outer whorl of rays as do the complete flowers.

The following description of the morphology of the fruit is given in order to compare the basic differences and similarities between the principal structures since the fruits are used to classify the Umbelliferae and are the sole means of separating Taenidia and Pseudotaenidia. Before describing the various parts of the fruit individually, a general description is given for purposes of orientation and for explaining the nomenclature that is used.

Taenidia and Pseudotaenidia are classified in their respective tribes on the basis of the direction of the flattening of their fruits and the uniformity or nonuniformity in the size of their primary ribs.

Members of the tribe Ammineae, which includes _Taenidia_, are characterized as having mericarps that are sub-terete in cross section and somewhat flattened laterally at right angles to the plane of coalescence of the mericarps. Their primary ribs are described as being all alike. Members of the tribe Peucedaneae, which includes _Pseudotaenidia_, are characterized as having mericarps that are narrow in cross-section, that is, flattened dorsally against the plane of coalescence of the mericarps. Their lateral primary ribs are characterized as being wing-like and much larger in size than the median primary ribs. Taxonomists, therefore, equate the lateral wings of the shizocarps of the Peucedaneae, with the lateral dorsal ribs of the shizocarps of the Ammineae.

In the Umbelliferae, the term _primary_ is used to designate the usually five conspicuous ribs of the mericarp with the term _secondary_ being used to designate those ribs located between the primary ones. Since there are no secondary ribs on the fruits of the Apioideae, the primary ribs will herein simply be referred to as ribs. What may on occasion appear to be irregularly formed secondary ribs between the primary ribs of _Pseudotaenidia_ are not true ribs in the usual sense in that they are not directly associated with vascular traces, but are simply produced as the result of an irregular wrinkling of the surface of the mericarp during the process of dorsal flattening. Such wrinkles are not present before extreme flattening occurs. The fruit of _Taenidia_ is not wrinkled between the ribs.

The three adjacent ribs located in the central area of the dorsal surface will herein be called the median dorsal ribs (Fig. 25). The two ribs located on the dorsal surface near the commissural plane of Taenidia will be called the lateral ribs (Fig. 57). The wing-like margins of the mericarp of Pseudotaenidia will be called the lateral wings (Fig. 26). The plane along which the two mericarps of the schizocarp separate, the commisurral plane, is the ventral surface (Fig. 15).

The five dorsal ribs of the mericarp of Taenidia appear externally as low rather inconspicuous, narrow, yellowish colored ridges running in a longitudinal direction from near the base to the apex of the mericarp and are very similar in appearance to the five dorsal ribs of Pseudotaenidia. The lateral ribs of Taenidia lie near the termination of the dorsal surface at the commissural plane (Fig. 57). In contrast, the lateral ribs of Pseudotaenidia lie at the base of the lateral wings (Fig. 26). The above description differs in part with published descriptive taxonomic works on the subject which equate the lateral wings of the Peucedaneae with the lateral ribs of the Ammineae. Both Taenidia and Pseudotaenidia have five low ribs each that are closely associated with the five dorsal traces. The lateral wings of Pseudotaenidia differ entirely from the ribs in origin and nature. The lateral wings of Pseudotaenidia are produced by the extreme dorsal flattening of the fruit and by the suberization of a considerable portion of the margins of the mericarps.

The color of the fruit of Pseudotaenidia is a light green from the time of its earliest development up until the time when the process of extreme dorsal flattening occurs and the relatively wide lateral wings develop. A change in color from light green to yellowish occurs on the lateral ribs and to varying degrees between and on the dorsal ribs and on the commissural or ventral surface as a result of the production of a thin film of yellowish corky cells. The lateral wings are made up entirely of identical appearing yellowish suberized cells. When mature, the dorsal surface of the mericarp is dark brown in areas where no corky cells are produced. Taenidia also has yellowish corky cells along the primary ribs but nowhere else. The young fruits of Taenidia are a light green in color as are those of Pseudotaenidia. The brown color of the fully mature fruit of Taenidia is identical to the brown color of Pseudotaenidia which lies beneath the surface layer of yellowish corky cells or which is exposed where no corky cells are produced.

Both Taenidia and Pseudotaenidia have a rather inconspicuous knob-like structure at the apex of their mericarps. This knob-like structure is not a stylopodium, as such a structure is completely lacking in both genera (Mathias and Constance 1945). It was determined in this work that the knob is formed by the fusion of the dorsal ribs at the apex of the mericarp. Viewed from above, the knob-like apex of the mericarp appears as a semicircular ridge. The shape of a knob on the apex of an unseparated schizocarp when viewed from above is that of a circular ridge with two breaks in the circle, each opposite the other in the plane of the commissure.

The schizocarp of Pseudotaenidia averages from 4 to 7 mm. in length, and from 3 to 5 mm. in width, including the lateral wings. The lateral wings average 0.75 mm. in width at their widest point mid-way between the base and apex of the fruit. The schizocarp of Taenidia averages 4 to 5 mm. in length and 3 to 4 mm. in width.

In both genera, the single vascular strand in the pedicel branches into two vascular strands in the receptacle (Figs. 16, 49). In the receptacle, each of the two vascular strands branches into six strands (Figs. 13, 68). Five strands from each of the two strands in the receptacle enter the mericarp and traverse its full length near the dorsal surface (Figs. 15, 55). The sixth strand, one from each of the two branches in the receptacle enter the schizocarp and traverse the central axis of the schizocarp near the ventral surface (Figs. 15, 55). When the schizocarps separate into two mericarps, the ventral strands become the carpophores. The two strands which will become the carpophores in the mature fruit lie in close proximity but are separated by a thin layer of parenchyma (Figs. 15, 64). For purposes of identification, the two commissural strands, one in each mericarp, will henceforth be called the ventral strands or carpophores, and the ten remaining strands, five in each mericarp, the dorsal strands.

The ten dorsal strands of vascular tissue are nearly evenly spaced in a semicircular arrangement near the epidermis of the schizocarp with five strands being located on either side of the commissure (Figs. 15, 55). A lacuna is associated with each one of the ten strands. The six dorsal strands of vascular tissue in each half of a schizocarp fuse at the apex of the ovary. It is from near this region of fusion that the vascular supply of the petals, stamens, styles, and ovules emanate. A single vascular strand goes to each petal, stamen, and style, but none goes to the rudimentary sepals. The region of fusion and the vascular supply to the ovules are discussed later.

The morphology of a single mericarp is used in describing the fruit structure. It is possible to describe the fruit morphology of *Taenidia* and *Pseudotaenidia* adequately and less repetitiously by describing only one of the two mericarps because the mericarps of a schizocarp are mirror images of each other.

The five lacunae or vittae associated with the five dorsal traces will herein be referred to as the dorsal lacunae. The remaining lacunae are spaced in a nearly circular arrangement within the mericarp close to the locule. These lacunae are not associated with vascular traces, are found in both dorsal and ventral positions and are closely associated with the locule. They are herein designated as *locular lacunae*, constituting new terminology (Figs. 24, 58).

The overall form and structure of the mericarps of *Taenidia* and *Pseudotaenidia* are shown in Figures 93 and 96.

Studies of free-hand sections of fresh mature fruits of both genera revealed that the endosperm completely fills the locule. The apparent space between the endosperm and the wall of the locule as it appears in Figure 24 and others was produced by shrinkage of the endosperm during processing the fruits for sectioning.

An area of sclerenchyma is present in the center of the ventral surface of *Pseudotaenidia* which was not observed to occur in *Taenidia* (Fig. 24, b). Before the separation of the carpophore from the mericarp the carpophore of *Pseudotaenidia* is attached to the ridge of sclerenchyma along its lateral surface (Figs. 32. 33).

In Figure 24 of Pseudotaenidia, the five dorsal traces and the five dorsal lacunae, one of which accompanies each trace, are clearly visible except for one dorsal lacuna at the base of the right hand lateral wing which is beyond the field of view. Three of the five dorsal traces and lacunae, i. e., the median dorsal ones, are located beneath the three ribs on the rounded dorsal surface as seen in the lower portion of the photograph. The two lateral dorsal traces and their accompanying lacunae may or may not form a rib on the dorsal surface. In Figures 24 and 25 a lateral dorsal rib is present. Lateral dorsal ribs occur in Pseudotaenidia when the lateral dorsal lacunae and traces lie close to the dorsal surface. The lateral dorsal ribs of Pseudotaenidia are therefore present irregularly, depending upon the meanderings of the lateral dorsal traces and the lacunae. No lateral dorsal rib is present when the lateral dorsal trace and lacuna lie relatively deep within the mericarp (Fig. 27). It is only the two lateral dorsal traces and lacunae of Pseudotaenidia that meander to any extent. The three median dorsal traces and lacunae of Pseudotaenidia and all five dorsal traces and lacunae of Taenidia lie close to the dorsal surface, do not meander and their associated ribs are always present in the mature fruit.

The locular lacunae of Pseudotaenidia can be seen in cross sectional view, as flattened tubes, the lumen of which is partially filled with dark staining deposits (Fig. 38). Usually in median cross sections of mericarps sixteen locular lacunae may be counted. A median cross section reveals that there are four locular lacunae on the ventral side of the mericarp with two spaced on each side of the ventral trace between the ventral trace and the lateral wings. In most cases twelve locular lacunae lie on the dorsal side of the mericarp with three each positioned between the dorsal ribs. Occasionally one of the three locular lacunae in each group may lie directly beneath one of the dorsal ribs.

Median cross sections of _Taenidia_ also reveal the presence of sixteen locular lacunae (Fig. 58). The locular lacunae of _Taenidia_ may be terete, ovoid or somewhat flattened in cross-section, but are usually not flattened to the extent of those of _Pseudotaenidia_. In mature fruits, dark staining deposits partially fill the lumens of the locular lacunae of _Taenidia_ in the same manner as those of _Pseudotaenidia_ (Fig. 61). Both _Taenidia_ and _Pseudotaenidia_ occasionally have 14 to 18 locular lacunae in median cross sections.

DETAILED MORPHOLOGY OF FRUIT STRUCTURE

The ventral trace, carpophore, and adjacent region

The employment of the term carpophore in referring to the ventral trace before the trace has physically separated from the mericarp is, strictly speaking, not appropriate. It is generally understrood that the ventral trace forms the carpophore. The terms are therefore used interchangeably by many writers. In this writing, also, these terms are used interchangeably and they are understood to include all of the sclerenchyma which forms the free, stalk-like structure and not just the very limited amount of discernable vascular tissue that is present.

Jackson (1933) concludes that the ventral trace may represent two more or less phylogenetically united traces. She considers this to be possible on the basis of the presence of two discrete or irregularly fused protoxylem traces in the carpophore halves of many species. The question has not been settled and for the purposes of this research, the ventral trace or carpophore will be considered as a single trace as it is described by most authors. The presence, however, of two somewhat discrete strands of vascular tissue in each carpophore half of Pseudotaenidia (Fig. 33) and Taenidia (Fig. 64) was observed in cross sections of the fruit. The two vascular strands of each carpophore half in both Pseudotaenidia and Taenidia tend to meander slightly and therefore are either nearly united or are distinctly separate at various cross sectional levels. The observation of this occurrence in Pseudotaenidia and Taenidia supports Jackson's (1933) conclusions that the ventral trace may represent two more or less phylogenetically united traces.

In cross sectional view, each of the protoxylem strands in the very immature fruit is surrounded by a small circular area of cells that appear to be parenchyma. Jackson (1933) concludes that in most species of Umbelliferae these cells are phloem-like conducting parenchyma. In Pseudotaenidia and Taenidia, and in the species studied by Jackson, the cells composing the two discrete areas of parenchyma or phloem-like parenchyma surrounding the two protoxylem strands of each carpophore mature into very thick walled sclerenchyma. In the mature fruits these lignified strands serve as the supporting structures, i. e., the carpophores, after they separate from the mericarps.

The carpophores of Taenidia and Pseudotaenidia have the characteristics that are, in general, typical of the Apioideae as described by Jackson in her comparative study of the carpophore of various representative genera in the subfamilies and tribes.

In the very immature fruit, the ventral traces of the two coalesced mericarps in Pseudotaenidia and in Taenidia are separated by a thin layer of parenchyma. This layer of parenchyma is sometimes called the separation layer (Essau, 1965). In the mature fruit of Taenidia and Pseudotaenidia cells in the region of the separation layer were observed to become strongly lignified and appear no different from the sclerenchyma throughout the carpophore. As a result of lignification, the parenchymatous separation layer ceases to exist in the mature fruit. This process was observed to occur in both genera under study. The lignification of the separation layer results in the two ventral traces of the schizocarp becoming, to all observable appearances, a single discrete structure separated by only a single layer of relatively thin walled cells in the plane of the commissure. The ventral traces of the coalesced mericarps separate along the plane defined by the single layer of cells with unthickened walls (Fig. 33, line a-c). The relatively thin walls of the cells in the plane of separation irregularly remain attached to one carpophore-half or the other.

Each of the essentially fused ventral traces of the coalesced mericarps, in additiion to separating from each other, must also separate from the mericarps in the formation of the two free, stalk-like structures, the carpophores, that support the mericarps of the mature fruit. There must be, therefore, three planes of separation, one being between the ventral traces as previously described, and with one being between each of the ventral traces and the mericarps. In Pseudotaenidia the separation of the ventral traces from the mericarps occurs in the same manner as that described above for the separation of the ventral traces from each other. Separation occurs along a plane of cells that have relatively thin walls (Fig. 33, line e-f). In Pseudotaenidia the ventral traces separate from a ridge of large celled sclerenchyma which is located along the ventral side of the mericarp (Fig. 32, line b-d).

In the cross sections of the mericarp of Pseudotaenidia in Figures 22-26, the carpophore is not present because at these particular levels it had previously separated from the mericarp and was broken off in processing for sectioning. The ridge of sclerenchyma from which the carpophore separated is clearly visible in the center of the ventral surface (Fig. 24, b). Fully separated carpophores of paired mericarps are shown in Figure 11. An enlarged view of the nearly separated carpophore (Fig. 33) shows that the carpophore of Pseudotaenidia is composed almost entirely of very thick walled sclerenchyma. Protoplasts are present in only a very few cells. The two protoxylem strands which are characteristic of the ventral trace of the immature fruit are discernible in the mature fruit and appear in cross section (Fig. 33) as very thick walled cells containing relatively small lumens. Also visible in the same photograph is the line along which the carpophore separates from the mericarp. At separation, the relatively thin walls of these cells irregularly remain attached to either the carpophore or to the sclerenchymatous ridge of the mericarp. The ridge of sclerenchyma from which the carpophore separates in Pseudotaenidia (Fig. 32) is absent in Taenidia. The carpophore of Taenidia separates from a relatively flat dorsal surface.

In Pseudotaenidia, a region of very thick walled sclerenchyma lies within the ventral mericarp wall just outside of the locule in the same radius as that of the carpophore. This region of sclerenchyma lies within that part of the mericarp wall that is crushed by the expansion of the ovule. The sclerenchyma is present at the level of the cotyledons and extends acropetally almost to the apex of the fruit. At the level of the cotyledons the mass of sclerenchyma is nearly terete in cross section (Fig. 27). At higher levels the sclerenchyma widens into a broad band (Fig. 32). No such sclerenchymatous region of the mericarp wall was observed to occur in Taenidia. The absence of sclerenchyma in Taenidia in the two areas noted above are the only apparent differences between the two genera in this particular portion of the mericarp.

The dorsal traces, dorsal lacunae, and dorsal ridges

Figure 17 depicts a cross section of an entire mericarp of Pseudotaenidia with the exception of the lateral wings which are beyond the field of view. The section shown is located near the base of the mericarp at the level of the receptacle. Since this section was made from a mericarp that had already separated from its opposing one, the receptacle is absent. It is at the level of the receptacle that the five dorsal traces and the five dorsal lacunae, which branch in the receptacle, enter the mericarp. A cross section of the schizocarp of Taenidia at approximately the same level of sectioning is shown in Figure 52.

Those parts of the mericarps which lie below the level of that shown in Figures 17 and 52 contain no vascular traces or lacunae. In the very immature fruits tissues of the mericarp are lacking below the level of the branching of the traces of the receptacle. With development of the fruit, the base of the schizocarp engulfs the receptacle and a very short section of the pedicel. As a result of this growth, a small basal portion of each mericarp lies below the branching of the traces.

A single lacuna accompanies and is very closely associated with each of the five dorsal traces. The dorsal lacunae are positioned on the outer or dorsal side of the dorsal traces. As previously absence of sclerenchyma in Taenidia in the two areas noted above are the only apparent differences between the two genera in this particular portion of the mericarp.

The dorsal traces, dorsal lacunae, and dorsal ridges

Figure 17 depicts a cross section of an entire mericarp of Pseudotaenidia with the exception of the lateral wings which are beyond the field of view. The section shown is located near the base of the mericarp at the level of the receptacle. Since this section was made from a mericarp that had already separated from its opposing one, the receptacle is absent. It is at the level of the receptacle that the five dorsal traces and the five dorsal lacunae, which branch in the receptacle, enter the mericarp. A cross section of the schizocarp of Taenidia at approximately the same level of sectioning is shown in Figure 52.

Those parts of the mericarps which lie below the level of that shown in Figures 17 and 52 contain no vascular traces or lacunae. In the very immature fruits tissues of the mericarp are lacking below the level of the branching of the traces of the receptacle. With development of the fruit, the base of the schizocarp engulfs the receptacle and a very short section of the pedicel. As a result of this growth, a small basal portion of each mericarp lies below the branching of the traces.

A single lacuna accompanies and is very closely associated with each of the five dorsal traces. The dorsal lacunae are positioned on the outer or dorsal side of the dorsal traces. As previously stated, in mature fruits of Pseudotaenidia in the region of the ovule the dorsal lacunae are usually flattened in cross section (Fig. 25). In Taenidia they may be somewhat flattened but are usually terete (Fig. 58). In both genera the dorsal lacunae are terete in cross section both above and below the level of the ovule. In both, dorsal lacunae enter the ventral side of the mericarp at a level slightly below that of their accompanying dorsal traces.

At the level of sectioning, as seen in Figure 17, four of the five dorsal lacunae are shown at their point of entrance into the mericarp. The four lacunae are located at or very near the ventral surface. Two of the lacunae are quite large and conspicuous in the photograph. All four lacunae may be identified and separated from the relatively large cells of the mericarp wall by the presence of a single layer of relatively minute cells surrounding each lacuna.. In Figure 17, only one dorsal trace, designated as c., is present entering the mericarp. It accompanies the lacuna, designated as d, located near the center of the ventral surface. The dorsal surface is unridged at this level and below.

Figure 52 of Taenidia shows the branching of the stele in the receptacle and the entrance of one median dorsal lacuna into the mericarp. In both genera, the centrally located median dorsal lacuna and trace enter the mericarp at a lower level than do the remaining dorsal traces (Figs. 17, 52). If one were observing cross sections of the mericarp in acropetal order, it would appear that the centrally positioned median dorsal lacuna and trace were the first to enter the mericarp. In both Pseudotaenidia and Taenidia, the two outer median dorsal traces enter the mericarp at a level only slightly above that of the centrally positioned one.

Figure 18 is of a cross section of the mericarp of Pseudotaenidia at a level only slightly above that shown in Figure 17, but still at the level of the receptacle. All five dorsal lacunae have entered the mericarp and are located about one-third of the distance through the mericarp from the ventral surface. Two of the five dorsal traces are present in the mericarp.

In Figure 19 the five dorsal lacunae are located approximately midway between the dorsal and ventral surfaces and all five dorsal traces have entered the mericarp. In the cross section shown in Figure 20 made at a slightly higher level than that shown in Figure 19 and near the apex of the receptacle, the five dorsal lacunae and the five dorsal traces are located about two-thirds of the distance from the ventral to the dorsal surface. Three relatively low, median dorsal ribs are well defined at this level. Each of the median dorsal ribs is associated with a median dorsal trace and lacuna. The three median dorsal ribs are present only in that part of the mericarp in which the three median dorsal traces and lacunae are close to the dorsal surface.

The two lateral dorsal traces and the two lateral dorsal lacunae of Pseudotaenidia, visible on the extreme right and extreme left in Figure 20, lie at the base of the lateral wings. The lateral dorsal traces and lacunae do not appear to be involved in the formation of the relatively large lateral wings as the wings extend well below the point of their entrance into the mericarp and well above the point of fusion of the lateral traces with the carpophore near the apex of the fruit. The lateral wings and the dorsal ribs are quite different in origin and structure. Lateral wings are not associated with the traces and lacunae as the dorsal ribs are. Lateral wings are formed as the result of the shape assumed by the mericarp during the process of dorsal flattening and by the suberization of a considerable portion of the margin of the mericarp. Lateral dorsal ribs occur in Pseudotaenidia at the base of the lateral wings where the meandering lateral traces and lacunae lie close to the dorsal surface (Figs. 25, 26, 27). This observation supports the contention of some that the dorsal ribs are formed by the presence of the relatively hard, lignified tissues of the traces.

In both Pseudotaenidia and Taenidia the lacuna accompanying each of the five dorsal traces is continuous from the branching of the traces from the stele in the receptacle and they follow the course of each trace. Near the point of convergence and fusion of the dorsal traces at the apex of the fruit the dorsal lacunae gradually separate from their associated dorsal traces. The dorsal lacunae continue in their upward course and enter the stamens and petals. On the anterior side of the schizocarp next to the axis of the umbellet, three of the dorsal lacunae enter the three petals located in this position. One lacuna enters each of the three petals. The two remaining dorsal lacunae enter the two stamens that are positioned on the anterior side of the schizocarp. One lacuna enters each stamen. On the opposite or posterior side of the schizocarp, two of the dorsal lacunae, one each, enter the two petals positioned on this side. Three dorsal lacuna, one each, enter the three stamens that are located on the posterior side of the schizocarp.

The single lacuna in each of the petals and stamens are, therefore, a continuation of the dorsal lacunae of the schizocarp. The lacuna in the petals nearly traverse full length of the petals. The lacuna in the stamens terminates near the base of the filament (Fig. 51). A branch trace from each dorsal trace follows the course of the lacunae and forms the vascular supply to petals and stamens (Fig. 68).

As previously stated, the five dorsal traces of both *Pseudotaenidia* and *Taenidia* traverse nearly the full length of the mericarp near the dorsal surface and converge and unite with the ventral trace near the apex of the fruit-half. The uniting of all six traces of *Pseudotaenidia* are shown in cross sectional view in Figures 39 through 44. Corresponding views of the uniting of the traces in *Taenidia* are shown in Figures 69 through 76. In both *Pseudotaenidia* and *Taenidia* the uniting of the traces occurs in nearly the same manner as described for *Pseudotaenidia* in the following paragraph.

In *Pseudotaenidia* the two lateral dorsal traces are each united with one of the outer median dorsal traces very near the apex of the mericarp and coincident with the apex of the locule (Fig. 39, g, h, j, k). At the level of the apex of the locule, the centrally positioned median dorsal trace is in a position near the dorsal surface (Fig. 39, d). At a slightly higher level, each of the lateral dorsal traces fuses with one of the median dorsal traces (Fig. 40, g, i). In the section depicted in Figure 40, the unfused median dorsal trace is in a position slightly closer to the ventral surface of the mericarp than it was at lower levels. At slightly higher levels the fused median dorsal and lateral dorsal traces fuse with the carpophore. The centrally positioned median dorsal trace (Fig. 40, d) arches over the apex of the locule and connects with the carpophore at about the same level as the two fused lateral dorsal and median traces. The ventral trace fuses with each set of the already fused lateral dorsal traces and median dorsal traces (Figs. 43, 44).

The vascular connection to the ovule consists of a trace originating from the fused lateral dorsal, outer median dorsal, and ventral traces (Figs. 41, 42). It would appear from Figures 41 and 42 that the ovule is supplied solely by the ventral trace, the outer median dorsal trace, and the lateral dorsal ~~trace. Jackson (1933), concluded that in~~ the Umbelliferae the ovule is supplied by the ventral and lateral dorsal traces. As explained in the previous paragraph, however, the two outer median dorsal traces fuse with the lateral dorsal traces and these fused traces in turn fuse with the carpophore and the centrally positioned median dorsal trace at the apex of the ventral trace or carpophore. A closed system is thus formed with all five dorsal traces and the ventral trace connected at the apex of the mericarp. Since all traces are connected, it appears that the vascular supply to the ovule is obtained directly from the fused ventral trace, outer median dorsal and lateral dorsal traces and indirectly by all six traces.

As noted previously, the fusion of the traces at the apex of the mericarp and the vascular supply to the ovule of <u>Taenidia</u> is nearly the same as that for Pseudotaenidia. In Taenidia each of the two lateral dorsal traces are united with the ventral trace (Fig. 69). These fused traces are shown here very close to their connection with the ventral trace (Fig. 69). Figure 70 also shows two branch traces originated from the fused lateral dorsal and ventral traces. These branch traces ultimately connect with the ovule. The same structures are also evident in the next serial section (Fig. 71). The connection of a lateral dorsal with the ventral trace are depicted in Figure 72. Also, a branch trace to an ovule is evident. Figure 73 shows a branch trace from a fused lateral dorsal and ventral trace at its point of entrance into the ovule. From these photomicrographs of Taenidia it would appear that the ovule is supplied only by the fused lateral dorsal and ventral traces. As in Pseudotaenidia, however, all six traces of the mericarp form a closed system and directly or indirectly furnish the vascular supply to the ovule. It is evident that there is some difference between the two genera in the manner of fusion of the traces and, therefore, a difference in the direct vascular supply to the ovule. In Pseudotaenidia, in each mericarp, the outer median dorsal and lateral dorsal traces fuse and then unite with the ventral trace. The branch trace to the ovule therefore originates from three fused traces. In Taenidia, the lateral dorsal trace connects with the ventral trace without any fusion with the outer median dorsal trace. The branch trace to the ovule therefore originates from two fused traces. The centrally positioned median dorsal trace arches over the apex of the locule and continues toward the ventral surface of the mericarp where it connects with the ventral trace

(Fig. 75). The fusion of the dorsal traces at the apex of the mericarp in Taenidia are shown in part in vertical section in Figures 67 and 68. These two figures also show that the traces to the petals branch from the region of fusion of the dorsal traces. Figure 90 depicts the entire vascular system of a schizocarp of Taenidia.

The locule and the locular lacunae

The anatomy of the locule in the mericarp of Taenidia and Pseudotaenidia was determined from serial sections. Photomicrographs of some pertinent sections are presented to substantiate the author's interpretations.

A cross sectional view of the locule of Pseudotaenidia below the level of the apex of the anatropous ovule is shown in Figure 22. This figure shows that Pseudotaenidia has a uniseriate inner epidermis of the mericarp and a uniseriate sub-inner epidermal layer. These layers are clearly a part of the mericarp wall, that is, they are not seedcoats because, as may be noted in the section pictured, this layer is well below the ovule itself. Sections made at higher levels and through the ovule reveal the presence of the same two layers of cells (Fig. 23). No differentiated seedcoat is discernible in the mature fruit; however, in the very young fruit a differentiated uniseriate layer which can be called a seedcoat is present (Fig. 15).

Taenidia has, as does Pseudotaenidia, a uniseriate layer or seedcoat surrounding the young ovule which is not discernible in the mature ovule (Fig. 55). Taenidia has a uniseriate inner epidermis of the mericarp wall as described for that of *Pseudotaenidia*. However, no differentiated sub-inner epidermal layer was observed to occur. The inner epidermis of the mericarp wall could also be designated as the locule wall.

A darkly staining substance accumulates in rather large quantities near the apex of the ovule, the base of the locule, of *Pseudotaenidia* (Fig. 22). This same, apparently mucilaginous, material lines the entire inner surface of the locule becoming progressively thinner in an acropetal direction (Fig. 23). To all observable appearances, the same type of mucilaginous material nearly fills the lumen or lines the walls of the locular lacunae (Fig. 38). This darkly staining mucilaginous material was observed to occur in the locular lacunae and locules of both *Taenidia* (Fig. 61) and *Pseudotaenidia*.

Before development of the ovule, the locular lacunae of the two genera are terete in cross sectional outline and are free of mucilaginous material (Figs. 15, 55). The strongly flattened locular lacunae of the mature fruit *Pseudotaenidia* are illustrated in Figure 22 and for *Taenidia* in Figure 61. When viewed in cross section, the immature fruits of both *Pseudotaenidia* and *Taenidia* usually have six locular lacunae spaced nearly equidistantly from one another in a circular arrangment around and very close to the locule. All of the six locular lacunae of the immature fruit originate at about the same level near the base of the locule and they follow the outline of the locule to their point of termination near the apex of the locule.

Taxonomic works ennumerate the number of lacunae in the mature friut as their being a certain number of lacunae positioned along the commissural side of the mericarp and a certain number positioned in the intervals between the dorsal ribs. Although these criteria are an excellent aid in the identification of species and deliniating position of the lacunae, the terminology tends to associate the locular lacunae with the commissure and the dorsal ribs; structures which, developmentally speaking, are not associated with the locular lacunae. In the immature fruit the locular lacunae lie deep within the mericarp very close to the locules and it is only after expansion of the ovule that the locular lacunae are forced into positions close to the commissure and the dorsal ribs.

With maturation of the fruit, additional locular lacunae are formed and add to the original six that are present in the immature fruit. These adventively produced locular lacunae are apparently formed schizogenously. Two are produced close to each of the original six lacunae; that is, one on each side. These late forming locular lacunae do not extend the full distance from near the base to near the apex of the locule as do the ones which originate in the immature fruit. Instead, they are of variable lengths with some occasionally extending nearly to the apices of the locule. Median cross sections of the mature fruits of *Pseudotaenidia* usually show sixteen locular lacunae to be present. Cross sections of mature fruits of *Pseudotaenidia* show that the locular lacunae lie close to the epidermis usually between the dorsal ridges and are not positioned as deeply in the mericarp as they are in the immature fruit. As a result of the growth of the ovule and dorsal flattening of the fruit, three locular lacunae are foreced into positions between each of the dorsal ridges and four are forced into a line near and closely parallel to the commissure. This change in position is a developmental one and the locular lacunae, as well as the wall of the mericarp are greatly flattened in the process (Fig. 37). In order for one to be able to ascertain the typical number of locular lacunae, one must examine fully mature fruits and truly median cross-sections must be used.

Pseudotaenidia was originally described as having usually one or sometimes two lacunae between the ribs and two to four along the commissure (Mackenzie, 1903). It was found in this research that the typical number of locular lacunae is three in the intervals between the ribs and four along the commissure. One specimen only was found with a single locular lacuna between each of the dorsal ribs, and only two specimens were found with two locular lacunae between the ribs. One specimen had four lacunae in the intervals and six along the commissure. The description of *Pseudotaenidia* as having one or two lacunae in the intervals between the ribs probably persists in the literature because of the difficulty in seeing the separate lacunae after the lacunae are flattened since they may appear as one with a hand lens, or because median cross-sections were not obtained, or because Mackenzie's (1903) original description of *Pseudotaenidia* as having one or two in the intervals has been carried over into later works without additional observation.

Similarly, it was determined in this research that *Taenidia* usually has three locular lacunae located in the intervals between the dorsal ribs and four locular lacunae are positioned on the commissural side of the mericarp. This observation coincides with the usual, published taxonomic description of the fruit. This number of locular lacunae, usually sixteen, corresponds to the number of locular lacunae present in the mericarp of *Pseudotaenidia* as determined in this work. Both *Pseudotaenidia*, and *Taenidia* have single locular lacuna located between the dorsal ribs of the very immature fruit; they are, however, located deep within the mericarp.

The endosperm

According to Isely (1947), the nucellus is absent in mature seeds and the abundant endosperm fills nearly the entire cavity in the Umbelliferae. In *Taenidia* and *Pseudotaenidia* the endosperm entirely fills the locule in each mericarp except for a relatively small space at the base and apex of the ovule. Examination of fresh, mature fruits of the two genera revealed that the endosperm is quite oily. Testing of the endosperm with iodine failed to reveal the presence of starch in the mature fruit. Also, starch grains were not observed to be present by microscopic examination of sections of the endosperm. Apparently the storage substance in the endosperm consists of an oil. Numerous oil droplets were observed in individual cells of the endosperm (Fig. 38). Comparative microscopic examinations of the endosperm of *Taenidia* and *Pseudotaenidia* revealed no basic differences between them.

The epidermis

The epidermis of the schizocarp of both *Taenidia* and *Pseudotaenidia* covers the entire dorsal side of each mericarp and ends at the plane of the commissure. The epidermis is unisereate in both genera and in both, there is a somewhat differentiated sub-epidermal layer (Figs. 35, 58). The sub-epidermal layer is not present in the ovary of the very young flower and apparently develops during maturation of the ovary and fruit.

The outer and inner walls of the uniseriate epidermis and the outer wall of the uniseriate sub-epidermal layer of both _Taenidia_ and _Pseudotaenidia_ become somewhat lignified in the mature fruit in that part of the mericarp lying below and above the locule. Cell walls of the epidermis are strongly lignified at the level of the locule.

It should be noted that the epidermal layer of the mericarp of _Taenidia_ and _Pseudotaenidia_ completely covers its dorsal surface and ends at the plane of the commissure. The presence of the epidermis on the dorsal surface of the lateral wings of _Pseudotaenidia_ and around its margin indicates that the lateral wings are an integral part of the mericarp and not just a proliferation of corky cells on the surface of the mericarp (Figs. 26, 36).

CHROMOSOME STUDIES

In an early study of the chromosomes of the Umbelliferae, Wancher (1934) wrote:

> In the Umbelliferae the chromosome numbers vary from 6 to 48 haploid....in the first two subfamilies,8 is probably the basic number, but in the third, 11 is the most common, being found in sixty-nine species. Probably 11 is of later origin than 8, both for the reason that 8 is found in most of the primitive genera investigated and for the reason of secondary pairing in a species with the haploid number 22, pointing to a lower primary origin of this number than 11 from which it, the species being tetraploid, has arisen secondarily by simple reduplication. Secondary associations pointing to 8 are also found in some species with 24 chromosomes haploid.

Chromosome studies made since those of Wancher substantiate his statement that 11 is the most common haploid number in the subfamily Apioideae (Darlington, 1956). However, both lower and higher haploid numbers occur quite frequently throughout the subfamily. Chromosome numbers of the Umbelliferae have been compiled and reported in the American Journal of Botany (Bell and Constance, 1957, 1960).

In this study, chromosome counts of *Taenidia* and *Pseudotaenidia* were made from microsporocytes. It was learned that in both *Taenidia* and *Pseudotaenidia* meiosis occurs well before emergence of the umbel from the sheathing leaf base. By the time of emergence of the umbel, apparently mature pollen is present.

Ten counts of the chromosome number of *Taenidia* were obtained with two counts each from five different plants. All counts indicated a haploid number of 11. The plant material for the counts was collected on Kate's Mountain in Greenbrier County, West Virginia, and in the West Virginia University Arboretum in Monongalia County from naturally growing plants. The ten counts of 11 haploid confirm a previous count of 11 for Taenidia made by Dr. C. R. Bell of the University of North Carolina at Chapel Hill. Dr. Bell's count was made from a plant collected in 1954 by Harry E. Ahles at Crystal Lake Park near Urbana, Champaign County, Illinois (Bell and Constance, 1957). A voucher specimen for Bell's original count is in the Carnegie Museum Herbarium at Pittsburgh, Pennsylvania (Ahles Collection No. 7926).

Seven counts of 11 haploid were obtained of the chromosomes of Pseudotaenidia. The counts were made from four plants. To the author's knowledge, this was the first time that a chromosome count of Pseudotaenidia had been made. All counts were made from specimens transplanted from a hillside between Wade's and White's Draft in Greenbrier County, West Virginia to the West Virginia University Arboretum. The transplanting procedure was followed because of the difficulty in separating Taenidia from Pseudotaenidia in early stages of growth and because of the relative remoteness of the natural range of Pseudotaenidia from West Virginia University. Plants were collected in late fall when in fruit and thus easily identified and then were planted in the Arboretum in an area where Taenidia does not occur. The plants were carefully marked and the umbels were collected from them the following spring. A voucher specimen for the chromosome count of Pseudotaenidia is on deposit in the Herbarium of the University of California at Berkeley. The count was reported in Documented Chromosome Numbers of Plants (1960).

In order to determine whether some relationship exists between the chromosome number, size, and shape of those species with laterally flattened fruits and those with dorsally flattened fruits, the published chromosome numbers and drawings of them were compiled in their respective categories for comparison. Tables 1 and 2 give the genus, chromosome numbers, and the number of species in the genus with a particular chromosome number. The drawings used in the comparison are given in Figures 104 through 125. Drawings and photomicrographs made in this research of _Taenidia_ and _Pseudotaenidia_ are also presented (Figs. 97-103).

The data in Tables 1 and 2 indicated that there is no relationship between chromosome number and the two basic types of fruits, based on presently known chromosome numbers. Haploid numbers of 6, 11, 18, and 22 occur in both classifications. Some numbers occur exclusively in one or the other classification. Haploid numbers of 8, 10, 17, 19, and 20 are found in genera with laterally flattened fruits, whereas 7, 14, 16, and 33 occur in genera with dorsally flattened fruits. Within both classifications the chromosome numbers from species to species within a single genus may vary considerably.

Extreme variation in size and shape of the chromosomes occurs between species within some genera in the two categories, whereas in other genera the chromosomes are quite uniform regardless of species. The chromosomes of some genera such as _Zizia_ and _Taenidia_ with laterally flattened fruits superficially resemble those of such genera as _Lomatium_ and _Pseudotaenidia_ with dorsally flattened fruits more so than others in their respective taxonomic classifications based on fruit shape.

On the basis of information compiled in this study, no basic

TABLE 1. Chromosome numbers of some genera with laterally flattened fruits*

Genus	Chromosome Number	Number of Species Counted
Bupleurum	n=8	2
Zizia	n=11	3
Cicuta	n=22	1
Cryptotaenia	n=10	1
	n=11	1
Carum	n=10	1
Taenidia	n=11	1
Pimpinella	n=10	1
	n=20	1
Perideridia	n=17	1
	n=18	1
	n=19	2
	n=20	1
	n=22	1
Sium	n=6	3
Berula	n=6	1

*Compiled from: Bell, C. Ritchie and L. Constance. 1954. Chromosome Numbers in Umbelliferae. Amer. J. Bot. 44:565-572.

____________. 1960. Chromosome Numbers in Umbelliferae II. Amer. J. Bot. 47:24-32.

TABLE 2. Chromosome numbers of some genera with dorsally flattened fruits*

Genus	Chromosome Number	Number of Species Counted
Ptilimnium	n=6	1
	n=7	1
	n=11	1
Ligusticum	n=11	4
	n=11 & 22	1
Thaspium	n=11	3
Conioselinum	n=11	1
Angelica	n=11	6
	n=33	1
Oxypolis	n=14	2
	n=16	1
	n=18	2
Pseudotaenidia	n=11	1
Polytaenia	n=11	1
Lomatium	n=11	16
	n=22	2
Heracleum	n=11	1

*Compiled from: Bell, C. Ritchie and L. Constance. 1954. Chromosome Numbers in Umbelliferae. Amer. J. Bot. 44:565-572.

____________. 1960. Chromosome Numbers in Umbelliferae II. Amer. J. Bot. 47:24-32.

difference between the tribes Ammineae and Peucedaneae can be correlated with chromosome number, size, or shape. A direct comparison across tribal lines between species that are apparently closely related on the basis of other morphological considerations appears to be valid. For purposes of comparison, outline drawings of the chromosomes of *Taenidia* and *Pseudotaenidia* are presented (Figs. 97, 98). These drawings were made by outlining the projected images of the chromosomes from negatives of several photomicrographs taken at different levels of focus in order to show best the outline form of each chromosome. Two sets of similar chromosomes are numbered 1 and 2 in each figure. Chromosome 1 of *Taenidia* (Fig. 97) is markedly similar to chromosome 1 of *Pseudotaenidia* (Fig. 98) in both size and shape. Chromosome 2 of *Taenidia* is somewhat comparable to chromosome 2 of *Pseudotaenidia*, but the resemblence here is less discernible than that between chromosomes designated as 1 in the two species. No chromosomes of the particular shapes of chromosomes 1 and 2 were found to be present in the published drawings of any other members of the tribes *Ammineae* or *Peucedaneae*. None of the remaining nine chromosomes in each of the respective complements of *Taenidia* and *Pseudotaenidia* are sufficiently similar in shape as to warrant a direct comparison either between *Taenidia* and *Pseudotaenidia* or any comparison between either of these species with any other species of their respective tribes or across tribal lines.

A comparison of the chromosomes of *Taenidia* and *Pseudotaenidia* revealed the following information:

1. Both plants have haploid numbers of 11.

2. Their chromosomes are approximately the same size, taking into account slight variations in shape.
3. Out of the complement of 11, two chromosomes of *Taenidia* are very similar in size and shape to two chromosomes of *Pseudotaeindia*. The remaining nine chromosomes in each plant are not directly comparable in shape but are quite similar in size.
4. The two comparable chromosomes of *Taenidia* resemble two chromosomes of *Pseudotaenidia* in size and shape more so than they resemble those of any other genera that have been investigated to date in either tribe *Ammineae* or *Peucedaneae*.
5. On the basis of chromosome number, size and shape there is no apparent reason for the very wide taxonomic separation made between *Taenidia* and *Pseudotaenidia*.

SUMMARY AND CONCLUSIONS

The evidence as evaluated in this research indicates that the present classification of the two monotypic genera, Taenidia and Pseudotaenidia, in different and widely separated tribes in the subfamily Apioideae is not justifiable and has thus resulted in an arbitrary separation of two very closely related genera. The taxonomic validity of the cross sectional shape of the fruit and the size of the lateral ribs as being the principal indicators of phylogenetic relationship in all taxa of the Umbelliferae may be, therefore, seriously questioned. A summary and discussion of the evidence for the above statements is given in the following paragraphs.

Based on purely descriptive taxonomy which recognizes the fruit of the Umbelliferae as the most reliable indicator of relationship, the plants Taenidia and Pseudotaenidia are readily separated into different genera and tribes. The laterally flattened schizocarps of Taenidia and the dorsally flattened ones of Pseudotaenidia are the primary features that enable the botanist to make a distinction between these plants. The morphology of only one structure i. e., the fruit, is, therefore, considered to be the primary indicator of phylogeny. Based upon descriptive taxonomy without taking into account the different morphology of the fruits, there is no apparent reason for the classification of Taenidia and Pseudotaenidia as two separate genera for in all other respects the genera are indistinguishable.

Because of the phylogenetic importance attributed to the fruits, the primary line of investigation in this research was to make a detailed study of the fruits of Taenidia and Pseudotaenidia and to evaluate the significance of their ultimate basic structure at maturity from a developmental standpoint and then to evaluate other taxonomic considerations including the chromosomal complements, ecology and range in order to assess the taxonomic relationship of the two genera.

The fruit is the product of a relatively long period of development and may be considered to have its beginning with the initiation of the flower primordium, followed by the initiation and development of the carpel primordia, the maturation of the carpels in the developing flower structure which produces the mature ovary, followed by maturation of the ovary to the mature fruit. This research began with a study of the flower primordium and followed the stages of development of the basic flower and fruit structures. This developmental sequence was studied in order to determine the stage of development in which the differences in the mature fruit first become evident and to ascertain whether the morphological differences between the mature fruits is fundamental in the development of the flower structure or whether the differences in morphology develop during the period of fruit maturation. It was reasoned that, if the direction of flattening of the fruits is a morphological feature that develops with maturation of the fruit and is not inherent in the morphology of the ovary, then it is more likely that the cross sectional shape of the fruit could have evolved independently in different taxa of the Umbelliferae. The shape of the fruits, therefore, may not always be the primary indicator of phylogeny. It was determined that the ultimate shape of the mature fruit is independent of the shape of the mature carpels or ovary and the fruits may actually be flattened in the opposite direction from that of the ovary of the flower.

The nature and sequence of primordial development of the flowers of both *Taenidia* and *Pseudotaenidia* was determined to be identical. A comparison of the morphological development of the flowers of *Taenidia* and *Pseudotaenidia* with the morphological development that has been studied in other genera of the Apiodeae by previous researchers indicates that the basic flower structure is produced in essentially the same manner. The fully developed flower structure is identical in *Taenidia* and *Pseudotaenidia*.

It was observed in this research that the shape of the ovaries of *Taenidia* and *Pseudotaenidia* are identical. As the fruit of *Taenidia* matures, the fruit maintains the same shape, i. e., laterally flattened, as that of the ovary, whereas the laterally flattened ovary of *Pseudotaenidia* remains laterally flattened only to the stage at which the fruit is approximatedly one-third of its mature size after which the maturing fruit becomes dorsally flattened. The lateral wings of the fruits of *Pseudotaenidia* become apparent only after the fruit has reached approximately one-half mature size. The cross sectional shape of the ovaries of *Taenidia* and *Pseudotaenidia* give no indication of the cross sectional shape of the mature fruits. On the basis of these two genera, the cross sectional shape of the fruit is, therefore, a morphological feature that is produced during maturation of the fruit, or, in other words, it is a morphological characteristic that is initiated by the stimulation of fruit development, after the process of pollination and/or fertilization. Rodgers (1950) has noted that the shape of the fruit may be very different from the shape of the ovary in some Umbelliferae. Rodgers stated that:

> In Hydrocotyle, lateral flattening of the ovary is evident in in very young buds, yet the ovaries are not as extremely flattened as the fruits. In Pastinaca sativa and Angelica triquinata the ovaries in the buds are actually laterally flattened while the fruits are dorsally flattened. In Angelica venenosa dorsal flattening is later, the ovaries of the flowers being somewhat laterally flattened. A further delay in dorsal flattening is in Oxypolis rigidior, O. ternata, and O. filiformis where the ovaries of buds and flowers are distinctly laterally flattened and where fruits mature distinctly dorsally flattened.

That the shape of the fruit of many Umbelliferae may be the same or the opposite, dorsally flattened as opposed to laterally flattened, of that of the ovary and that the shape of the fruit is not fundamental to the nature and development of the carpels is a strong morphological indication that dorsal or lateral flattening of the fruit could have evolved independently in various taxa of Umbelliferae. A taxonomic scheme, therefore, based largely on the shape of the fruit would result in relatively unrelated plants being grouped together in the same taxon.

Morphological features other than the direction of the flattening of the fruits that have been noted in taxonomic works as being different in Taenidia and Pseudotaenidia concern the number of lacunae and the size of the lateral dorsal ribs. As was noted in this work, there is no difference between Taenidia and Pseudotaenidia in respect to the number and morphology of these features. Both genera have three lacunae located between adjacent dorsal ridges and four lacunae located along the commissure or ventral side of the mericarp for a total of sixteen lacunae. These have been designated as locular lacunae in this work but are simply called lacunae or oil tubes in other works. The schizocarps of Taenidia are described in taxonomic works as having five low dorsal ribs, whereas Pseudotaenidia is described as having three low dorsal ribs, the median dorsal ones, and two relatively wide wing-like lateral dorsal ribs which are equated with the low lateral dorsal ribs of Taenidia. As was clearly shown in the present study, both genera have five low dorsal ridges. The laterally positioned wing-like structures of the mericarp of Pseudotaenidia are structures that are in addition to the five low dorsal ribs and are in reality the suberized lateral margins of the dorsally flattened mericarp. The wing-like lateral margins of the mericarp of Pseudotaenidia and other Umbelliferae with dorsally flattened fruits are often described as being nerved on the dorsal surface. The so called nerve of Pseudotaenidia is the structure that may be accurately equated with the low lateral dorsal ribs of Taenidia and other Ammineae. The nerve is actually the lateral dorsal rib of Pseudotaenidia and is closely associated with a dorsal trace and lacuna as is typical of dorsal ribs. The number of lacunae and the number and size of the dorsal ribs, therefore, cannot be used to separate these two genera as they are the same in both. The vascular pattern, i. e., the ramifications of the dorsal and ventral traces and vascular supply to the ovules were determined to be nearly identical. The only difference in the vascular system between the fruits of *Taenidia* and those of *Pseudotaenidia* is in the sequence of anastomosis of the dorsal traces near the apex of the mericarp. In *Pseudotaenidia*, the outer median dorsal trace fuses with the lateral dorsal trace before the branching of the trace to the ovule. In *Taenidia* a trace to the ovule branches before the fusion of the outer median dorsal trace with the lateral dorsal trace. To the writer, this does not appear to be a taxonomically significant difference between the genera. As in *Pseudotaenidia*, the outer median dorsal and lateral dorsal traces of the mericarp of *Taenidia* fuse. ~~In *Taenidia* the fusion occurs slightly~~ higher, in an acropetal direction than it does in *Pseudotaenidia*. In other words, the manner of fusion is the same but it occurs at slightly different levels in the two genera.

The only apparent difference between the schizocarp of *Taenidia* and that of *Pseudotaenidia* is the direction of flattening, the suberization of the lateral margins of the mericarps of *Pseudotaenidia*, and a very slight difference in size.

In addition to a close phylogenetic relationship being indicated by identical morphological features with the exception of those noted above, there are other features which support the same conclusion. As noted in a prior section entitled Chromosome Studies, *Taenidia* and *Pseudotaenidia* have the same haploid chromosome number of eleven. The haploid number is in itself not a strong indication of comparatively close relationship for eleven is by far the most common haploid chromosome number throughout the very large sub-family Apioideae. Two chromosomes, however, in the haploid set of Taenidia greatly resemble two chromosomes in the haploid set of Pseudotaenidia in respect to both shape and size. Based on a study of the published descriptions and drawings of other genera in the same sub-family, chromosomes with this particular morphology were not observed in other taxa. These two easily identified chromosomes in both Taenidia and Pseudotaenidia were observed by the author in all smears of microsporocytes. The similar morphology of these chromosomes that occurs in these two genera but not noted elsewhere in the taxa that have been studied by others is an additional indication of a close phylogenetic relationship between Taenidia and Pseudotaenidia.

That the taxa Taenidia and Pseudotaenidia are distinct is indicated by the presence of a reproductive barrier between them. As was determined in the section of this work under Reproductive Isolation, cross-pollination must be a very common occurrence but no plants have ever been found that exhibit morphological features that would indicate hybridization, that is, the fruits are always distinctly laterally flattened or dorsally flattened. Taenidia and Pseudotaenidia are two nearly identical plants of apparently common evolutionary origin, but are separated not by range, ecological, or developmental barriers, but nevertheless maintain themselves as distinct taxa. The absence of hybridization between these morphologically similar plants indicates that they are distinct comparia, a biosystematic category that is usually comparable to the traditional category of the genus. Since a genetic barrier is indicated by morphological studies and field observations, Taenidia and Pseudotaenidia should remain as separate genera as they are now classified. Future studies of a cytogenetic nature involving controlled attempts at hybridization could determine the nature and degree of the apparent genetic barrier resulting in additional information as to the degree of relationship. It is possible that successful hybrid offspring are produced but one fruit shape is dominant.

This writer concludes from the morphological, geographical and ecological evidence that the closest phylogenetic relative of Pseudotaenidia is Taenidia in spite of the fact that they produce differently shaped fruits. Such a conclusion is supported by the work of Rodgers (1950) who has stated that:

> The lumping together of all species with extreme dorsal flattening does not seem to reflect their true origin. Some members have little in common except extreme flattening. It is more likely that this tendency has several origins.

The following conclusions may be drawn from this study of Taenidia and Pseudotaenidia:

1. Taenidia integerrima (L.) Drude and Pseudotaenidia montana Mackenzie should remain as they are now classified in separate genera.
2. The nearest phylogenetic relative of Taenidia is Pseudotaenidia.
3. Taenidia and Pseudotaenidia should not be classified as they are at present in separate tribes at nearly the opposite ends of the very large sub-family Apioideae. The present

taxonomic criteria that are used to define the two tribes would not permit, because of the differences in the flattening of the fruits, either _Taenidia_ being placed in the Peucedaneae with _Pseudotaenidia_ or for _Pseudotaenidia_ to be placed in the Ammineae with _Taenidia_. A new basis for such a classification should be devised, but because of the great number of species and the morphological complexities involved, the likelihood of such a drastic reclassification being made lies well into the future.

4. The use of the cross sectional shape of the schizocarp and the presence or absence of lateral wings as the primary indicators of phylogenetic relationship in the Apiodeae of the Umbelliferae is seriously questioned. Other morphological features may be of equal or greater significance.

Explanation of Plate 1

Pseudotaenidia. Development of flower primordia.

Fig. 1. Three stages of flower primordial development, longitudinal section, X1191. a. Early primordium; b. Disk stage; c. Petal developing; d. Supporting stalk of older disk stage; e. Apex of umbellete ray.

Fig. 2. Two stages of flower primordial development, longitudinal section, X976. a. Disk stage; b. Stage intermediate between a. and b., Fig. 1; c. Apex of umbellete ray.

Fig. 3. Late disk stage of flower primordial development, longitudinal section, X912. a. Supporting stalk of older disk stage; b. Early stamen primordium; c. Base of developing petal, apex removed in sectioning.

PLATE - 1

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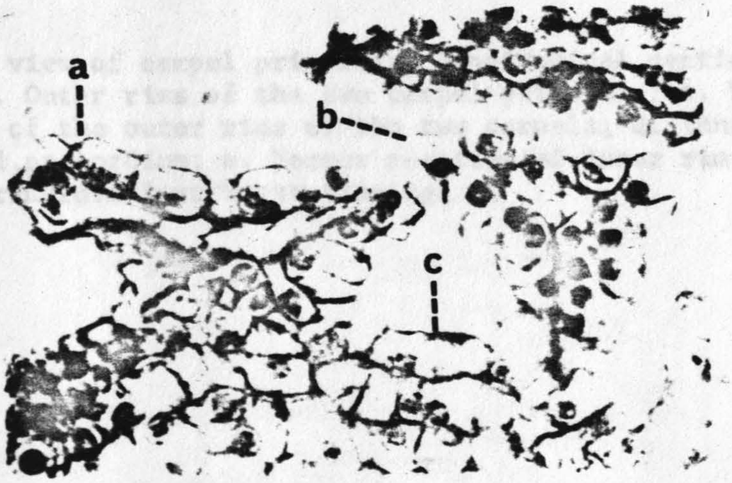

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Explanation of Plate 2

Pseudotaenidia. Development of carpels and locules.

Fig. 4. Immature flower with most floral structures present, longitudinal section, X478. a. Inner rim of carpel primordium; b. Basal portion of petal; c. Apical portion of petal; d. Stamen; e. Inner rim of carpel primordium; f. and g. Outer rims of carpel primordia.

Fig. 5. Close-up view of carpel primordia, longitudinal section, X1290. a. and b. Outer rims of the two carpel primordia; c. Plane of adnation of the outer rims of the two carpels; d. Inner rim of carpel primordium; e. Former position of inner rim of carpel primordia lost in sectioning.

Fig. 6. Close-up view of carpel primordia, longitudinal section, X2425. a. and c. Fully adnate outer rims of the two carpel primordia; b. Plane of adnation; d. Locule.

PLATE-2

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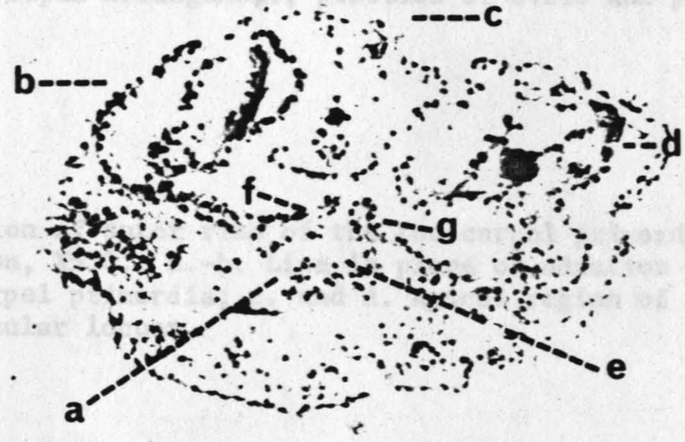

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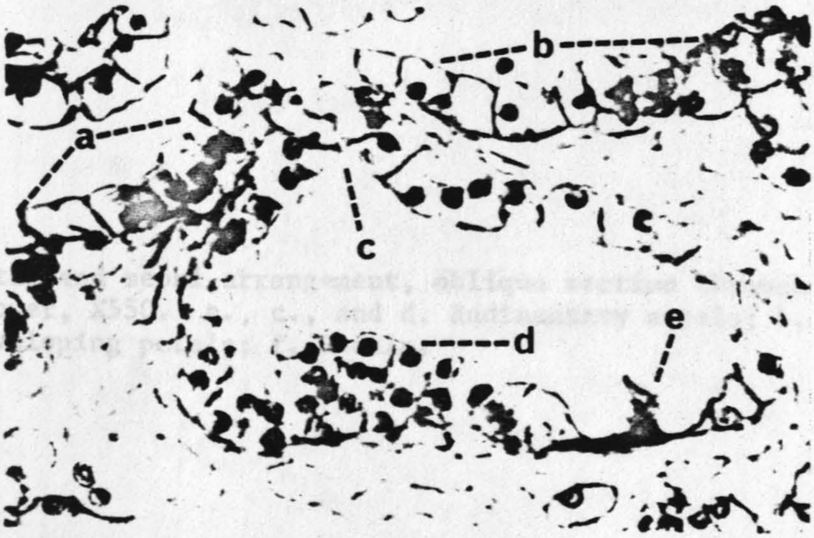

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Explanation of Plate 3

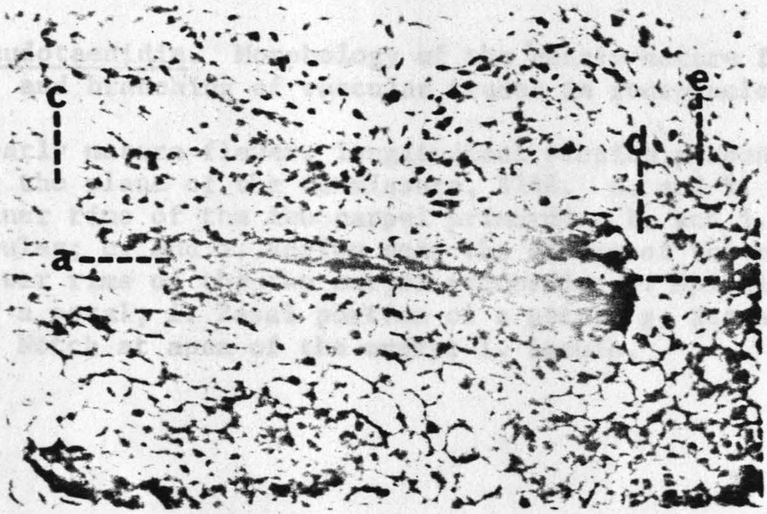
Pseudotaenidia. Development of carpels and locules, petal and sepal arrangement, position of ovule and polyembryony.

Fig. 7. Adnation of outer rims of the two carpel primordia, cross section, X550. a.-b. Line in plane of adnation of outer rims of carpel primordia; c. and d. Apical region of locules; e. Locular locuna.

Fig. 8. Petal and sepal arrangement, oblique section through immature flower, X550. a., c., and d. Rudimentary sepals; b. and e. Developing petals; f. Locule.

Fig. 9. Anotropous ovules, longitudinal section, X558. a. Normally developing ovule; b. and c. Funiculi; d. Second ovule that is usually not present or aborts.

PLATE-3



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Explanation of Plate 4

Pseudotaenidia. Morphology of the nearly mature flower and branching of vascular traces in receptacle.

Fig. 10. Nearly mature flower, longitudinal section perpendicular to the plane of the commissure, X146. a. and k. Matured inner rims of the two carpel primordia; b. and j. Anatropous ovules; c. and i. Region near the center of the matured outer rims of the two carpel primordia; e. Apical portion of a petal; f. Basal portion of a petal; g. Stamen; h. Notch at apex of the ovary; l. Locule.

Fig. 11. Young developing sytles, longitudinal section perpendicular to the plane of the commissure, X357. a. and b. Immature styles; c. Notch formed along plane of adnation of outer rims of the two carpel primordia in same position as h. Fig. 10.

Fig. 12. Young developing styles, longitudinal section parallel to the plane of the commissure, X1612. a. Knob-like stigma; b. Style; c. Apex of the mericarp.

Fig. 13. Branching of traces in receptacle, longitudinal section, X614. a. Stele; b. and h. Lacunae; c. d. e. f. and g. The five dorsal traces of a mericarp.

PLATE-4

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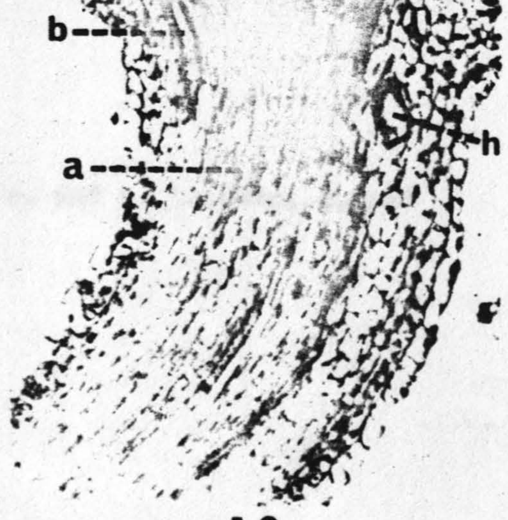

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Explanation of Plate 5

<u>Pseudotaenidia</u>. Morphology of immature mericarp, anatomy of ovary-half and receptacle.

Fig. 14. Immature flower, longitudinal section, X550. a. Locule; b. and h. Basal portion of petal; c. Stamen; d. Apical portion of petal; e. Adnate outer rims of the two carpel primordia; f. Petal; g. Stamen.

Fig. 15. Immature mericarp, cross-section, X375. a. - n. Line in the plane of the commissure; b. and l. Lateral dorsal lacunae, each with accompanying lateral dorsal trace; c. Uniseriate inner epidermis of mericarp; d. f. and h. Median dorsal lacunae, each with accompanying median dorsal trace; e. Seed coat; g. Uniseriate sub-epidermal layer; i. Uniseriate epidermal layer; j. Locular lacuna (one of three visible in photomicrograph); k. Cavity in ovule containing a megaspore nucleus; m. Beginning development of a lateral wing; o. and p. Ventral traces of opposing mericarps.

Fig. 16. Receptacle, cross-section, X500. a. and b. Lacunae; c. and d. Discrete traces.

PLATE-5

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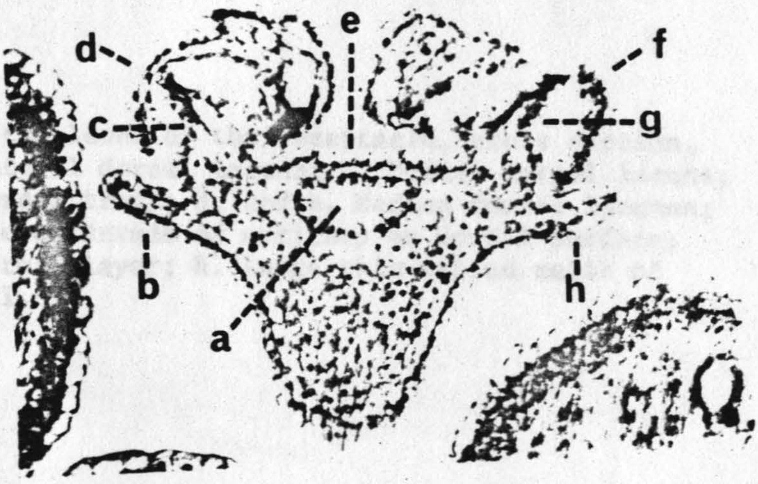

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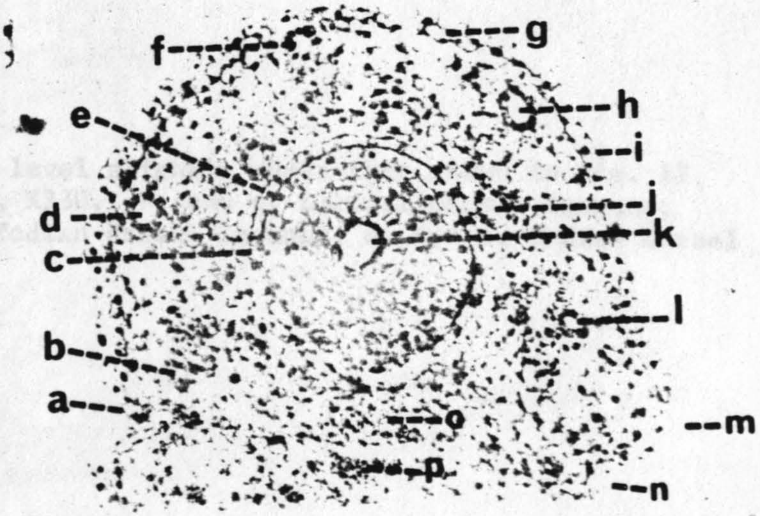

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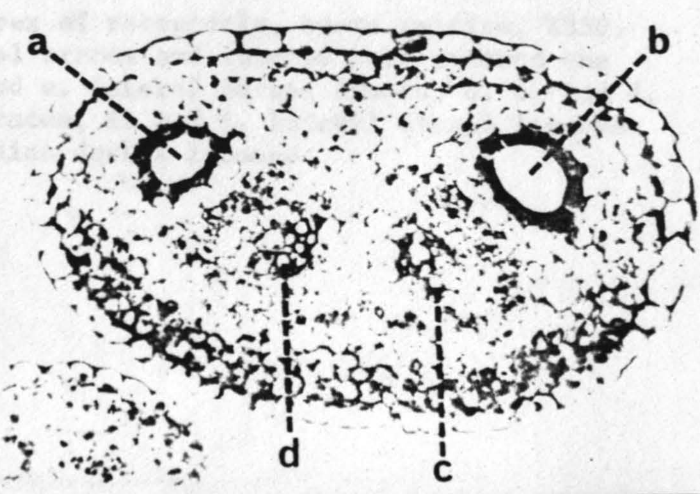


Explanation of Plate 6

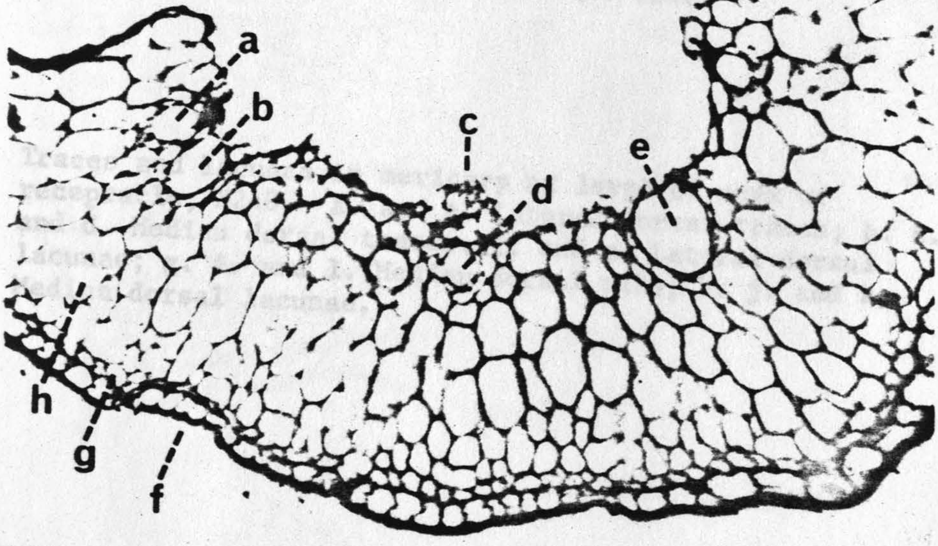
Pseudotaenidia. Entrance of traces and lacunae into mericarp. Note - Lateral wings are out of field of view.

Fig. 17. Mericarp at the level of the receptacle, cross section, X330. a. Lateral dorsal lacuna; b. Median dorsal lacuna; c. Median dorsal trace; d. and e. Median dorsal lacunae; f. Uniseriate epidermis of mericarp on dorsal surface; g. Sub-epidermal layer; h. Large thin-walled cells of mericarp wall.

Fig. 18. Mericarp at a level slightly above that shown in Fig. 17, cross section, X330. a. and g. Lateral dorsal lacunae; b. c. and f. Median dorsal lacunae; d. and e. Median dorsal traces.

Fig. 19. Mericarp near apex of receptacle, cross section, X350. Note - All dorsal traces and lacunae have entered the mericarp. a. and e. Lateral dorsal traces; b. c. and d. Median dorsal traces; f. and j. Lateral dorsal lacunae; g. h. and i. Median dorsal lacunae

PLATE-6



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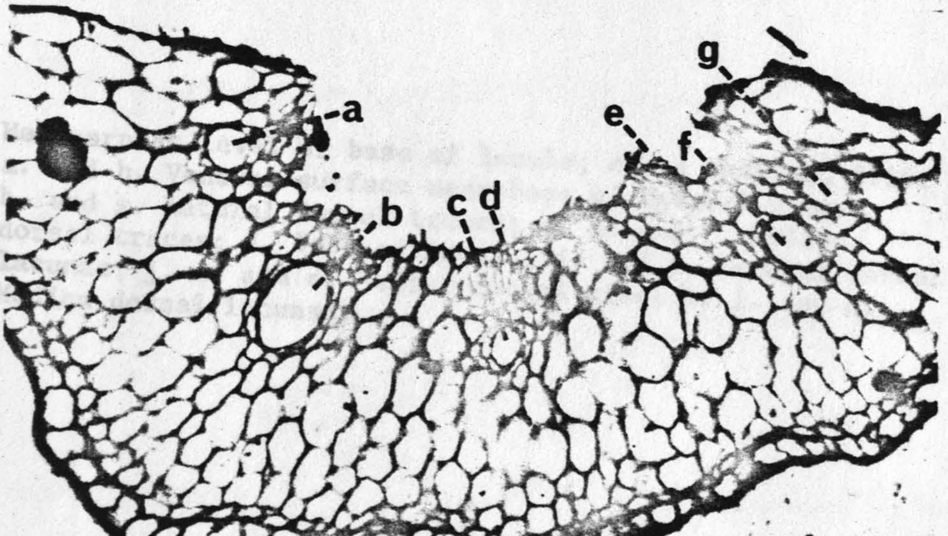

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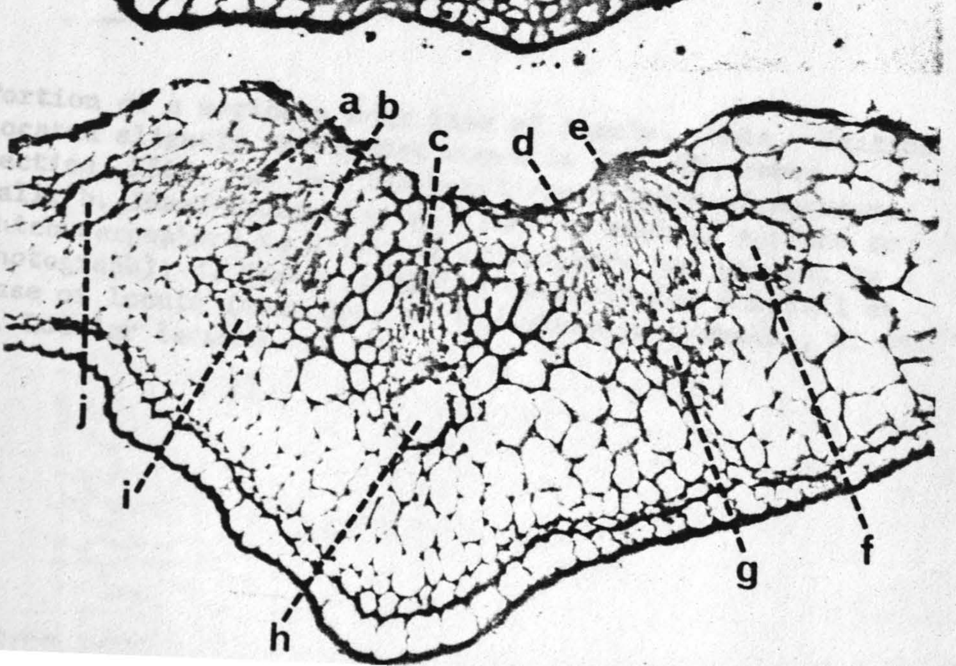

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Explanation of Plate 7

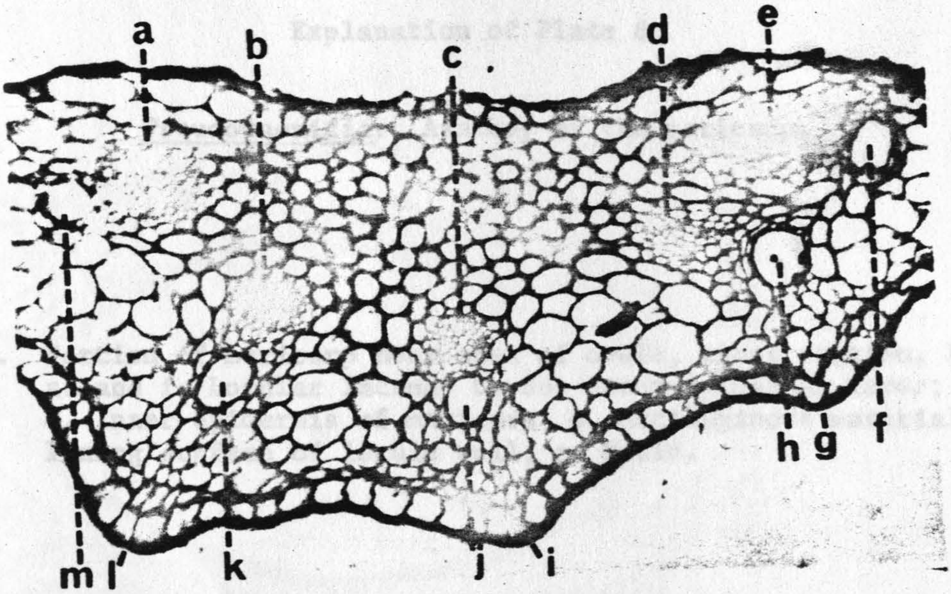
<u>Pseudotaenidia</u>. Anatomy of the mericarp. Note - Lateral wings are out of field of view.

Fig. 20. Traces and lacunae in mericarp at level of apex of receptacle, X240. a. and e. Lateral dorsal traces; b. c. and d. Median dorsal traces; f. and m. Lateral dorsal lacunae; g. i. and l. Median dorsal ribs; h. j. and k. Median dorsal lacunae.

Fig. 21. Mericarp at level of base of locule; cross section, X215. a. and h. Ventral surface near base of lateral wings; b. and g. Lateral dorsal traces; c. e. and f. Median dorsal traces; d. Base of locule; i. and p. Lateral dorsal lacunae; j. m. and o. Median dorsal ribs; k. l. and n. Median dorsal lacunae.

Fig. 22. Portion of a mericarp near base of locule. Note - Section located slightly above that shown in Fig. 21, cross section, X502. a. Sub inner-epidermal layer of mericarp wall; b. Inner-epidermis; c. Ridge on ventral surface to which carpophore is attached (carpophore not present in photograph); d. Darkly staining mucilaginous material at base of locule (near apex of the anatropous ovule); e. and f. Locular lacunae.

PLATE-7



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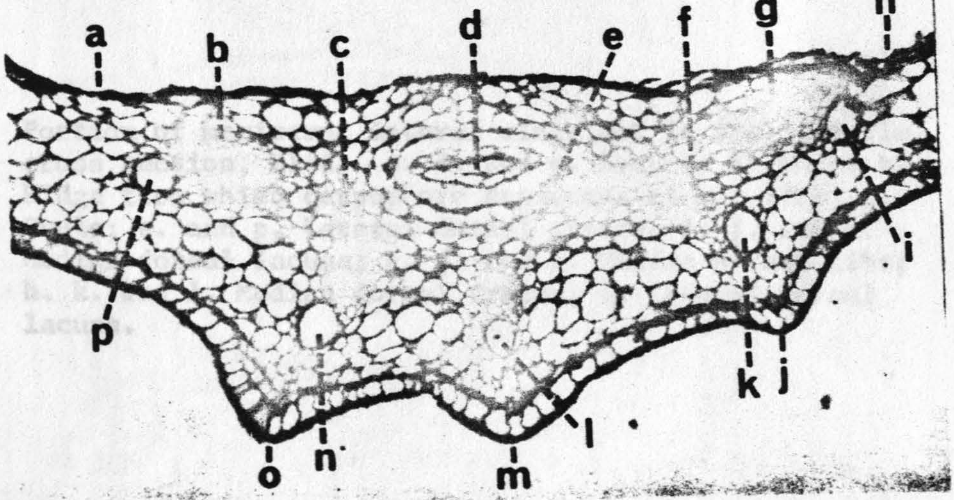

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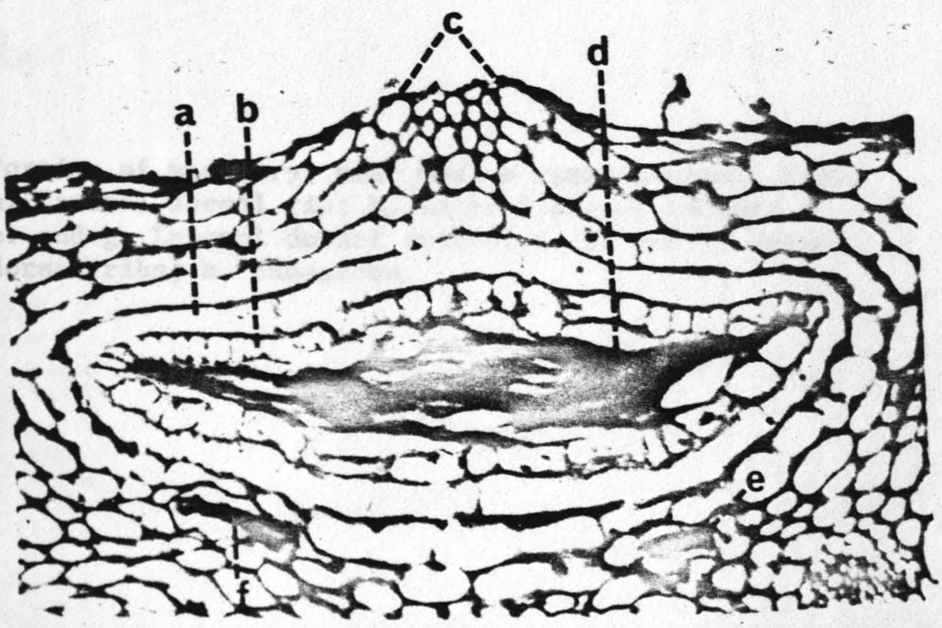

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Explanation of Plate 8

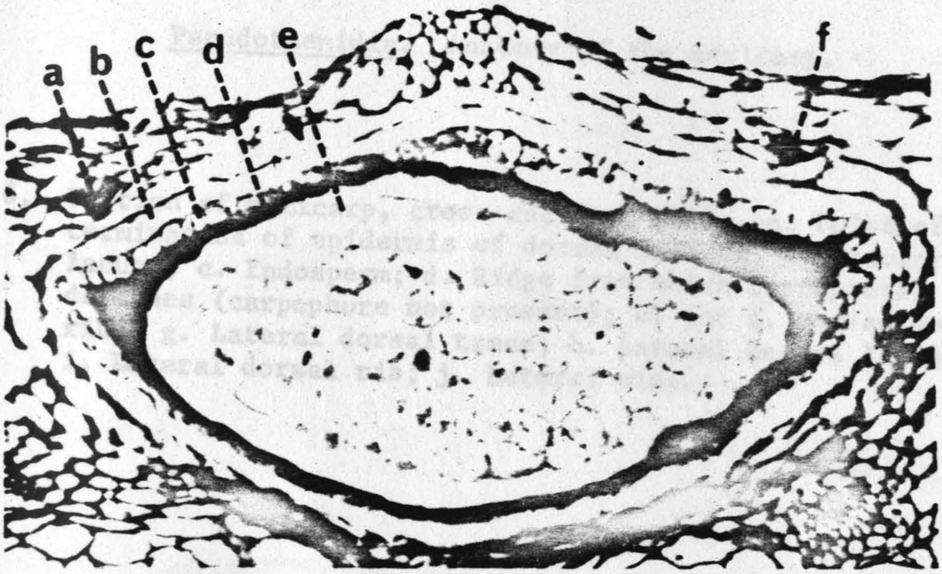
Pseudotaenidia. Anatomy of the mericarp.

Fig. 23. Portion of mericarp near apex of ovule, cross section, X384. a. and f. Locular lacuna; b. Sub inner-epidermal layer; c. Inner-epidermis of mericarp; d. Mucilaginous material lining surface of locule wall; e. Ovule.

Fig. 24. Portion of mericarp, lateral wings not in field of view, cross section, X144. a. d. and o. Locular lacunae; b. Ridge from which carpophore separates at maturity; c. Ovule; e. and p. Lateral dorsal traces; f. i. and m. Median dorsal lacuna; g. j. and n. Median dorsal ribs; h. k. and l. Median dorsal traces; q. Lateral dorsal lacuna.

Fig. 25. Portion of mericarp, near median cross-section, X105. a. Lateral dorsal rib; b. Lateral dorsal lacuna; c. and g. Lateral dorsal traces; d. e. and f. Median dorsal ribs; h. Endosperm.

PLATE-8



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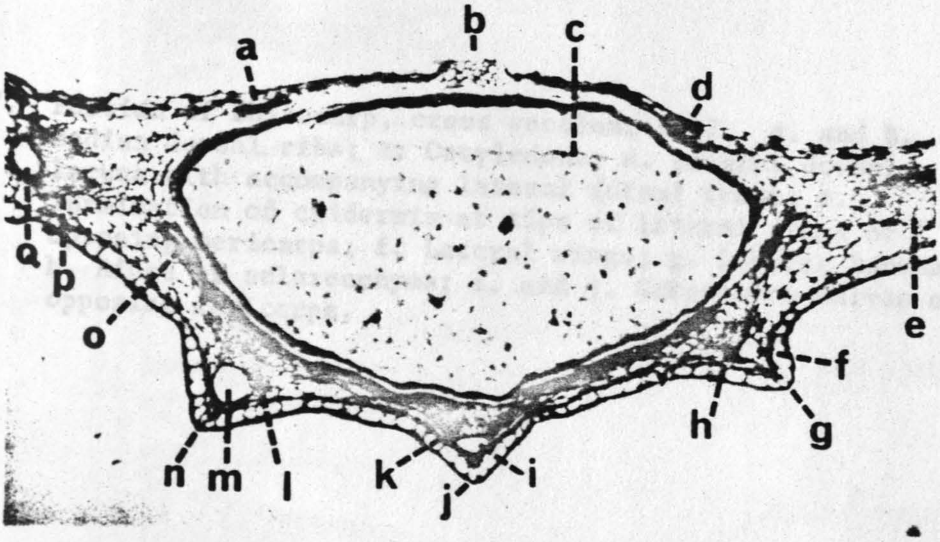

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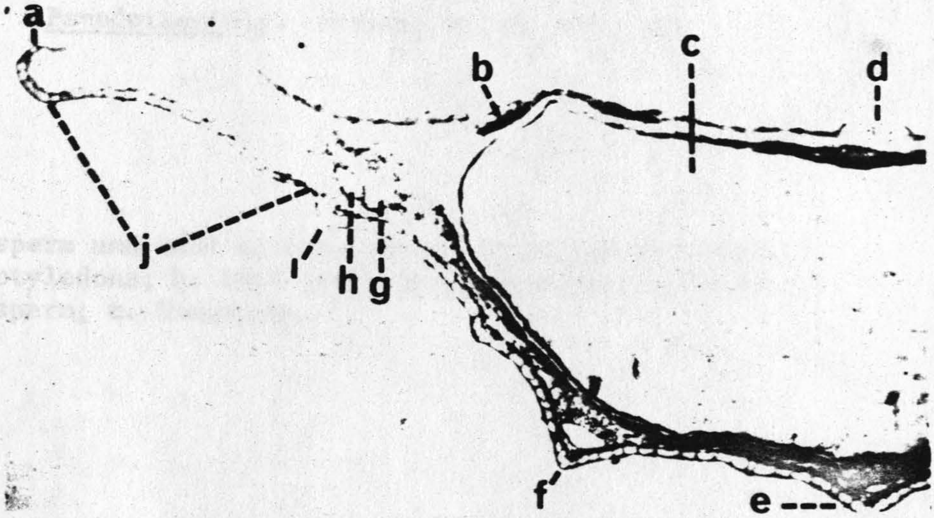
Explanation of Plate 9

Pseudotaenidia. Anatomy of the mericarp.

Fig. 26. Portion of mericarp, cross section, X115. a. Point of termination of epidermis of dorsal surface; b. Locular lacuna; c. Endosperm; d. Ridge from which carpophore detaches (carpophore not present); e. and f. Median dorsal ribs; g. Lateral dorsal trace; h. Lateral dorsal lacuna; i. Lateral dorsal rib; j. Lateral wing.

Fig. 27. Portion of shizocarp, cross section, X137. a. and b. Median dorsal ribs; c. Cotyledons; d. Lateral dorsal lacuna with accompanying lateral dorsal trace; e. Termination of epidermis at tips of lateral wings of opposing mericarps; f. Lateral wings; g. Locular lacuna; h. Ridge of sclerenchyma; i. and j. Carpophore halves of opposing mericarps.

Fig. 28. Endosperm and apex of cotyledons, cross section, X611. a. Cotyledons; b. Differentiated uniseriate layer in endosperm; c. Endosperm.



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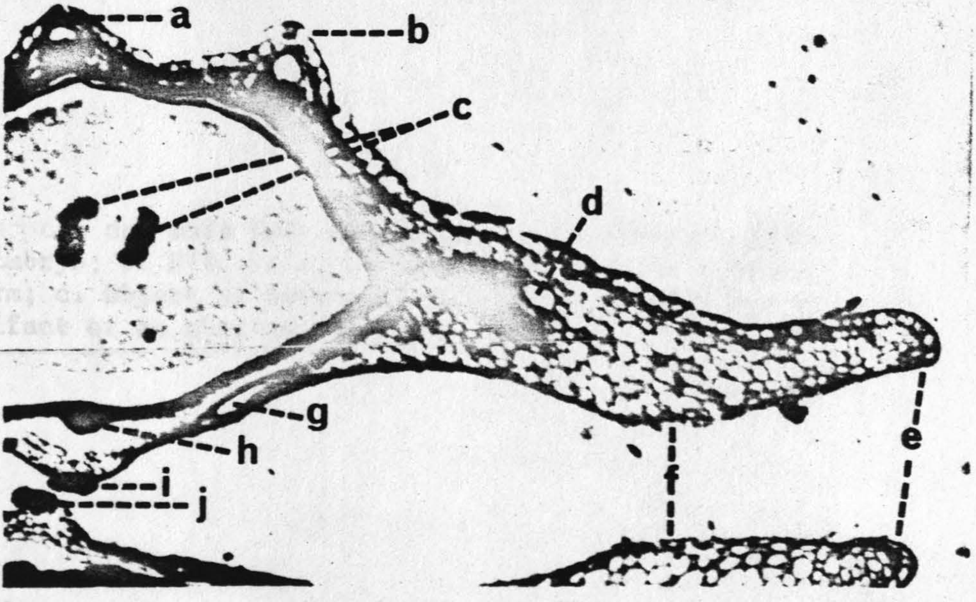

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Explanation of Plate 10

Pseudotaenidia. Anatomy of the mericarp.

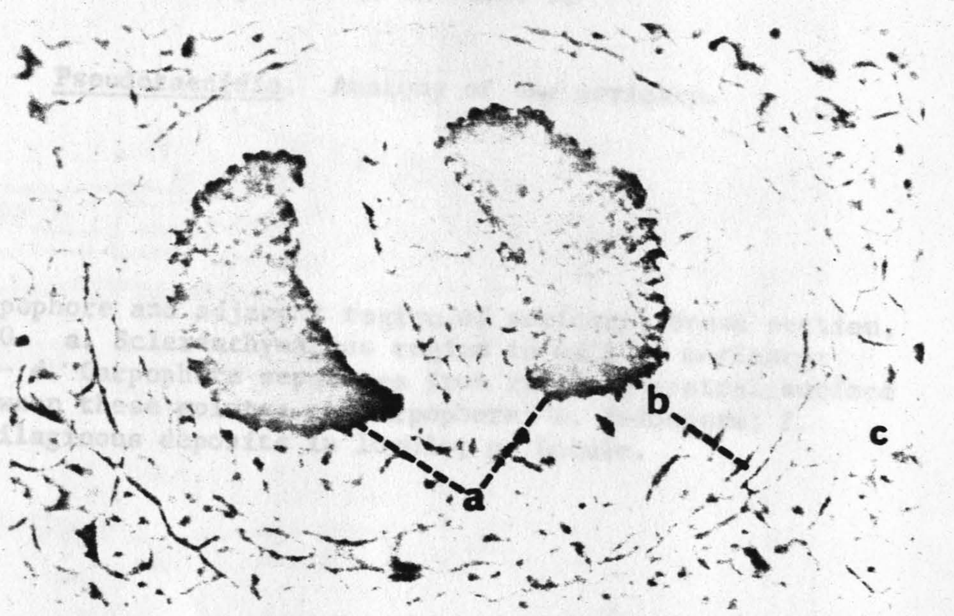
Fig. 29. Endosperm and base of cotyledons, cross section, X616. a. Cotyledons; b. Differentiated uniseriate layer in endosperm; c. Endosperm.

Fig. 30. Endosperm and main body of embryo, cross section, X596. a. Embryo; b. Differentiated uniseriate layer in endosperm; c. Object of undetermined nature, perhaps an artifact or an aborted embryo; d. Endosperm.

Fig. 31. Ridge of sclerenchyma on ventral surface of mericarp, cross section, X1324. a. - b. Carpophore separates from surface of ridge between these points; c. Sclerenchymatous cells in wall of mericarp; d. Locule.

PLATE-10

29



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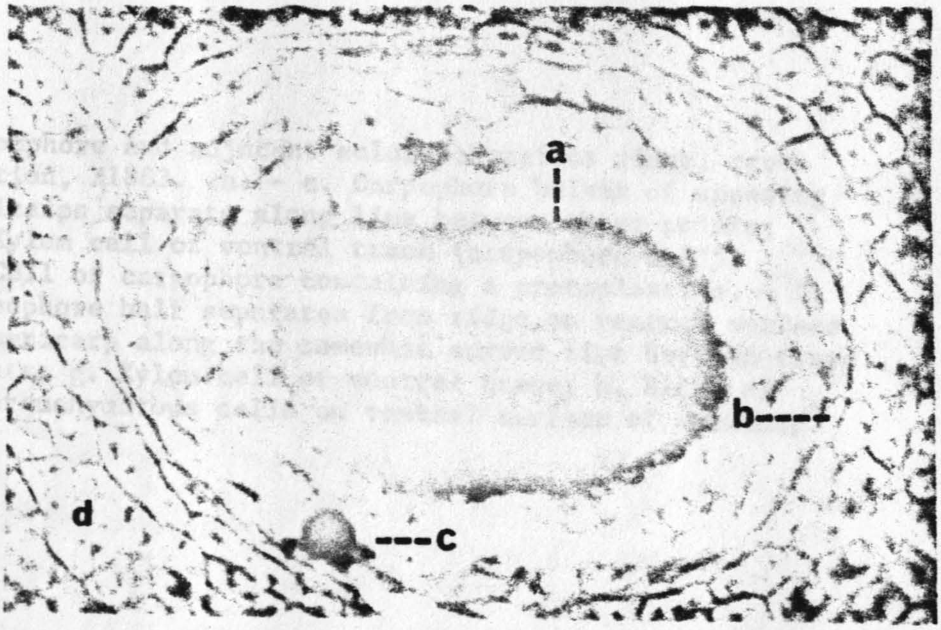

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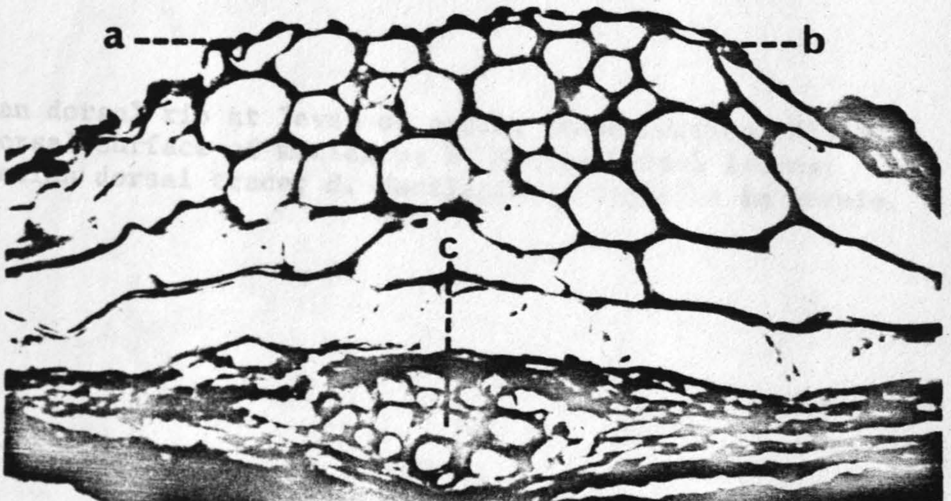


Explanation of Plate 11

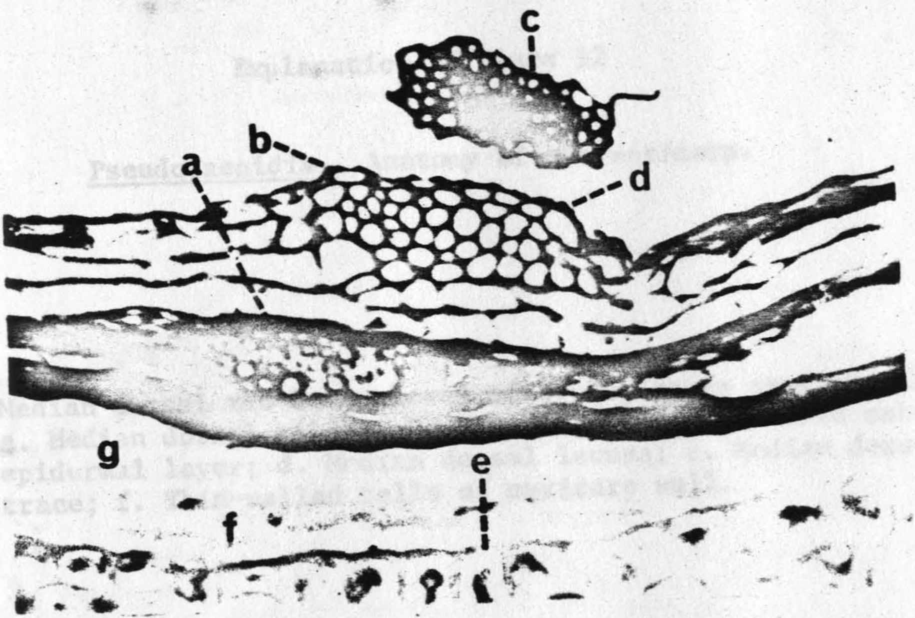
Pseudotaenidia. Anatomy of the mericarp.

Fig. 32. Carpophore and adjacent region of mericarp, cross section, X650. a. Sclerenchymatous region in wall of mericarp; b. - d. Carpophore separates from ridge on ventral surface between these points; c. Carpophore; e. Endosperm; f. Mucilaginous deposits in locule; g. Locule.

Fig. 33. Carpophore and adjacent sclerenchymatous ridge, cross section, X1883. a. - c. Carpophore halves of opposing mericarps separate along line between these points; b. Xylem cell of ventral trace (carpophore half); d. Cell of carpophore containing a protoplast; e. - f. Carpophore half separates from ridge on ventral surface of mericarp along the somewhat curved line between these points; g. Xylem cell of ventral trace; h. Ridge of sclerenchymatous cells on ventral surface of mericarp.

Fig. 34. Median dorsal rib at level of ovule, cross section, X1518. a. Dorsal surface of mericarp; b. Median dorsal lacuna; c. Median dorsal trace; d. Mucilaginous deposits in locule.

PLATE-11



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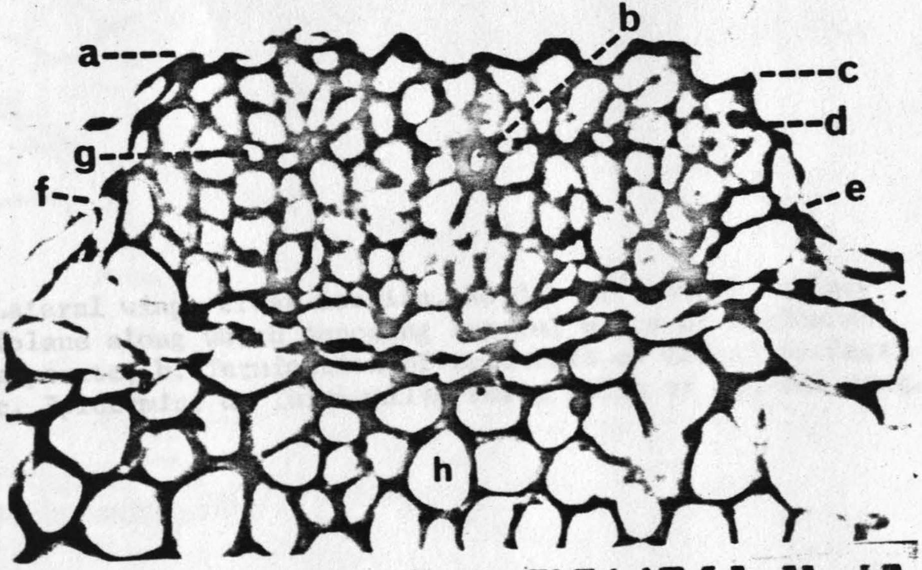

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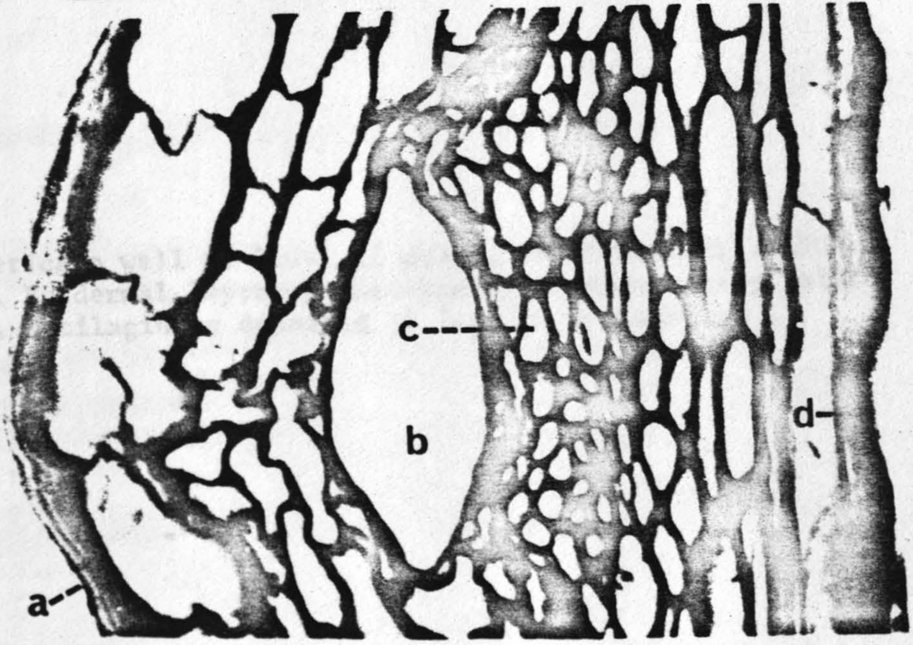

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Explanation of Plate 12

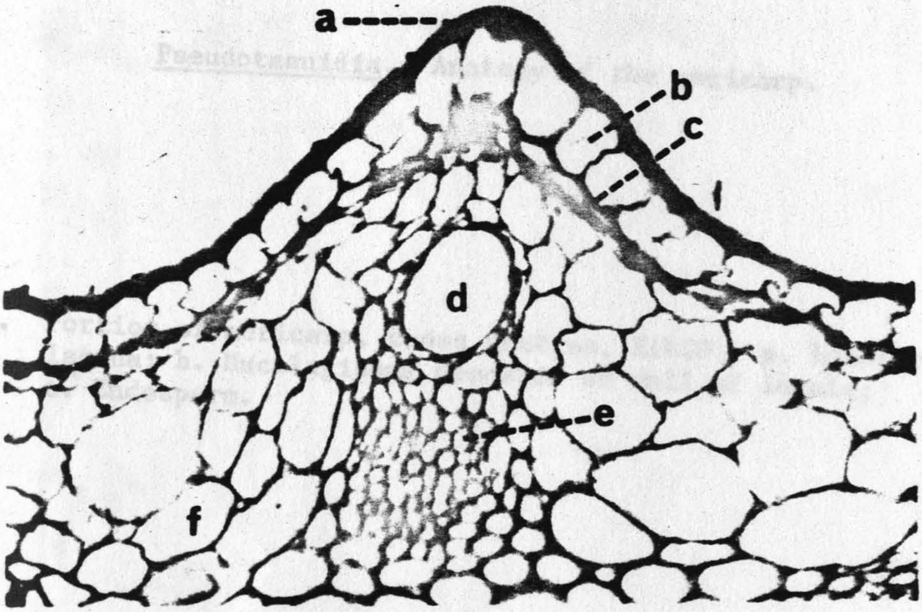
Pseudotaenidia. Anatomy of the mericarp.

Fig. 35. Median dorsal rib below level of ovule, cross section, X500. a. Median dorsal rib; b. Epidermal layer; c. Crushed subepidermal layer; d. Median dorsal lacuna; e. Median dorsal trace; f. Thin-walled cells of mericarp wall.

Fig. 36. Lateral wing, cross section, X680. a. Ventral surface (plane along which opposing lateral wings of mericarps separate; b. Termination of epidermis of dorsal surface; c. Epidermis; d. Thin-walled corky cells of lateral wing.

Fig. 37. Mericarp wall at level of ovule, cross section, X1509. a. Epidermal layer; b. Crushed cells of mericarp wall; c. Mucilaginous deposits in locule; d. Endosperm.

PLATE-12



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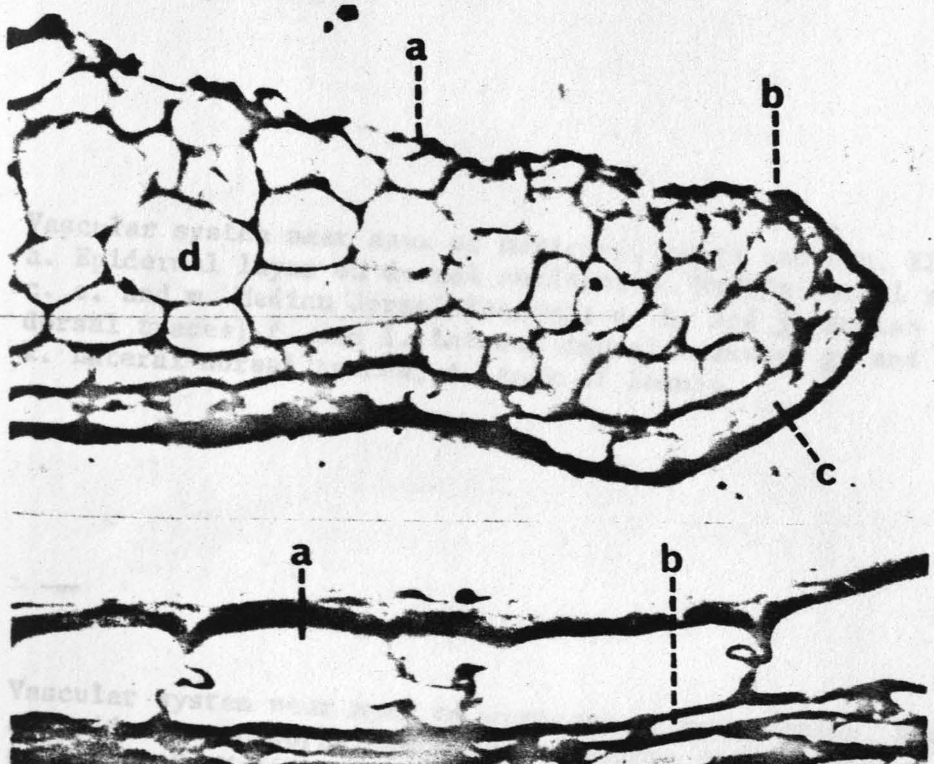

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Explanation of Plate 13

Pseudotaenidia. Anatomy of the mericarp.

Fig. 38. Portion of mericarp, cross section, X1619. a. Locular lacuna; b. Mucilaginous deposits on wall of locule; c. Endosperm.

Fig. 39. Vascular system near apex of mericarp, cross section, X245. a. Epidermal layer on dorsal surface; b. Median dorsal rib; c. e. and m. Median dorsal lacunae; d. h. and j. Median dorsal traces; f. and l. Lateral dorsal lacunae; g. and k. Lateral dorsal traces; i. Apex of locule.

Fig. 40. Vascular system near apex of mericarp, cross section, X245. a. Epidermis on dorsal surface; b. Median dorsal rib; c. e. and k. Median dorsal lacunae; d. Median dorsal trace; f. and j. Lateral dorsal lacunae; g. United lateral dorsal and median dorsal traces (g. and h. of Fig. 39); h. Cells that form the apical portion of the wall of the locule; i. United lateral dorsal and median dorsal trace (j. and k. of Fig. 39).

PLATE-13

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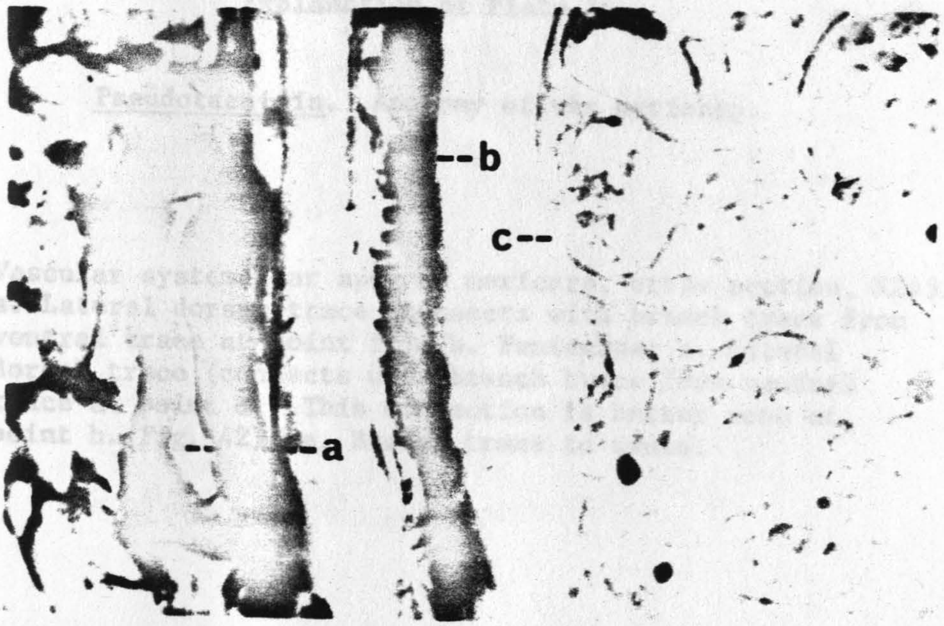

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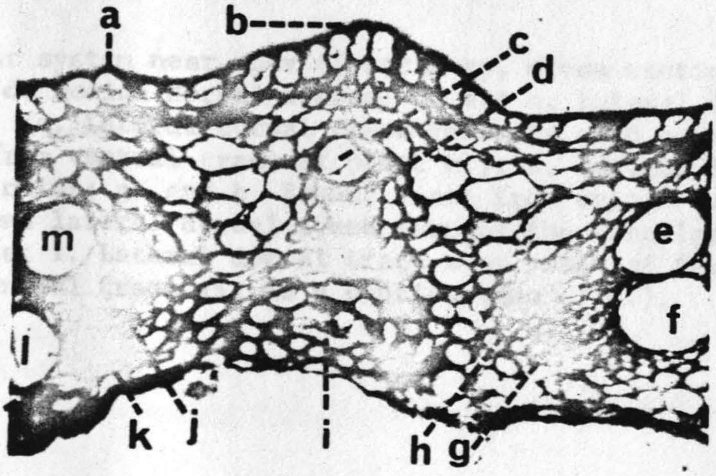

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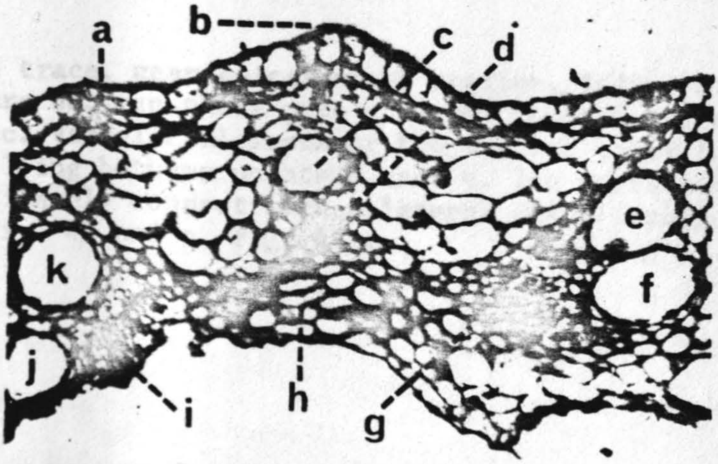


Explanation of Plate 14

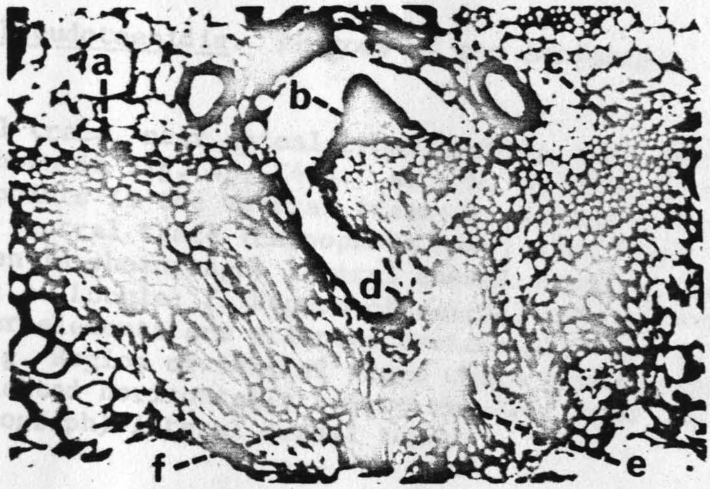
Pseudotaenidia. Anatomy of the mericarp.

Fig. 41. Vascular system near apex of mericarp, cross section, X245. a. Lateral dorsal trace (connects with branch trace from ventral trace at point f.); b. Funiculus; c. Lateral dorsal trace (connects with branch trace from ventral trace at point d; This connection is better seen at point h. Fig. 42); e. Branch trace to ovule.

Fig. 42. Vascular system near apex of mericarp, cross section, X245. a. and d. Median dorsal traces; b. and e. Lateral dorsal traces (e. Lateral dorsal trace connects with branch trace from ventral trace at point h.); c. Locular lacuna; f. Funiculus; g. and h. Branch trace from united ventral trace and lateral dorsal trace forming the vascular supply to ovule; i. Lateral dorsal trace near point of fusion with ventral trace (i. is a continuation of b.).

Fig. 43. Ventral trace, near apical cross section, X472. a. and b. Structure between these points is the ventral trace; b. and c. Vascular elements of the ventral trace in the region lying between points b. and c. lie horizontally and ultimately connect with a lateral dorsal trace (as in h. Fig. 42 and c. Fig. 44).

PLATE-14



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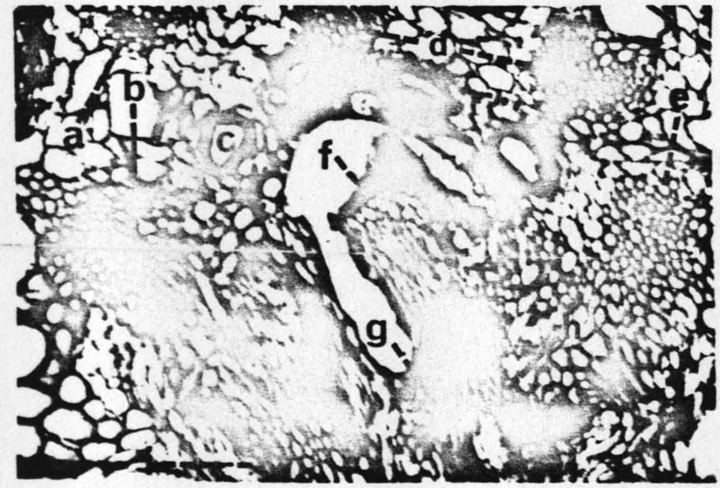

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Explanation of Plate 15

Pseudotaenidia. Anatomy of the mericarp.

Fig. 44. Ventral trace, near apical cross section, one section above that shown in Fig. 43, X486. a. - b. Structure between these points is the ventral trace; c. Region of connection of the ventral trace (carpophore half) with right hand (as seen in photograph) lateral dorsal trace; d. Locular lacuna; e. Locule; f. Region of ventral trace where vascular elements are oriented horizontally toward the ovule; g. Region of ventral trace where vascular elements are oriented horizontally toward the left hand (as seen in photograph) lateral dorsal trace.

PLATE-15

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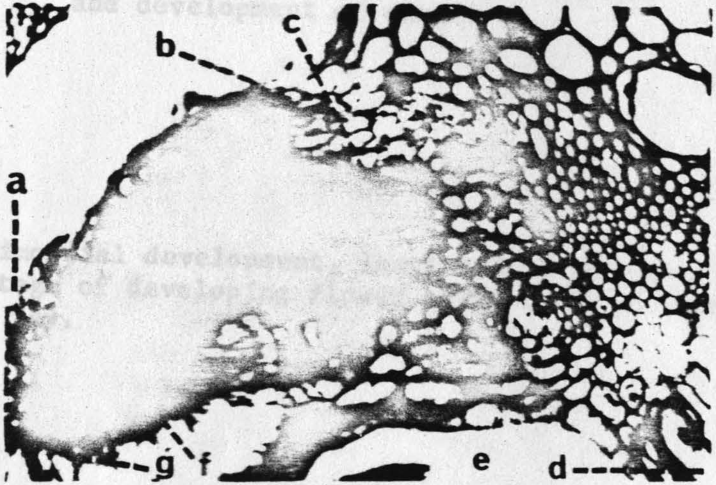

Explanation of Plate 16

Taenidia. Early flower primordial development and development of carpels.

Fig. 45. Flower primordial development, longitudinal section, X1632. a. Disk stage of developing flower primordium; b. Apex of umbellete ray.

Fig. 46. Development of carpels, longitudinal section, X2330. a. Outer rims of the two carpel primordia; b. Base of locule.

Fig. 47. Development of carpels, longitudinal section, X1978. a. and b. Outer rims of the two carpel primordia; c. Line in plane of adnation of outer rims of the two carpel primordia; d. Locule.

PLATE-16

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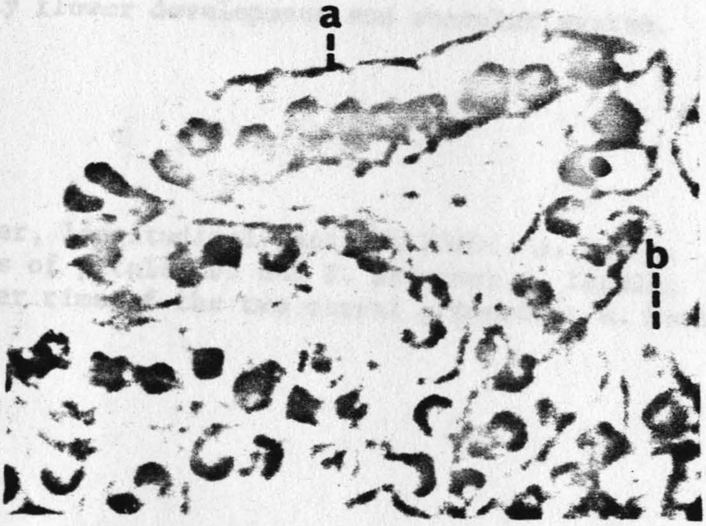

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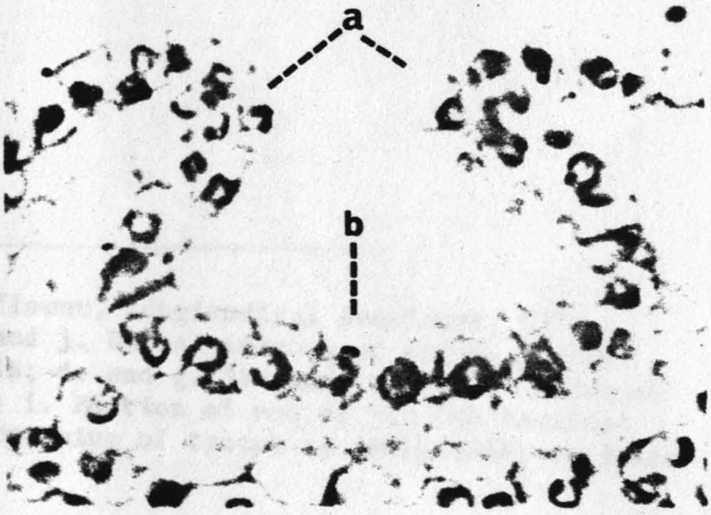

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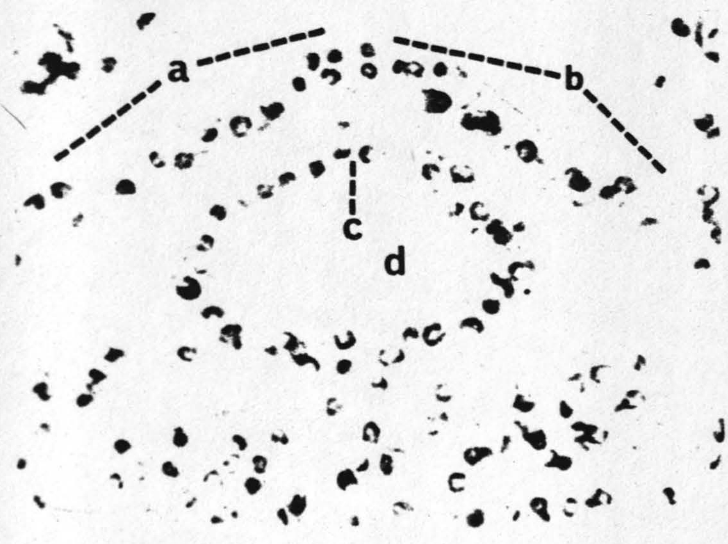


Explanation of Plate 17

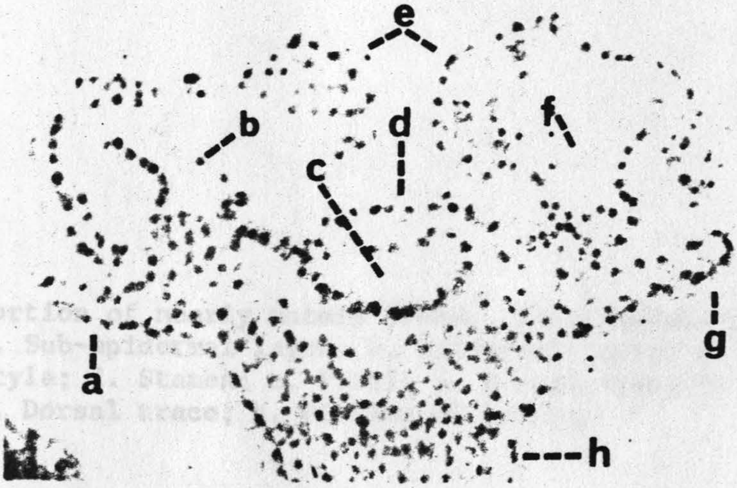
Taenidia. Early flower development and vascular system.

Fig. 48. Immature flower, longitudinal section, X500. a. and g. Basal portions of petals; b. and f. Stamens; c. Locule; d. Adnate outer rims of the two carpel primordia; e. Petals; h. pedicel.

Fig. 49. Nearly mature flower, longitudinal sectional, X372. a. Lacuna; b. and j. Dorsal traces; c. and h. Branch traces to petals; d. and g. Stamens; e. and f. Bases of the two styles; i. Portion of one of the two locules; k. Region of branching of traces in receptacle; l. Trace in pedicel.

PLATE-17

48



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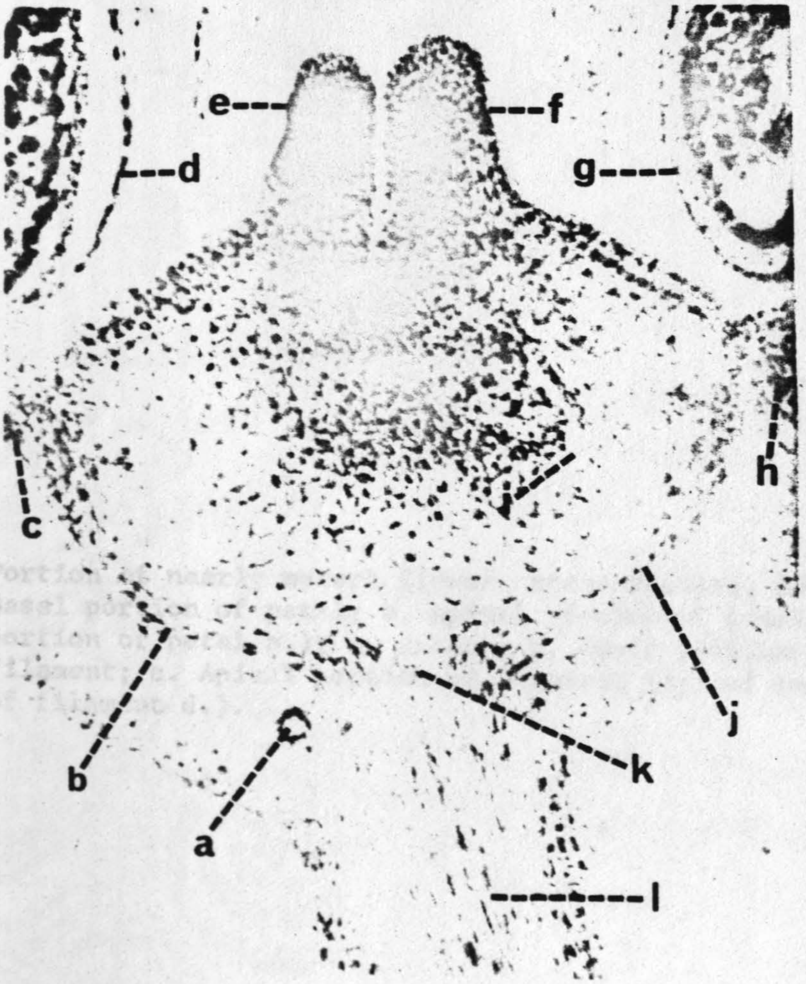


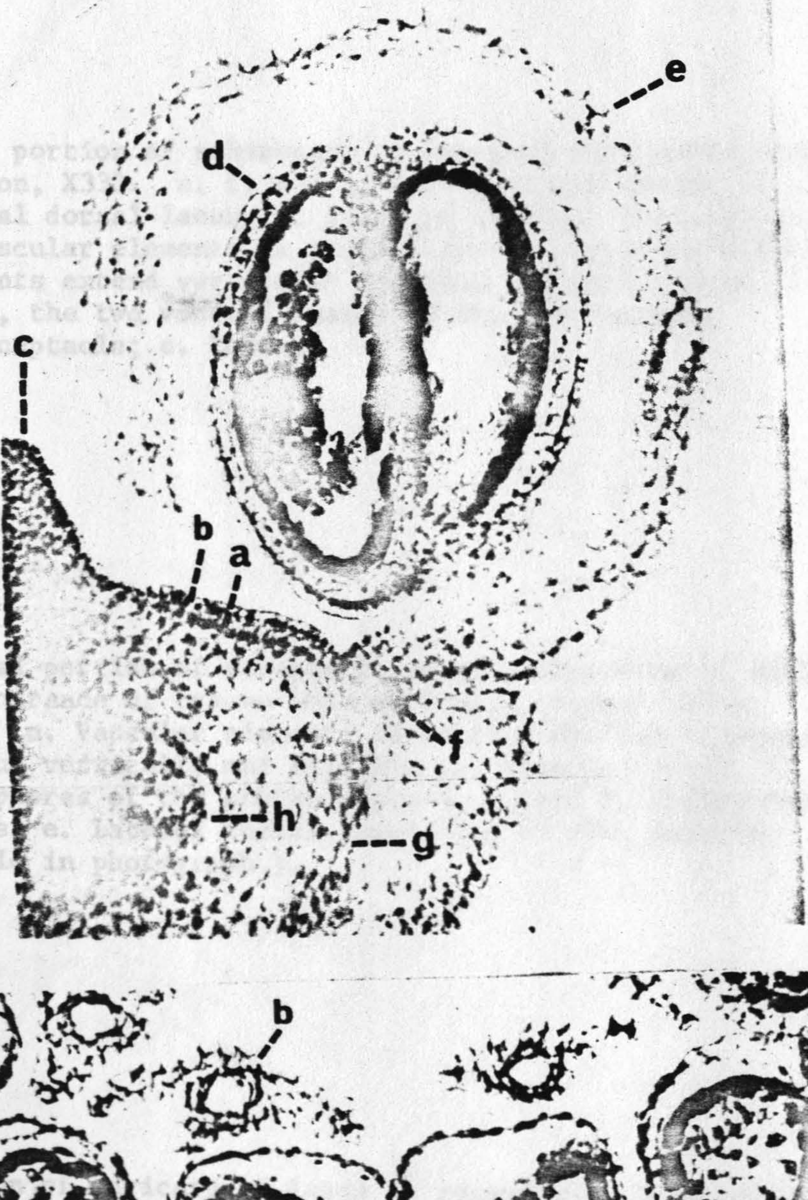
Explanation of Plate 18

Taenidia. Flower structure.

Fig. 50. Portion of nearly mature flower, longitudinal section, X586. a. Sub-epidermal layer; b. Epidermal layer; c. Portion of style; d. Stamen; e. Petal; b. Branch trace to petal; g. Dorsal trace; h. Portion of locule.

Fig. 51. Portion of nearly mature flower, cross-section, X566. a. Basal portion of petal; b. Apical portion of petal (apical portion of petal a.); c. Anther; d. Basal portion of filament; e. Apical portion of filament (apical portion of filament d.).

PLATE-18



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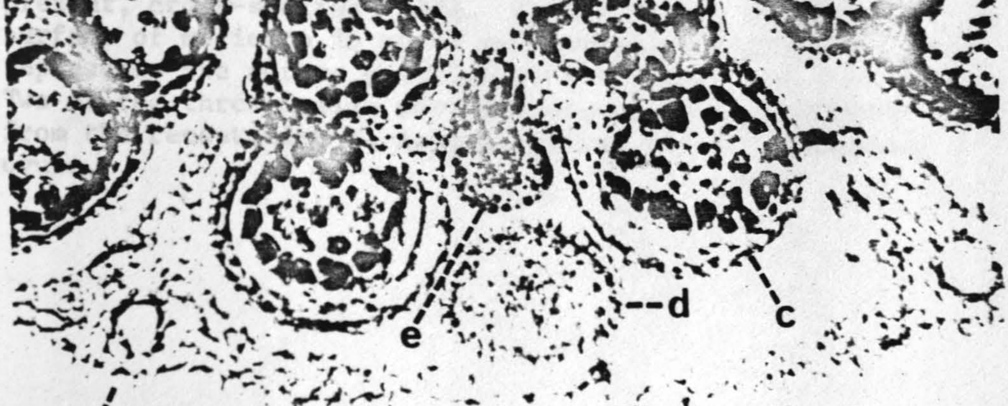

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Explanation of Plate 19

Taenidia. Branching of stele in receptacle and entrance of traces into mericarp.

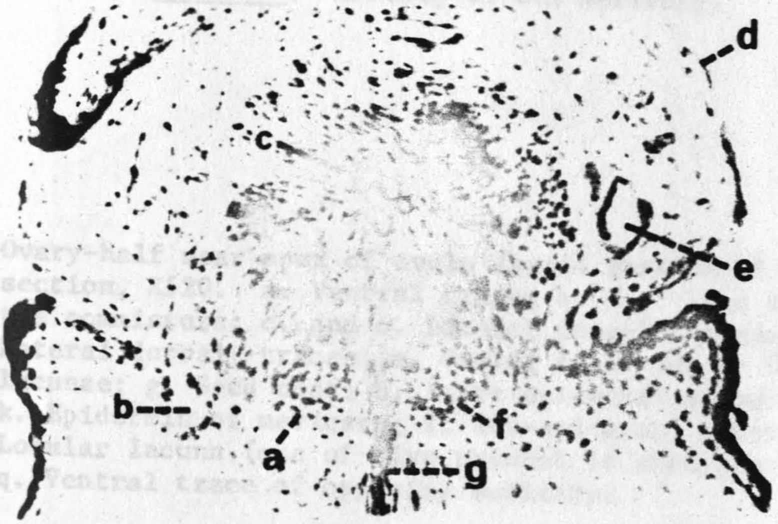
Fig. 52. Basal portion of schizocarp at level of receptacle, cross-section, X333. a. f. and g. Median dorsal traces; b. Lateral dorsal lacuna at point of entrance into mericarp; c. Vascular elements in central portion of stele (these elements extend vertically and form the carpophores, i. e., the two ventral traces of the schizocarp); d. Receptacle; e. Lacuna.

Fig. 53. Central portion of receptacle showing branching of stele and entrance of traces into mericarp, cross-section, X500. a. Vascular elements in central portion of stele (extend vertically and form the two ventral traces; i. e. carpophores of the schizocarp); b. c. and d. Median dorsal traces; e. Lateral dorsal trace (one of two, only one visible in photograph.).

Fig. 54. Portion of mericarp at level of receptacle, receptacle not present, cross-section, X332. Note - Curved ventral surface of mericarp in upper portion of photograph represents the former position of the receptacle. a. Two of the three median dorsal traces entering mericarp from the receptacle; b. Apical portion of the anatropous ovule.

PLATE-19

52



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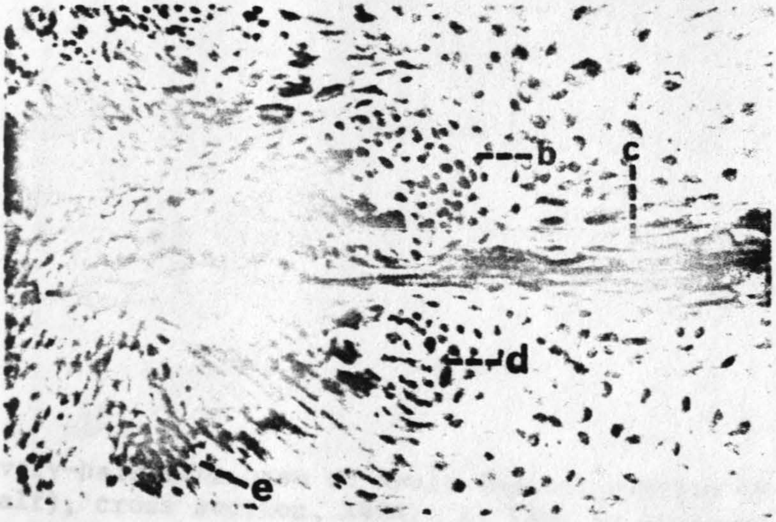

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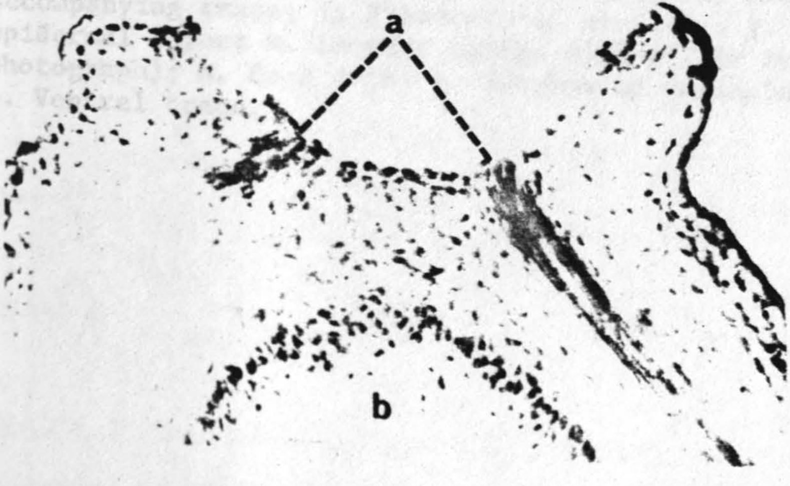

Explanation of Plate 20

Taenidia. Anatomy of the mericarp.

Fig. 55. Ovary-half near apex of ovule (basal portion of ovary), cross section, X520. a. Ventral trace; b. - p. Line in plane of the commissure; c. and o. Lateral dorsal lacunae; d. and n. Lateral dorsal traces; e. Ovule; f. i. and j. Median dorsal lacunae; g. Seed coat; h. Inner epidermis of mericarp; k. Epidermis of mericarp; l. Sub-epidermal layer; m. Locular lacuna (one of five present in photograph); q. Ventral trace of opposing mericarp.

Fig. 56. Ovary-half near base of ovule (apical portion of ovary-half), cross section, X424. a. Line in plane of commissure; b. and m. Lateral dorsal lacunae; c. and l. Lateral dorsal traces; d. Inner epidermis of mericarp; e. Ovule; f. g. and h. Median dorsal lacunae, each with accompanying trace; i. Epidermis of mericarp; j. Sub-epidermal layer; k. Locular lacuna (one of six in photograph); n. Seed coat; o. Portion of funiculus; p. Ventral trace.

PLATE-20

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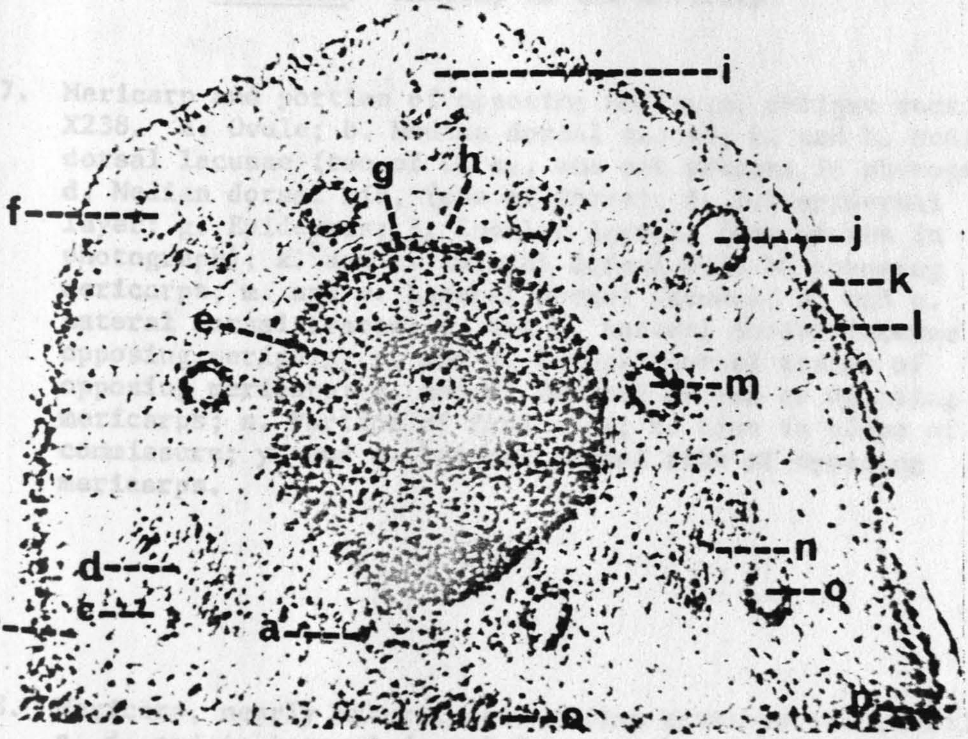

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Explanation of Plate 21

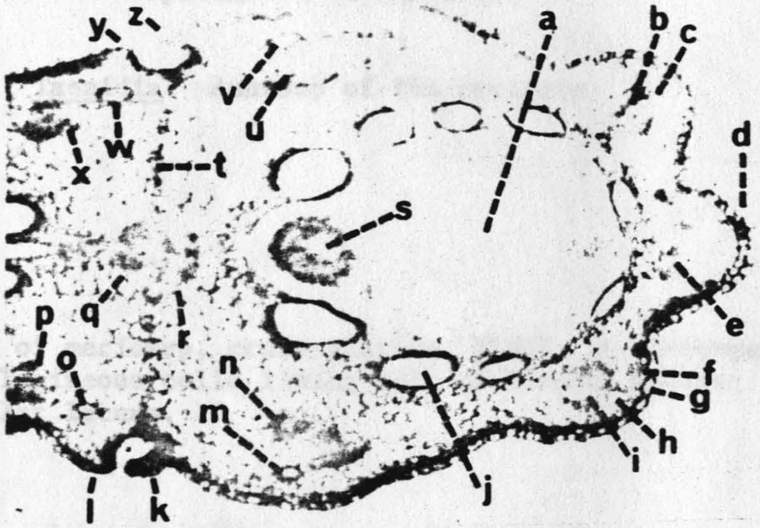
Taenidia. Anatomy of the mericarp.

Fig. 57. Mericarp and portion of opposing mericarp, oblique section, X238. a. Ovule; b. Median dorsal traces; c. and h. Median dorsal lacunae (two of three, one not present in photograph); d. Median dorsal rib, (one of three); f. Sub-epidermal layer; g. Epidermis; j. Locular lacuna, (one of ten in photograph); k. and l. Lateral dorsal ribs of opposing mericarps; m. and v. Lateral dorsal lacunae; n. and u. Lateral dorsal traces; o. and w. Lateral dorsal lacunae of opposing mericarp; p. and x. Lateral dorsal traces of opposing mericarp; g. and r. Ventral traces of opposing mericarps; s. Portion of funiculus; t. Line in plane of commissure; y. and z. Lateral dorsal ribs of opposing mericarps.

Fig. 58. Mericarp, nearly mature, near median cross-section, X253. a. d. and j. Lateral dorsal lacunae; b. c. and i. Lateral dorsal traces; e. Median dorsal rib (one of three, the apices of two ribs are not in field of view); f. Uniseriate epidermis; g. Sub-epidermal layer; h. Locular lacuna (one of sixteen present); k. Ovule (shrunken and distorted by fixation process).

Fig. 59. Locular lacuna; cross-section, X1470. a. Cell of endosperm; b. Mucilaginous cells lining wall of lacuna; c. Locular lacuna.

PLATE-21



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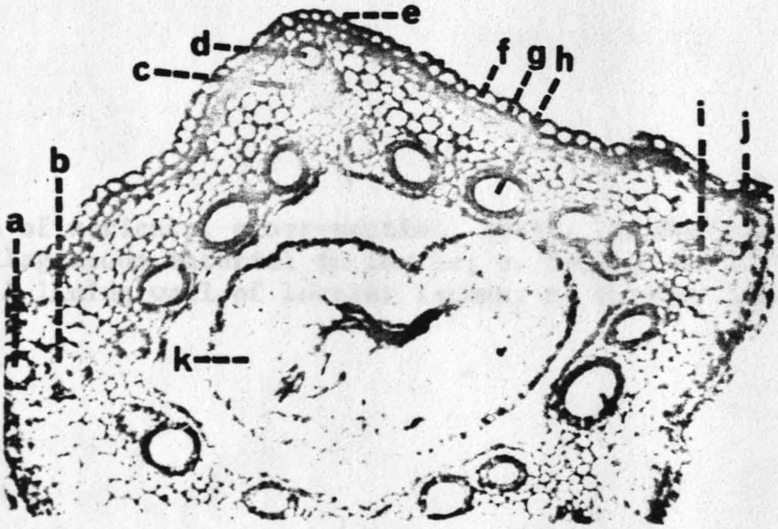

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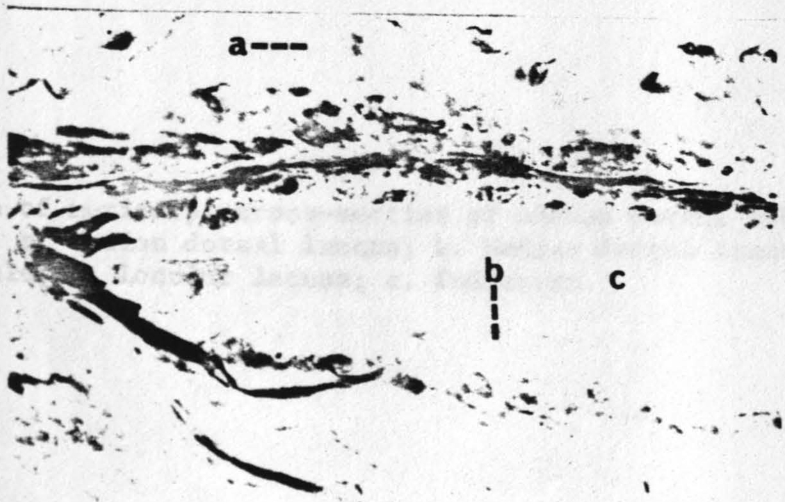

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Explanation of Plate 22

Taenidia. Anatomy of the mericarp.

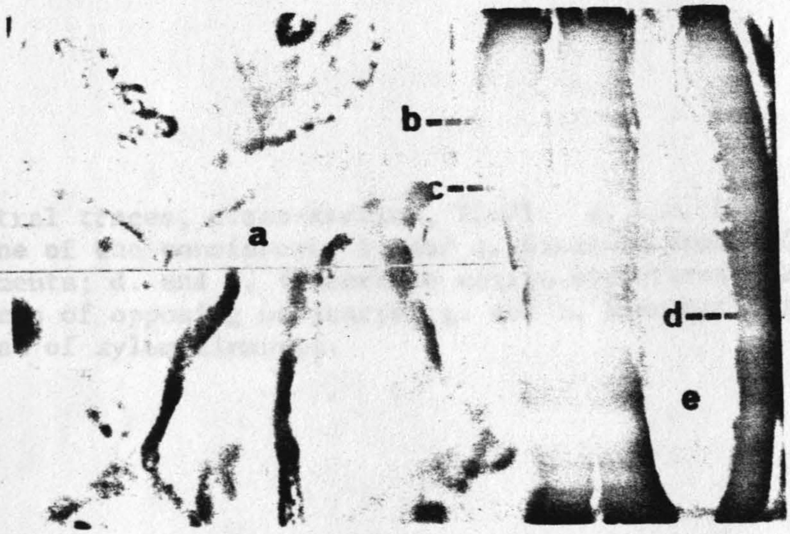
Fig. 60. Portion of mericarp, cross-section, X1088. a. Endosperm; b. Mucilagineous cells lining wall of locular lacuna; c. Locular lacuna.

Fig. 61. Portion of mericarp, cross-section, X1455. a. Endosperm; b. Mucilagineous material in locule; c. Locule; d. Mucilagineous material lining wall of locular lacuna; e. Locular lacuna.

Fig. 62. Portion of mericarp, cross-section of median dorsal rib, X1092. a. Median dorsal lacuna; b. Median dorsal trace; c. Locule; d. Locular lacuna; e. Endosperm.

PLATE-22

60



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Explanation of Plate 23

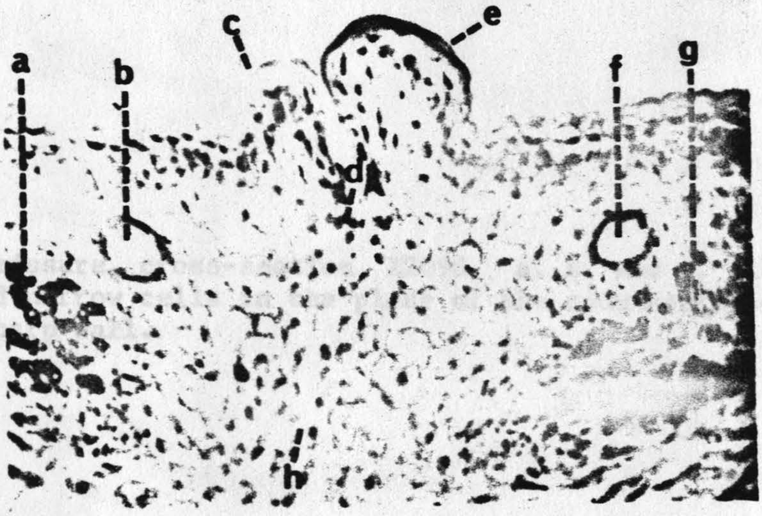
Taenidia. Anatomy of the mericarp.

Fig. 63. Portion of mericarp, cross-section, X1118. a. and g. Lateral dorsal traces of opposing mericarps; b. and f. Lateral dorsal lacunae of opposing mericarps; c. and e. Lateral dorsal ribs of opposing mericarps; d. - h. Line in plane of the commissure.

Fig. 64. Ventral traces, cross-section, X1671. a. - e. Line in plane of the commissure; b. and c. Discrete areas of xylem elements; d. and f. (refers to entire structures) Dorsal traces of opposing mericarps; g. and h. Somewhat discrete areas of xylem elements.

Fig. 65. Portion of mericarp, cross-seciton, X302. a. b. and c. Locular lacunae; d. Embryo; e. Endosperm.

PLATE-23



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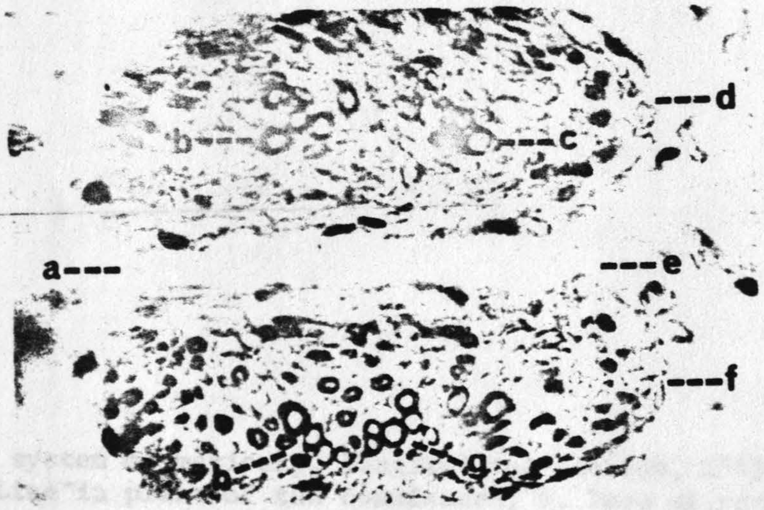

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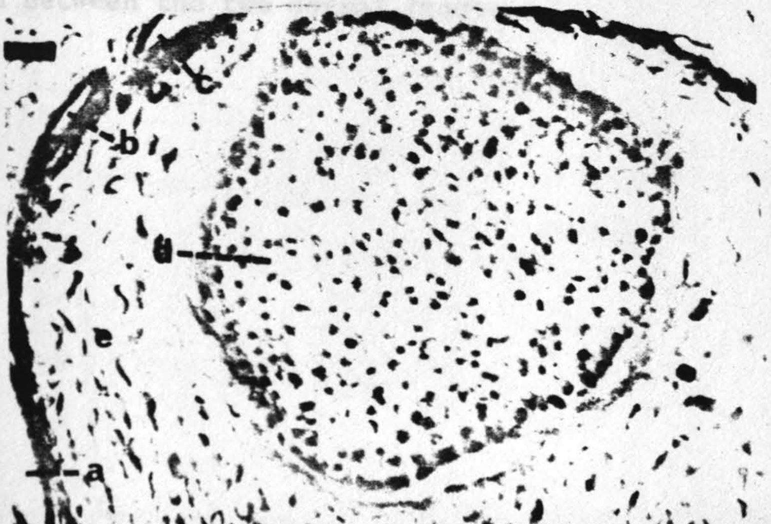

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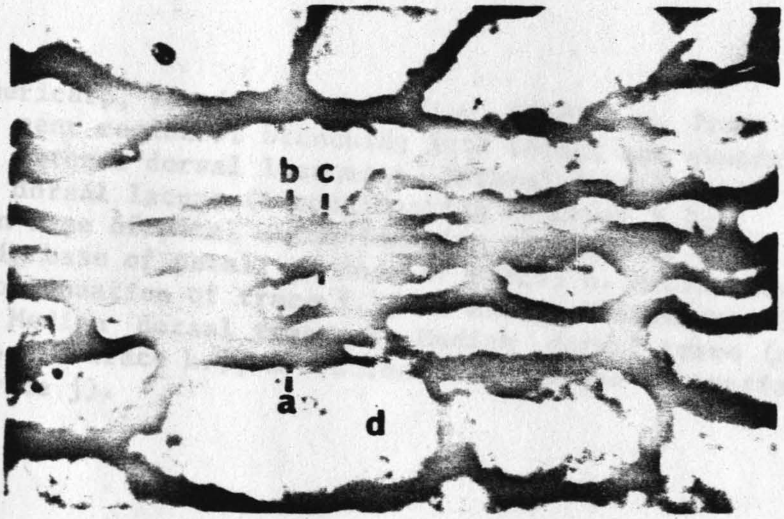
Explanation of Plate 24

Taenidia. Anatomy of the mericarp.

Fig. 66. The commissure, cross-section, X2098. a. b. and c. Relatively long and narrow cells in the plane of the commissure; d. Cell of mericarp wall.

Fig. 67. Vascular system of mericarp, longitudinal section, X545. a. - h. Line in plane of the commissure; b. Base of petal; c. Branch trace to petal; d. Median dorsal trace; e. Median dorsal lacuna; f. Lateral dorsal trace; g. Vascular connection between the two dorsal traces.

PLATE-24



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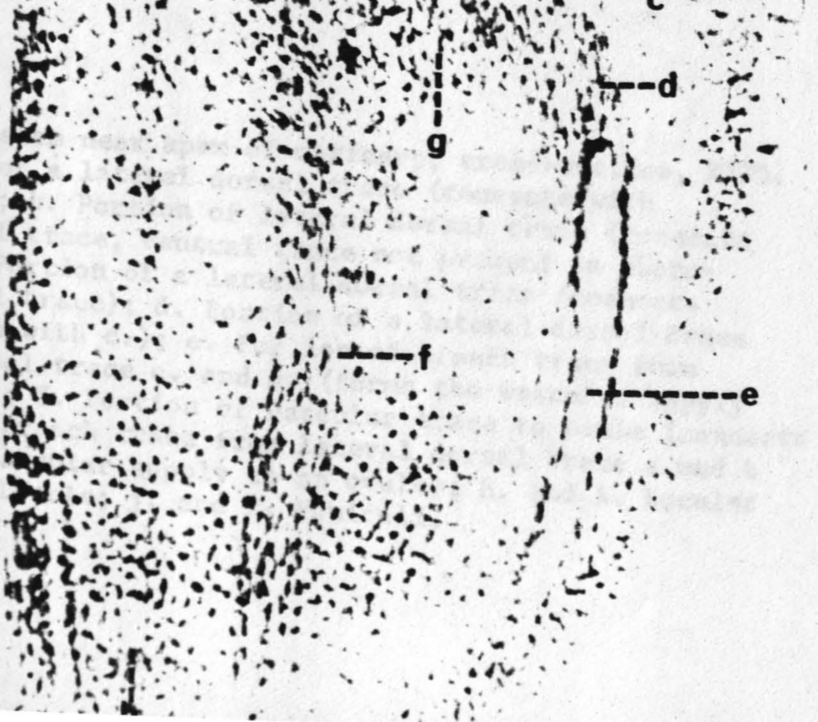

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Explanation of Plate 25

Taenidia. Anatomy of the mericarp.

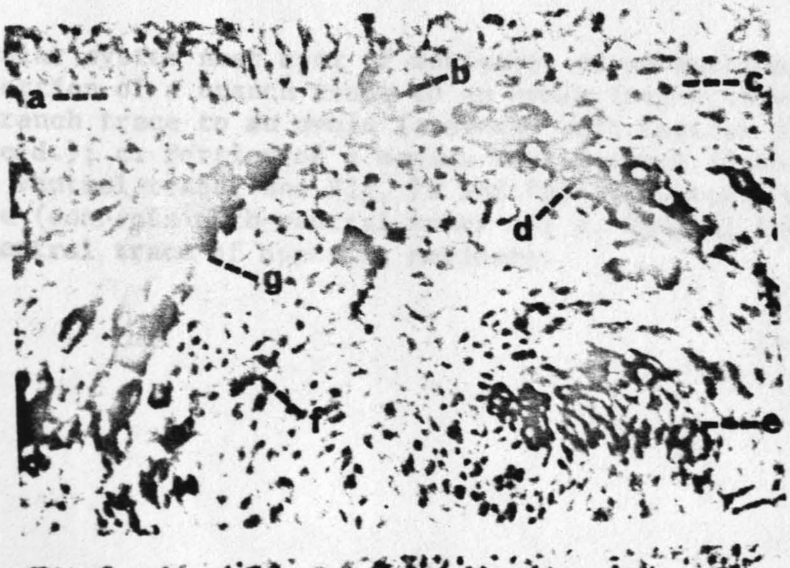
Fig. 68. Immature mericarp, longitudinal section, X1485. a. Trace in receptacle near region of branching into dorsal and ventral traces; b. Lateral dorsal lacuna; c. Lateral dorsal trace; d. Lateral dorsal lacuna (a continuation of lacuna b.); e. Trace in base of petal a continuation of trace k. and l.); f. Lacuna in base of petal; g. Base of petal; h. Median dorsal trace (a continuation of trace i.); i. and j. Median dorsal traces; k. Median dorsal trace; l. Median dorsal trace (a continuation of trace k.); m. Median dorsal trace (a continuation of trace j).

Fig. 69. Vascular system near apex of mericarp, cross-section, X530. a. - c. Line in plane of the commissure; b. Ventral trace; d. Lateral dorsal trace (connects with ventral trace b.); e. Portion of the branch trace from lateral dorsal trace d. (Branch trace e. forms the vascular supply of an ovule.); f. Portion of the branch trace from lateral dorsal trace g. (Branch trace f. forms the vascular supply of an ovule.); g. Lateral dorsal trace (connects with ventral trace b.).

Fig. 70. Vascular system near apex of mericarp, cross-section, X375. a. Portion of a lateral dorsal trace (connects with portion b.); b. Portion of lateral dorsal trace (connects with ventral trace, ventral trace not present in photograph); c. Portion of a lateral dorsal trace (connects with ventral trace); d. Portion of a lateral dorsal trace (d. connects with c.); e. Portion of branch trace from lateral dorsal trace c. and d. (forms the vascular supply to an ovule); f. Portion of vascular trace to ovule (connects with e); g. Branch trace from lateral dorsal trace a and b (forms the vascular supply to an ovule); h. and l. Locular lacunae; i. Locule; j. and k. Funiculi.

PLATE-25

68



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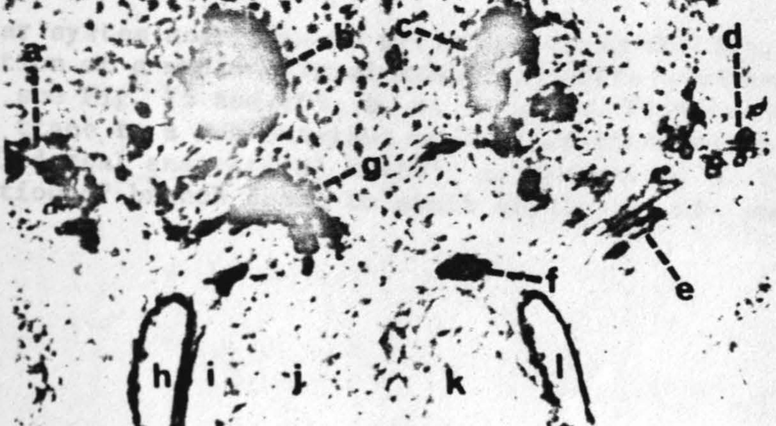

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Explanation of Plate 26

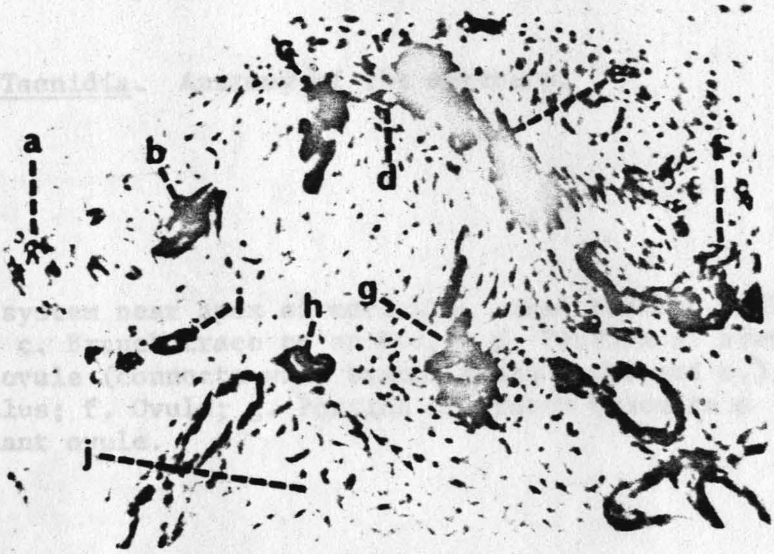
Taenidia. Anatomy of the mericarp.

Fig. 71. Vascular system near apex of mericarp, cross-section, X325. a. b. and c. Portions of the same lateral dorsal trace (connects with ventral trace d.); d. Ventral trace; e. and f. Portions of the same lateral dorsal trace (connects with ventral trace d.); g. Branch trace from lateral dorsal trace e. and f. (forms vascular supply to a non-existant ovule); h. Portion of branch trace from lateral dorsal trace a. b. and c. (forms vascular supply to an ovule); i. Portion of branch trace to an ovule (connects with h. and lateral dorsal trace a. b. and c.).

Fig. 72. Vascular system near apex of mericarp, cross-section, X518. a. Portion of a branch trace to an ovule (connects with b.); b. Branch trace to an ovule (connects with lateral dorsal trace d.); c. Portion of a median dorsal trace (connects with ventral trace, see Fig. 75 and 76); d. Lateral dorsal trace (connects with ventral trace e); e. Ventral trace; f. ventral trace of opposing mericarp.

Fig. 73. Vascular system near apex of mericarp, cross-section, X399. a. Portion of a median dorsal trace (connects with ventral trace, see Fig. 75 and 76); b. c. d. and e. Portions of a branch trace to a non-existant ovule (branches from a fused lateral dorsal and ventral trace); g. Funiculus; h. Ovule; i. Portion of branch trace to ovule (connects with portion f.).

PLATE-26



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Explanation of Plate 27

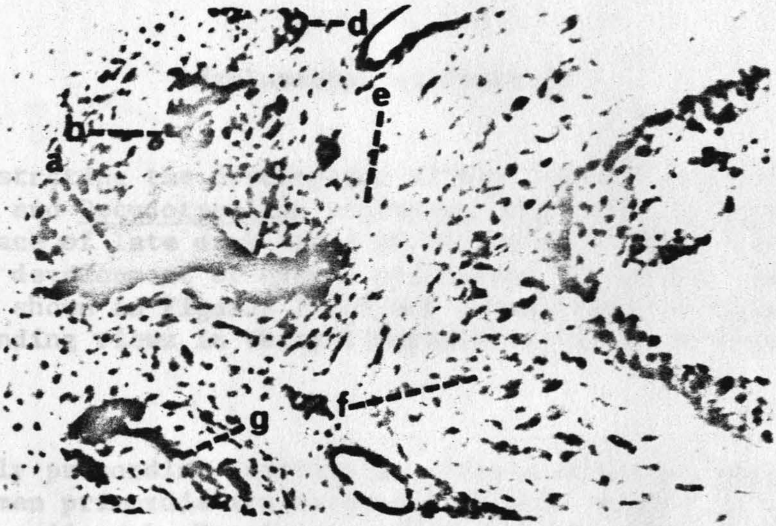
Taenidia. Anatomy of the mericarp.

Fig. 74. Vascular system near apex of mericarp, cross section, X398. a. b. and c. Branch trace to an ovule; d. Portion of branch trace to ovule (connects with branch trace a. b. and c.); e. Funiculus; f. Ovule; g. Portion of branch trace to a non-existant ovule.

Fig. 75. Vascular system near apex of mericarp, cross section, X275. a. Portion of a median dorsal trace (one of three median dorsal traces), (a. is a continuation of portion e.); b. Portion of a median dorsal trace; c. Portion of apex of locule (c. and i. are portions of the same locule); d. Bridge of tissue at apex of locule through which median dorsal trace a. - e. passes; e. Portion of median dorsal trace (connects with portion a.); f. Median dorsal rib (one of three, two are not visible in photograph); i. Portion of apex of locule; j. Portion of a median dorsal trace.

Fig. 76. Vascular system near apex of mericarp, cross section, X371. a. Region of fusion of the three median dorsal traces (c. f. and h.). In region a., the three traces curve downward and connect with the lateral dorsal trace (the connection occurs at a level slightly below the section shwon in this photograph); b. Line in the plane of the commissure; c. Portion of a lateral dorsal trace; d. Portion of apex of locule (d. and g. are portions of the same locule); e. Bridge of tissue at apex of locule through which median dorsal trace f. passes; f. Portions of a median dorsal trace; g. Portion of apex of locule; h. Portion of a median dorsal trace.

PLATE-27



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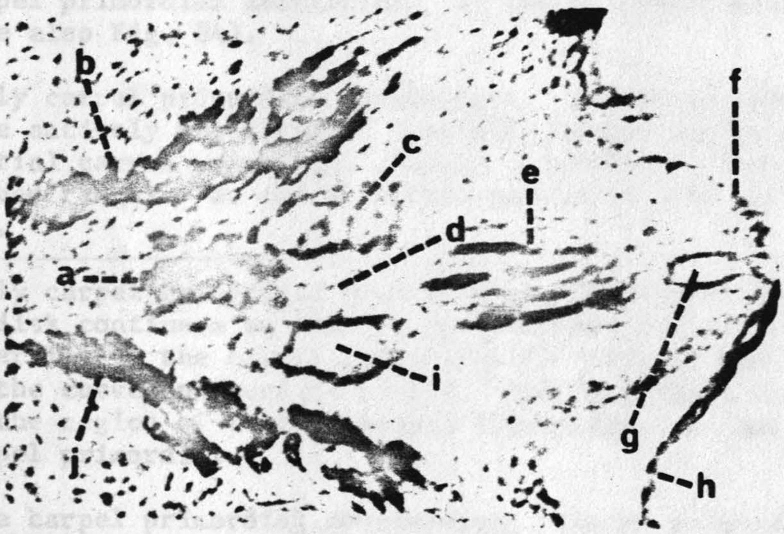

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Explanation of Plate 28

Drawings illustrating the development of the basic flower structure of both Taenidia and Pseudotaenidia beginning with cross sectional views of upper surface of late disk stage of flower primordium. Shows primarily the development of carpel primordia. Petal and stamen primordia are shown in Figures 77-79 but are omitted in Figures 80-82. Corresponding views in three dimension are given in Figures 83-88.

Fig. 77. Early primordial initiation. Only alternating petal and stamen primordia are initiated at this stage. a. Stamen primordium; b. Petal primordium (see also Fig. 83.).

Fig. 78. Carpel primordial initiation. a. and b. Carpel primordia (see also Fig. 84).

Fig. 79. Early carpel primordial development. Tissue of disk becomes more actively meristematic laterally to the region of the initial carpel primordia. Carpel primordia develop as curved ridges. a. and b. Carpel primordia (see also Fig. 85).

Fig. 80. Early carpel primordial development. Additional tissue of disk continues to become more actively meristematic laterally to the carpel primordia and increase the length of the curved primordial ridges. The two ridges are highest in the region of their original initiation. a. and b. Carpel primordia.

Fig. 81. Late carpel primordial development. Carpel primordia develop inward from the ends of the curved ridges. a. and d. Outer rims of the two carpel primordia; b. c. e. and f. Beginning development of inner rims of the two carpel primordia (see also Fig. 86).

Fig. 82. Basic structure of carpel primordia fully formed. a. and b. Outer and inner rims of one carpel; c. and d. Inner and outer rims of second carpel. (See also Figs. 87-88).

PLATE-28

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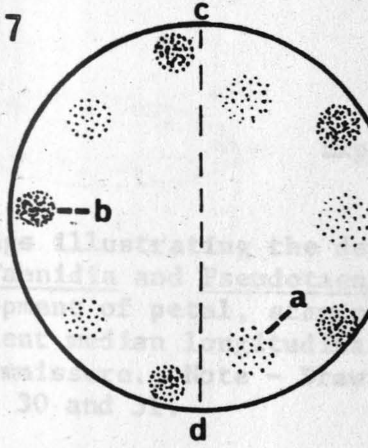

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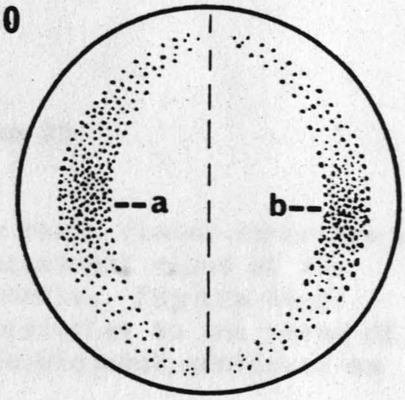

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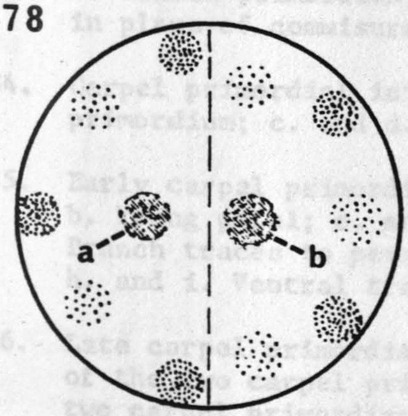

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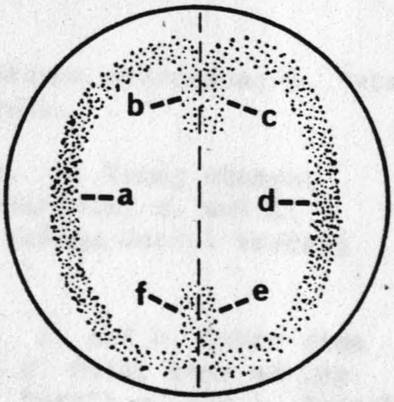

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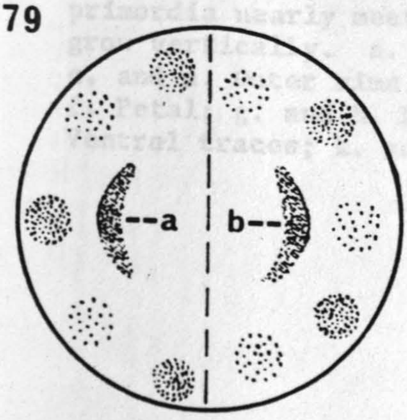

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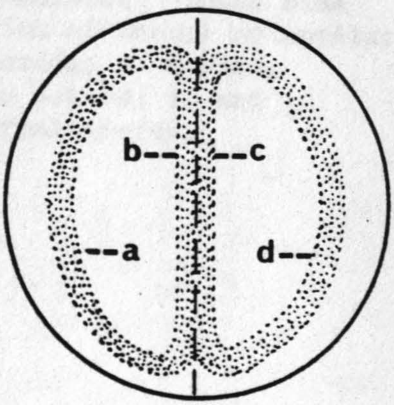


Explanation of Plate 29

Drawings illustrating the development of the basic flower structure of both *Taenidia* and *Pseudotaenidia*. Three dimensional views of the development of petal, stamen and carpel primordia. Figures 84-87 represent median longitudinal sections perpendicular to the plane of the commissure. Note - Drawings of flower development continued on plates 30 and 31.

Fig. 83. Late disk stage of flower primordium with early stage of petal and stamen primordial development on upper surface. a. Stamen primordium; b. Petal primordium; c. - d. line in plane of commisure.

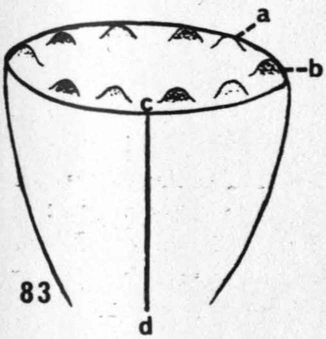
Fig. 84. Carpel primordial initiation. a. Stamen primordia; b. Petal primordium; c. and d. Carpel primordia.

Fig. 85. Early carpel primordial development. a. Young stamen; b. Young petal; c. and d. Carpel primordia; e. and f. Branch traces to petals; g. and j. Median dorsal traces; h. and i. Ventral traces.

Fig. 86. Late carpel primordial development. a. and b. Inner rims of the two carpel primordia; c. and d. Outer rims of the two carpel primordia; e. Stamen; f. Petal; g. and h. Branch traces to petals; i. and j. Ventral traces; k. and l. Median dorsal traces.

Fig. 87. Late carpel primordial development. Outer rims of carpel primordia nearly meet in plane of commisure. Inner rims grow vertically. a. and b. Inner rims of carpel primordia; c. and d. Outer rims of carpel primordia; e. Stamen; f. Petal; g. and h. Branch traces to petals; i. and j. Ventral traces; k. and l. Median dorsal traces.

PLATE-29



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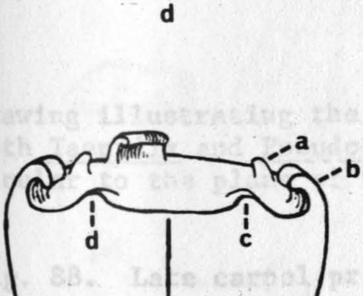

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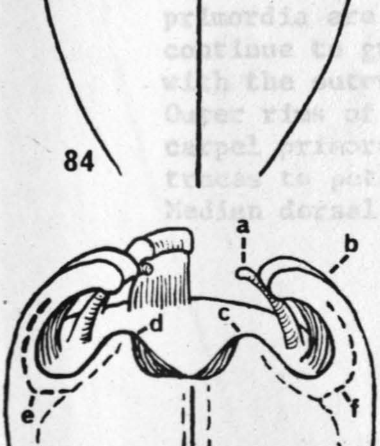

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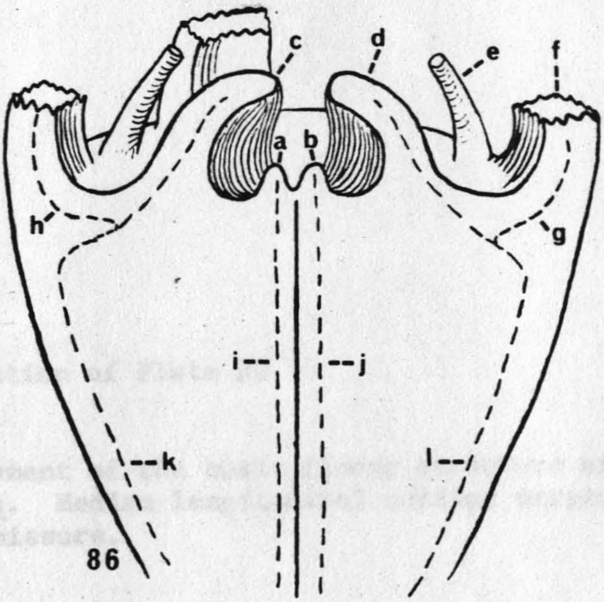

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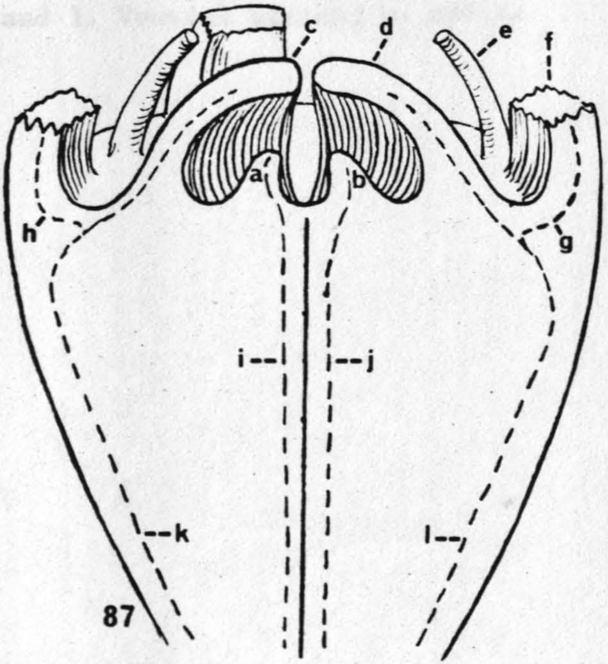

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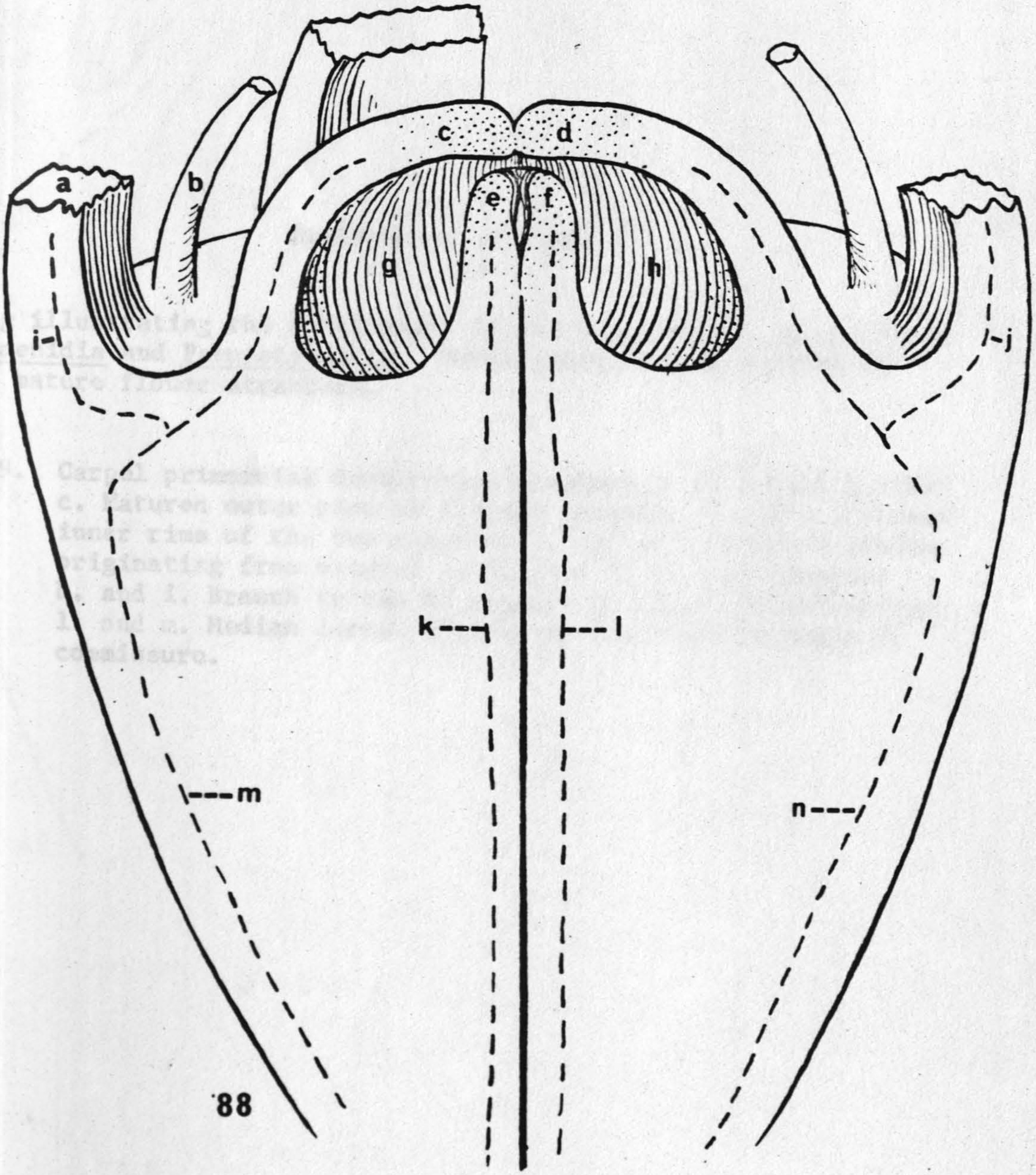
Explanation of Plate 30

Drawing illustrating the development of the basic flower structure of both <u>Taenidia</u> and <u>Pseudotaenidia</u>. Median longitudinal section perpendicular to the plane of the commissure.

Fig. 88. Late carpel primordial development. Outer rims of carpel primordia are adnate. Inner rims of carpel primordia continue to grow vertically and are nearly in contact with the outer rims. a. Petal; b. Stamen; c. and d. Outer rims of carpel primordia; e. and f. Inner rims of carpel primordia; g. and h. Locules; i. and j. Branch traces to petals; k. and l. Ventral traces; m. and n. Median dorsal traces.

PLATE - 30



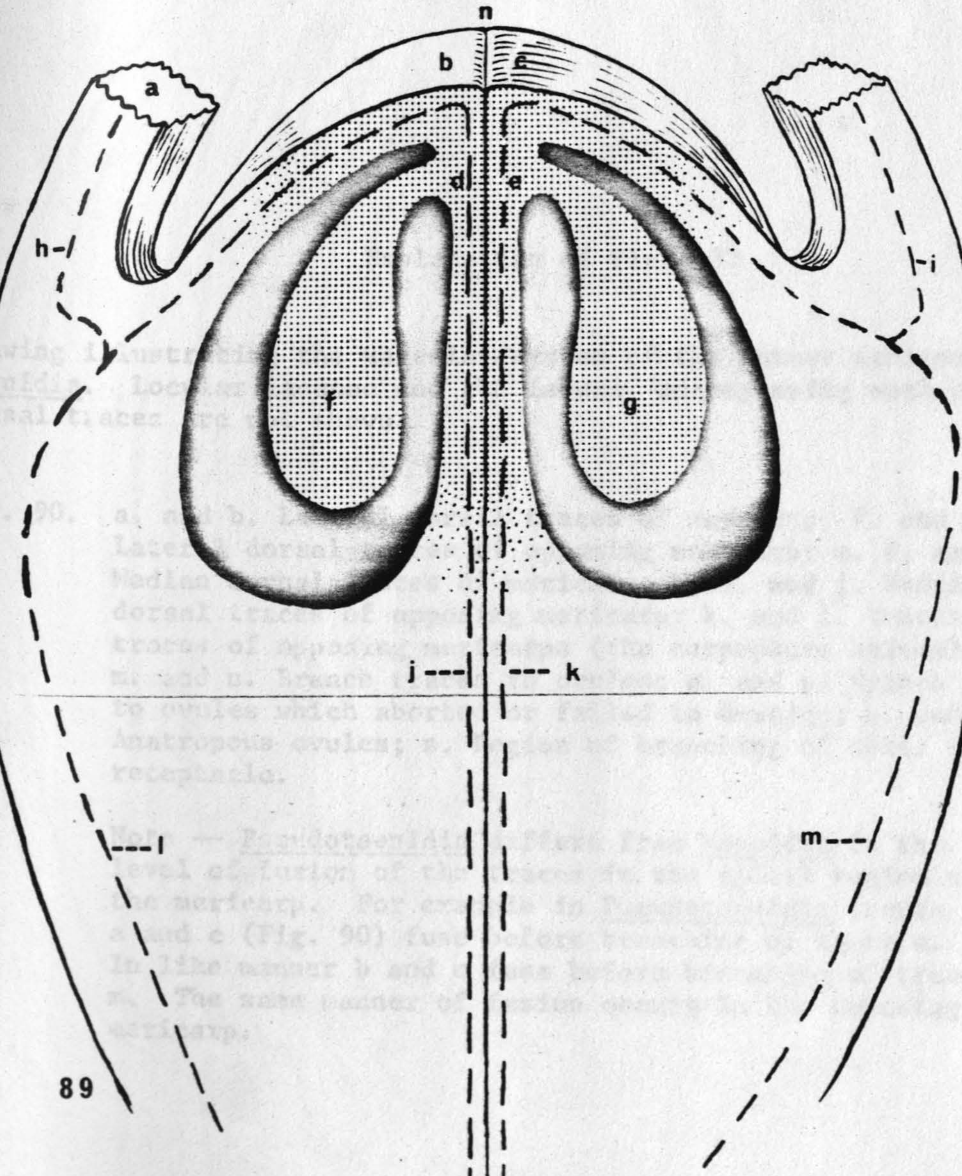
88

Explanation of Plate 31

Drawing illustrating the development of the basic flower structure of both _Taenidia_ and _Pseudotaenidia_. Median longitudinal section of nearly mature flower structure.

Fig. 89. Carpel primordial development completed. a. Petal; b. and c. Matured outer rims of the two carpels; d. and e. Matured inner rims of the two carpels; f. and g. Anatropous ovules originating from matured inner rims of the two carpels; h. and i. Branch traces to petals; j. and k. Dorsal traces; l. and m. Median dorsal traces; n. - o. Line in plane of commissure.

PLATE-31



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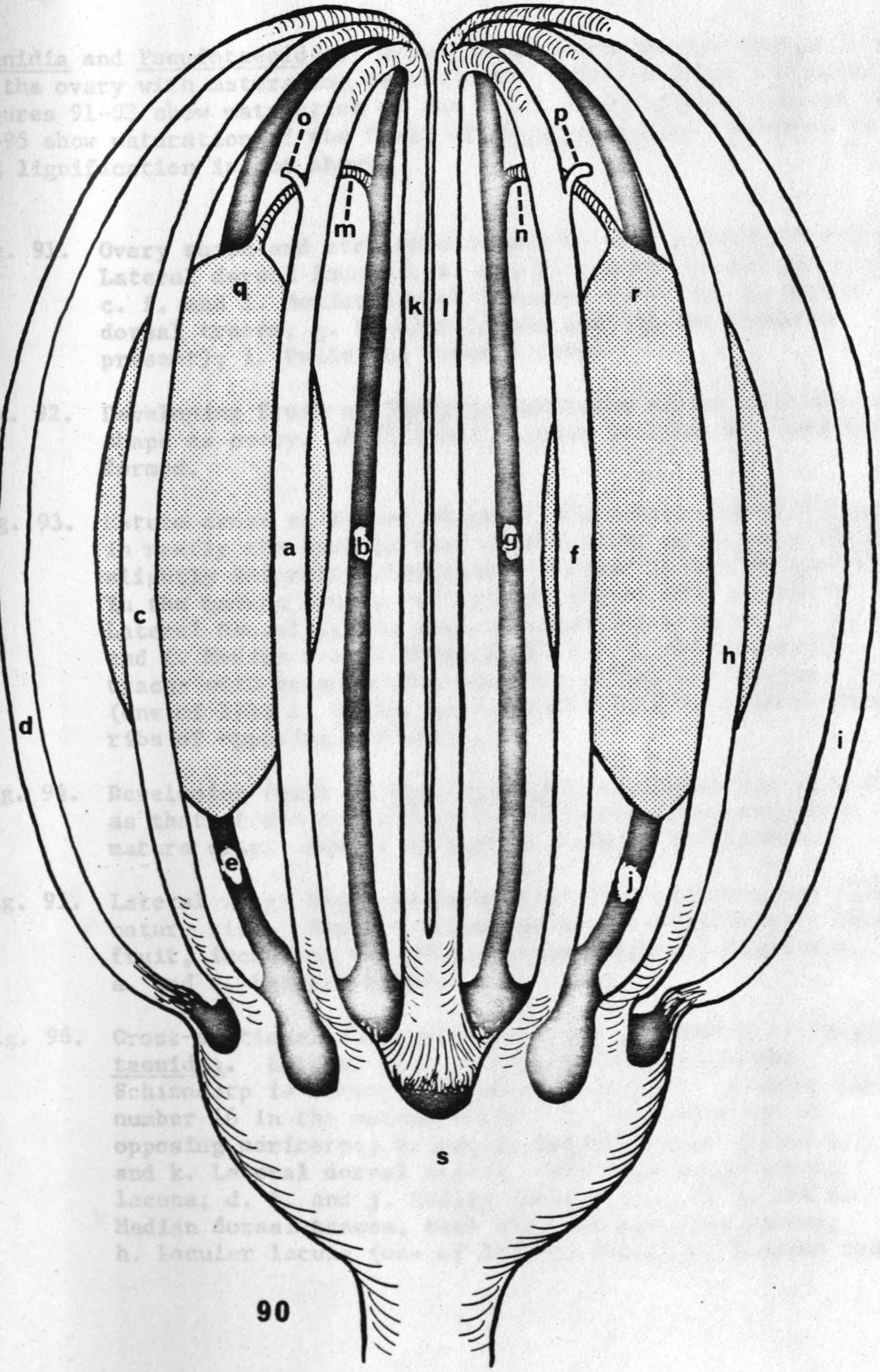
Explanation of Plate 32

Drawing illustrating the vascular system of the mature schizocarp of *Taenidia*. Locular lacunae and the lacuna accompanying each of the dorsal traces are not shown.

Fig. 90. a. and b. Lateral dorsal traces of mericarp; f. and g. Lateral dorsal traces of opposing mericarp; c. d. and e. Median dorsal traces of mericarp; h. i. and j. Median dorsal traces of opposing mericarp; k. and l. Ventral traces of opposing mericarps (the carpophore halves); m. and n. Branch traces to ovules; o. and p. Branch traces to ovules which aborted or failed to develop; q. and r. Anatropous ovules; s. Region of branching of stele in receptacle.

Note -- *Pseudotaenidia* differs from *Taenidia* in the level of fusion of the traces in the apical region of the mericarp. For example in *Pseudotaenidia* traces a and c (Fig. 90) fuse before branching of trace o. In like manner b and e fuse before branching of trace m. The same manner of fusion occurs in the opposing mericarp.

PLATE-32



90

Explanation of Plate 33

Taenidia and *Pseudotaenidia*. Drawings illustrating the change in shape of the ovary with maturation to the fruit. Median cross sectional views. Figures 91-93 show maturation of the fruit of *Taenidia*. Figures 91 and 94-95 show maturation of the fruit of *Pseudotaenidia*. Increase in size and lignification is not shown.

Fig. 91. Ovary shape and structure common to both genera. a.and k. Lateral dorsal lacunae; b. and j. Lateral dorsal traces; c. f. and i. Median dorsal lacunae; d. e. and h. Median dorsal traces; g. Locular lacuna (one of six normally present); l. Ovule; m. Ventral trace.

Fig. 92. Developing fruit of *Taenidia* maintains essentially the same shape as ovary. Additional locular lacunae are schizogenously formed.

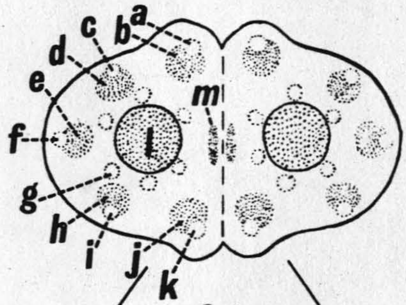
Fig. 93. Mature cross sectional shape of the schizocarp of *Taenidia* is nearly the same as that of the ovary except for being slightly laterally flattened. Locular lacunae number 16 in the mature fruit. a. Lateral dorsal rib; b. and j. Lateral dorsal traces with accompanying lacunae; c. e. and i. Median dorsal ribs; d. f. and h. Median dorsal traces with accompanying lacunae; g. Locular lacuna (one of 16); l. Ovule; m. Ventral trace; k. Lateral dorsal ribs of opposing mericarps.

Fig. 94. Developing fruit of *Pseudotaenidia* maintains the same shape as that of the ovary (Figure 91) until about one-third mature size. Number of locular lacunae increases.

Fig. 95. Lateral wings begin to form after fruit reaches one-third mature size. Number of locular lacunae increases. Entire fruit, including the ovule becomes dorsally flattened. a. and b. Lateral wings.

Fig. 96. Cross-sectional shape of the mature schizocarp of *Pseudotaenidia*. Lateral wings are prominent structures. Schizocarp is strongly dorsally flattened. Locular lacunae number 16 in the mature fruit. a. Lateral wings of opposing mericarps; b. and l. Lateral dorsal ribs; c. and k. Lateral dorsal traces, each with accompanying lacuna; d. f. and j. Median dorsal ribs; e. g. and i. Median dorsal traces, each with accompanying lacuna; h. Locular lacuna (one of 16); n. Ovule; o. Ventral trace.

PLATE-33



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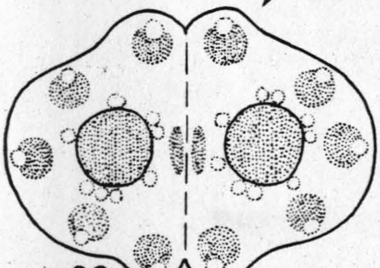
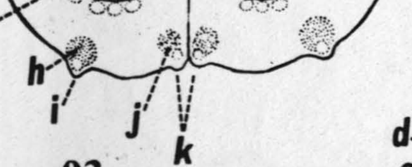
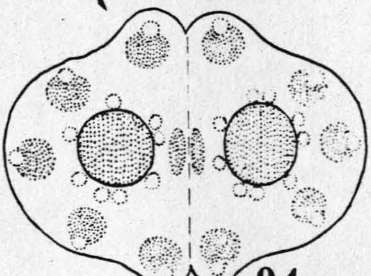


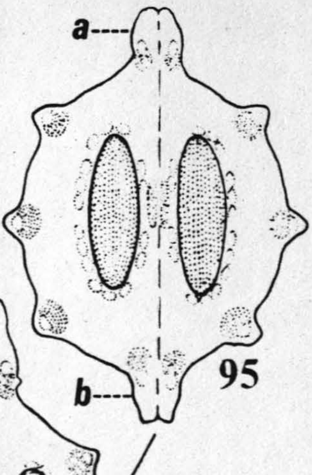
92



93



94



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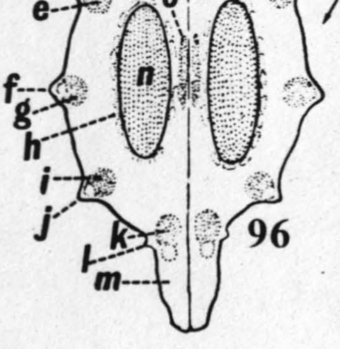
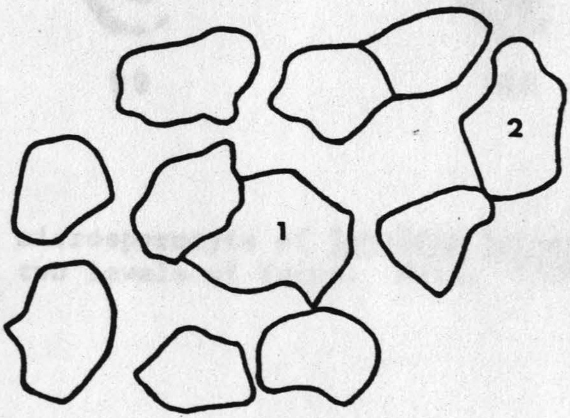


96

Explanation of Plate 34

Drawings of chromosomes of Taenidia and Pseudotaenidia, approximately 5,894X, anaphase II. Drawings made by tracing projected images from photomicrograph negatives. Those chromosomes of Taenidia, Fig. 97, designated as 1 and 2, correspond closely in size and shape with those of Pseudotaenidia, Fig. 98, designated as 1 and 2.

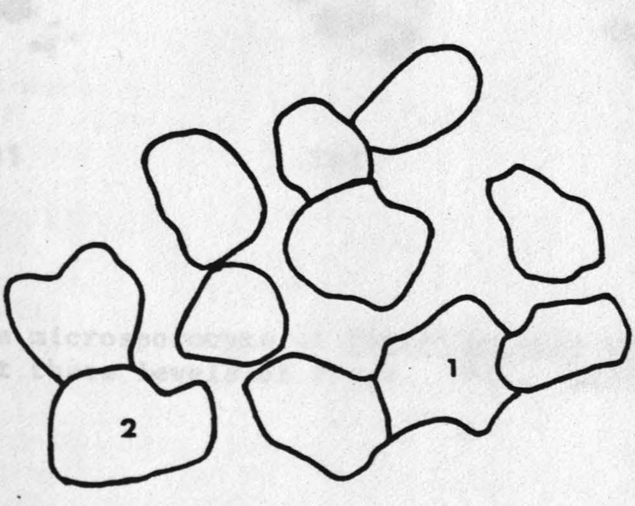
PLATE-34



97

Taenidia

n = 11



98

Pseudotaenidia

n = 11

PLATE-35

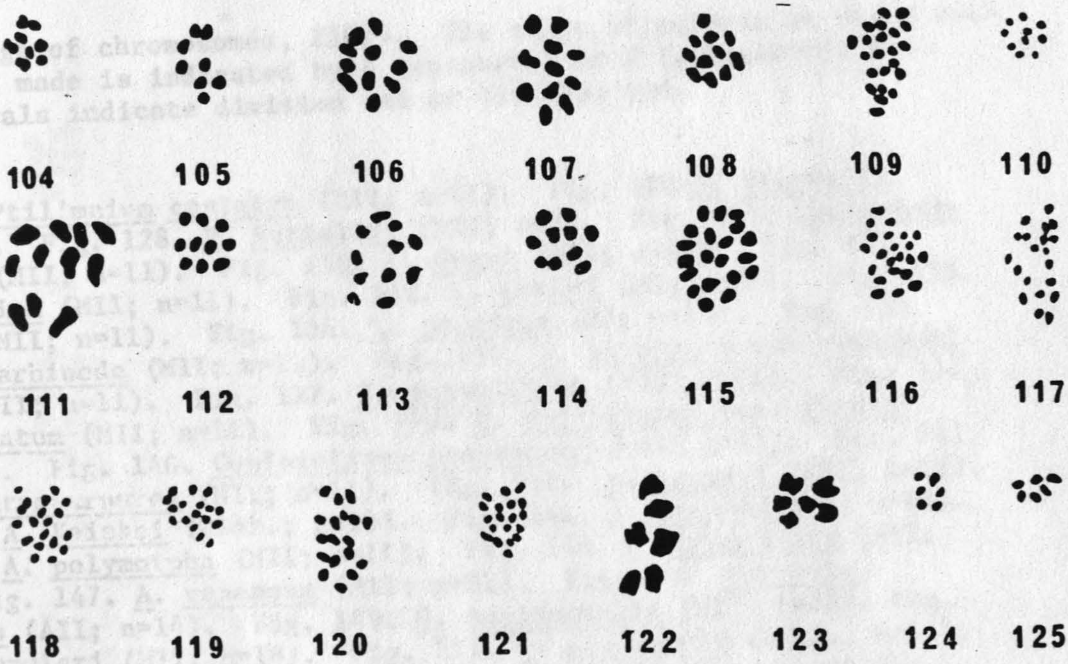
99 100

A portion of a microsporocyte of Taenidia integerrima showing its chromosomes at two levels of focus. N=11. 2500 X. Anaphase II.

101 102 103

A portion of a microsporocyte of Pseudotaenidia montana showing its chromosomes at three levels of focus. N=11. 2105 X. Anaphase II.

PLATE-36
CHROMOSOMES OF SOME SPECIES WITH LATERALLY FLATTENED FRUITS



Drawings of chromosomes, X1050. The stage of meiosis at which each drawing was made is indicated by A (anaphase) or M (metaphase); The roman numerals indicate division one or division two.

Fig. 104. Bupleurum falcatum (MI; n=8). Fig. 105. B. longiradiatum (MI; n=8). Fig. 106. Zizia aptera (MI; n=11). Fig. 107. Z. aurea (MII; n=11). Fig. 108. Z. trifoliata (MII; n=11). Fig. 109. Cicuta Bolanderi (AII: n=22). Fig. 110 Cryptotaenia canadensis (MII; n=10). Fig. 111. C. japonica (MI; n=11). Fig. 112. Carum carvi (MII; n=10). Fig. 113. Taenidia integerrima (MII; n=11). Fig. 114. Pimpinella anisum (MI; n=10). Fig. 115. P. Saxifraga (MII; n=20). Fig. 116. Perieridia californica (MII; n=22). Fig. 117. P. americana (MII; n=20). Fig. 118. P. Bolanderi (MII; n=19). Fig. 119. P. Gairdneri (MII; n=17). Fig. 120. P. oregana (AI; n=18). Fig. 121. P. Parishii (MII; n=19). Fig. 122. Sium floridanum (MII; n=6). Fig. 123. S. suave (MII; n=6). Fig. 124. S. suave (AII; n=6). Fig. 125. Berula erecta (AII; n=6). (Adapted from Bell and Constance, 1957 and 1960.)

Explanation of Plate 37

Drawings of chromosomes, X1050. The stage of meiosis at which each drawing was made is indicated by A (anaphase) or M (metaphase); the roman numerals indicate division one or division two.

Fig. 126. *Ptilimnium costatum* (MII; n=11). Fig. 127. *P. fluviaile* (MII; n=6). Fig. 128. *P. Nuttallii* (MII; n=7). Fig. 129. *Ligusticum canadense* (MII; n=11). Fig. 130. *L. Grayi* (MII; n=22). Fig. 131. *L. apiifolium* (MII; n=11). Fig. 132. *L. Canbyi* (MI; n=11). Fig. 133. *L. Grayi* (MII; n=11). Fig. 134. *L. scoticum* (MI; n=11). Fig. 135. *Thaspium barbinode* (MII; n=11). Fig. 136. *T. barbinode* var. *Chapmani* C. & R. (MII; n=11). Fig. 137. *T. pinnaifidum* (MII; n=11). Fig. 138. *T. trifoliatum* (MII; n=11). Fig. 139. *T. trifoliatum* var. *flavum* (MI; n=11). Fig. 140. *Conioselinum scopulorum* (MII; n=11). Fig. 141. *Angelica atropurpurea* (MII; n=11). Fig. 142. *A. Breweri* (MII; n=33). Fig. 143. *A. Keickei* (Diak.; n=11). Fig. 144. *A. pinnata* (MI; n=11). Fig. 145. *A. polymorpha* (MII; n=11). Fig. 146. *A. triquinata* (MII; n=11). Fig. 147. *A. venenosa* (MII; n=11). Fig. 148. *Oxypolis filiformis* (AII; n=14). Fig. 149. *O. occidentalis* (MII; n=18). Fig. 150. *O. Fendleri* (MII; n=18). Fig. 151. *O. greenmanii* (Diak.; n=14). Fig. 152. *O. rigidior* (MII; n=16). Fig. 153. *Polytaenia Nuttallii* (AI; n=11). Fig. 154. *Lomatium angustatum* (MII; n=11). Fig. 155. *L. californicum* (MII; n=11). Fig. 156. *L. ciliolatum* var. *Hooveri* (MII; n=11). Fig. 157. *L. Congdonii* (MII; n=11). Fig. 158. *L. dasycarpum* (MII; n=11). Fig. 159. *L. Hundle* (MI; n=11). Fig. 160. *L. macrocarpum* (AII; n=11). Fig. 161. *L. marginatum* (MII; n=11). Fig. 162. *L. marginatum* var. *purpureum* Jepson (MII; n=22). Fig. 163. *L. nevadense* var. *Parishii* (MII; n=11). Fig. 164. *L. repostum* (MII; n=22). Fig. 165. *L. Torreyi* (MII; n=11). Fig. 166. *L. triternatum* (MII; n=11). Fig. 167. *L. utriculatum* (MII; n=11). Fig. 168. *L. ambiguum* (MII; n=11). Fig. 169. *L. Cous* (MII; n=11). Fig. 170. *L. dissectum* (MII; n=11). Fig. 171. *L. dissectum* var. *multifidum* (MII; n=11). Fig. 172. *Heracleum lanatum* (MI; n=11). (Adapted from Bell and Constance, 1957 and 1960.)

PLATE-37

CHROMOSOMES OF SOME SPECIES WITH DORSALLY FLATTENED FRUITS

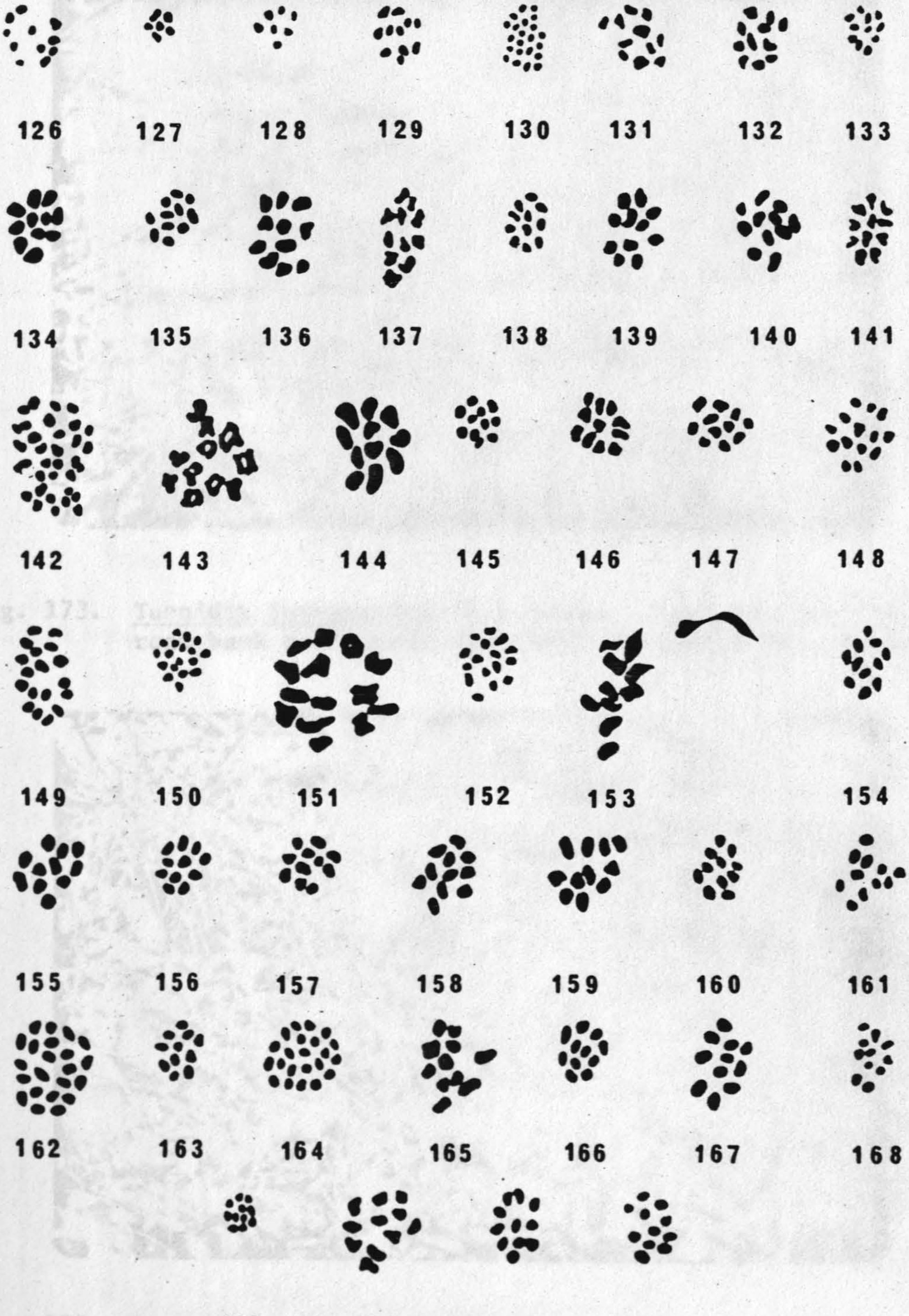


PLATE-38

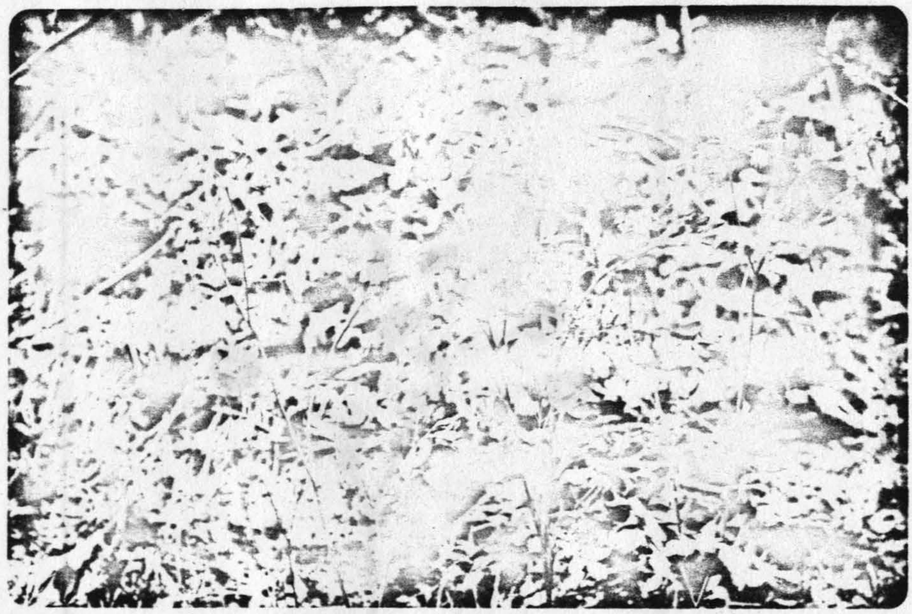


Fig. 173. *Taenidia integerrima* (L.) Drude. Plants in flower along road bank near Cheat Lake Dam, Monongalia Co., W. Va.

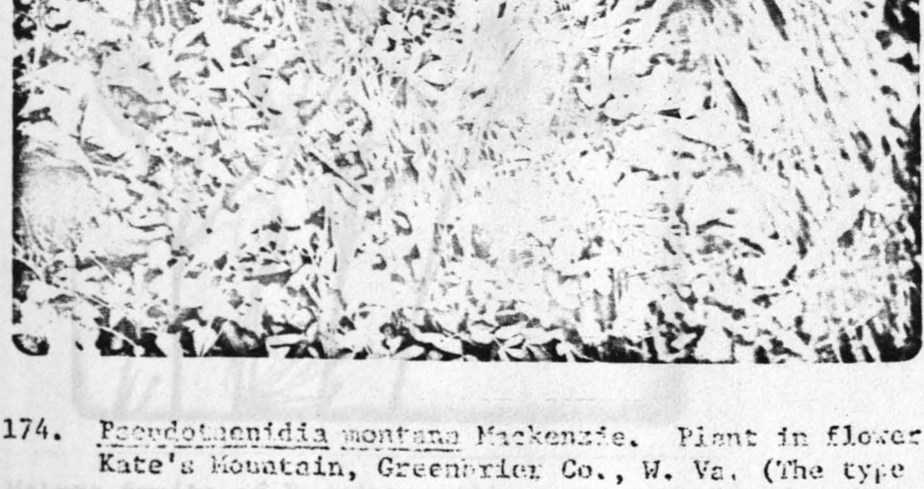


Fig. 174. *Pseudotaenidia montana* Mackenzie. Plant in flower on Kate's Mountain, Greenbrier Co., W. Va. (The type locality)

PLATE - 39

Fig. 175. Mature fruits of Taenidia integerrima (L.) Drude. (2X).

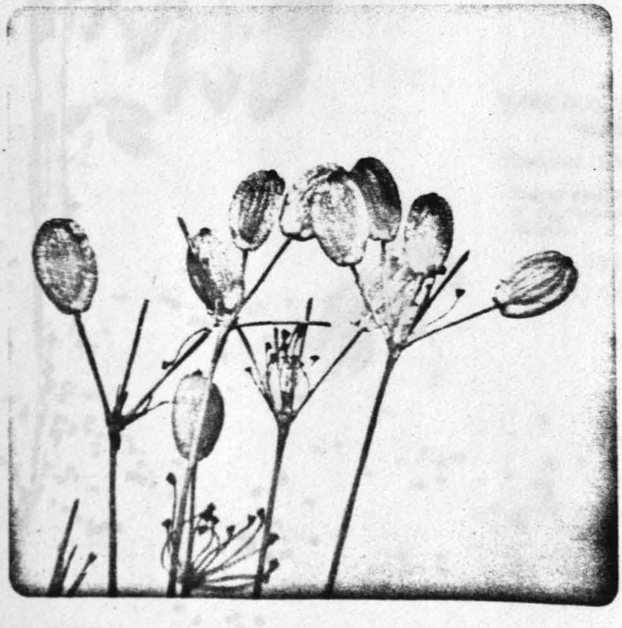
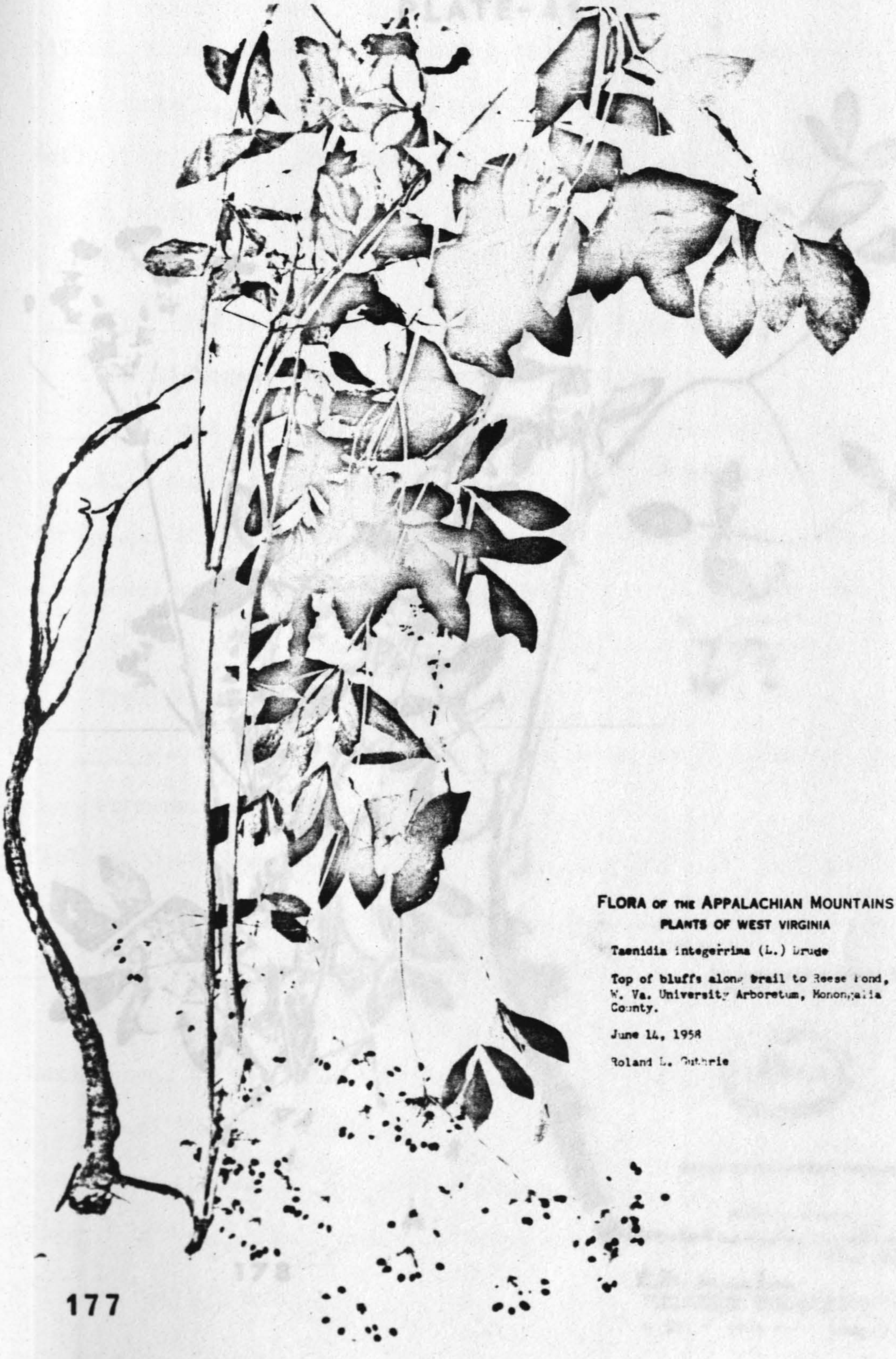


Fig. 176. Mature fruits of Pseudotaenidia montana Mackinzie. (2X).

PLATE-40



FLORA OF THE APPALACHIAN MOUNTAINS
PLANTS OF WEST VIRGINIA

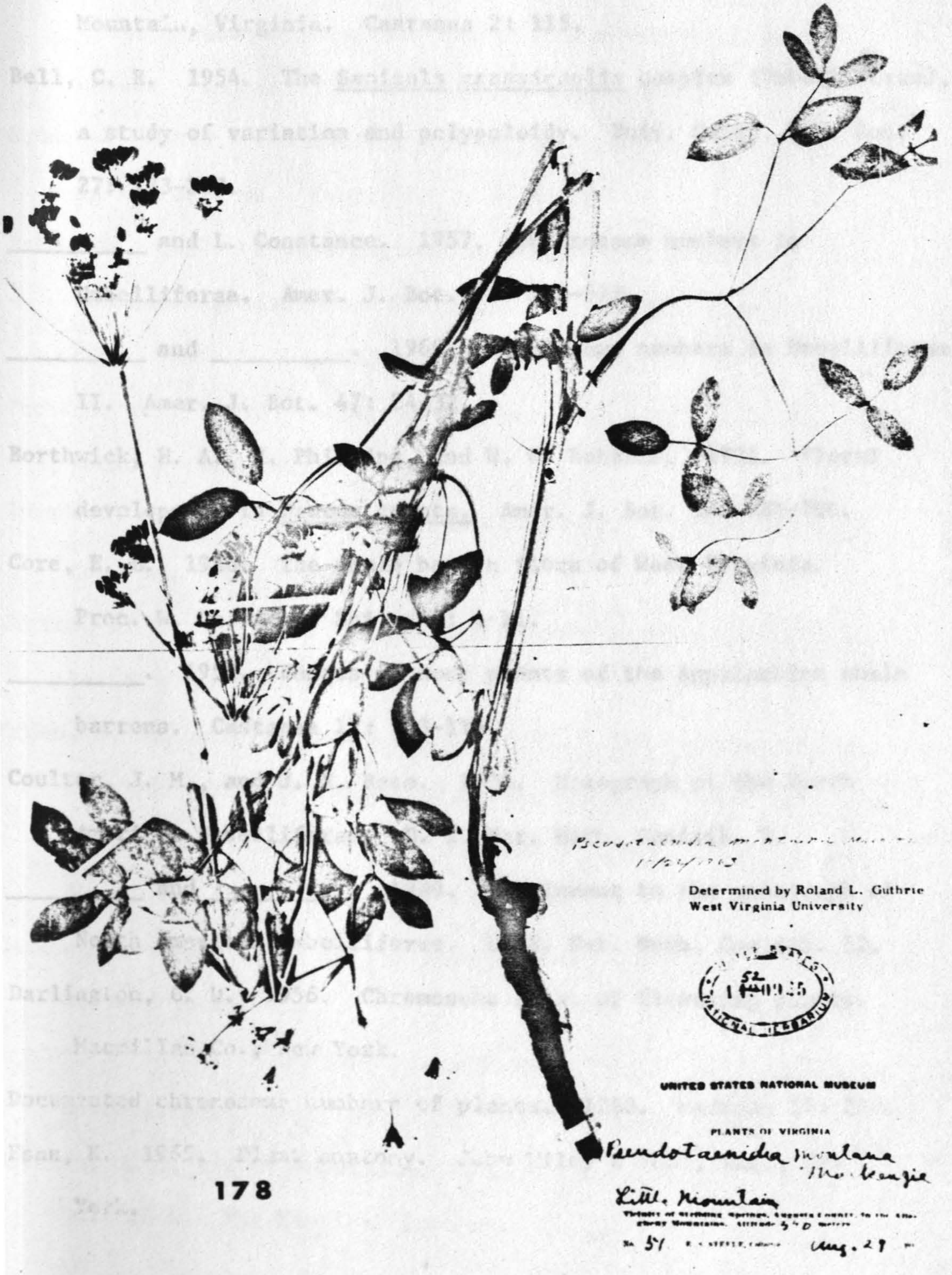
Taenidia integerrima (L.) Drude

Top of bluffs along trail to Reese Pond, W. Va. University Arboretum, Monongalia County.

June 14, 1958

Roland L. Guthrie

PLATE- 41


Pseudotaenidia montana Mackenzie
11/24/1963
Determined by Roland L. Guthrie
West Virginia University
52
1409935
NATIONAL HERBARIUM
UNITED STATES NATIONAL MUSEUM
PLANTS OF VIRGINIA
Pseudotaenidia montana
Mackenzie
Little Mountain
Vicinity of Stribling Springs, Augusta County, in the Allegheny Mountains. Altitude 5?0 meters
No. 57
Aug. 29

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APPENDIX. INSTITUTIONS FROM WHICH HERBARIUM SPECIMENS WERE BORROWED FOR GROSS MORPHOLOGICAL STUDIES.

Institution	No. of Specimens
Brooklyn Botanical Garden	24
Carnegie Museum	84
Dartmouth College	13
De Paul University	13
Duke University	27
Florida Agricultural Experiment Station	9
Florida State University	24
Indiana University	45
Iowa State University	75
Kansas State University	15
Marshall University	4
Michigan State University	55
Missouri Botanical Garden	124
New York Botanical Garden	75
North Carolina State College	13
Ohio State University	38
Ontario Agricultural College	27
Pennsylvania State University	33
Randolph-Macon Woman's College	2
Rutgers University	26
Southern Methodist University	41

APPENDIX (Cont.)

Southwestern Missouri State College	8
Stanford University	16
Texas A & M University	4
Texas Research Foundation	4
United States National Museum	130
University of Arkansas	21
University of California (at Berkeley)	62
University of California (at Los Angeles)	5
University of Cincinnati	7
University of Georgia	27
University of Illinois	106
University of Kansas	15
University of Kentucky	8
University of Louisville	5
University of Maryland	3
University of Minnesota	116
University of Nebraska	8
University of North Carolina (Chapel Hill)	51
University of Notre Dame	13
University of Oklahoma	33
Universityof Pennsylvania	120
University of Tennessee	52
University of Texas	25
University of Vermount	17
University of Wisconsin	100
Virginia Polytechnic Institute	25

APPENDIX (Cont.)

West Virginia University	69
West Virginia Wesleyan College	8
Yale University	26
Total Specimens	1851

ABSTRACT

The objectives of this research work were to determine the phylogenetic relationship between the Umbelliferous species Taenidia integerrima (L.) Drude, Yellow Pimpernel, and Pseudotaenidia montana Mackenzie, Mountain Pimpernel. The research involved morphological and cytological investigations as well as range and ecological considerations. Based on the findings of this investigation, the phylogenetic significance of the fruits of the Umbelliferae as indicators of relationship was evaluated.

The development of the flower structure was investigated beginning with the growth of the flower primordium and continuing to the mature flower. The structure of the immature and mature fruits were investigated and evaluated. A study of chromosome numbers and chromosome morphology was included in the work. Gross morphological studies were made from herbarium specimens and from naturally growing plants in the field. The results of this original research were correlated with range and ecological studies of previous investigators.

The genera studied are monotypic and the species differ in gross morphology only in their fruits. The identical morphology with the exception of the fruits provided a unique opportunity for the evaluation of fruit structure as a phylogenetic indicator in the Umbelliferae. The present system of classification places Taenidia in the tribe Ammineae and Pseudotaenidia in the tribe Peucedaneae. This classification results in the two genera being placed at nearly

opposite ends of the very large sub-family Apioideae even though the plants are indistinguishable except during the fruiting stage.

On the basis of the evidence of this study the conclusions were:

1. Taenidia integerrima (L.) Drude and Pseudotaenidia montana Mackenzie should remain as they are now classified in separate genera.
2. The nearest phylogenetic relative of Taenidia is Pseudotaenidia.
3. Taenidia and Pseudotaenidia should not be classifed as they are at present in separate tribes at nearly the opposite ends of the very large sub-family Apioideae. The present taxonomic criteria that are used to define the two tribes would not permit, because of the differences in the flattening of the fruits, either Taenidia being placed in the Peucedaneae with Pseudotaenidia or for Pseudotaenidia to be placed in the Ammineae with Taenidia. A new basis for such a classification should be devised, but because of the great number of species and the morphological complexities involved, the likelihood of such a drastic reclassification being made lies well into the future.
4. The use of the cross sectional shape of the schizocarp and the presence or absence of lateral wings as the primary indicators of phylogenetic relationship in the Apiodeae of the Umbelliferae is seriously questioned. Other morphological features may be of equal or more significance.

VITA

Roland Lee Guthrie was born in Charleston, West Virginia, on April 5, 1928. He received his early education in the public schools of Cabell County at Huntington, West Virginia. After serving in the U. S. Army in 1946 and 1947, he entered Marshall College in 1948 where he completed his freshman year. In September, 1948 he entered the Division of Forestry of West Virginia University. During his junior year, he was recalled to active service in the Army Reserves and he served in Germany during 1950 and 1951. Returning to West Virginia University in September of 1951, he received the Bachelor of Science degree in Forestry in January, 1953. In August, 1953 he received the Master of Science degree with a major in Botany from West Virginia University. From 1953 until 1956, he was employed as Forester-Naturalist by the Isaac W. Bernheim Foundation of Louisville, Kentucky. In September of 1956, he re-entered Graduate School at West Virginia and after serving a three year period as a graduate assistant, he was appointed Arboretum Assistant, a position he held until 1965 when he was made Assistant Professor of Biology and Arboretum Director. He is a candidate for the degree of Doctor of Philosophy in Botany to be conferred in August, 1968.

APPROVAL OF EXAMINING COMMITTEE

Charles H. Baer

Dr. Charles H. Baer

H. L. Barnett

Dr. H. L. Barnett

W. Newman Bradshaw

Dr. W. Newman Bradshaw

Earl L. Core

Dr. Earl L. Core

Gerald E. Bennett

Dr. Gerald E. Bennett,
Chairman

e August 9, 1968