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A NATURAL HISTORY AND CLASSIFICATION OF THE GENUS PARTHENICE (COMPOSITAE)

by

Jane Reese Sauck

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF BIOLOGICAL SCIENCES

In Partial Fulfillment of the Requirements

For the Degree of

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THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Jane Reese Sauck entitled A Natural History and Classification of the Genus Parthenice (Compositae) be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Charles T. Mason Jr. — April 22, 1969
Dissertation Director — Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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ABSTRACT

The genus Parthenice (Compositae-Heliantheae) which contains the single species P. mollis occurs along washes and on rocky hillsides in the semi-arid mountain ranges of south central Arizona and adjacent parts of northern Mexico as well as southern Baja California. Since its description by Gray in 1853, its taxonomic position within the Heliantheae has been questioned by several workers. In this study the natural history of P. mollis is examined as a requisite leading to the eventual classification of the genus in the Compositae.

As both traditional and neoclassical methods are used, data are obtained from a wide variety of disciplines. Field studies indicate that P. mollis is well adapted to the periodic rainy season in southern Arizona in that it is able to withstand considerable drouth. A chemical inhibitor is present in the seed coat which detains germination until sufficient rain has fallen to insure establishment of seedlings. Morphological data indicate that P. mollis is an unbranched annual with a wide variety of leaf sizes and shapes. The morphology of the flower is similar to that of Parthenium. Several distinct differences are indicated. Vegetative anatomy is characterized by the presence of secretory canals of schizogenous origin in the pith and cortex of the stem and leaf. A peculiar elevated stomatal apparatus located in the stem epidermis is described and figured. Trichomes are either uniseriate and non-glandular or biseriate and glandular. Both types of trichomes originate with a single papillate epidermal cell. Floral anatomy is discussed in detail. Sections are devoted to the

floral apex, peduncle, phyllaries, ray flower, the disk flower, pales, vasculature of the capitulum, as well as pollen. A chromosome analysis revealed a count of n = 18. Meiosis is normal, and reproduction is strictly sexual. Megasporogenesis is of the monosporic type while embryogenesis is of the Capsella type. P. mollis is self fertile. Two fungal parasites are found on the leaves, a rust and an imperfect. Insects normally found on the leaves and stem are ants and aphids. Leaf injury is caused primarily by the lace bug (Stephanitis). An analysis of certain chemical constituents using pharmaceutical methods reveals that P. mollis possesses a tertiary alkaloid, a saponin in the leaves, a flavonoid in the inflorescence, and rubber in the stems.

The study resulted in the description of a new variety of P. mollis endemic to Baja California. Although no new conclusions as to the taxonomic position of Parthenice are made, a list of over two hundred characters of taxonomic value is given.

INTRODUCTION

For several years I have observed that students of plant taxonomy almost traditionally select a monographic approach to their dissertation topic. Frequently, because of the size of the selected genus or family, only a few of the major botanical disciplines are employed to describe the taxonomic relationships of the group. According to Davis and Heywood (1963), Adanson, a contemporary of Linneaus, put forth the idea that a true and meaningful taxonomy of organisms can only be ascertained if the sum total of all characteristics of the organisms are used. To apply Adanson's philosophy to genera which contain a large number of species presents serious difficulties. The enormous quantity of data which would be accumulated in a study of fifteen species in one genus could scarcely be assimilated by one worker. Until the taxonomist avails himself of tools such as computer analysis to hasten his task, the Adansonian approach is undoubtedly best applied to those genera with only a few species. Further, sufficient funds might not be available for extensive analysis of the chemical components of a large group of plants. Finally, greenhouse space for hybridization and growth studies may be limited.

A taxon ideally suited to an Adansonian study is Parthenice. Parthenice is a little-known monotypic genus of doubtful taxonomic position in the angiosperm family, Compositae. The one species P. mollis A. Gray is native to Arizona, and Sonora and Baja California, Mexico. Although it has no known use and no common name, natives in

Mexico have reported it a nuisance in their milpas (corn fields) (Johnson 1966). One of Howard Scott Gentry's collections (#1622) from Rio Mayo, Sonora does bear the vernacular epithet of "kotasulu," the meaning and origin of which is not known at the present time. "Kotasulu" has been applied to Abutilon lignosum whose vegetative leaves look very much like those of Parthenice.

The father of American botany Asa Gray first described Parthenice in 1853 using Mexican collections sent to him by Charles Wright. Gray grew Parthenice from seed in the Cambridge Botanic Garden and described it as a paniculately branched herb with the aromatic odor of an Artemisia. Taxonomically Gray considered Parthenice closely related to Parthenium (guayule) in the Melampodinae of the tribe Heliantheae. He distinguished Parthenice from Parthenium by the former's deciduous and less ligulate ray corollas, the reduction of the paleae of the disk to minute rudiments, and the want of a pappus (Gray, 1853, p. 85).

Since 1853 little has been done to alter the taxonomic position of Parthenice. Baillon (1882, p. 233) gave Parthenice and Aiolotheca, a name of a scarcely known genus from San Luis Potosi, Mexico, as synonyms of Parthenium yet recognized them as sections of that genus. No new nomenclatural combinations were made or was any justification given for such a treatment. Rollins (1950) has pointed out that the differences between these genera are so apparent that no modern taxonomist would consider them as co-generic. Recently Rzedowski (1968) has reviewed the material identified as Aiolotheca and found it to be in the genus Zaluzania in the subtribe Verbesininae.

Although Parthenice has been traditionally placed in the Melampodinae, a taxon which Gray (1884, p. 245) regards as artificial, its true affinity has not yet been established. Bentham (1873) has suggested the intermediate nature of the genus in his frequently quoted passage wherein he relates the Anthemideae with the Melampodinae through Parthenice. His observations, however, are based on megamorphic and distributional features alone.

Work by palynologists have led to other speculations. Wodehouse (1935) relates Parthenice to the subtribe Ambrosiinae (Heliantheae) because its pollen possesses a combination of characters which makes it appear to be an ideal prototype for that tribe.

Recent pollen studies with the electron microscope (Skvarla and Larson 1965) substantiate the work of Wodehouse only in part. Instead the pollen of Parthenice appears to be the prototype for only certain members of the tribe. They conclude ". . . Parthenice is not an easy genus to place and it might be that the genus, phyletically speaking, stands somewhere within the aggregate triangle Heliantheae-Ambrosieae-Anthemideae."

Morphological and palynological data alone may have failed to properly relate Parthenice to other Compositae. Therefore the Adansonian philosophy has been used to develop a fuller knowledge of this interesting desert annual. Information concerning the natural history of Parthenice has been obtained from a variety of disciplines including cytology, ecology, chemistry, anatomy, and morphology. Although taxonomic conclusions cannot be made from this study alone, it is hoped that data

obtained here will provide a basis for future studies in the helianthoid Compositae.

DISTRIBUTION AND HABITAT

Charles Wright made the first known botanical collection of P. mollis in 1851 near the tiny Mexican town of Santa Cruz, Sonora on his historical journey which began in Texas. Since that time sporadic collections have been made in Arizona, and Sonora, Sinaloa, and Chihuahua, Mexico, and in the southern part of Baja California (Figure 1). In addition, P. mollis has been reported from New Mexico and Colorado in several floras: Arizona Flora (Kearney and Peebles 1960), Flora of Arizona and New Mexico (Tidestrom and Kittell 1941), Flora of the Rocky Mountains and Adjacent Plains (Rydberg 1922), and Vegetation and Flora of the Sonoran Desert (Shreve and Wiggins 1964).

Weber (1966) has recently published a note concerning Parthenice in Colorado. He states that he has been unable to verify the report of P. mollis in Colorado, that it is probably not there, and that "the species is far out of range and should be rejected." Furthermore, examination of herbarium material by Weber at University of Colorado, Gray Herbarium, and the New York Botanical Garden and examination of herbarium material by the author at The University of Arizona, California Academy of Sciences, University of California at Berkeley, and Dudley Herbarium at Stanford has failed to turn up any evidence of occurrence in Colorado. Iva xanthifolia which occurs in Colorado has a very similar appearance to Parthenice (Figure 2). It is possible that the report from Colorado has arisen from a mistake in identification.

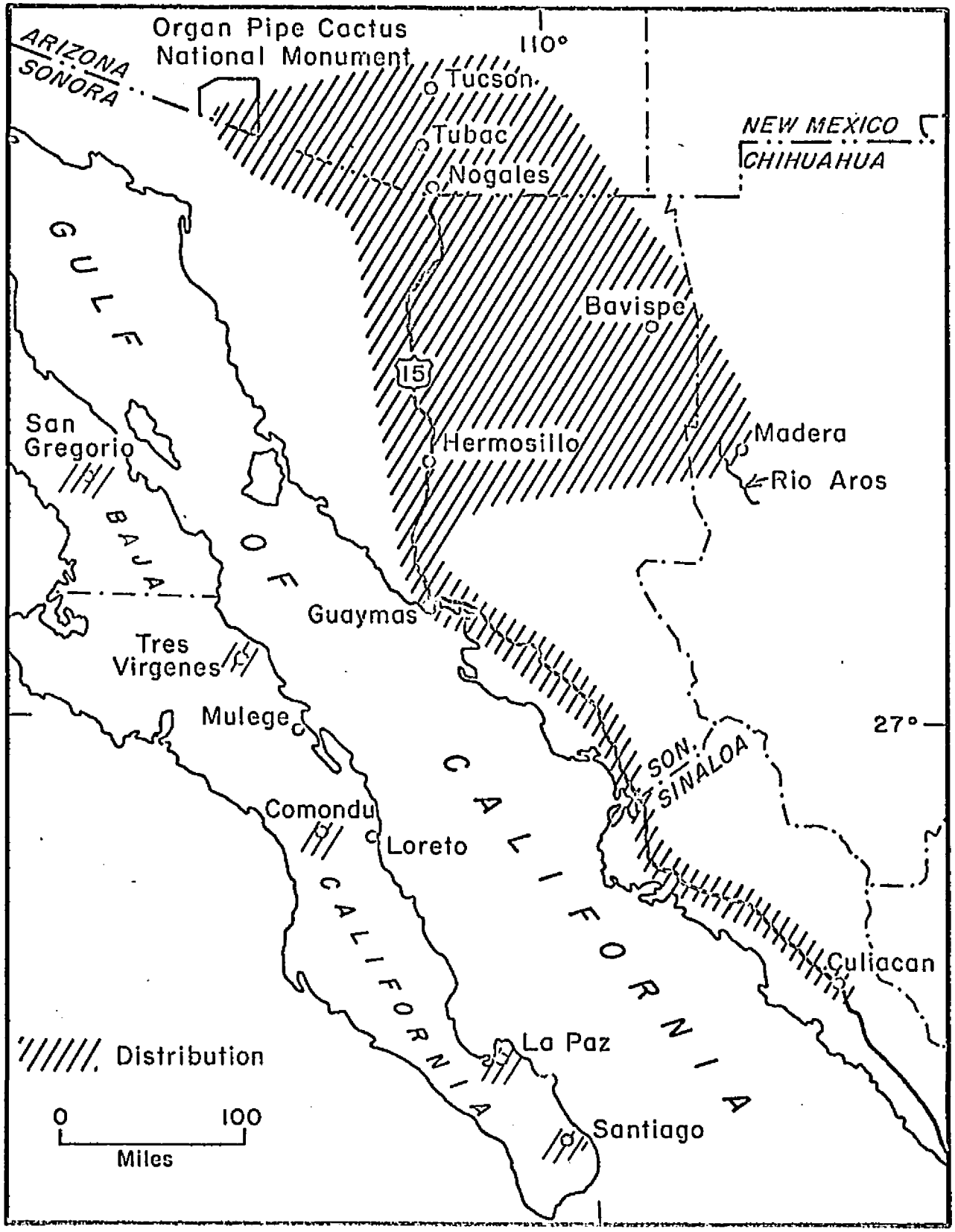


Figure 1. The Distribution of Parthenice mollis

A

B

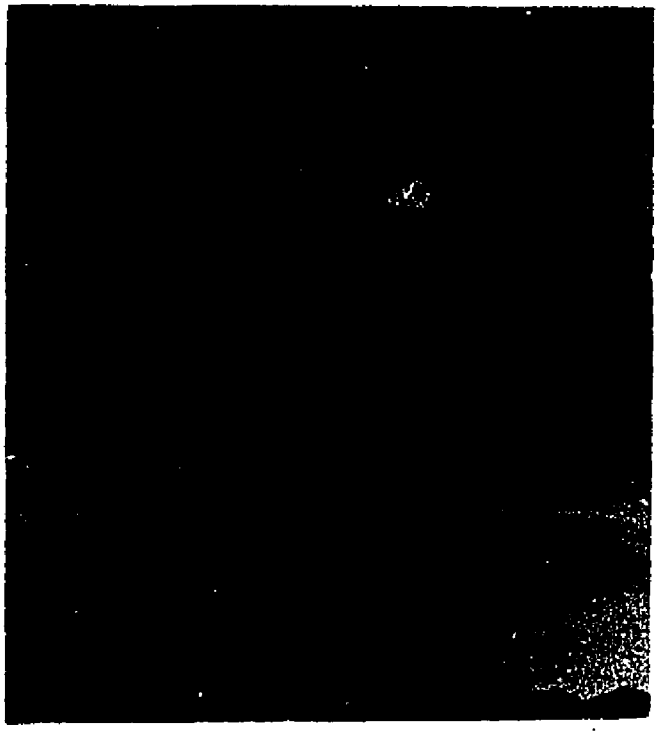


Figure 2. Comparison of Habit of Parthenice mollis and Iva xanthifolia

A. P. mollis on hillside in southern Arizona. B. I. xanthifolia along roadside in southern Colorado.

Also the report from New Mexico seems doubtful. There are no records of the plant in New Mexico in the above-mentioned herbaria. Martin (1967) at Albuquerque and Gordon (1967) at Las Cruces have reported that they have no record of it in their herbaria. The type specimen, however, bears the handwritten inscription "collected in N. Mex." which might have been interpreted to mean New Mexico instead of northern Mexico thereby giving rise to a report from that state. The type, #1208, according to Gray in Plantae Wrightianae, was collected near Santa Cruz, Sonora, Mexico. It is interesting to note that Wright's previous collection #1207 was collected in New Mexico and the plant collected was Iva xanthifolia. It is suggested that the two plants were confused again, and that the report from New Mexico should be disregarded.

In Arizona, P. mollis has been found in many of the southern mountain ranges. Collections have been made in Wild Burro Canyon in the Tortolito Mountains, Canon del Oro, Sabino Canyon, Pontatoc Wash and in the Fort Lowell area in the Santa Catalina Mountains, Toro Canyon, Baboquivari Canyon and Brawley Wash in the Baboquivari Mountains. P. mollis has been observed at Buenos Aires, Arizona, an old port of entry from Mexico at the foot of the Baboquivari Mountains. Other mountain ranges in which Parthenice has been collected or observed include: Alamo Canyon in the Ajo Mountains, Mendoza Canyon in the Coyote Mountains, Sycamore Canyon, near Ruby, and Sycamore Canyon along the road to Lochiel (county A-2), west of Manzana Mountain and in the Patagonia Mountains respectively. Also it occurs in Box Canyon and in Stone Cabin Canyon of the Santa Rita Mountains, as well

as along the Redington Road (county A-5) which lies between the Rincon Mountains and the Santa Catalina Mountains.

The Ajo Mountains represent the western limit of distribution in Arizona while the Patagonia Mountains apparently limit it to the east. Parthenice is conspicuously absent from the Huachuca Mountains and the Chiricahua Mountains. To date the Tortolito Mountains are the most northern site. There is no southern limit in Arizona; Parthenice extends far south of the border into Mexico.

In Mexico, the distribution of Parthenice is somewhat more complex. During August 1966, P. mollis was found by the writer to be a conspicuous roadside weed all along Highway 89-15 from Tubac, Arizona to Culiacan, Sinaloa, a distance of more than 600 miles. Earlier an herbarium survey by the author had indicated that P. mollis was disjunct between Santa Cruz, Sonora and Culiacan, Sinaloa. Presently, the center of distribution appears to be northern Sonora. North of Hermosillo, the species can be found on hillsides and in washes associated with the west and north flowing river basins of the Rio Magdalena and the Santa Cruz. South of Hermosillo, it is restricted to roadcuts and milpas near Highway 15. This weedy tendency suggests that it is not native in the southern areas but that it may have been introduced there by the activities of man. This seems especially feasible considering that the achene is very light and due to the presence of the associated pales it clings easily to any textured surface.

In the Mexican state of Chihuahua one collection of Parthenice has been made by Harde Le Sueur (s. n.) near the Papigochico River north of the Rio Aros. This locality is about 150 miles directly east of

Hermosillo. Because overland travel in Chihuahua is difficult the author was unable to determine the extent of Parthenice's distribution in that state.

Various collections have been made in Baja California with populations being found near La Paz, Canipole, Comondu, Tres Virgenes, and San Gregorio. Though there is no known way of estimating how long P. mollis has been present on the peninsula, it has been present long enough for certain morphological dissimilarities to arise which distinguish Baja California material from that of Arizona and Sonora. The extent of these differences is discussed more fully in the chapter on morphology.

Parthenice is essentially a plant of the Sonoran Desert in the sense of Shreve and Wiggins (1964). Although it is most often found in the Upper Sonoran Life Zone in Arizona at elevations of 3,000 to 4,500 feet, plants were observed by the author to be growing at sea level near Guaymas, Sonora. Little data are available for elevations of Parthenice in Baja California. One herbarium collection, Carter 5050, indicates an elevation of 1,200 feet near San Javier.

Associates frequently found with Parthenice in Arizona include Atriplex canescens, Rumex hymenosepalus, Prosopis juliflora, Haplopappus sp., Acacia constricta, Condalia lycioides, Salsola kali, Erodium cicutarum, Sphaeralcea sp., Opuntia engelmanii, Celtis pallida, and Cercidium floridum. Herbarium collections indicate the following plants to be associated with Parthenice in Baja California: Jatropha cinerea, Acacia brandegeeana, Bumelia occidentalis, Lemaireocereus thurberi, Celtis pallida, Olneya sp., Cercidium sp., Lysiloma candida,

Bursera microphylla, B. odorata, Sapium biloculare, Pachycereus pringlei, and Parkinsonia sp.

Despite the fact that Parthenice possesses no apparent morphological adaptations for desert environments the genus appears to prefer hot, dry, southern slopes with few trees. Figure 3A shows P. mollis near Tubac, Arizona in such a habitat. The writer walked much of the length of Alamo Canyon in the Ajo Mountains and observed hundreds of seedlings of P. mollis on the south-facing slope of the canyon. Not a single seedling was to be found on the north slope. Populations have also been observed growing among boulders where catchment water is available. Soil is usually damp in the areas near such boulders. Figure 3B is a photograph of P. mollis among boulders along the Redington Pass road near Tucson, Arizona.

The habitat of Parthenice in southern Sonora and northern Sinaloa is not like that in Arizona and northern Sonora. The plant occupies disturbed sites along Highway 15 such as roadcuts or milpas. Exposure of such sites is not consistently southern but rather Parthenice is found in those roadside areas which offer good runoff (Figure 4). In Baja California P. mollis has been reported to be found along the margins of dry lake beds as well as along the margins of moist arroyos.

Soil samples from two localities in the Tucson area were analyzed by the Soils and Water Testing Laboratory at The University of Arizona for potassium and nitrate content, water holding capacity, calcium carbonate content, and pH. The results of these analyses are recorded in Table 1. It is interesting to note that the potassium and nitrate content of the soil is nearly ten times that of a "normal desert soil."

A

B

Figure 3. Habitat Photographs of P. mollis in Arizona

A. Southern slope 1 mile south of Tubac, Arizona. B. P. mollis among boulders near Redington Road, Tucson, Arizona.

A

B

Figure 4. Habitat of P. mollis in Mexico

A. South of Hermosillo along roadside. B. Near Culiacan. East facing roadcut.

TABLE 1

Analysis of Soil Samples from Two Habitats of P. mollis

	Pontatoc Wash	Cañon del Oro
ppm NO_3	100	112
ppm PO_4	59	71
% $CaCO_3$	1.91	0.83
ppm soluable salts	1505	1141
pH	7.2	7.2
field capacity 1/3 atm	11.9%	11.3%

ECOLOGICAL BEHAVIOR (PHENOLOGY)

To observe the ecological behavior of Parthenice many trips were made to various localities in the Tucson area over a period of four years. Populations were studied at Cañon del Oro, Box Canyon, Pontatoc Wash, and Redington Pass because of their proximity to The University of Arizona. Seedlings from these areas as well as from Buenos Aires, Arizona were transplanted to the greenhouse for study. Plants were also grown from seed collected from these localities.

Germination of Seeds

In nature germination of seeds of Parthenice takes place primarily in February and March after winter rains. It is interesting to note that only one population of Parthenice could be found in the Tucson area in the spring of 1967 after an exceptionally dry winter season. In February of 1969 after relatively good rains as many as 22 seedlings per square decimeter were observed in the Canon del Oro area as well as in Pontatoc Wash near Tucson. It would appear that winter precipitation is a significant factor in the initiation of the life cycle of P. mollis. In south central Arizona summer precipitation occurs during July and August; occasionally Parthenice has been observed to germinate after the summer rains. Attempts to germinate seeds in the laboratory and greenhouse were successful only after a treatment of 36-48 hours of continual washing in tap water. This was conveniently done by placing the seeds in a fine-mesh sieve under a faucet and allowing the water to drip rapidly. After one week of such a regime up to 70 percent germination was obtained.

Ungerminated seeds may be forced to develop by excising the embryo from both the achene and the seed coat. The seeds must be soaked for at least 12 hours so that the embryo will be turgid enough for dissection. The separation of the embryo from the seed coat is a tedious, delicate operation because of the small size of both structures. Great care must be exercised not to injure the embryo while removing all traces of the seed coat. If a portion of the coat remains attached to the embryo, growth of that part is inhibited, and embryos of unusual shapes develop. The above data seem to indicate the presence of a water-soluble growth inhibitor in the seed coat. Common sewing needles filed to a fine point and attached to dissecting needle handles are good tools to remove the seed coat. The naked embryos should be washed in a 0.525 percent solution of sodium hypochlorite (10 percent solution of Clorox in tap water) and transferred to a petri dish lined with moist filter paper. In excised embryos the development of the radicle is rapid as is the appearance of chlorophyll in the cotyledons. The root may develop to a centimeter long in 12 hours, and chlorophyll may appear in 6 to 8 hours.

Germination in intact seeds is detected by the emergence of the radicle at the base of the achene where its growth splits the achene lengthwise along several sutures. When the young root reaches about a centimeter in length, growth of the cotyledons causes the shedding of the ovary wall and seed coat. Subsequently, the cotyledons develop chlorophyll within a few hours. Within three days the cotyledons develop short petioles, and the hypocotyl elongates and elevates the cotyledons above the surface of the soil. When a germinating seed is about four days old the first foliage leaves are visible. The development of the

shoot axis is rapid, and the cotyledons wither and die. Though the cotyledons are short lived, the buds in their axils may become active after the plant is several decimeters high. Here a short lateral branch is produced which bears several small leaves. A semidiagrammatic outline of the germination of P. mollis seeds is given in Figure 5.

Vegetative Growth and Flowering

In the field, seedlings develop rapidly after germination. Such development is continuous from February or March until rains cease in May or June. At this time the vegetative shoot may have grown to a height of 50 centimeters, and although internodes are very short numerous leaves are present. At this time Parthenice has a rather caespitose aspect. Figure 6 is a photograph which shows P. mollis at the onset of the summer dry season when all vegetative growth appears to cease. As temperatures rise lower leaves become wilted while younger upper leaves remain in a state of partial expansion. Figure 7 shows Parthenice near Buenos Aires, Arizona in such a condition. Parthenice may remain under a state of water stress for several weeks. During this time many of the less hardy seedlings die. With the onset of Arizona's summer rains in late July and early August vegetative growth commences again. This second period of development is characterized by a great increase in in height, the addition of many new leaves, and the production of a large, paniculate inflorescence. Flowers appear in August, and flowering may continue until December. A diagram of the phenology of Parthenice mollis is shown in Figure 8. Herbarium collections indicate that flowering occurs in February and March in Baja California. According to Hastings and Turner (1965) most of the meagre rainfall in southern

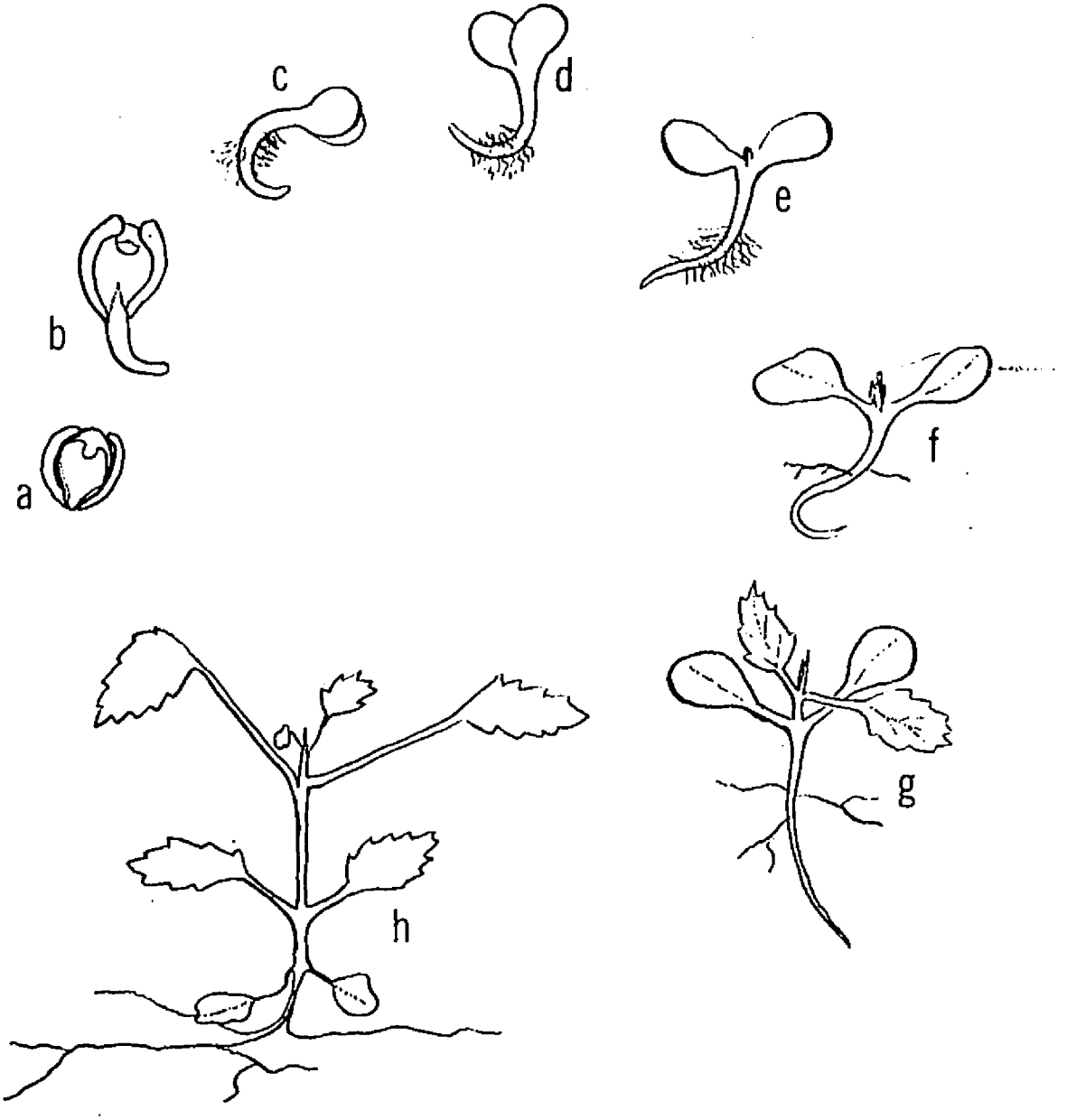


Figure 5. Semidiagrammatic Drawing of the Morphology of Germination

a. dormant achene; b. appearance of the radicle at the base of the achene; c-e. development of the cotyledons; f-g. growth of the foliage; h. seedling one week old.

Figure 6. P. mollis at the Onset of the Summer Dry Season near Tucson, Arizona

The leaves are in a state of partial expansion and vegetative growth has temporarily ceased.

Figure 7. P. mollis near Buenos Aires, Arizona

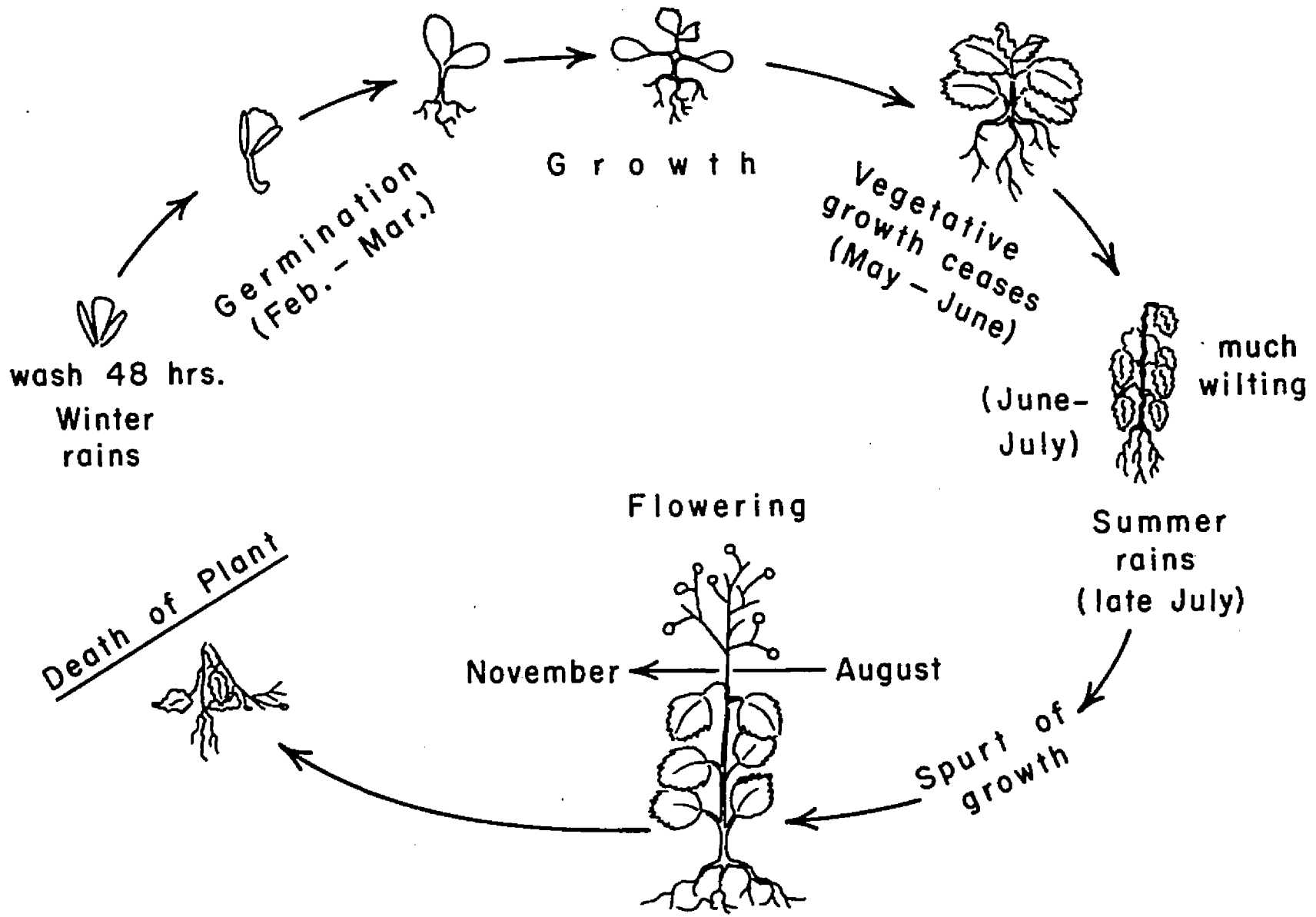


Figure 8. The Phenology of Parthenice mollis

Baja California occurs in the winter and spring with very little in summer and fall. Differences in seasonal precipitation may account for flowering-time differences. Plants grown from seed obtained in Baja California as well as Arizona may flower at any time of the year when grown under greenhouse conditions.

The behavior and appearance of Parthenice grown from seed in the greenhouse is distinctly different from that in the field. Under uniform greenhouse conditions Parthenice shows no "periodicity," flowering may take place when plants are less than 10 centimeters tall and few flowers are produced. The appearance of the plants is marked by pale instead of dark green leaves, long spindly internodes, and the production of few instead of many leaves. Seedlings transplanted from the field to the greenhouse when they are at least two months old are much more similar to field-grown plants than those grown from seed germinated in the greenhouse. Seedlings are easily and successfully transplanted because they show a remarkable ability to recover from the effects of uprooting. Such plants may be simply pulled out of the soil and tossed in a plastic sack with a little moisture. Several hours may pass before they must be planted in the greenhouse. Once in the greenhouse transplants must be well watered and kept in the shade. Under these conditions they recover with the loss of only a few lower leaves.

Summary

In the ecological behavior of Parthenice certain patterns have been described which enable this mesophytic-appearing annual to cope with the harsh environment of the Sonoran Desert. Parthenice can withstand periodic rainy seasons, it can tolerate considerable drouth, and a

chemical inhibitor is apparently present in the seed coat which may detain germination until enough rain has fallen not only to insure germination but also to insure the establishment of seedlings.

GROSS MORPHOLOGY

Parthenice mollis is an erect, aromatic, grayish-green, annual herb, generally reaching heights of 1 to 1.5 meters. A few individuals have been observed to reach a height of two meters under exceptionally good moisture conditions. The stem, which may reach a diameter of several centimeters, is typically unbranched except in the inflorescence. Here branching is often profuse. The root is of the taproot type described by Cannon (1949). It is like his types II or IV in which laterals are acropetal in development; the oldest are nearest the surface of the soil. The root of P. mollis is stout and woody near the soil surface but it is quite slender at depths of 20 centimeters. Cannon characterizes such a root as a mesophytic type.

Cotyledons

The cotyledons are very small (scarcely one square millimeter in surface area), glabrous, ovoid structures, with entire margins as they emerge from the seed. At maturity they are petiolate, the blade is about three millimeters in length, and it possesses a slight midrib.

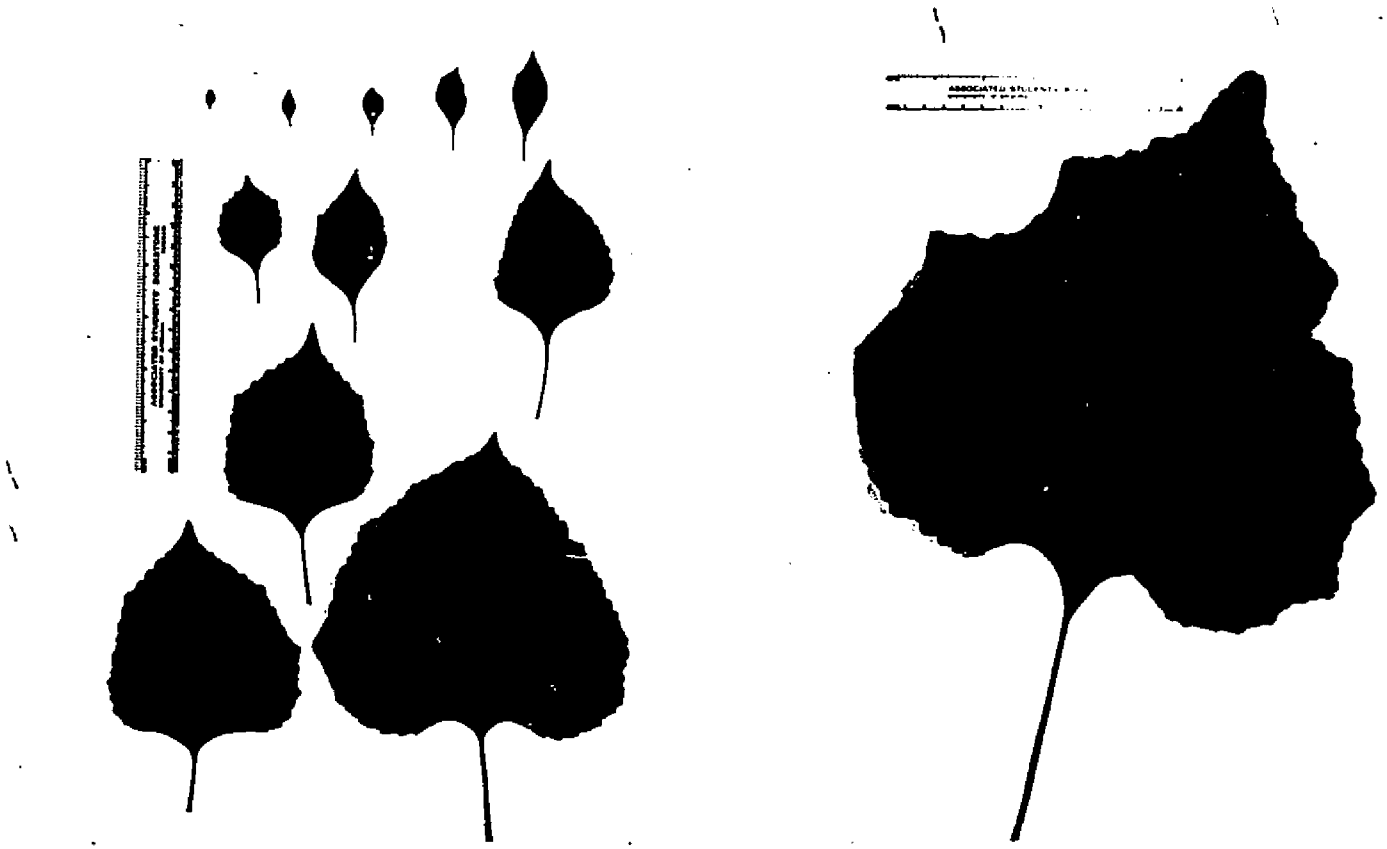
Foliage Leaves

True foliage leaves are simple, glandular, and felty-tomentose. When crushed slightly they emit a curious aromatic odor that reminds one of the odor of either geraniums or ragweeds. This strong odor may be responsible for the fact that Parthenice is not relished by livestock.

The shape of the leaves is highly variable on any one plant. Figure 9 shows a series of leaves collected from one individual. Leaves tend to fall into two classes: those found below the inflorescence, and those found associated with the inflorescence. The type above the inflorescence is coarsely toothed to entire and may vary in length from one to seven centimeters. The blades of such leaves are lance-ovate to ovate and are acute at both the base and the apex. Furthermore, the venation is distinctly pinnate. The leaf below the inflorescence is typically much larger than the one above. This is especially true of the lower stem leaves whose blades may be as long as 30 centimeters and whose petioles may reach a length of 15 centimeters. Figure 9B is such a leaf. Lower stem leaves also differ from upper ones in that they are distinctly cordate at the base and they may have a sinus as much as three centimeters deep. The lamina at the base of the sinus may be decurrent on the petiole for several centimeters.

The margin of such leaves is always coarsely crenate to coarsely toothed. The venation is palmate with the branching of the three main veins occurring well within the lamina. The main branches are very prominent on the undersurface of the blade but are slightly depressed on the upper surface.

Except for the coyledons and the first pair of foliage leaves, which are opposite, all leaves are alternate in arrangement with a phyllotaxy of 2/5. A spatial arrangement of leaves after the method of Saunders (1922) is shown in Figure 10. With such a diagram an excellent visual representation is obtained which can be useful in comparative studies.



A B

Figure 9. Variation in Size of Leaves from an Individual Plant

A. From left to right the first six leaves are from the inflorescence, the remaining five from below. B. Large lower leaf. Note that venation ranges from pinnate to palmate.

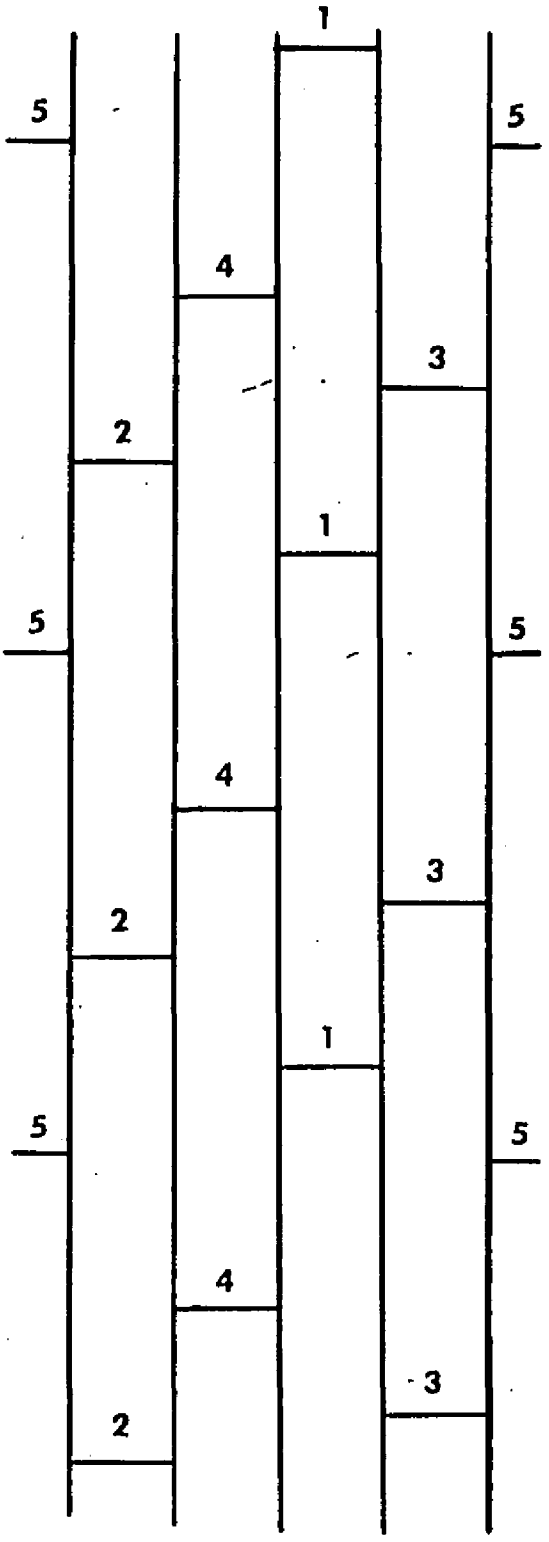


Figure 10. Graphic Representation of Phyllotaxy after the Method of Saunders (1922)

The Arrangement of Capitula

The small hemispherical capitula are clustered in tight groups of from 5 to 50 individuals which vary both in size and age. Figure 11A is a sketch of such a group. These groups are in turn disposed in large, lax panicles, a portion of which is shown in Figure 11B. Heads of the clusters are either pedunculate or sessile. The pedunculate heads, located at the tip of the clusters, mature first and nod, spilling pollen on the leaves below. Payne (1963) has stated that if the oldest head in a cluster terminates a stem or a branch upon which it is borne the head arrangement may be said to be determinate. Such is the case with Parthenice. In addition, the order of maturation of capitula is basipedal which, as Payne notes, is the case in all composites with branched inflorescences. In Parthenice the order of maturation of capitula will be substantiated by anatomical data in the present paper.

The Structure of the Capitulum

In spite of its small size (five to six millimeters in diameter), the capitulum is morphologically complex consisting of over 70 minute structures closely invested by phyllaries. The overall arrangement of structures is very similar to that of Parthenium which has been figured by Artschwager (1943). Some of the capitular differences between Parthenium and Parthenice are mentioned in the descriptions that follow.

The Phyllaries

The phyllaries are present in two distinct series (Figure 12A). The outer series consists of five, slightly overlapping, persistent, involucral leaves, which are somewhat reflexed in age. These are ovate,

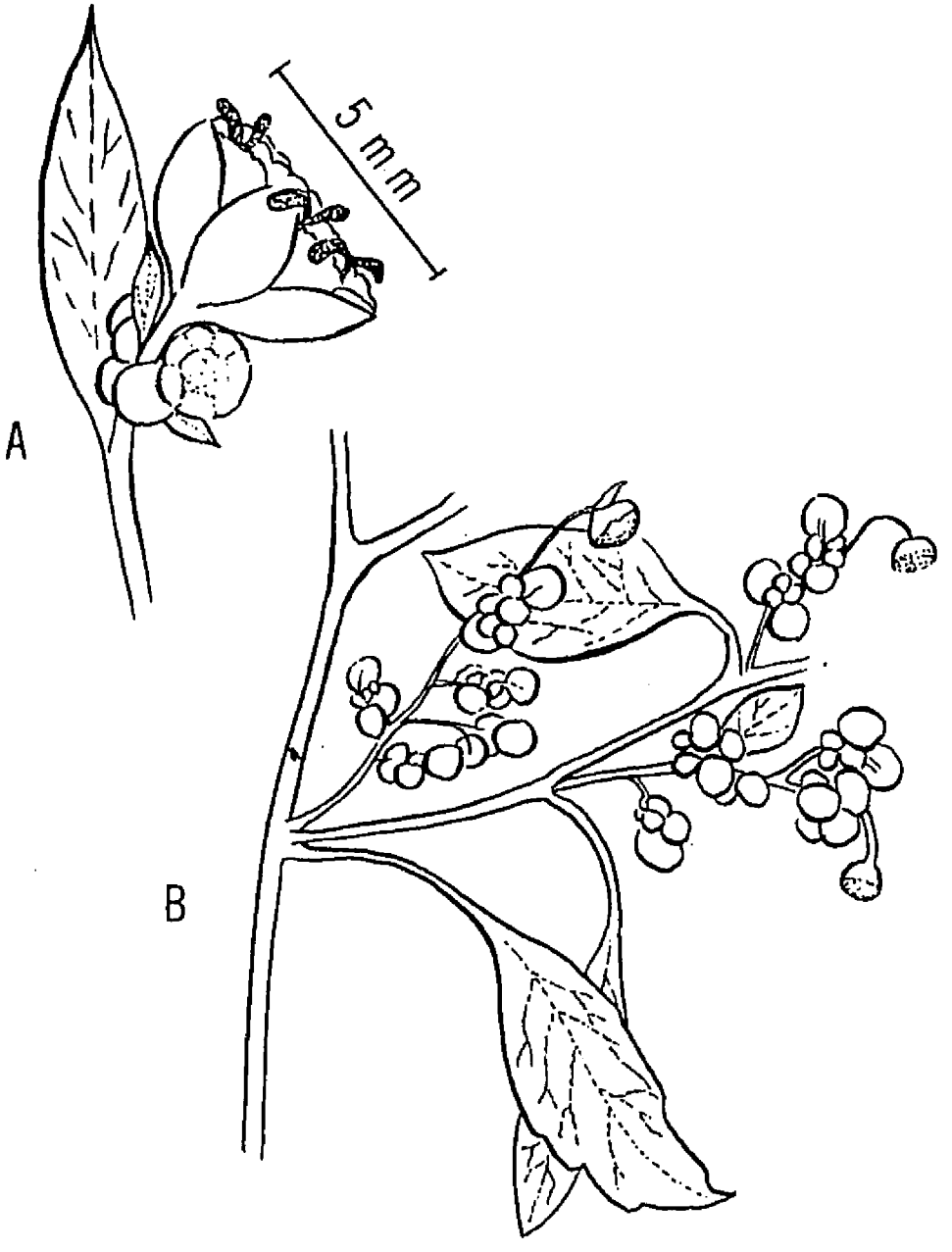


Figure 11. The Arrangement of Capitula

A. Single branch of the inflorescence showing the position of the pedunculate capitulum (X5). B. Portion of the panicle showing several branches with pedunculate capitula (X1).

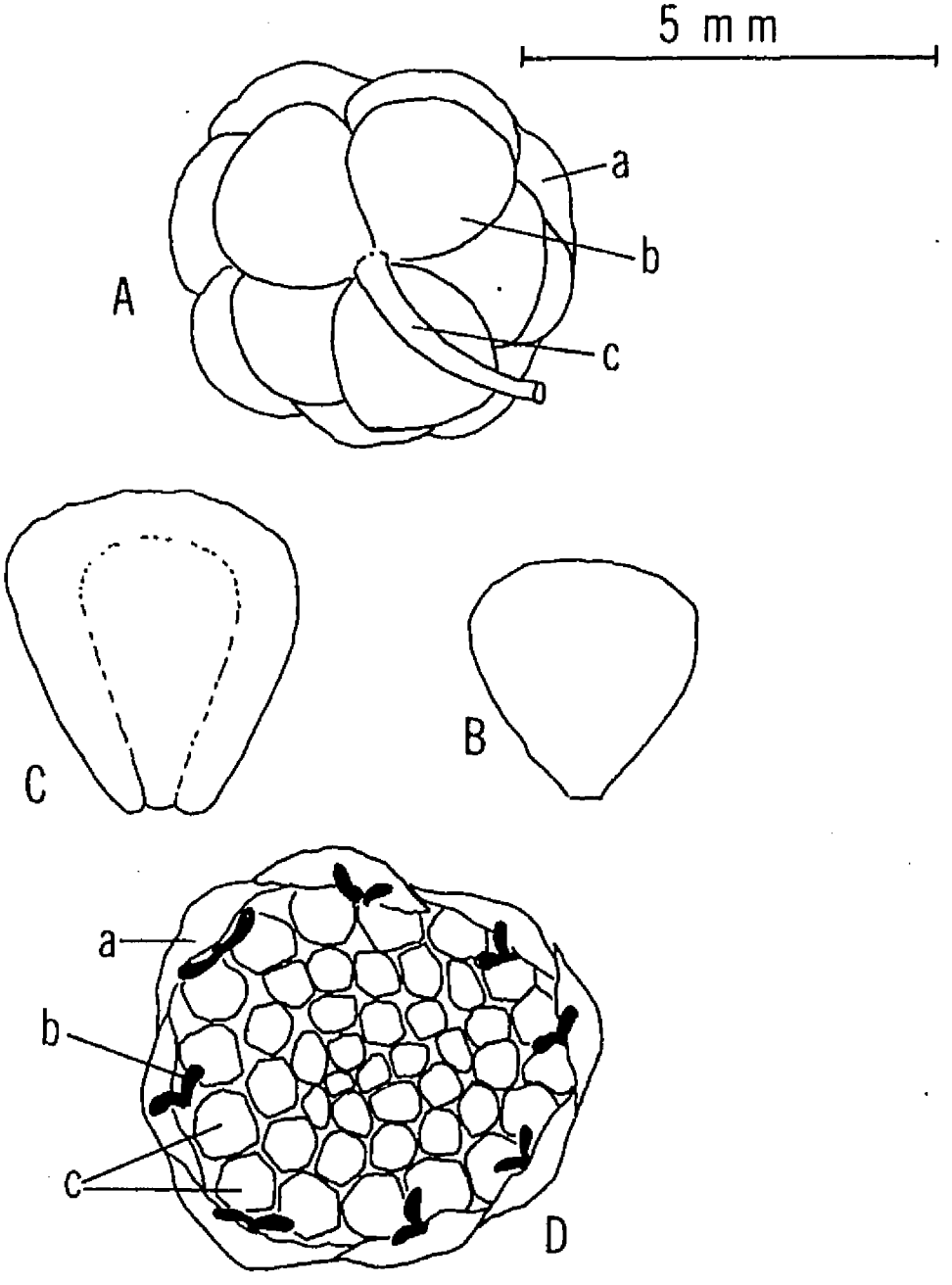


Figure 12. The External Morphology of the Capitulum

A. Basal view showing the position of the two series of phyllaries. a. inner phyllary; b. outer phyllary; c. peduncle. B. The outer phyllary. C. The inner phyllary. D. Apical view of the capitulum. a. inner phyllary; b. stigma; c. disk flowers.

herbaceous, and pubescent (Figure 12B). The inner series consists of eight, hyaline, broadly ovate to nearly round phyllaries, each of which has in its axil one pistillate ray flower (Figure 12C). Such phyllaries are conspicuously cupped to fit the shape of the achene. In Figure 12D the phyllaries enclose all but the stigma of the pistillate flower. They are deciduous with the achene, although they do not remain attached to it as in Parthenium where two disk flowers, their associated pales, a phyllary, and the pistillate flower all fall as a unit of dehiscence.

The Ray Flower

There are eight pistillate ray flowers in each capitulum (note, five in Parthenium), each of which consists of a single pistil or ovary derived from two carpels, a short style that terminates into two stigmatic lobes of equal length, and a small deciduous corolla. The corolla is definitely ligulate as well as shortly cleft in front and so minute that it can be seen only by dissecting away the phyllary which obscures it from view. The corolla has a greenish cast and is covered with curling hairs and biseriate glands. Figure 13 shows front and side views of the pistillate flower and associated structures.

The achene (ovary) when mature is a dorsoventrally flattened, obovate, tuberculate, sessile structure which is about 1.5 to 2 millimeters long and 1 millimeter wide. Adnate to the base of the achene are the two pales which originally subtended the disk flowers immediately adjacent to the achene. These two pales and the attached achene fall from the head as a unit of dispersal. Such pales differ considerably in structure and texture from those which subtend other disk flowers. Pales attached to the achene are purple mottled as well as coriaceous whereas

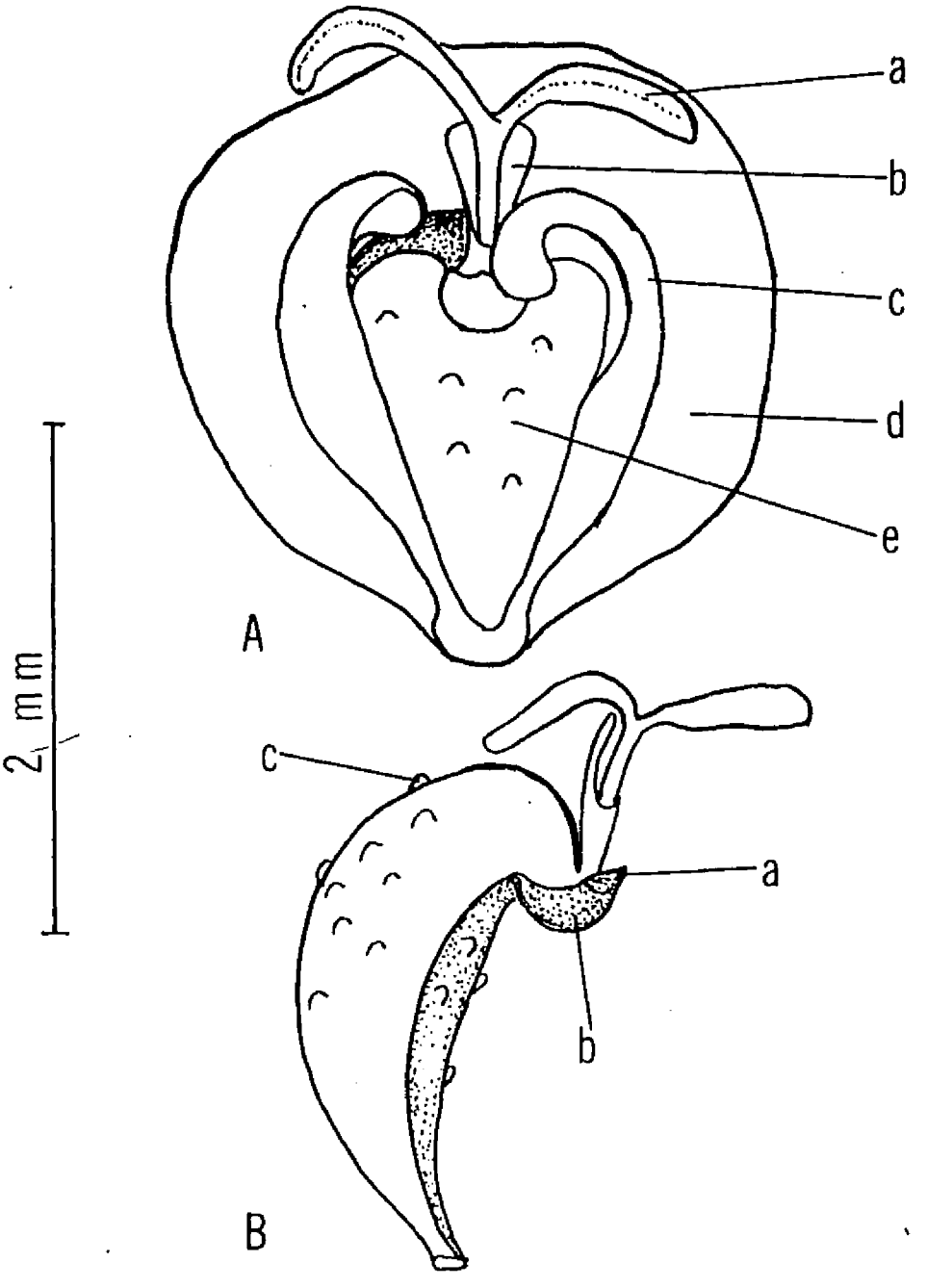


Figure 13. The Morphology of the Ray Flower

A. Ventral view showing attached pales and associated inner phyllary. a. stigma; b. corolla; c. winglike pale; d. phyllary; e. achene. B. Lateral view with pales removed. a. tooth; b. bulbous apiculation; c. tubercle.

disk pales are transparent and fragile. The pales of the achene in material from Baja California are shorter than those in Arizona, Sonora, and Sinaloa and that has prompted the description of a new variety of P. mollis, var. peninsularis, in the taxonomic section of the present paper.

At the apex of the achene just below the point of attachment of the corolla there is a peculiar bulbous structure the function of which is not known. Occasionally a minute tooth or mucro is visible at the top of the structure. This suggests that the peculiar structure may represent a rudimentary or modified pappus although pappus is generally considered to be absent in Parthenice. In Figure 13B the position of the mucro is indicated.

The Disk Flower

Thirty to forty disk flowers, each staminate with a minute, transparent, conical subtending pale, fill the remaining surface of the receptacle. The disk flower is morphologically similar to disk flowers of many other Compositae (Figure 14A). It consists of a five-toothed, actinomorphic corolla with a short tube which expands abruptly into a funnelform corolla. The outside of the corolla especially near the lobes is covered with glands and curling interlocking hairs which tend to hold the disk flowers together as they fall from the head after anthesis. The five loosely coherent stamens are adnate to the corolla by their slender filaments at a place just above the reduced ovary or pistillodium (Figure 14C). The anthers are truncate at the base and bear hollow, deltoid, terminal appendages. The stigma is of the brush type and is unlobed (Figure 14B). It is attached directly to the top of the pistillodium and is deciduous with the corolla. The style is shorter than the stamens at first. As

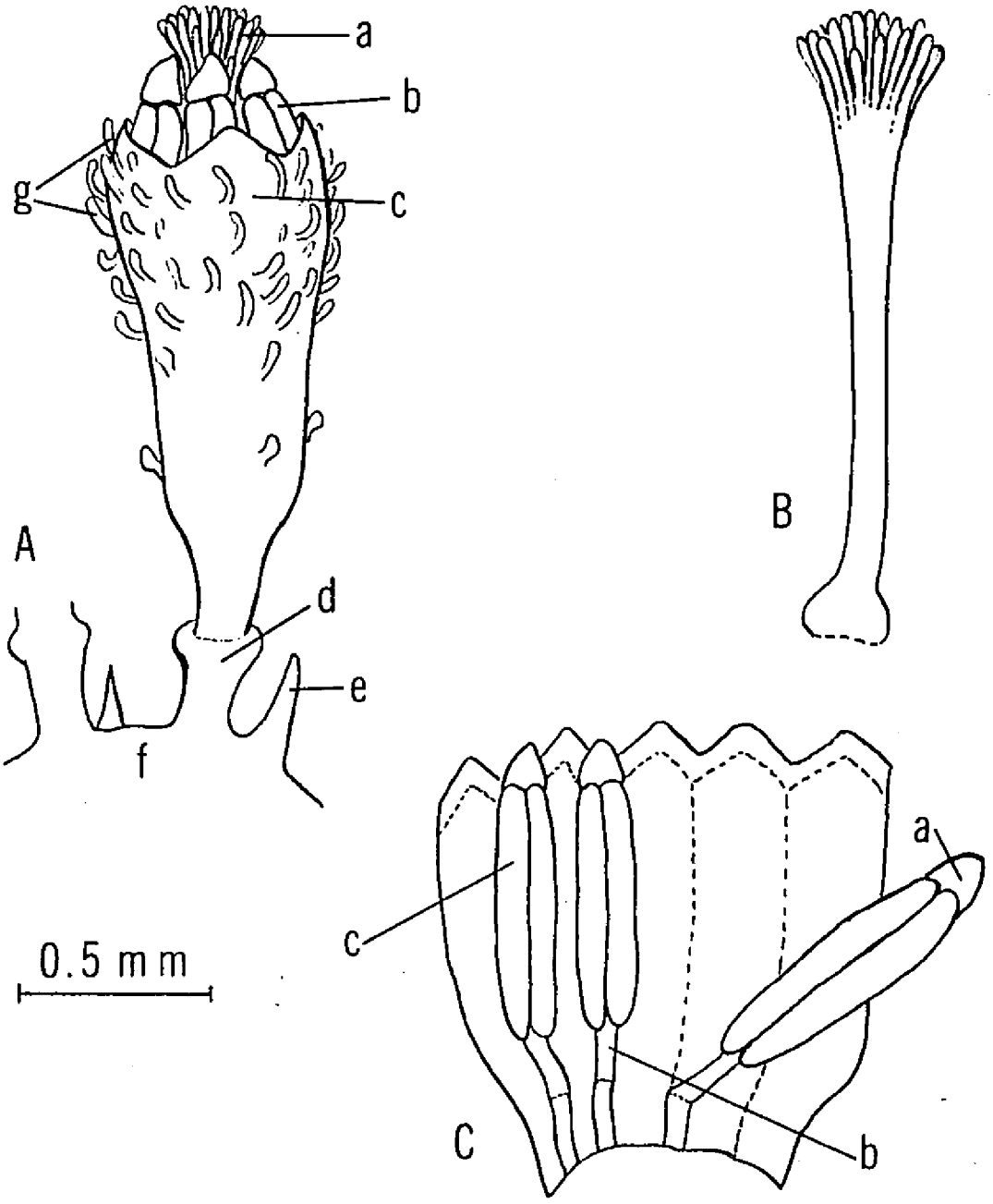


Figure 14. The Morphology of the Disk Flower

A. Disk flower and associated conical pale. a. stigma; b. stamen; c. corolla; d. pedicel; e. pale; f. receptacle; g. trichomes. B. Stigma. C. Portion of corolla showing attachment of stamens. a. deltoid appendage; b. filament; c. anther.

the flower matures the style elongates pushing the pollen up and out of the anthers to the top of the corolla. The abundant pollen is yellowish, globose, tricolpate, and echinate.

Each disk flower, unlike the ray flower, is elevated above the surface of the compound receptacle by a short pedicel which remains attached to the receptacle after the abcission of the flower. In Parthenium disarticulation occurs on the receptacle.

As in Parthenium, when the achenes mature the entire head disintegrates, and the seeds are dispersed as a consequence. In Parthenice the reflexed outer phyllaries, the pedicels of the disk flowers and the pales of the disk flowers remain attached to the stalk of the inflorescence while in Parthenium only the phyllaries and the pales remain attached. Rollins (1950) states that the sterile disk florets are shed as a unit in Parthenium and individually in Parthenice. The present writer has not observed this difference. Due to the presence of glands and curling interlocking hairs on the corolla, disk flowers tend to fall as a unit in Parthenice as in Parthenium.

VEGETATIVE ANATOMY

Materials for anatomical studies were obtained from various populations of Parthenice in the vicinity of Tucson, Arizona as well as from San Javier, Baja California. Formalin-Aceto-Alcohol made with 50 percent ethyl alcohol was used for killing and fixing. Staining was accomplished by the usual technique with safranin and fast green. Hand sections of living material were made to determine the presence and position of the starch sheath with iodine. Maceration of the xylem was carried out satisfactorily in Jeffery's solution, a mixture of equal parts of 10 percent chromic acid and 10 percent nitric acid. Safranin was used to stain the xylem. Leaves and peels of stem epidermis were cleared according to the method of Foster (1953) in which clearing is achieved by first boiling the material in alcohol and then treating it with sodium hydroxide and chloral hydrate. Such material was stained in a 1 percent solution of safranin "O" in equal volumes of absolute alcohol and xylene.

The Cotyledon

The mature cotyledon possesses a distinct epidermis in which is found a few stomata on both the abaxial and adaxial surfaces. The mesophyll exhibits a modest amount of differentiation between palisade and spongy parenchyma. The one palisade layer is loosely packed and abuts upon several spongy layers. Both cell types possess chloroplasts when the cotyledon is mature. The blade is vasculated by a midrib and two laterals which enter from the short petiole and branch to give a

reticulate pattern. Secretory canals are absent from both the blade and the petiole.

The Foliage Leaf

Lamina. The epidermal system consists of an abaxial (lower) and an adaxial (upper) surface densely covered with glandular and non-glandular trichomes and interrupted by stomata of the anomocytic type (that is, no special subsidiary cells) (Figure 15). Typical epidermal cells in the areole between the veinlets have undulate cell walls when viewed from the surface of the leaf. Such cells vary from 20 to 30 microns in width and possess no chloroplasts. Epidermal cells along veins are elongate parallel with the vein.

Although there are no specialized subsidiary cells present around the guard cells there are, however, no more than five cells in contact with their edges. Most often there are four adjacent cells arranged so that there is one cell on each end and one cell on each side of the stomatal apparatus (Figure 15B). The guard cells possess chloroplasts, a nucleus, and are about 25 microns in length. The shape of the stomatal apparatus changes considerably with changes in turgor. When the stoma is open the guard cells are broadly ovate in outline; however, when the stoma is closed the guard cells are elliptical in outline. The walls of the guard cells are somewhat thickened in the region adjacent to the stoma.

Beneath the stoma of both the upper and lower surfaces there are conspicuous substomatal chambers. The substomatal chamber associated with the adaxial epidermis is longer than that of the abaxial epidermis. It extends from the stoma through the palisade layer to the

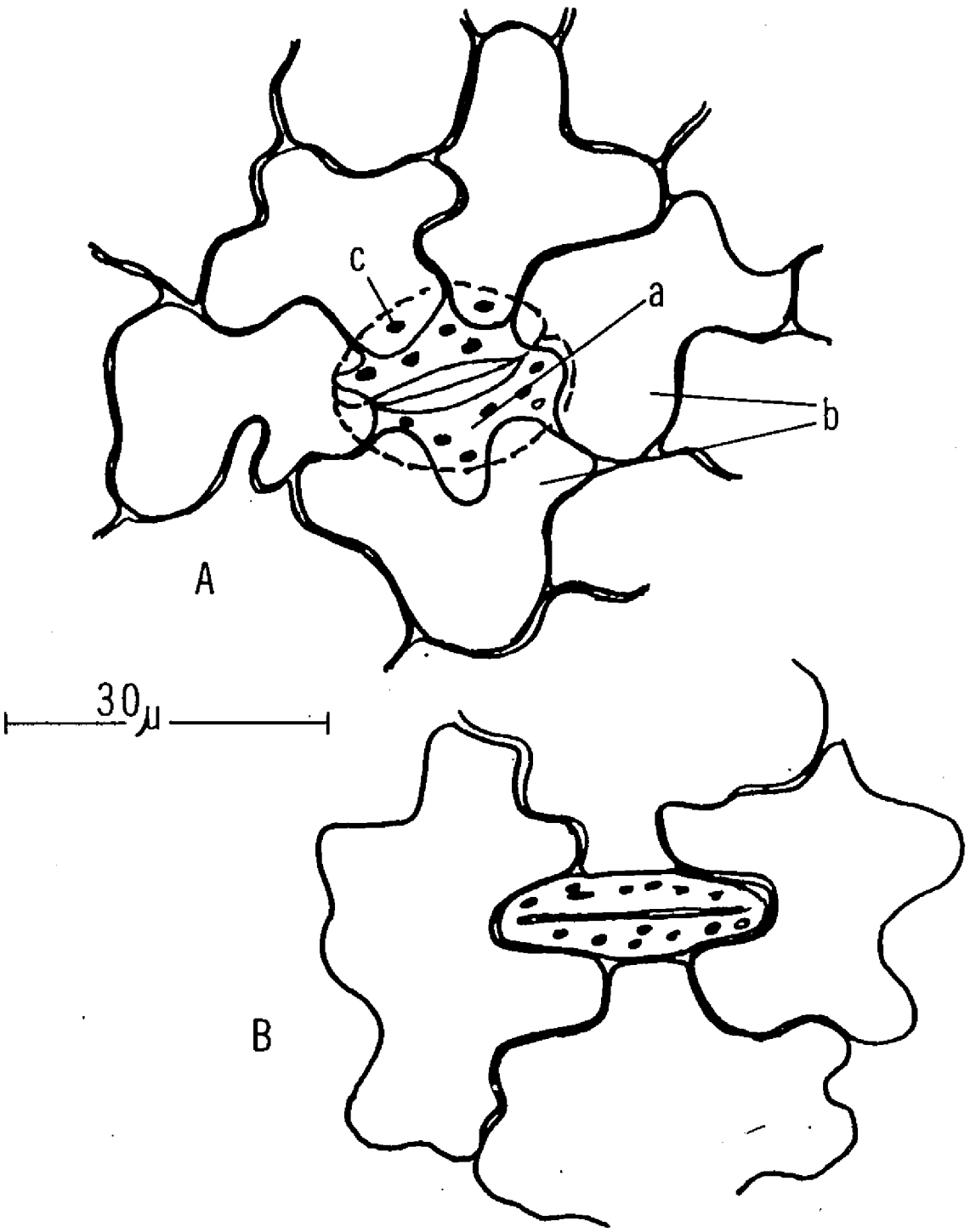


Figure 15. Stomata of the Foliage Leaf

A. Stoma open (internal view). a. guard cell; b. adjacent cells; c. chloroplast. B. Stoma closed (external view). Note the arrangement of adjacent cells.

spongy layer. The substomatal chamber of the abaxial epidermis is relatively shallow, extending only a short way into the spongy layer.(Figure 16A). The abaxial epidermis has about 100 stomata per square millimeter while the adaxial surface has only 50 stomata per square millimeter. On both surfaces the stomata are slightly elevated above the other epidermal cells (Figure 16B); also they are evenly spaced, and there are no concentrations of stomata in special areas.

The mesophyll internal to the epidermis is a well-differentiated tissue, characterized by distinct palisade and spongy layers, similar in cross section to those seen in many typical mesophytic leaves. The two-storied palisade layer is adjacent to the adaxial epidermis. The layer immediately adjacent to the epidermis is composed of elongate palisade cells which measure 60 by 15 microns in a cross-sectional view of the lamina. Chloroplasts are present in the cytoplasm adjacent to the cell wall. The lower layer of palisade differs only in the length of the cells (about 30 microns). The lower palisade cells are in contact with the spongy parenchyma. The spongy layer is several cells deep and consists of the usual polymorphic parenchyma with chloroplasts. Conspicuous intercellular spaces exist between spongy cells whereas the palisade parenchyma are closely packed.

Veins of several distinct sizes are present in the vascular system. The largest veins, which branch at the base of the blade and extend toward the margins, occur in conspicuous ribs on the underside of the leaf and are not directly associated with the mesophyll proper. Such ribs consist of two or three layers of collenchyma near the epidermis internal to which is found cortical-type layers with their associated

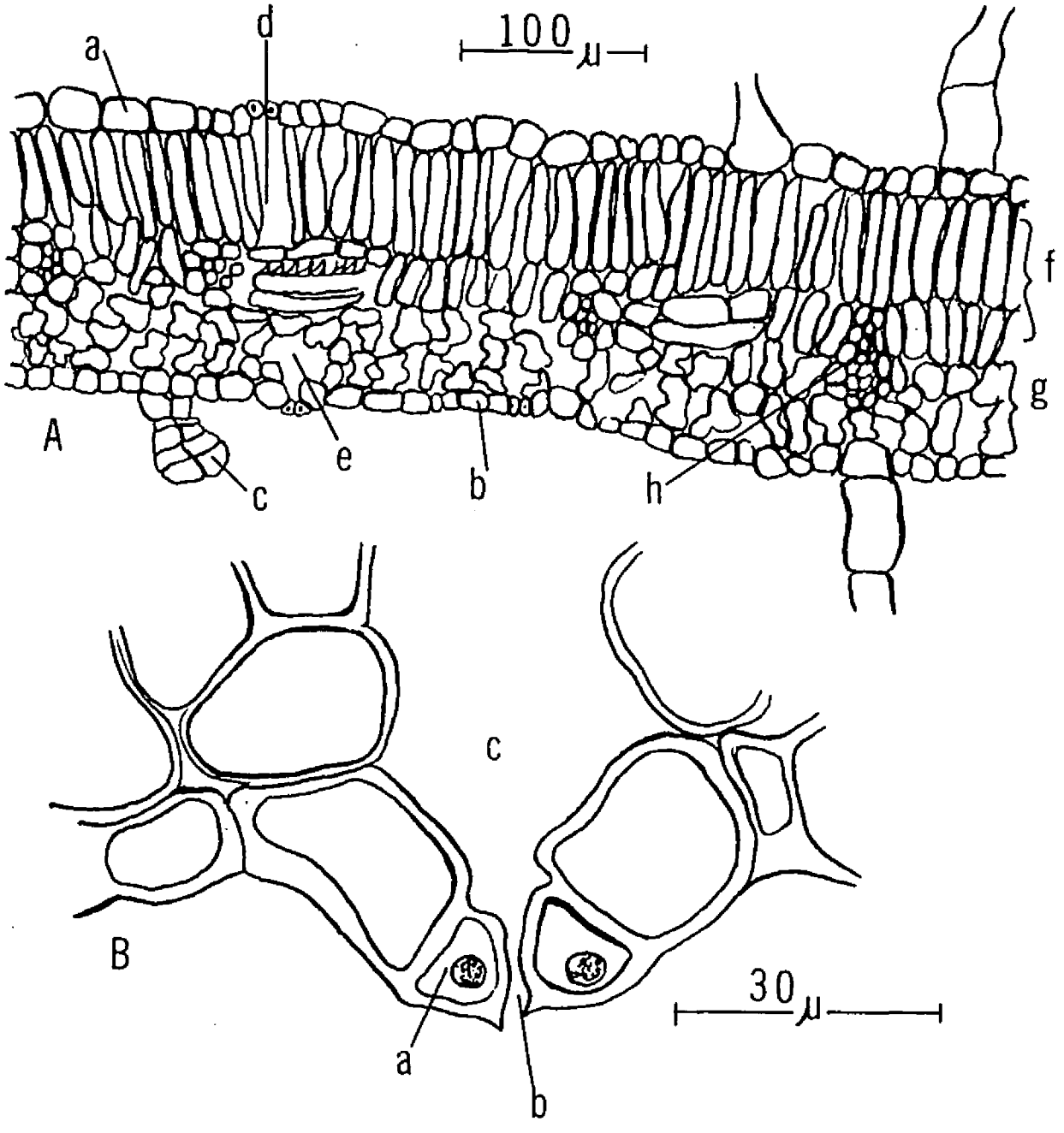


Figure 16. Structure of the Stomatal Apparatus as Seen in the Cross Section of the Leaf

A. Cross section of the lamina. a. upper epidermis; b. lower epidermis; c. glandular trichome; d. substomatal chamber in the palisade parenchyma; e. substomatal chamber in the spongy parenchyma; f. palisade parenchyma; g. spongy parenchyma; h. vascular bundle. B. Enlarged view of a single stoma. Note that the guard cells are slightly elevated from the surface of the lamina. a. guard cell; b. stoma; c. substomatal chamber.

vascular bundles and secretory canals. A large rib may have as many as five vascular bundles, each with one or more secretory canals associated with the phloem (Figures 17 and 18A). The smaller veins, unlike the veins of the ribs, occur in close association with the palisade layer of the mesophyll. These veins traverse the mesophyll at the level where the lower palisade layer abuts upon the spongy layer. Three main sizes of veins are present in the mesophyll. The largest of these consists of over 15 phloem elements and several xylem elements. The bundle sheath possesses bundle-sheath extensions which reach both the upper and lower epidermis. Such a bundle sheath extension is capped by parenchyma and collenchyma so as to form a small rib on the lower surface of the leaf. Medium-sized bundles, which consist of four or five phloem elements and two or three xylem elements, have bundle-sheath extensions which reach only the abaxial epidermis. The smallest veins, which consist of only a very few elements of xylem and phloem, have only a bundle sheath and no extensions. Unlike the vascular bundles of the large ribs, no secretory canals are present in the veins associated with the mesophyll proper.

Areoles are irregular in shape and vary from 0.5 millimeters to 1.0 millimeters in width. There is no definite number of free vein endings per areole, and anywhere from two to seven were observed. In toothed leaves at the apex of each tooth several veins appear to converge into a mass of peculiar sclerenchyma. Figure 19 shows line drawings made from leaves of Parthenice cleared by the method of Foster (1953).

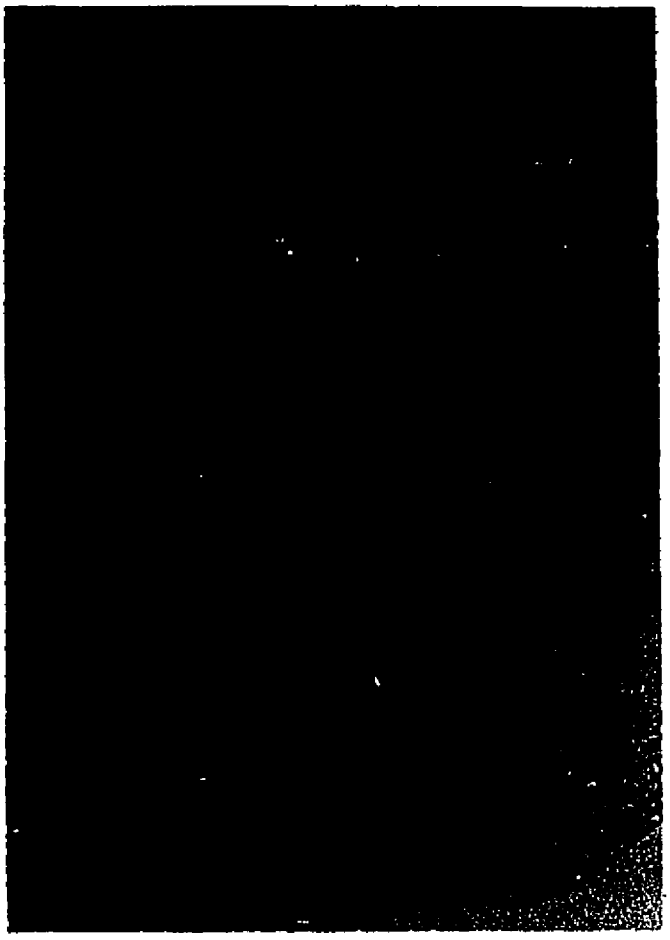


Figure 17. Cross Section Through a Major Rib of the Lamina

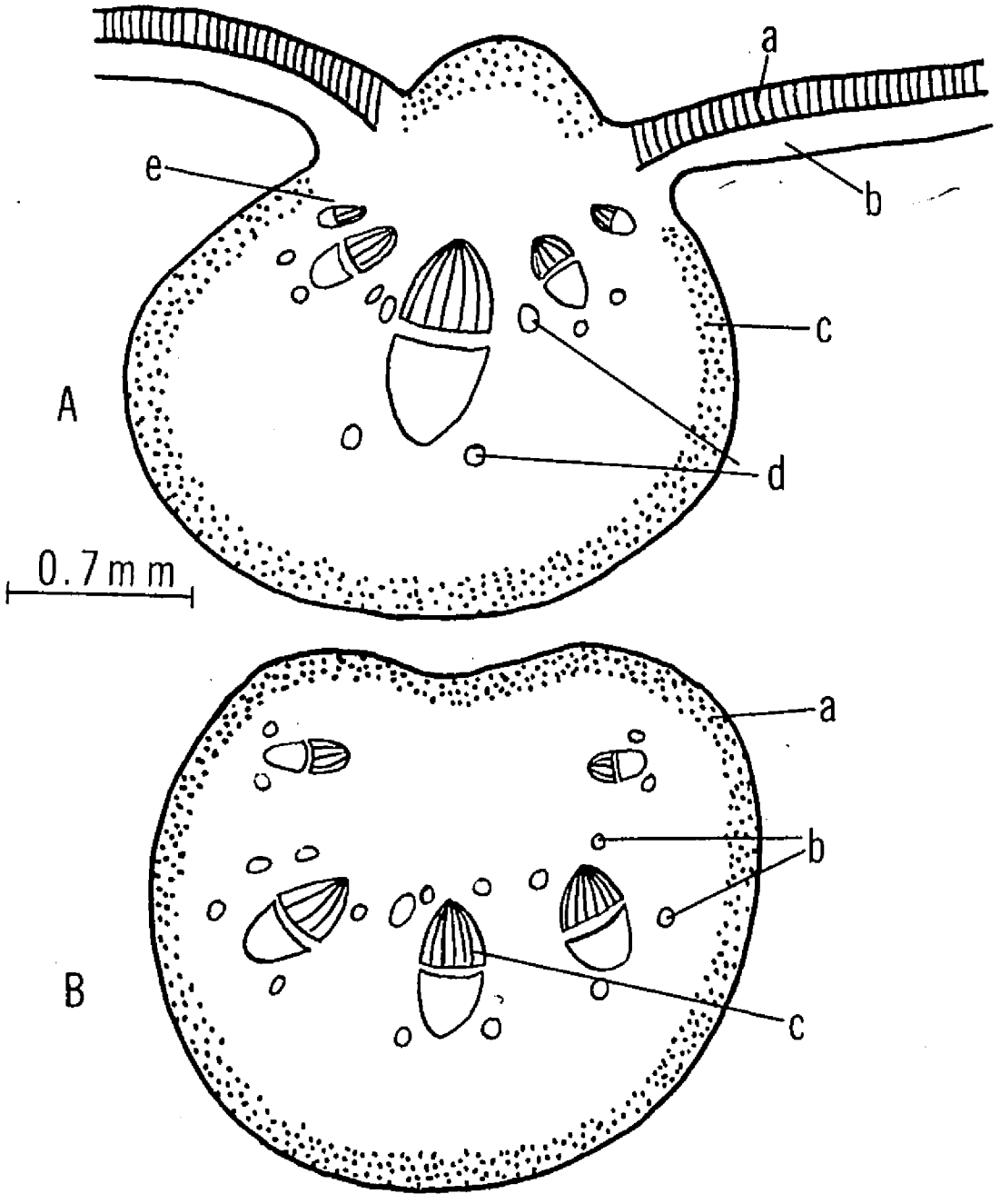


Figure 18. Diagram of the Structure of the Laminal Rib and the Petiole

A. The laminal rib. a. palisade parenchyma; b. spongy prenchyma; c. collenchyma; d. secretory canals; e. vascular bundle. B. The petiole at a point distal to the lamina. a. collenchyma; b. secretory canals; c. vascular bundle.

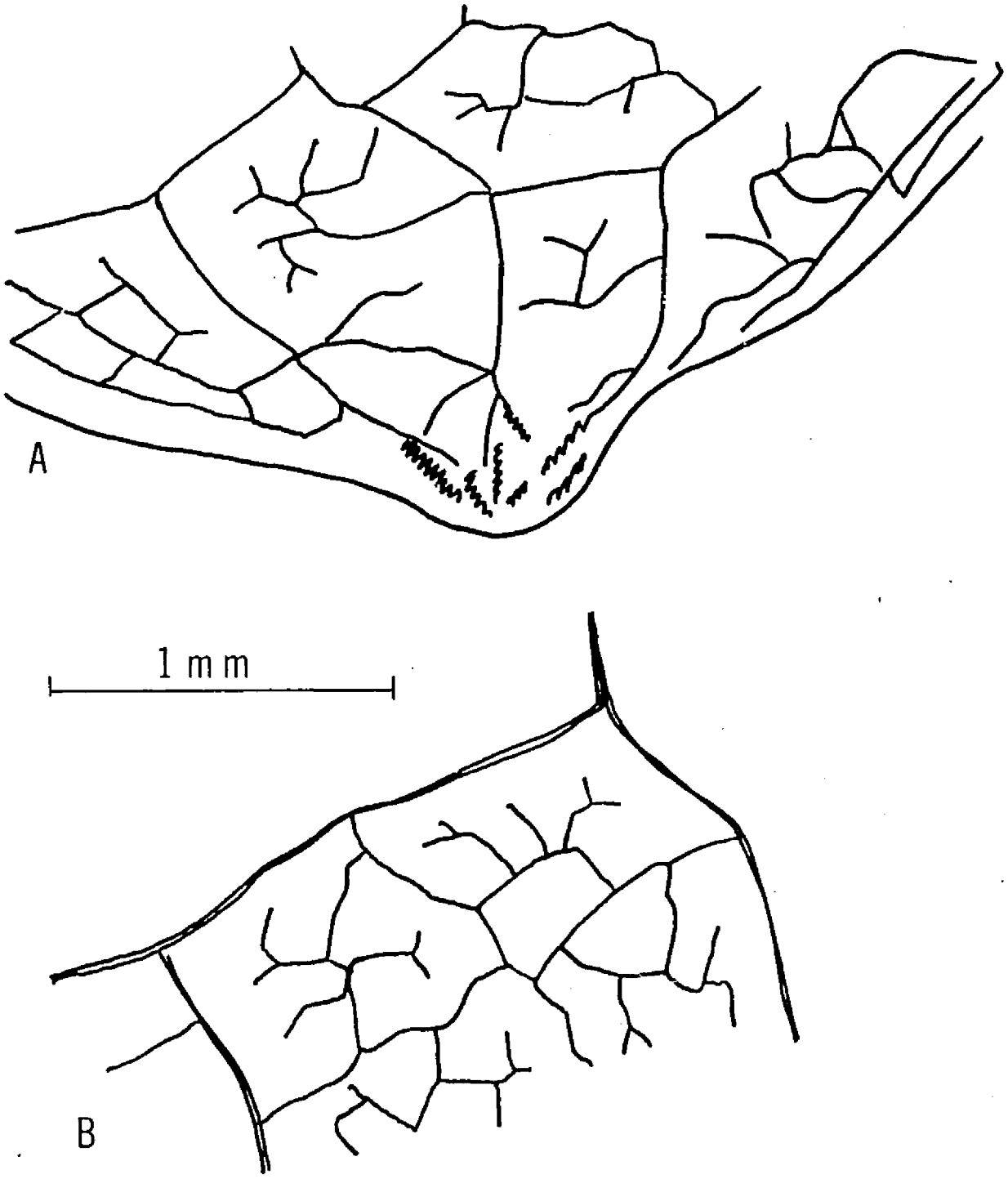


Figure 19. Patterns of Vasculation in Leaves Cleared in Chloral Hydrate

A. Vascular pattern near tooth. B. Central portion of lamina near juncture of two large veins.

Petiole. The tissues of the petiole are comparable to the primary tissues of the stem and to the ribs of the lamina (Figures 20 and 18B). Glandular and nonglandular trichomes are present as well as stomata. The stomata are more nearly like those of the stem than those of the leaf in that they are surrounded by epidermal cells which do not have undulate cell walls.

The ground tissue just under the epidermis is composed of several layers of collenchyma while typical parenchyma containing chloroplasts are found toward the inside of the petiole. Such parenchymatous tissue possesses intercellular spaces. Secretory canals similar to those found in the stem are found in the petiole near the larger vascular bundles on both the abaxial and adaxial sides. A starch sheath was not detectable following staining with iodine.

The vascular bundles are arranged in a multistranded arc which is open toward the adaxial side of the petiole. In the petiole, distal to the lamina, five vascular bundles are present. This number increases as the lamina is approached giving rise to the vasculature of the leaf blade.

The Stem

The anatomy of the stem is typical of many herbaceous dicots (Figures 21 and 22) (see Esau, 1960, pp. 203-237). In the epidermis, the ground mass of tissue consists of a single layer of epidermal cells proper, which are the least specialized members of the system and contain no chloroplasts. Dispersed among these cells are the guard cells of the stomatal apparatus and two types of trichomes. The mature epidermal cells are slightly wider than deep (14 X 10 microns) and are elongate parallel to the stem axis. Although their average length is 40 to 50

Figure 20. Cross Section of the Petiole at a Point Distal to the Lamina

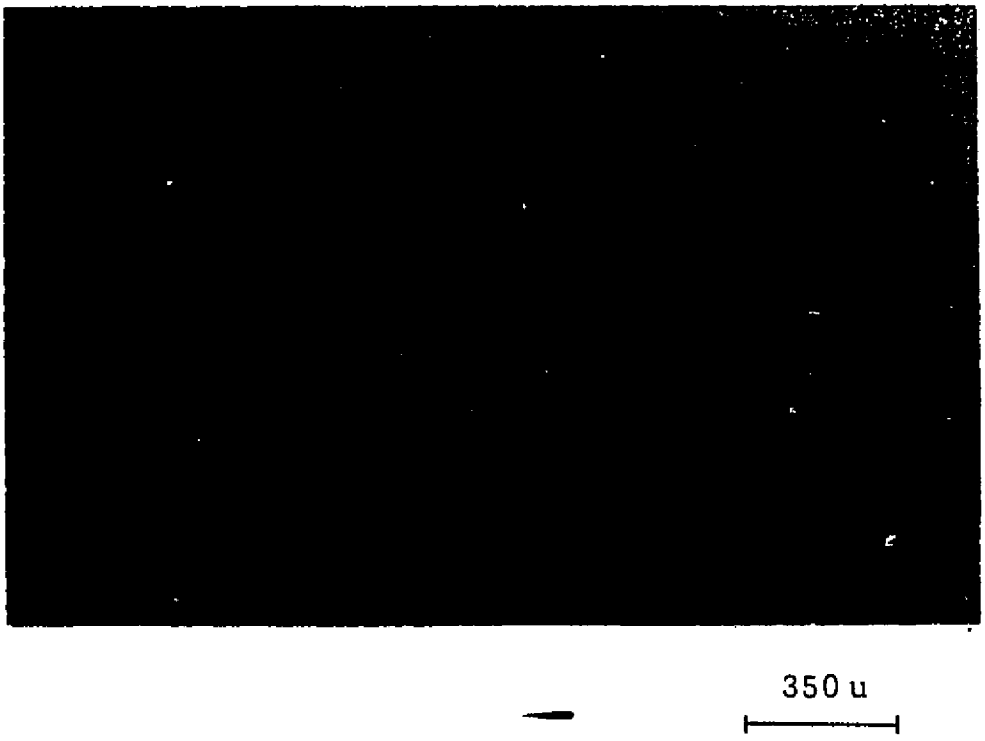


Figure 21. Portion of the Stem Showing Several Vascular Bundles

Note the presence of secretory canals near the largest bundle. An elevated stomatal apparatus is visible in the lower right hand corner.

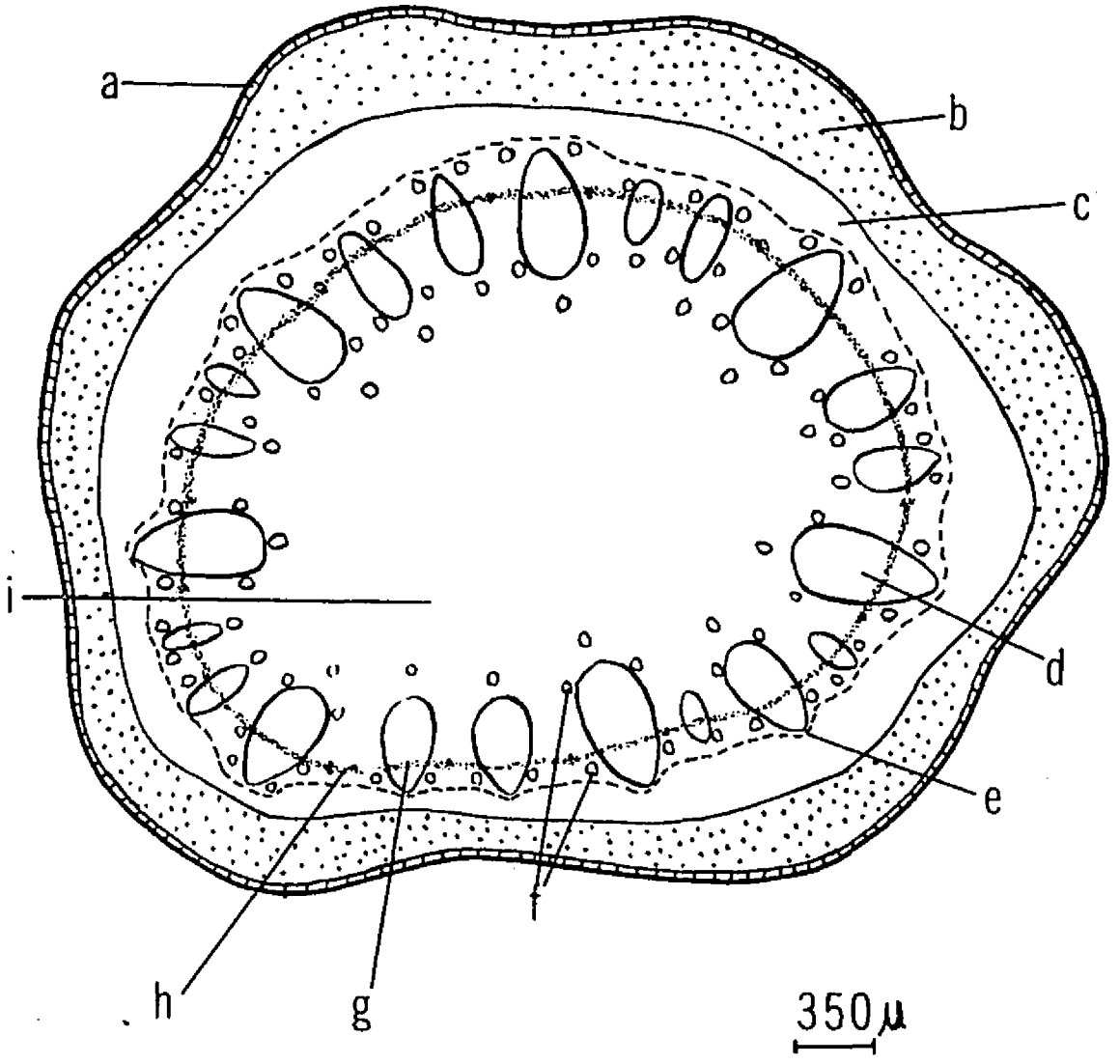
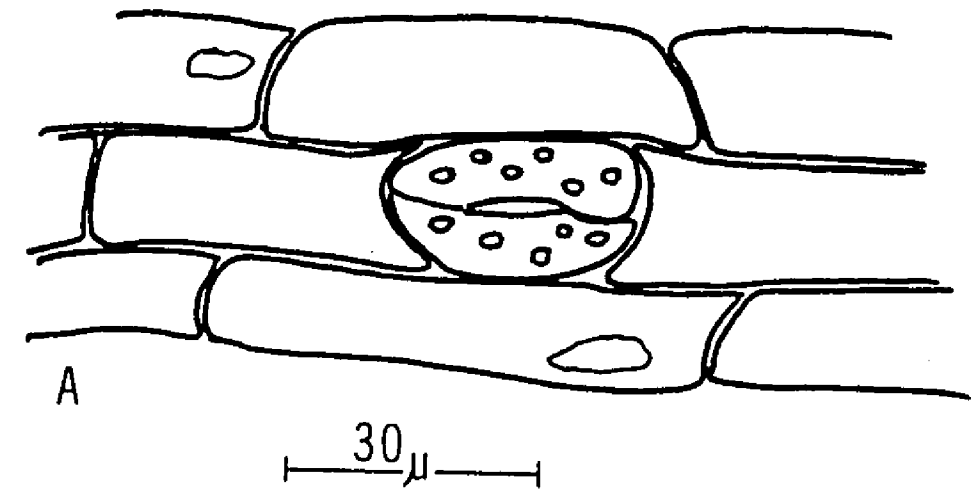


Figure 22. Diagrammatic Interpretation of the Structure of the Stem

a. epidermis; b. collenchyma; c. cortical parenchyma; d. vascular bundle; e. starch sheath; f. secretory canals; g. fascicular cambium; h. interfascicular cambrium; i. pith.

microns, lengths of 135 microns have been observed by the author in greenhouse-grown material. The outer wall of epidermal cells, thicker than the inner wall, is covered by a thin cuticle. As the stem matures the epidermis may appear multiple in prepared sections. This is due to the structure of the sub-epidermal collenchyma whose cells are similar in size and shape to epidermal cells. The original epidermis remains intact even on very old stems in which considerable secondary growth has occurred. Repeated anticlinal divisions in the epidermal tissue give rise to the increase in tissue which covers the stem in age.

Two types of stomata are present: one which occurs at the same level as other epidermal cells and one which occurs at the apex of a chimneylike bump (Figure 23, A and B). The first consists of two chloroplast-bearing guard cells, each of which is about 15 microns wide and 30 microns long. Elongate epidermal cells surround the stomatal apparatus much as in the petiole of the leaf. Beneath the guard cells there is a small substomatal chamber. Loosely organized parenchyma surrounds the chamber and extends into the collenchyma to the cortical parenchyma. The elevated stomatal apparatus is a most curious structure. With the aid of a dissecting microscope at a magnification of 40X it appears as a small mound or pimple of tissue capped by a brownish exudate. Figure 24A is a photomicrograph of the structure as seen when cleared by chloral hydrate and stained with safranin. Such structures are rather irregularly and distantly spaced from one another. The anatomy of this peculiar structure is easily seen in a cross section of the stem (Figure 24B). It consists of a hollow cylinder of cells elevated above the other epidermal cells some 70 to 100 microns (about the same



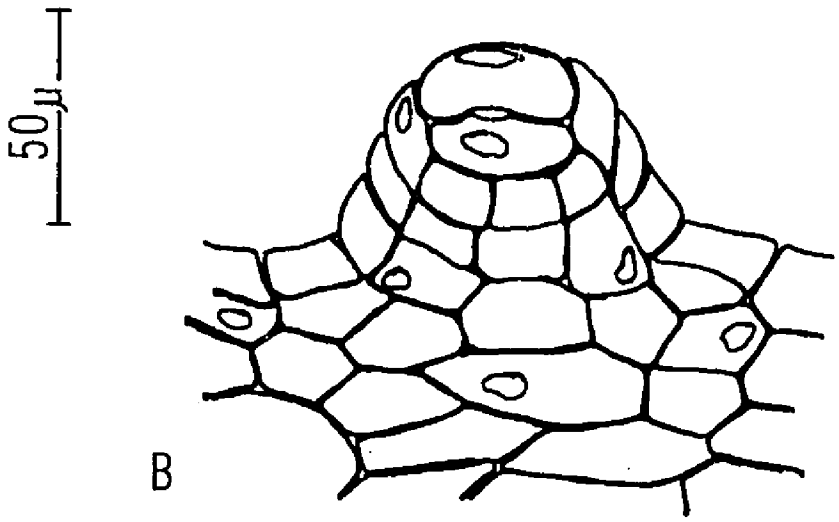
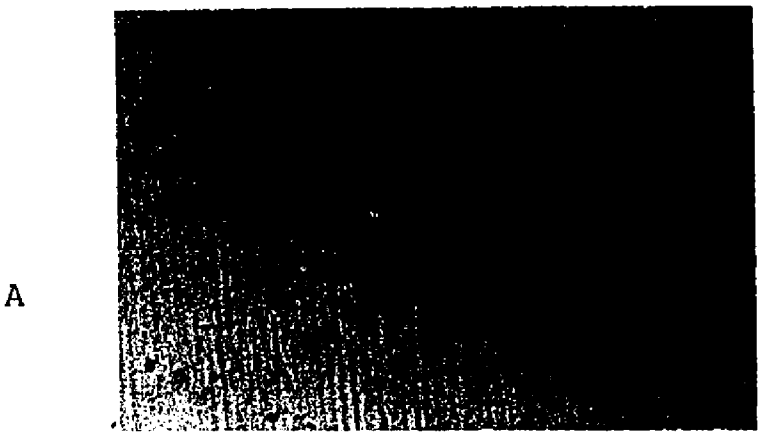


Figure 23. Types of Stem Stomata

A. "Normal" stoma and associated epidermal cells. B. Elevated stomatal apparatus.



A

50 u

B

50 u

Figure 24. The Elevated Stomatal Apparatus

A. Surface view of the stoma seen in stem epidermis cleared with chloral hydrate and stained with safranin. B. Longisection as seen in the cross section of the stem.

height as a young glandular trichome). At the apex of the cylinder there are two kidney-shaped guard cells which form a stomatal opening. These cells appear in every way to be like the "normal" guard cells of the stem and leaf. The cylinder of cells forms a porelike entrance to a shallow sub-substomatal chamber. The chamber is bound by loosely organized parenchyma like that which is found around other substomatal chambers of the stem. Similar structures have been described for the Burseraceae (Santiria mollis) by Solereder (1908, p. 190) and the Malvaceae (Hibiscus octifolius) by Linsbauer (1930, p. 215). Solereder has interpreted the structure to be an adaptive feature of plants found in moist habitats. Linsbauer refers to the structure as an Intumescenz. An intumescence is a peculiarity in epidermal structure thought to be induced by a virus.

The presence of an elevated stomatal structure is difficult to interpret in such a plant as Parthenice. Solereder's explanation for raised stomata is unsuitable as Parthenice is most often found growing on hot, dry, southern slopes, not in moist habitats. That the apparatus may be virus induced, as was suggested by Linsbauer for Hibiscus, may be possible, but demonstration of the presence of such a virus is beyond the scope of the present paper.

Perhaps a little speculation is justified here with regard to the physiological implications of such a structure. Meyer and Anderson (1939, p. 203) have pointed out that the length of a diffusion gradient is one of the factors governing its steepness and that diffusion through a small hole is slower if the gas must pass through a relatively long tube to an orifice than if it passes through a short tube. The pore of the elevated stoma could represent a means to lengthen the diffusion gradient

from the substomatal chamber to the stoma itself to curtail transpiration. One might expect, however, that if such a system is to be effective there would be numerous, well-spaced, specialized stomata and that these would be found primarily on the leaves. In Parthenice these structures are few in number, sporatic in occurrence, and present on the stem rather than the leaves. There appears to be no evidence that this unusual stoma is a specialized structure adapted to reduce water loss through transpiration.

The cortex. The cortex, which occupies a relatively small area when compared with the pith, consists of five or six layers of collenchymatous cells adjacent to the epidermis and six to nine layers of cortical parenchyma internal to the collenchyma. The collenchyma is interrupted by thin-walled parenchyma in the areas associated with substomatal chambers. Cortical parenchyma are thin-walled and often are separated by conspicuous intercellular spaces. A starch sheath can be detected in fresh sections stained with iodine as a continuous band of cells just outside the vascular cylinder and secretory canals.

Secretory canals are present in the cortex near the phloem and in the pith near the xylem. Canals located in the pith are termed medullary canals by Metcalf and Chalk (1950, p. 784). The term secretory canal will be used here in preference to the term resin canal. Tetley (1925) has pointed out that the term resin canal should be restricted to those structures known to conduct resin. The presence of resin in the canals of Parthenice has not yet been demonstrated. An analysis of the contents of the secretory canals is presented elsewhere in the present paper.

Typically, from four to six secretory canals flank the xylem and phloem of larger vascular bundles (Figure 22). Smaller vascular bundles may have only one secretory canal which is usually located near the phloem. In cross section a canal is about 30 microns in diameter and round in shape (Figure 25). The canal is lined with one or two secretory layers. The cells of the secretory layer contain densely staining cytoplasm and one conspicuous nucleus. Such cells are smaller and more compact than the surrounding parenchyma cells. Canals originate from the apical meristem very near the stem apex. Small dark-staining patches of meristematic tissue appear near the procambial stands. In the midst of these cells a noncellular canal is formed by the separation of the young secretory cells in the region of an intercellular space. Thus, the canal is schizogenous in origin. No canals are secondary in origin; however, as the stem enlarges the canal becomes somewhat distorted parallel to the cambium. Secretory canals have been described for many plants. Interesting from the taxonomic standpoint is the fact that they have been found in Artemisia, Anthemis, Ambrosia, and Parthenium. Medullary canals have been seen in Artemisia and Ambrosia (Metcalf and Chalk 1950, p. 784). These genera belong in the tribes Heliantheae, Ambrosieae, or Anthemideae; all tribes with which Parthenice may have some connection.

Pith. The large pith is of uniform structure except for the presence of secretory canals described above. It is composed of large thin-walled parenchyma cells which become sclerotic in age. In older stems the pith may collapse giving rise to a hollow internode.

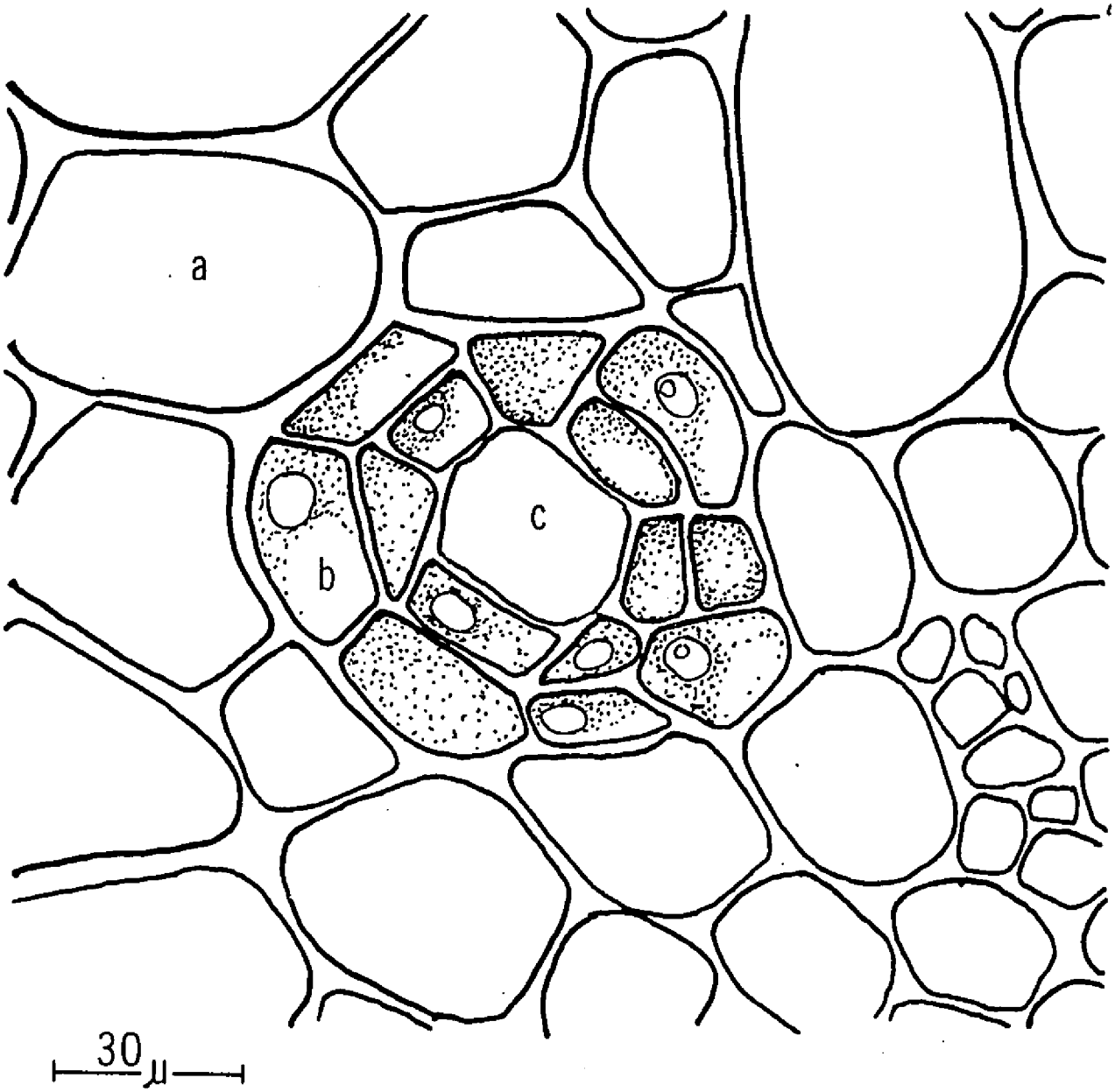


Figure 25. The Structure of the Secretory Canal

a. parenchyma; b. secretory cell; c. secretory canal.

The vascular system. The vascular system of a stem in which some secondary growth has occurred consists of a single series of distinct collateral vascular bundles arranged in a circle around the pith. Vascular bundles are of various sizes, and there may be more than 30 at a single level. There are distinct interfascicular regions in which an interfascicular cambium arises. Secondary development occurs first in the fascicular regions as seen in Figure 26. The interfascicular cambium becomes active soon after the fascicular cambium giving rise to secondary tissues in fairly young internodes. In older stems the vascular tissue becomes a continuous ring of primary and secondary tissues interrupted only by conspicuous pith rays.

The structure of the primary phloem was examined in both cross section and longi-section in young stems. It was found to be composed of the usual sieve tubes, companion cells, and parenchyma. Sieve plates were difficult to locate, but several were seen. These possessed about 15 perforations per plate. Primary phloem becomes fibrous in age giving rise to a cap of heavily sclerified cells at intervals around the secondary phloem. Secondary phloem appears to be very much like primary phloem in structure.

The primary xylem is composed of vessels and parenchyma. These vessels are smaller and rounder than those of the secondary xylem. Also they are arranged in neat rows perpendicular to the vascular cambium. The secondary xylem is composed of vessels, fibers and parenchyma. Vessels are numerous there being as many as 68 per square millimeter (Figure 27). In cross section they are sometimes roundish, but more often they are angular, and they may be solitary or in bunches of four or five.

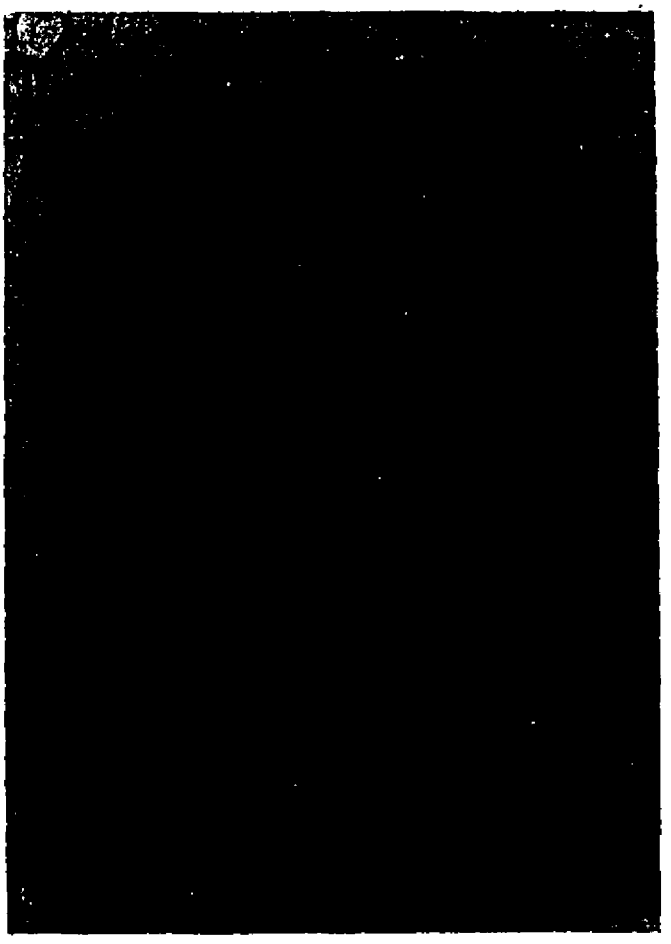


Figure 26. Single Vascular Bundle of P. mollis Showing the Development of the Fascicular Cambium

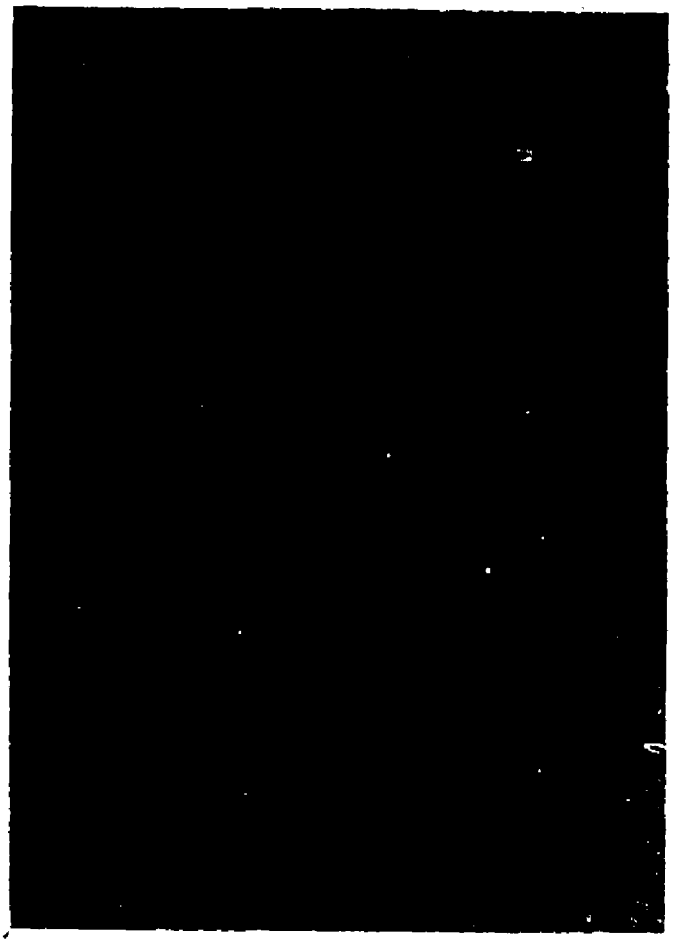


Figure 27. Portion of the Secondary Xylem Showing Distribution of Vessels

Vessel members may be cylindrical or fusiform in shape when viewed longitudinally and with or without ligular projections. Perforation plates may be horizontal or oblique. In length vessels vary from 40 to 175 microns while widths vary from 20 to 50 microns. Fibers are numerous, long (up to 300 microns), and narrow (6-8 microns). Figure 28, a-d, represents drawings made from secondary xylem macerated in chromic and nitric acid.

Trichomes

The indumentum consists of several types of multicellular hairs or trichomes. These lend to Parthenice its velvety texture and greyish color. The density of the hairs is variable especially on the leaves where fewer hairs are found along veins than in areolar regions. Trichomes are present on all parts of the plant except the cotyledons. Trichomes of Parthenice fall into two categories: the uniseriate clothing hair and the biseriate glandular hair.

The uniseriate clothing hair. The uniseriate clothing hairs are also of two types. Those hairs found associated with the inflorescence bear a blunt terminal cell supported by four or five subterminal cells which vary from 40 to 80 microns in length. Such hairs are slightly curved and are found primarily on the branches and peduncles of the inflorescence as well as on the phyllaries and corollas of the ray and disk flowers (Figures 29, 30a). Hairs found below the inflorescence represent the second type of uniseriate clothing hair. These hairs consist of four to ten cells. The terminal cell, however, is long and taper pointed rather than blunt. While subterminal cells never reach a greater length than 80 microns, taper-pointed terminal cells may reach lengths as great

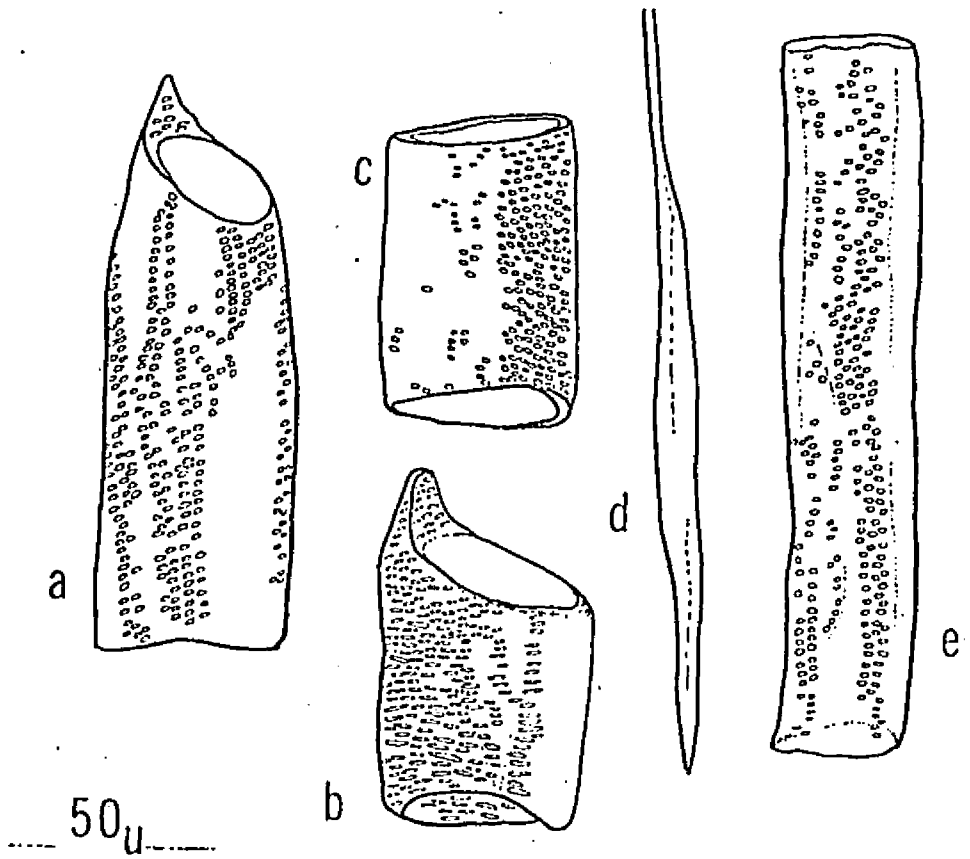


Figure 28. Cell Types from the Xylem

a-b. caudate, barrel-shaped vessels; c. non-caudate vessel; d. fiber; e. elongate, non-caudate vessel.

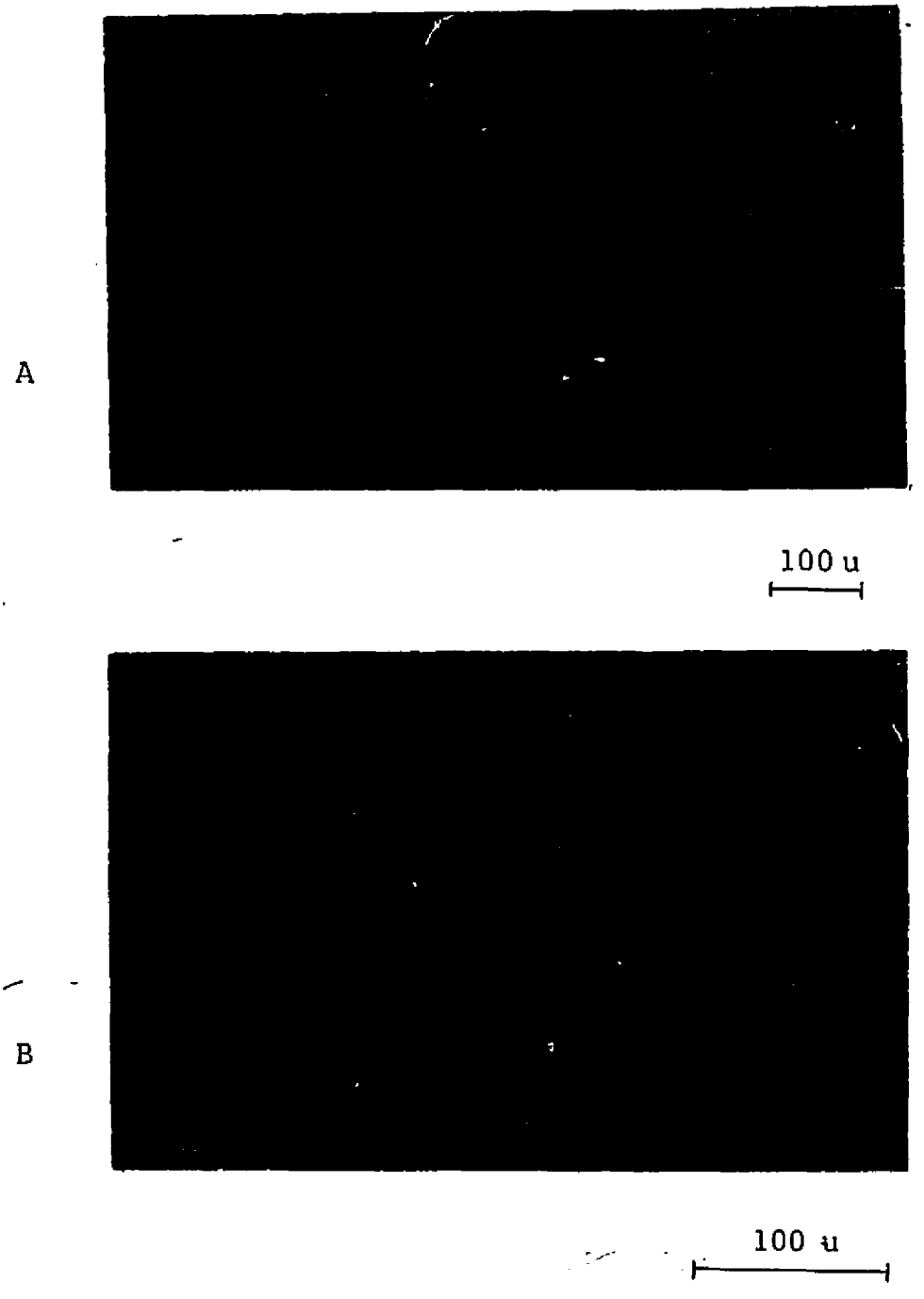


Figure 29. Uniseriate Clothing Hairs

A. Blunt-celled hair associated with the inflorescence.
B. Taper-pointed hair of the vegetative stems and leaves.

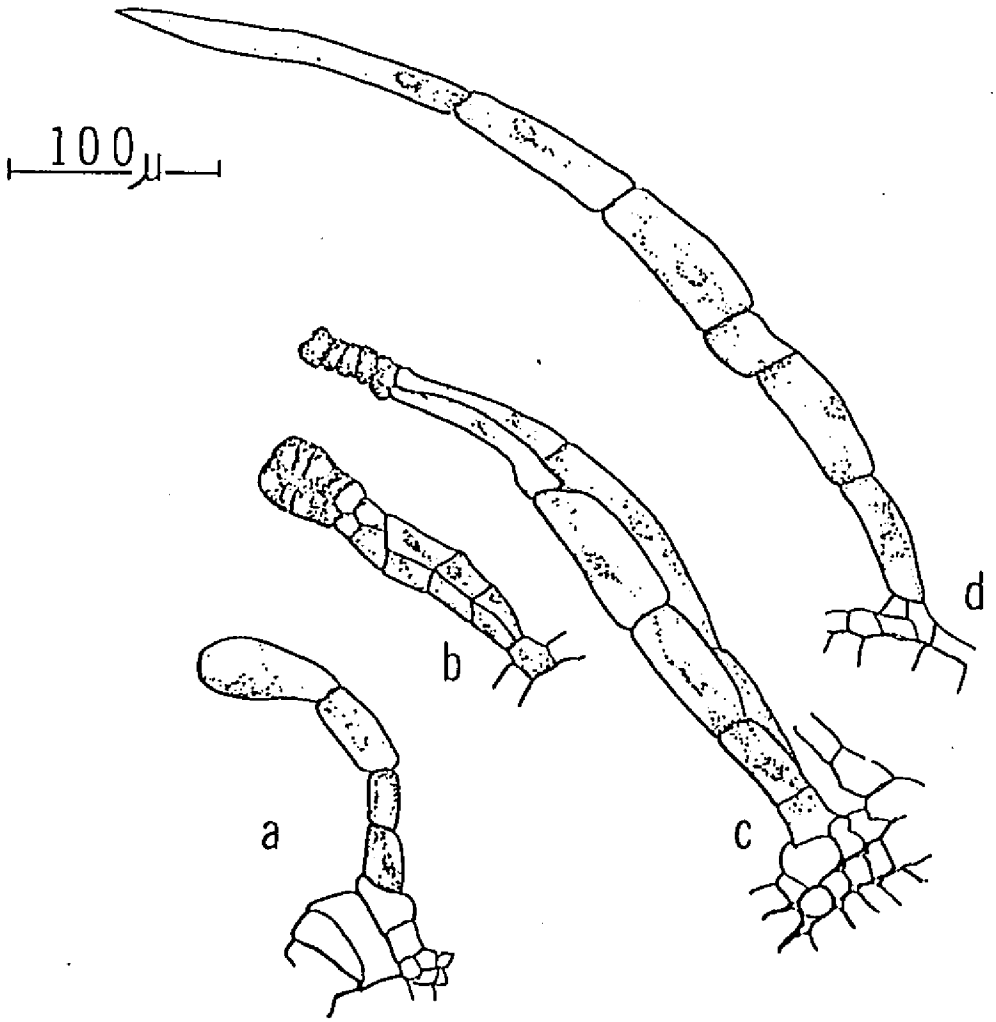


Figure 30. Types of Trichomes

a. uniseriate hair of the inflorescence; b. young biseriate glandular hair; c. mature biseriate glandular hair; d. uniseriate hair of the vegetative stem and leaves.

as 150 microns. These hairs are uncurved and are found on the leaves and stems below the inflorescence (Figures 29B, 30d). The development of these hairs is typical of uniseriate hairs whose origin begins with the papillate elongation of a single epidermal cell.

The biseriate glandular hair. The biseriate glandular hair is found on all aerial parts of the plant (Figure 30, b and c, and Figure 31). Their density varies from occasional on the pales of the receptacle to very dense on young foliage. The biseriate glandular hair varies from 0.2 millimeters to 0.4 millimeters in length depending primarily on its stage of development. The hair is composed of two parts, a head and a stalk. The head consists of ten cells which are arranged in two rows of five each. These cells are densely staining and possess conspicuous nuclei. The cells of the stalk are usually six in number but as many as ten cells have been observed in mature hairs. The stalk cells are arranged in two rows, possess a lightly staining protoplast, and elongate greatly at maturity elevating the head well above the epidermis.

The biseriate glandular hair originates much like those of the Madineae described in detail by Carlquist (1958). A single papillate structure arises from a single cell in very young epidermal tissue. The nucleus of the papilla divides anticlinally giving rise to two cells, the division products of which form the biseriate structure characteristic of the glandular hair. Subsequent divisions are periclinal and give rise to the length of the hair. The filamentous structure thus produced shows early differentiation into stalk and head cells. The developing hair at first appears sessile; as the stalk cells elevate the head above the epidermis they become elongate and slender. At maturity when all of the

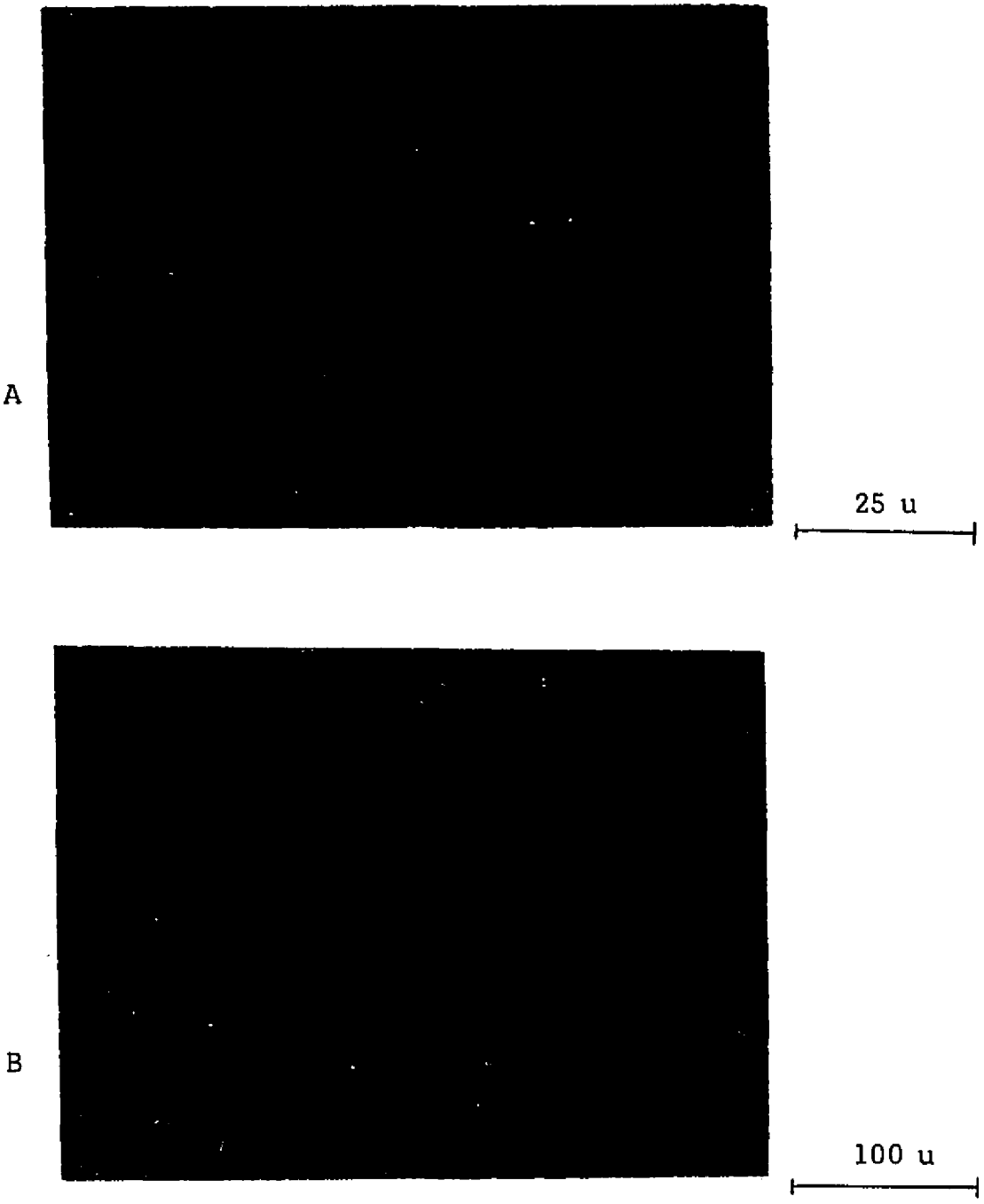


Figure 31. The Biseriate Glandular Hair

A. Young hair before elongation of stalk cells. B. Mature hair after the droplet of exudate has appeared.

stalk cells have elongated, a droplet of clear exudate appears at the top of the head. At this time the cells of the head appear shrivelled.

The Root

The primary root of a seedling two days old (Figure 32) is characterized by a central core of vascular tissue limited on the outside by an endodermis. The surrounding cortex is four to five layers deep and consists of the usual thin-walled parenchyma interrupted by intercellular spaces. The peripheral cells of the cortex are covered with root epidermis members which are about one half the diameter of the cortical parenchyma. Many of these elongate into unicellular root hairs. In Parthenice the primary xylem develops like many dicot roots in which the direction of maturation of xylem is exarch. The number of cells in the primary xylem is small; usually there are less than ten elements. Primary roots are usually diarch and a patch of primary phloem is found on either side of the xylem.

Secondary development is apparent in seedlings less than two weeks old (Figure 33). What appears to be the first formed secondary xylem is not derived from the cambium but rather from a proliferation of vascular parenchyma between the primary xylem and phloem. Artschwager (1943) has interpreted this peculiar tissue to be metaxylem. Structurally it consists of numerous fibers and parenchyma with conspicuous vessels scattered about. The oldest of these is near the primary xylem. Surrounding this tissue are groups of phloem and small rectangular cells which appear to be giving rise to cambium. Although secondary phloem is produced in small amounts, the endodermis remains intact for several weeks compensating for stelar enlargement by first increasing in cell size and

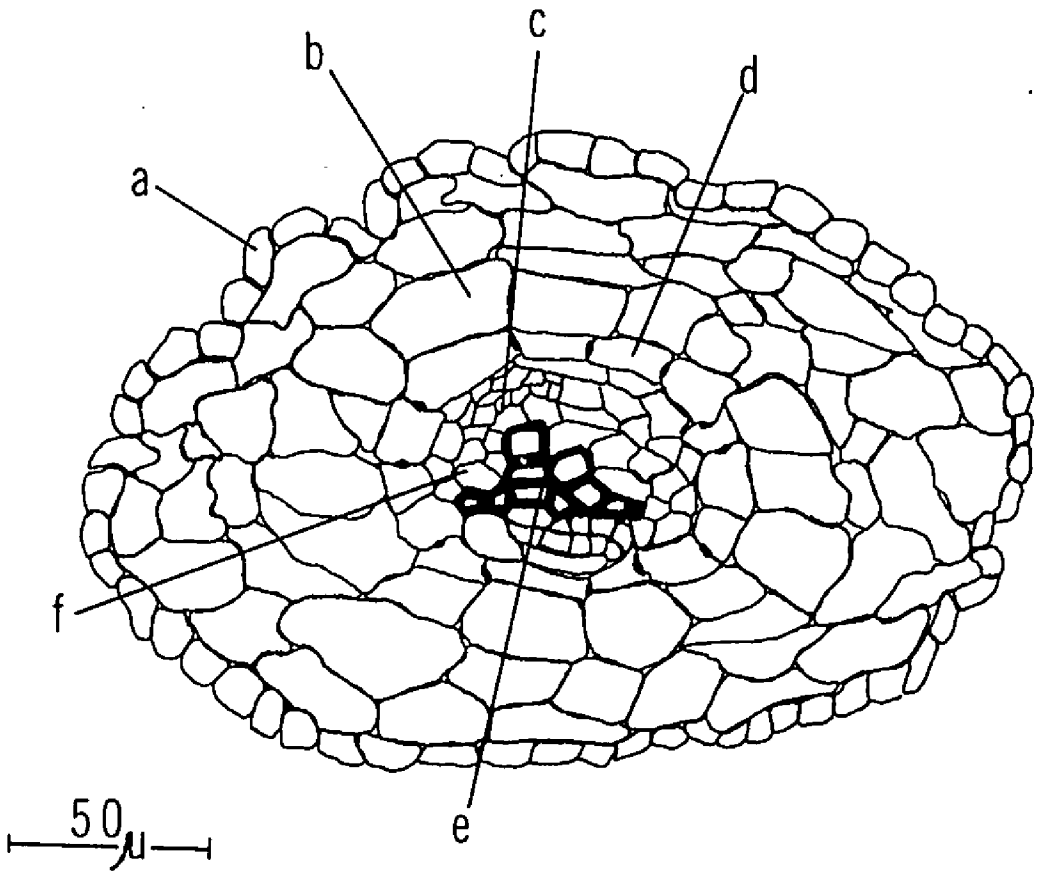


Figure 32. The Tissues of the Primary Root

a. epidermis; b. cortex; c. primary phloem; d. endodermis; e. primary xylem; f. pericycle.

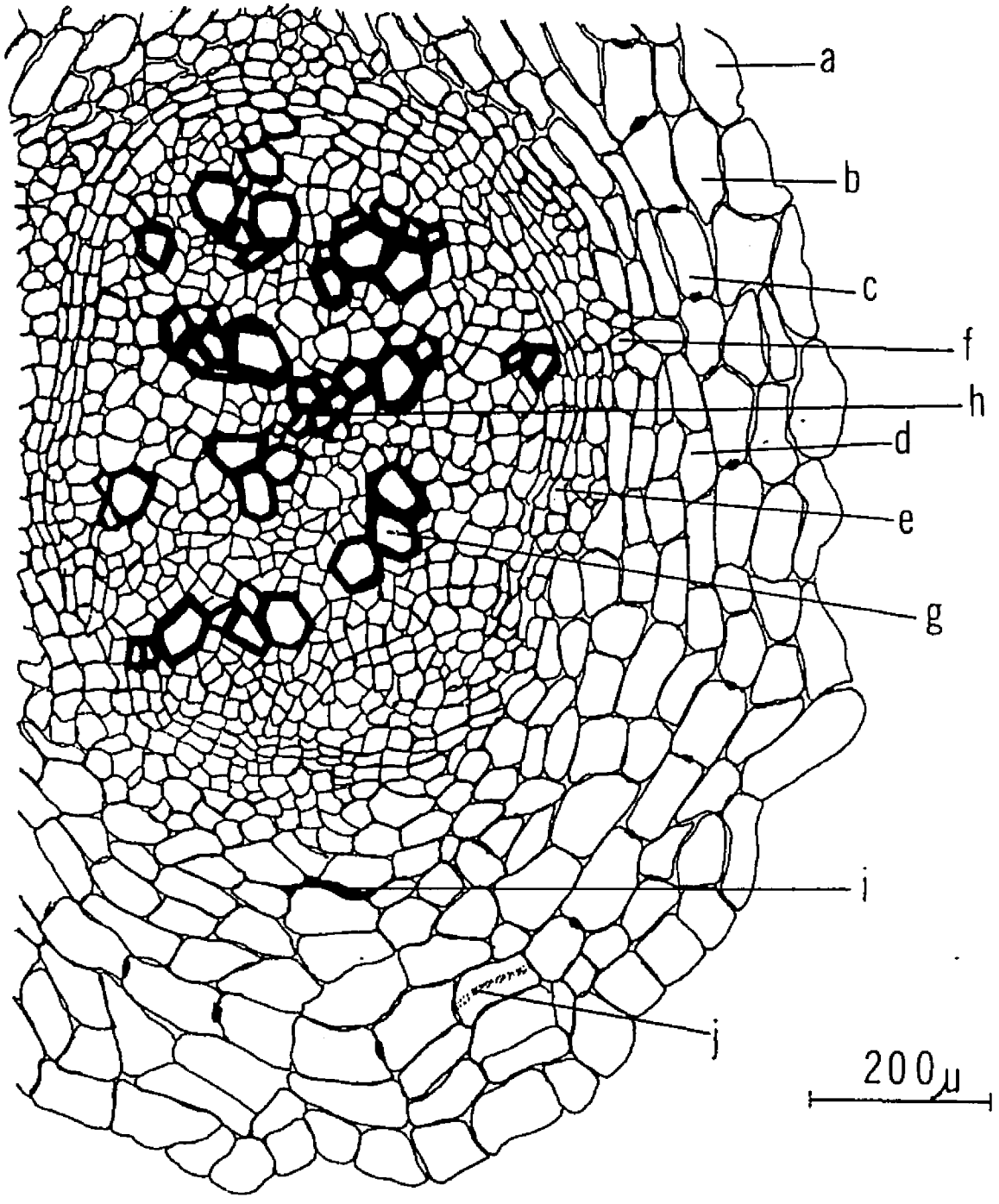


Figure 33. Cross Section of the Root of a Two-week-old Seedling

a. epidermis; b. cortex; c. endodermis; d. pericyle; e. developing cambium; f. secondary phloem; g. xylem formed from the activity of the vascular parenchyma; h. primary xylem; i. crushed primary phloem; j. casparian strip.

then increasing in cell number. In Parthenium the development of the endodermis includes the formation of secretory ducts through the production of a localized two-layered endodermis (Artschwager 1943). No such development was observed for Parthenice.

When the root reaches a diameter of about five millimeters and the seedling is about two months old, secondary tissues derived from the cambium begin to develop. Xylem formed from the cambium has an entirely different character than that derived from vascular parenchyma. The cells are relatively small, being arranged in neat compact linear rows. Such an arrangement of tissues gives the root the aspect of a stem since the first formed xylem resembles pith (Figure 34).

In mature roots much secondary development is seen. Here the cortex, epidermis, and endodermis are completely replaced by a cork which originates in the pericycle.

The Vegetative Shoot Apex

The vegetative shoot apex of Parthenice is typical of many herbaceous dicots in which a two-layered tunica surrounds a massive corpus. Relative to the floral apex discussed elsewhere in the present paper the shoot apex is broad and somewhat flattened in shape. Figure 35 is a photomicrograph of the shoot apex of Parthenice mollis.

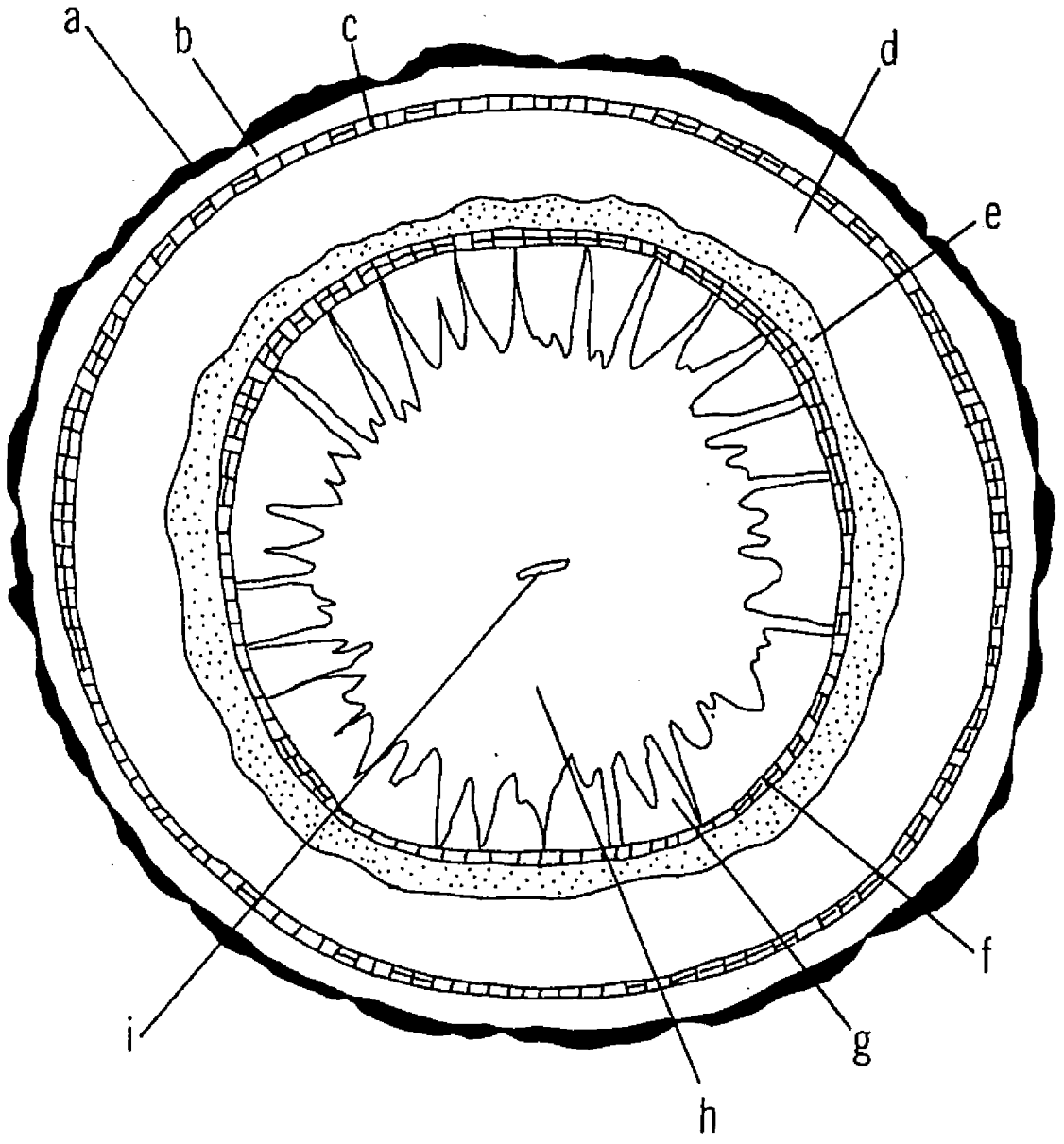


Figure 34. Mature Root in Which Secondary Development Has Begun

a. sloughed epidermis and cortex; b. cork; c. cork cambium; d. pericycle; e. secondary phloem; f. vascular cambium; g. secondary xylem; h. xylem formed from activity of the vascular parenchyma; i. primary xylem.

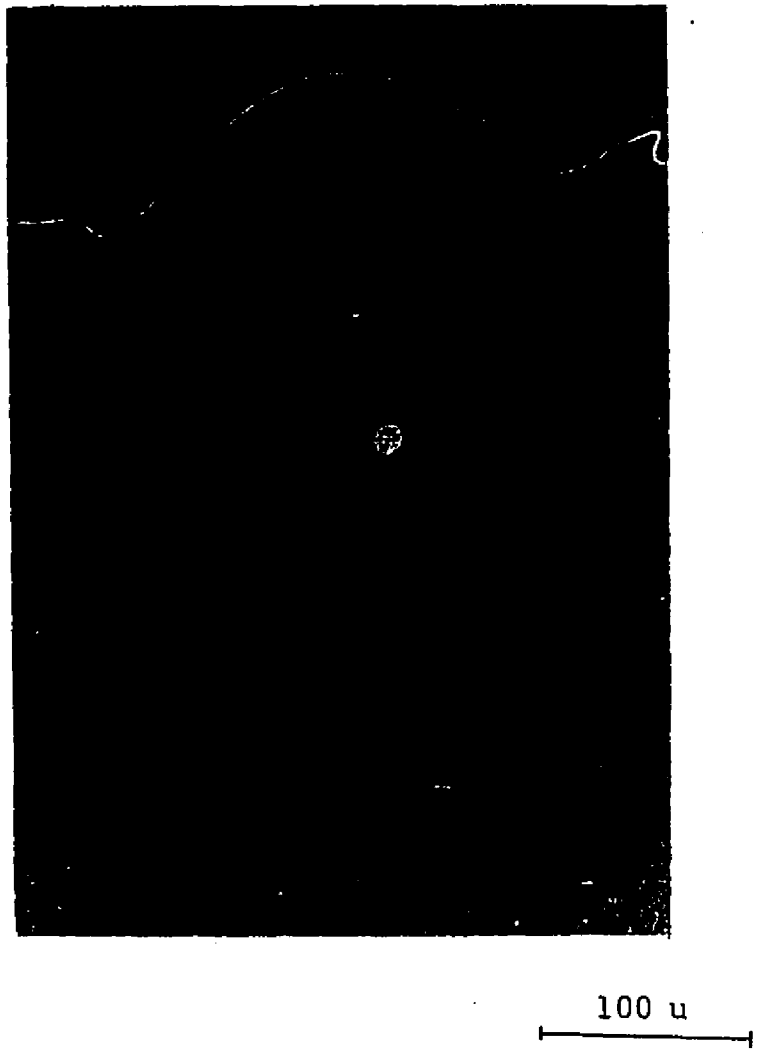


Figure 35. The Vegetative Shoot Apex

FLORAL ANATOMY

The anatomical observations recorded here were derived from three main sources: fresh, dried, and preserved material. Capitula from Baja California and Tucson, Arizona were used. Dried herbarium material was prepared by boiling entire heads gently in detergent and tap water until a brownish yellow color appeared in the solution. Heads were lifted onto a slide and teased apart. The teased material was then mounted in lactophenol and covered with a cover slip for observation. Such preparations were ringed with paraffin for storage. Material preserved in the field in Formalin-Aceto-Alcohol using 50 percent ethyl alcohol was used for paraffin sections. Most sections were cut at 10 microns, but sections through the receptacle were cut at 50 microns in order to study vasculation more effectively in serial section (Kasapligil 1965).

The capitulum is composed of a variety of structures, the morphology of which has already been discussed. The structure of the peduncle, though a stem, is discussed here because of its intimate relation to the vasculation of the receptacle. The anatomy of the capitulum will be discussed in the following order: the floral apex, peduncle, phyllaries, ray flower, disk flower, pales, pollen, and vasculature of the capitulum.

Floral Apex

The shoot apex in which flowering has been initiated (Figure 36A) is strikingly different from the vegetative shoot apex previously

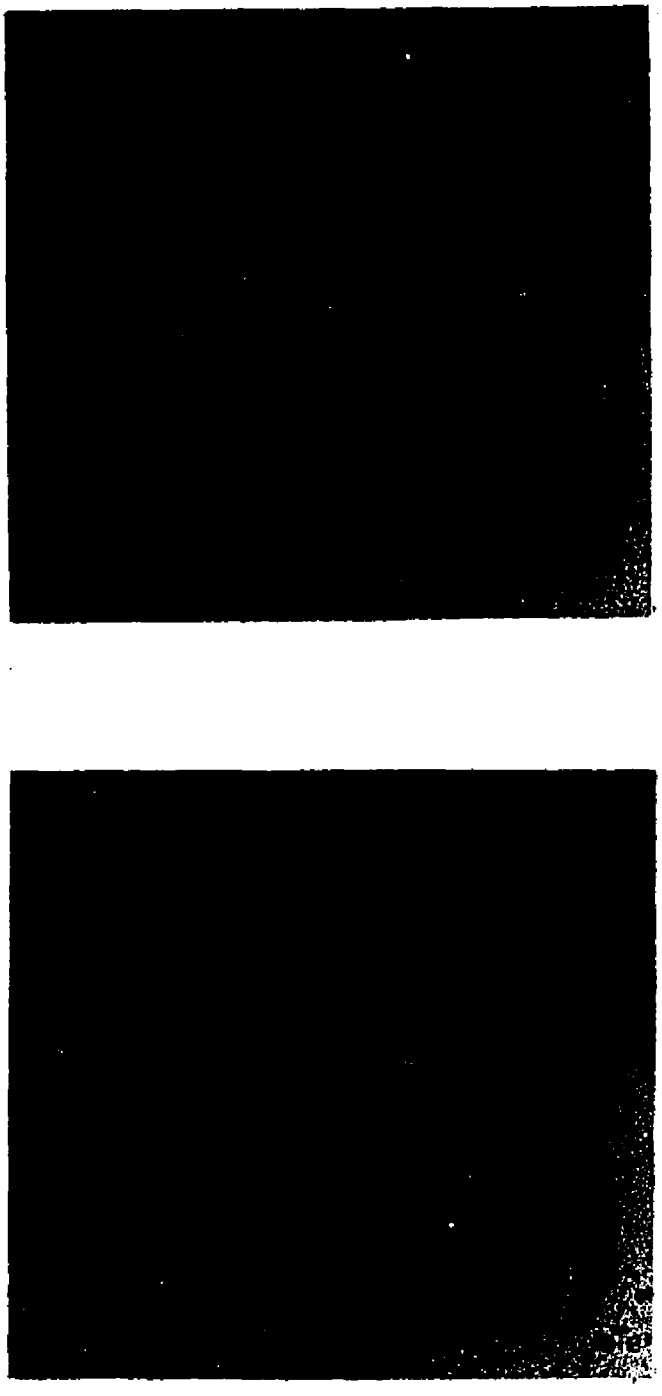


Figure 36. The Shoot Apex in Which Flowering Has Been Initiated

A. Just prior to the formation of phyllary primordia. B. The phyllary primordia present. Divisions in the tunica will give rise to ray and disk flower primordia.

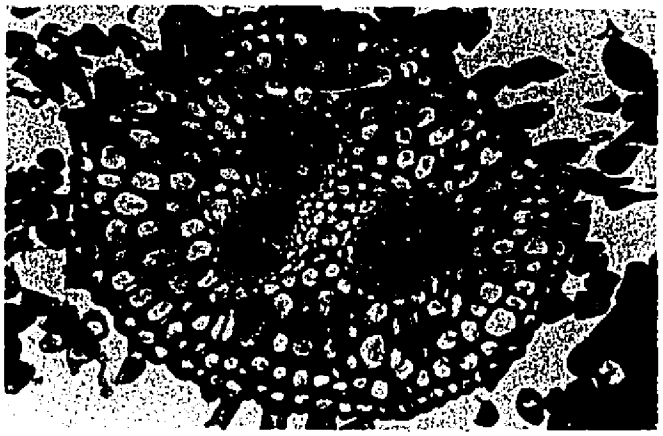
discussed. Although the tunica is two layered around the corpus, the shape of the entire structure is distinctly bulbous when compared to the flattish vegetative apex. In a median section of the developing capitulum as seen in Figure 36B, phyllary primordia nearly enclose the globose, meristematic receptacle. However, in the axil of the phyllary primordium there is no sign of a developing axillary bud; instead, meristematic activity is scattered, that is, it occurs in patches over the entire surface of the receptacle. These tiny primordia give rise to the ray and disk flowers as well as their associated structures.

Within the single capitulum the order of maturation of the flowers is centripetal as in all other Compositae. That the order of maturation of capitula of a particular branch within the inflorescence is basipetal is substantiated by anatomical data. In Figure 36, the oldest capitulum is at the tip of the stem, while the younger capitula are lateral. Thus, very early in the development of the inflorescence a basipetal order of maturation is established.

The Peduncle

Typically, peduncles possess a single-layered epidermis which bears biseriate glands and uniseriate, blunt-tipped clothing hairs. A heavily collenchymatized cortex surrounds from two to five bicollateral vascular bundles. The pith is scanty and secretory canals are present only near the phloem in the cortex. The number of bundles present in a given section depends upon its proximity to the capitulum; the closer to the head the larger the number of bundles. Figure 37A is a photograph of

A



0.5 mm

B

Figure 37. Structure of the Peduncle and Phyllaries

A. The peduncle 0.5 mm from the capitulum with three vascular strands. B. The phyllaries; the upper structure is the outer phyllary, the lower is the inner phyllary.

a cross section of the peduncle taken about 0.5 millimeter below the receptacle.

The Phyllaries

The outer phyllary. The outer phyllary or involucral bract is composed of an epidermis with stomata under which there are roundish substomatal chambers. Such stomata occur on the abaxial surface only. The mesophyll shows little differentiation, its aspect being more like that of a petal than a leaf. Embedded in this loosely organized spongy parenchyma and closely associated with vascular tissue are secretory canals similar to those already described for the stem and leaf. The reticulate vascular system is composed of collateral veins of small dimensions. The upper structure of Figure 37B is a cross section of such a phyllary.

The inner phyllary. The inner phyllary is basically similar to the outer in that both are covered with uniseriate and biseriate trichomes, and the mesophyll is poorly differentiated. Secretory canals are present but somewhat smaller in diameter than those of the outer phyllary. Stomata are completely absent from the inner phyllary. At maturity the mesophyll apparently collapses causing the phyllary to become thin and scarious. The lower structure in Figure 37B is a photograph of a cross section of the inner phyllary.

The Ray Flower

The ray or ligulate flower consists of a short style which branches into a bilobed stigma, a tiny deciduous corolla, and an achene derived from two carpels. Stamens are absent. The stigma and style are

composed of parenchymatous ground tissue traversed by two vascular bundles each of which diverges from the apex of the style into the lobes of the stigma. The stigmatic surface is composed of specialized papillate collecting hairs which are elongate perpendicular to the long axis of the stigma. Other epidermal cells are elongate parallel to the long axis of the stigma. Figure 38A is a camera lucida drawing of the stigma showing the densely staining collecting hairs. Collecting hairs are restricted to the lateral surfaces of the stigmatic lobes. Figure 38B is a diagrammatic representation of the distribution of collecting hairs at two places along the stigmatic lobe.

In cross section, the corolla is characterized by a thin-walled epidermis possessing no stomata and a uniform parenchymatous mesophyll of only three layers. The vasculature of the ligule is poorly developed in comparison to that of many Compositae. According to Koch (1930) most ligulate corollas possess either four or five corolline vascular bundles, the terminal branches of which anastomose at the tip of the lobes of the corolla. In Parthenice there are from two to five corolline bundles. Such bundles may be variously branched and fused. Figure 39 is a diagrammatic comparison of the vasculature of the ligule of a typical composite and Parthenice. Numerous corollas from Parthenice were mounted in lactophenol for observation of vasculature. Two examples were photographed. These are shown in Figure 40. Note the lack of development of lateral branches in several of the bundles. At the base of both the style and the corolla an abcission layer is formed which causes both structures to fall away together at maturity.

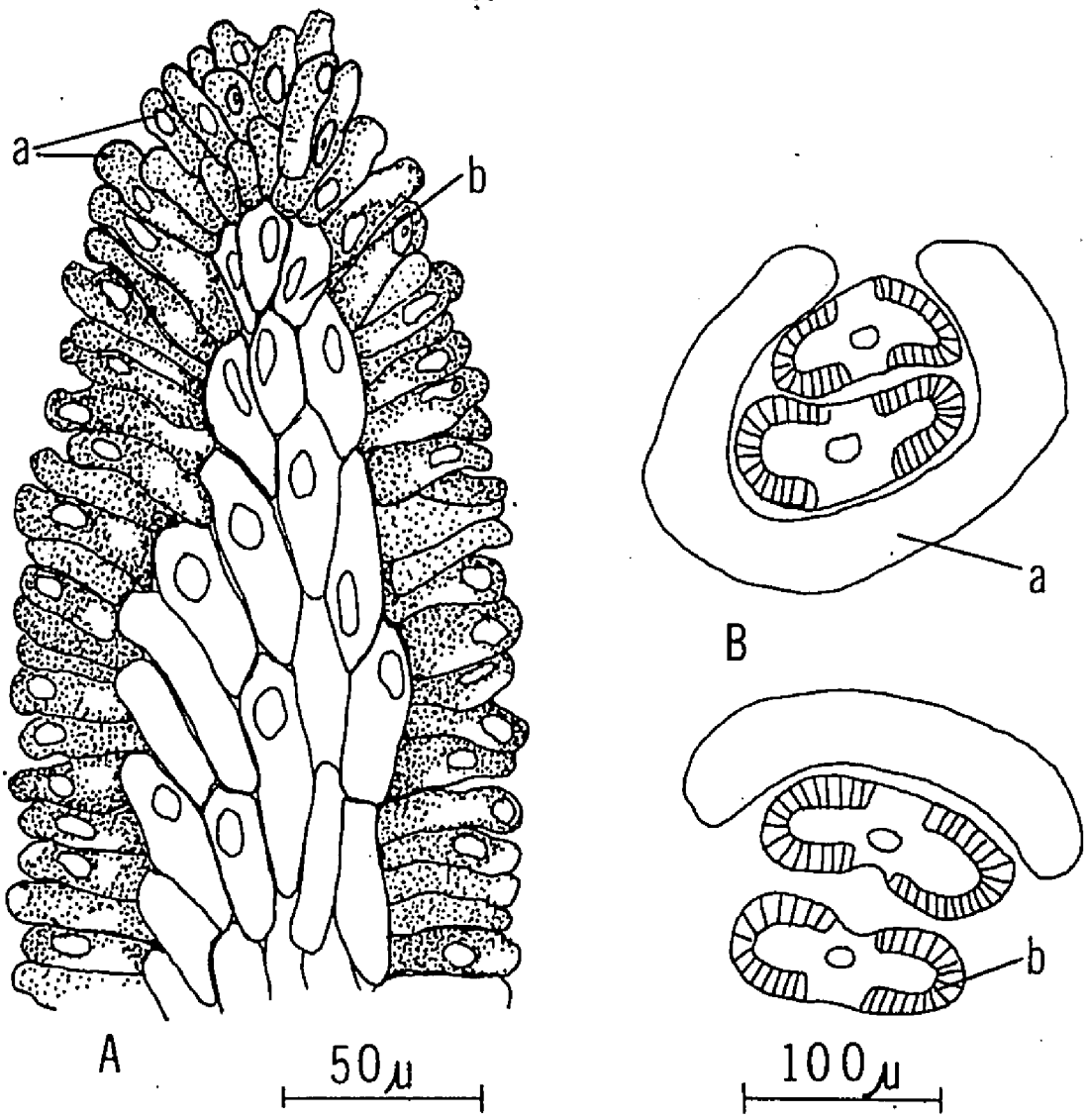


Figure 38. The Structure of the Stigma

A. Portion of the stigma. a. papillate collecting hairs; b. ground parenchyma. B. Diagrams of the cross section of the stigma to show the distribution of collecting hairs. a. corolla; b. collecting hairs.

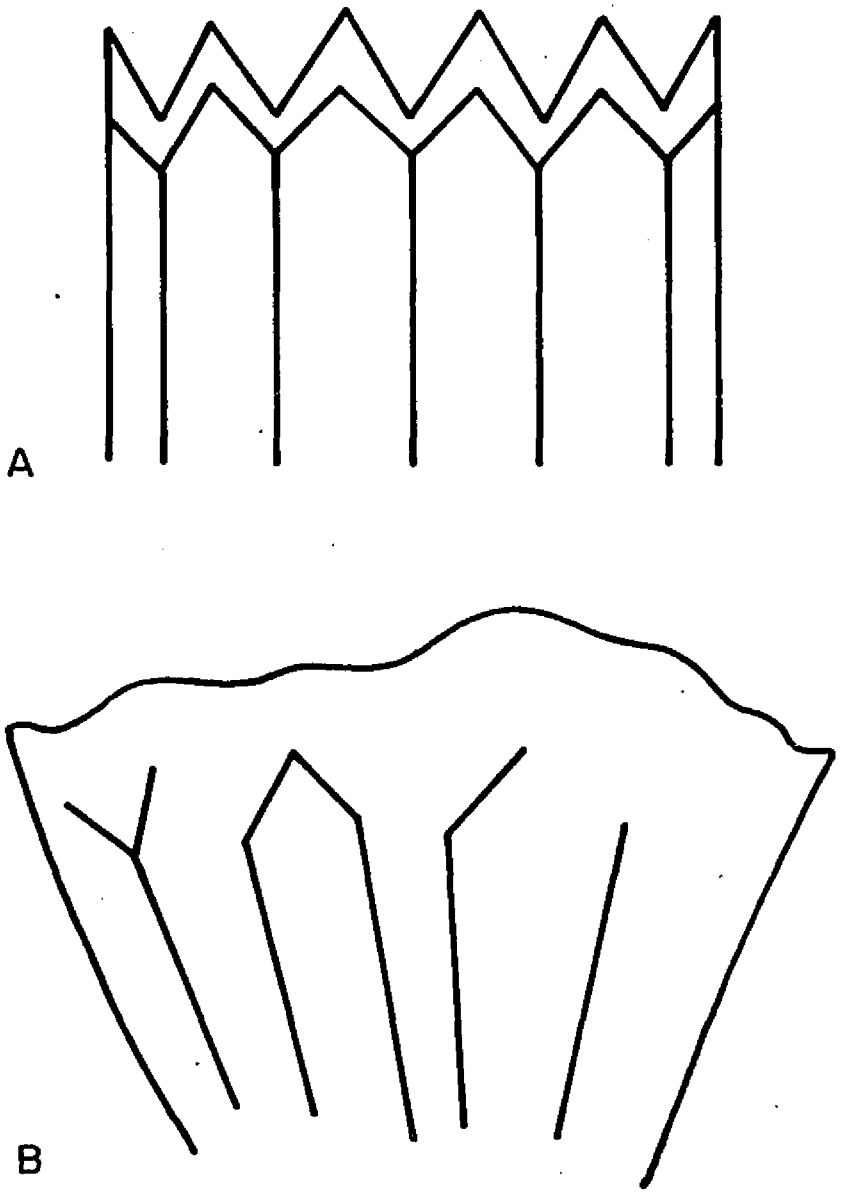


Figure 39. Comparison of the Vasculation of the Corollas of a Typical Helianthoid Composite and Parthenice

A. Typical composite with five vascular strands which anastomose at the tips of the corolla lobes. B. Corolla of P. mollis showing the various types of patterns of vasculation.

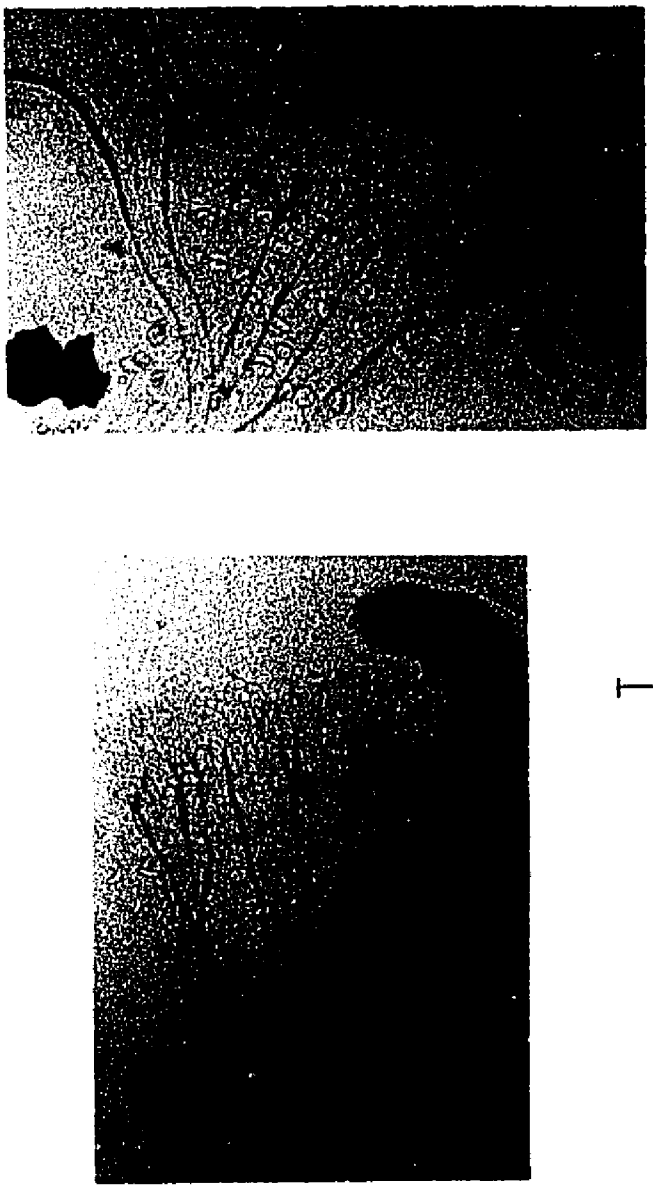


Figure 40. Photographs of Corollas of P. mollis Mounted in Lactophenol

A. Four veins present with some anastomosing at the tip of the corolla. B. Five veins present, branching, obscure, and no anastomoses present.

The peculiar bulbous structure present just under the point of attachment of the corolla and style to the achene is composed of a mass of sclerenchyma and a few elongated cells which appear to be fibrous in nature.

The structure of the achene is very like that described for Parthenium by Artschwager (1943). In the ovary wall (Figure 41A) there is a single-layered epidermis which abuts upon a row of oblong, palisade-like cells which possess densely staining cytoplasm. Localized periclinal and anticlinal divisions in this layer give rise to the tubercles which are present on the surface of the mature achene. Internal to the palisade-like layer is a space approximately 40 microns wide which becomes filled with pigment as the achene matures. This pigment is deposited in large scleriform patches (Figure 41b, 42) when the ovary wall is flaccid and little lignification has taken place. When the ovary is mature and the achene is hard a solid mass of pigment is present which gives the achene its dark brown color. Internal to the pigment space are several rows of small thick-walled fibers, which, because of their proximity to the endocarp have been interpreted to be mesocarp in Parthenium (Artschwager 1943). The layer of mesocarp cells adjacent to the pigmented layer possesses peculiar conical papillae. The endocarp is made of large amorphous parenchyma cells which resemble endosperm. The single anatropous ovule present in the ovarian locule may possess from three to five procambial strands.

The Disk Flower

The disk flower is similar in structure to many other staminate disk flowers (Figure 43). The five-lobed corolla is composed of a

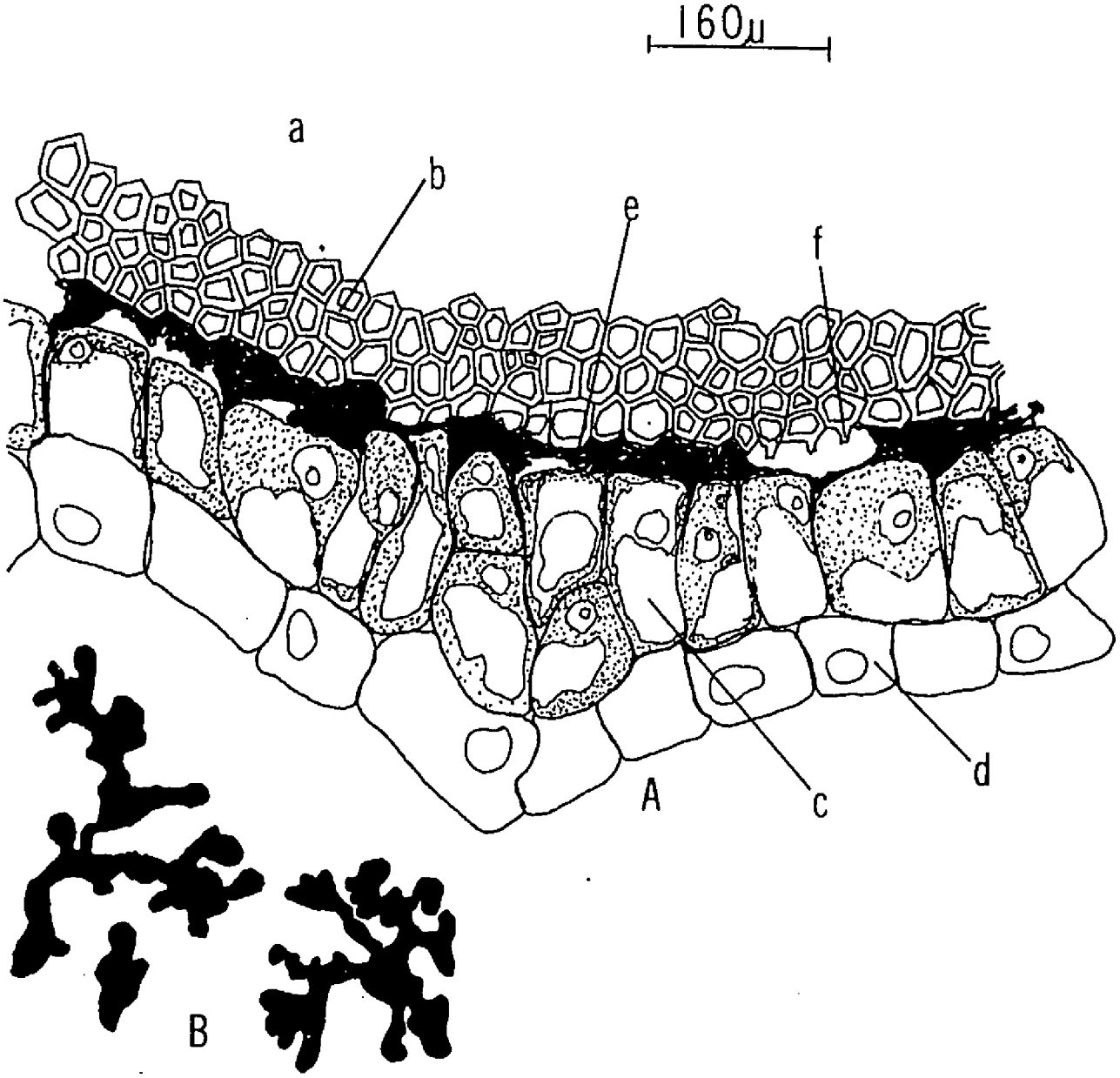


Figure 41. Camera Lucida Drawings of the Wall and Pigmentation of the Achene

A. Cross section of portion of the wall of the mature achene. a. endocarp; b.. fibrous mesocarp; c. exocarp. d. epidermis; e. pigmented layer; f. papilla of the mesocarp fibers which abut upon the pigmented layer. B. Appearance of early pigmentation patches as seen from the surface of a young achene.

Figure 42. Young Achene Mounted in Lactophenol to Show Early Stages in Pigmentation

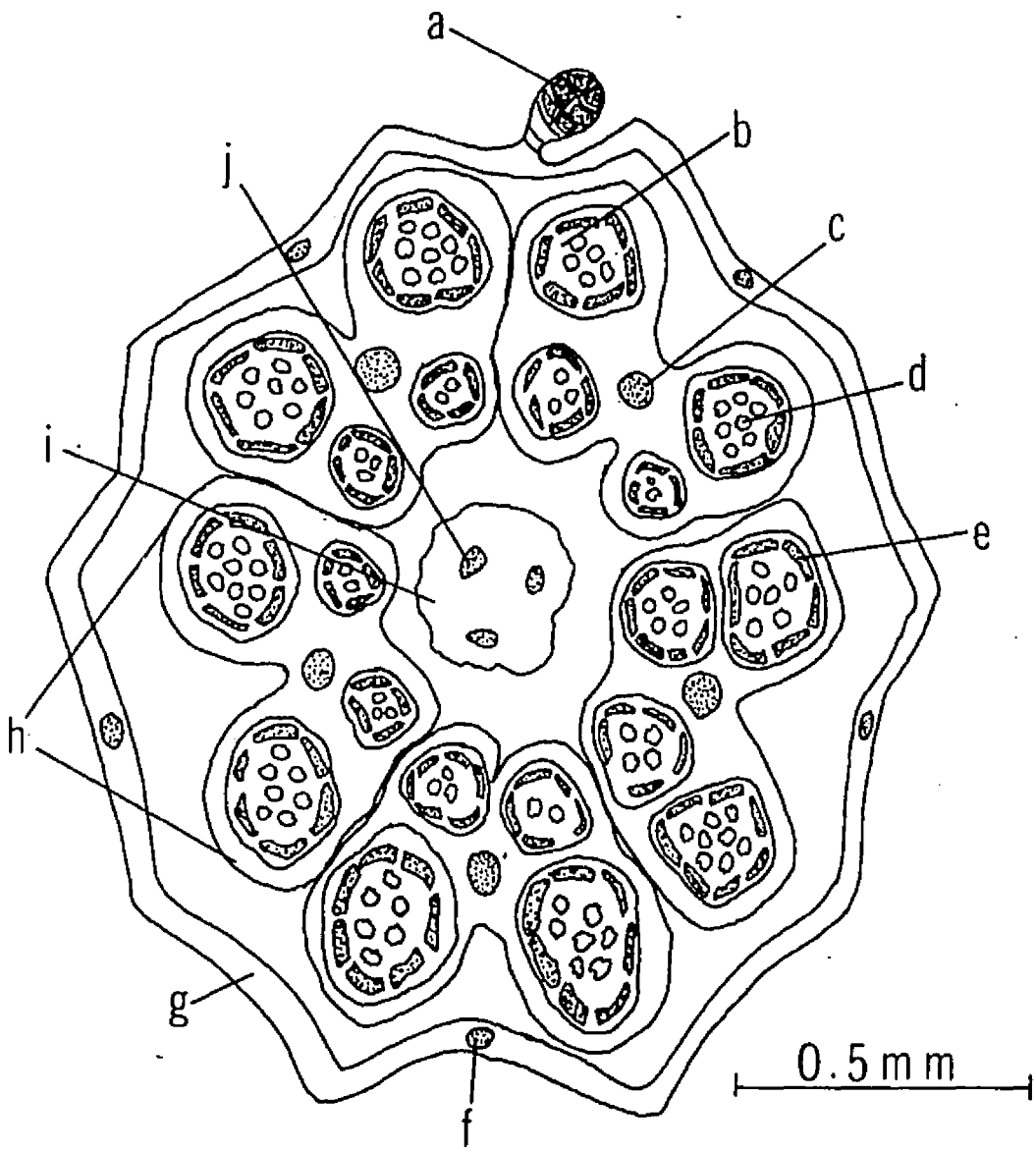


Figure 43. Structure of the Disk Flower

a. glandular trichome; b. locule; c. stamen bundle; d. microspore; e. tapetum; f. corolline bundle; g. corolla; h. anther; i. stigma; j. stigma bundle.

mesophyll of two to three layers bound by an inner and outer epidermis in which there are no stomata. The five vascular bundles alternate with the lobes of the corolla and show the usual pattern of branching and fusion. The outer epidermis is densely clothed with biseriate glands and curling hairs.

The five stamens are supported by slender flattish filaments each of which possesses a single vascular strand. The vein is surrounded by two or three layers of thin-walled parenchyma cells and a cutinized epidermis. The anthers are loosely coherent and tend to separate readily in age. Each anther is elongate and possesses a hollow, deltoid, terminal appendage. The body of the anther is two lobed; each lobe possesses two locules. The locules adjacent to the corolla are almost twice as large as those near the stigma. The anther wall is two to three layers thick. Internal to this is a tapetal layer whose cells are characterized by densely staining protoplasts and prominent nuclei. They appear flattened parallel to the inner periphery of the anther wall. The sporogenous tissue is of closely packed and densely staining cells which become separate from one another as cell division proceeds. Meiosis results in four microspore nuclei whose protoplasts are walled off simultaneously. After wall formation is complete the microspores become separated and develop echinate wall ornamentation. Pollen is shed from the anther with a generative nucleus and a tube nucleus.

Pollen

The structure of the mature pollen has been studied by Wodehouse (1935, p. 519) with the light microscope and by Skvarla and Larson (1965) with the electron microscope. Wodehouse describes the

grain of P. mollis as echinate and provided with spines essentially the same as those of Oxytenia, tricolpate, with long furrows reaching almost from pole to pole, and with the surface texture only finely granular. He also gives diameter measurements of 15.4 to 15.8 microns stating that the grains are small, somewhat smaller than those of Parthenium. Measurements made by the present writer on acetolyzed pollen grains from Baja California and Arizona showed that the average size of the grain was 15.6 microns for ten grains examined from each locality. The wall at its thickest point is about 2.5 microns while the inner aperture is about 10.6 microns in diameter. Average spine length is about 1.1 microns. Figure 44, A-D, is several views of P. mollis as seen in the light microscope. Note that the dry pollen grain is oblong in shape rather than round as it is when mounted in tap water.

Wodehouse (1935, p. 525) further points out that the grains of Parthenice possess a combination of primitive characteristics through which the other members of the Ambrosieae may have been derived.

Skvarla and Larson (1965) have examined and discussed the ultrastructure of pollen in helianthoid Compositae. The following description is based on their work. The fine structure of the wall of the typical pollen grain of the Compositae is considered to be divided into two distinct layers, a unipartite layer and a tripartite layer as sketched in Figure 45A.

The unipartite layer is located to the interior of the wall near the protoplasm and is termed the endexine. The tripartite layer is known as the ektexine. It consists of three layers: (1) the foot layer, (2) the columellae, and (3) the tectum with (or without) associated spinules.

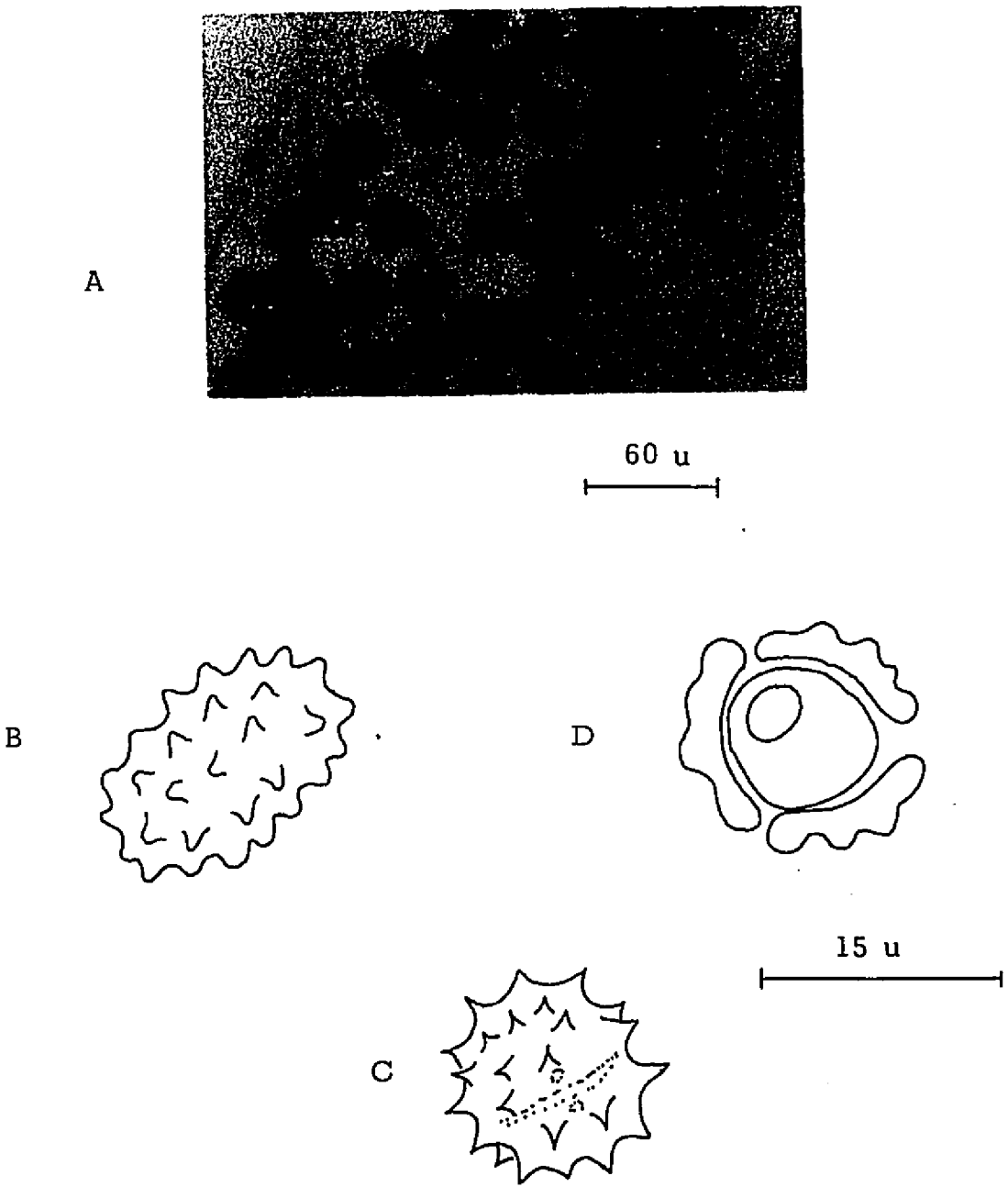
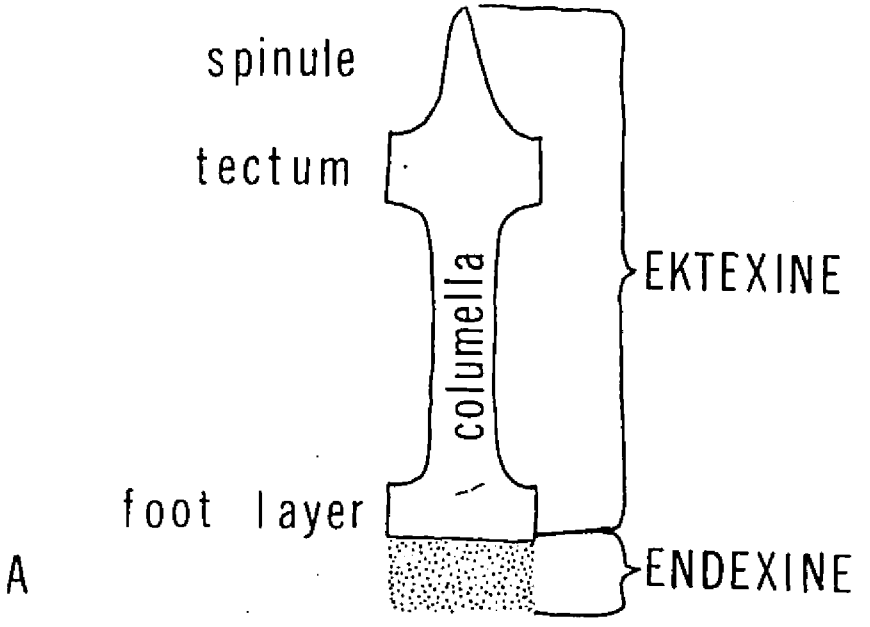


Figure 44. Pollen of P. mollis

A. Photograph of pollen in the anther. B. Dry grain. Note the oblong shape. C. External view (after Wodehouse). D. Median view of acetolyzed pollen.



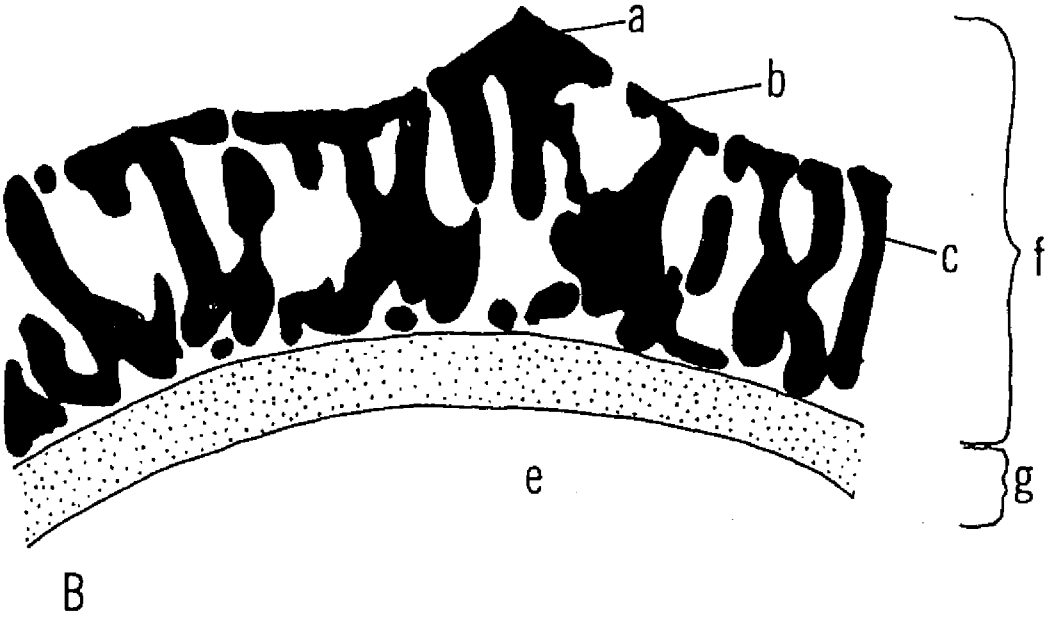


Figure 45. The Ultrastructure of Pollen Grain Walls in General Compositae and in Parthenice mollis.--(After Skvarla and Turner 1966)

A. Diagram of the basic wall structure in general compositae. B. Tracing made from photograph by Skvarla and Larson (1965) of structure of P. mollis (X13000). a. spinule; b. tectum; c. branched columellae; e. inside of grain; f. ektexine; g. endexine.

The layers described above define the basic layers common to all Compositae. Within each layer there exists a multitude of complex configurations an excellent summary of which is given by Skvarla and Turner (1966).

Parthenice mollis possesses a singular pollen grain when compared with the other members of the tribe Melampodinae (Figure 45B). In all the species examined by Skvarla and Larson (1965) in the Melampodinae, P. mollis showed the greatest detailed structural variation. One of the distinctive features is that some of the columellae are connected to adjacent columellae by lateral branches. The result is a rather loosely organized internal tectum. A second major feature of P. mollis is that foramina, or holes in the columella, which are present in all other species of the Melampodinae are absent in P. mollis.

Earlier it was suggested by Wodehouse (1935) on the basis of observations made with the light microscope that P. mollis pollen may be a prototype for pollen types found in the ambrosioid group. Electron microscopy tends to corroborate this notion only in part according to Skvarla and Larson (1965). While certain species in the ambrosioid group (Iva ambrosiaefolia Gray and I. axillaris Pursh.) are similar to P. mollis in having an ektexine with a discontinuous internal tectum and lacking internal foramina, other species of the ambrosioid group are very distinct.

In other morphological characteristics Parthenice pollen is typical of the tribe Heliantheae in general. Spines ornamenting the exine are short and conical. The thin, perforate tectum is supported by predominantly conjunctate columellae. Caveae, the pockets between the

columellae and the foot layer, are weakly developed and not observable in the light microscope. The foot layer is thin and appressed to the thick endexine (Skvarla and Larson 1965).

Pales

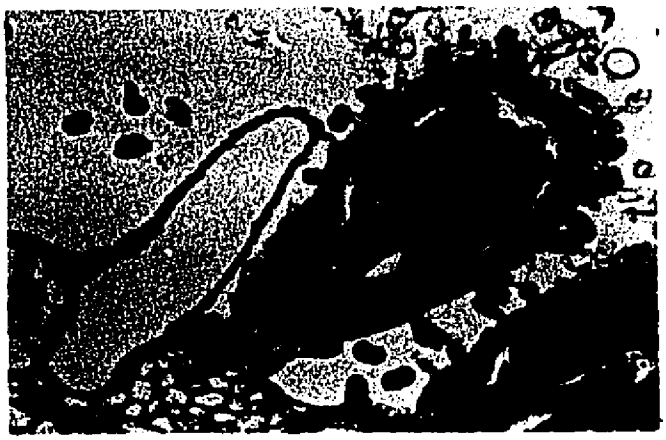
Pale associated with the disk flower (Figure 46A). The pale which subtends most of the disk flowers is small, hollow, inconspicuous, unvasculated, and it remains attached to the receptacle after the fall of the ray and disk flowers. In cross section the wall of the cylindrical pale is two cell layers thick. The cells are elongate parallel with the long axis of the pale. The inner cell layer of the pale is densely staining and possesses conspicuous nuclei. Such cells are very similar to the cells which line secretory canals. The base of the pale is bulbous and appears sunken in the receptacle.

Pale associated with the achene of the ray flower (Figure 46B). Unlike the pale associated with the disk flower the one associated with the achene of the ray flower is conspicuous, vasculated by two fibrous vascular strands, and deciduous. At maturity the pale is coriaceous due to the sclerification of the ground tissue. In cross section the inside portion of the curved pale possesses parenchyma which looks rather like aerenchyma due to large intercellular spaces. Two such pales are fused to the base of the achene and fall with it as a unit of dispersal.

The Vasculation of the Capitulum

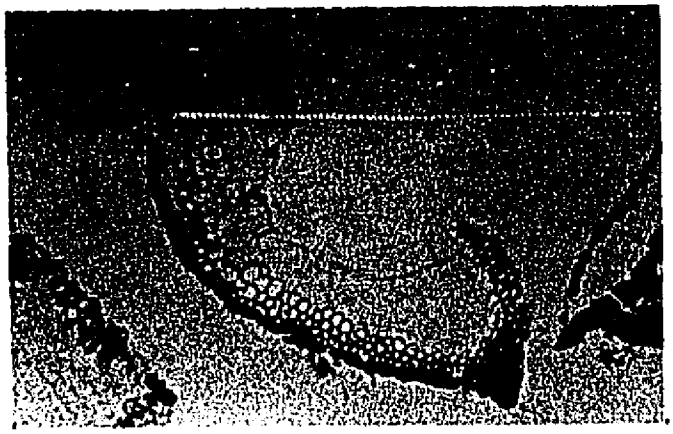
A separate section is devoted to the vasculation of the capitulum in order to emphasize its continuity. Over 70 tiny structures are amassed in the capitulum in an area less than 5 millimeters in diameter.

A



0.25 mm

B



0.5 mm

Figure 46. The Anatomy of the Pales of the Receptacle

A. Longisection of the pale associated with the disk flower.
B. Cross section of the pale associated with the ray flower.

Each of these structures has a vascular connection with the receptacle. The presence of xylem is the criterion used for determining vasculation. Observations were made from material which prior to paraffin preparation was cleared in sodium hydroxide and chloral hydrate according to the method of Foster (1953). Sections prepared in this manner were stained with safranin and fast green and cut at 50 microns (Kasapligil 1965). Material from locations in Arizona and Mexico including Baja California was examined. For ease of discussion the pattern of vasculation has been diagrammed and divided into seven stages (Figure 47).

Xylem reaches the base of the capitulum after passing through the peduncle in the form of three collateral vascular bundles (Stage 1). Nearing the receptacle two of the three bundles bifurcate to produce a total of five peduncular vascular bundles just below the receptacle (Stage 2). Each of these bundles bifurcates producing a total of ten bundles, five of which vasculate the five outer phyllaries (Stage 3). Subsequently, three of the remaining five bundles bifurcate creating a total of eight bundles (Stage 4). A trace derived from each of these eight vascular bundles vasculates the eight inner phyllaries (Stage 5). The remaining eight vascular bundles enter the pistillate flowers (Stage 6). Traces derived from the vein which entered the pistillate flower vasculate the two disk flowers immediately adjacent to the pistillate flower (Stage 6). Disk flowers centripetal to those associated with the achene receive their vasculature from traces derived from the bundles which entered the disk flowers near the achene (Stage 7).

The vasculature of the capitulum of P. mollis consists of repeated bifurcations which approach being dichotomous. No fusions of

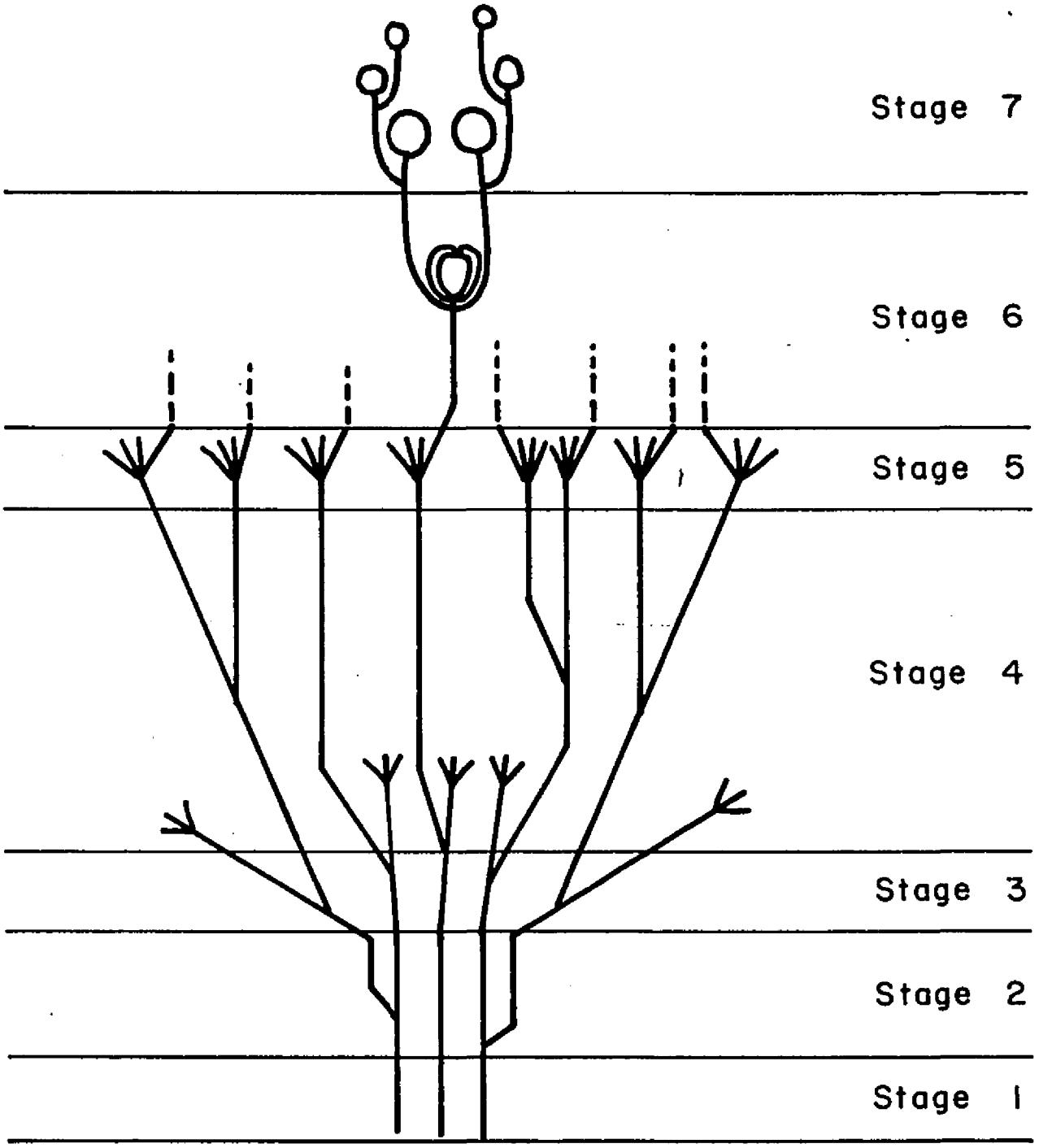


Figure 47. The Vasculation of the Capitulum

See text for explanation.

bundles were observed, only branching. Secretory canals are absent from the receptacle which consists primarily of thin-walled parenchyma.

CHROMOSOME ANALYSIS

Good meiotic figures (Figure 48) were obtained from capitula two millimeters in diameter and whose stamens possessed no yellowish color. A modified Carnoy's solution containing four parts chloroform, three parts ethyl alcohol, and one part glacial acetic acid was used for killing and fixing. Material was stored for several weeks in the refrigerator in 70 percent ethyl alcohol, but immediate use of fresh material gave better results. Collections made between 8:30 and 9:30 AM gave the greatest number of dividing pollen mother cells although figures were obtained at any time of day. Disk flowers were removed from the capitula and then mashed in acetocarmine with a rusty dissecting needle. Considerable pressure is required on the cover slip of the preparation to obtain an adequate squash.

Material transplanted from the Redington Pass road and from Buenos Aires, Arizona was used for the counts. Unfortunately, fresh material from Baja California was unavailable for examination. In five counts a diploid number of $2n = 36$ was obtained. Pairing appeared normal, but the chromosomes of P. mollis are very small and difficult to see. Sizes range from 1 micron to 1.2 microns.

Mitotic figures were also obtained in Parthenice using root tips of two and three day old seedlings. A pre-treatment of .005 M hydroxyquinone for three hours was given for the purpose of reducing chromosome length. After the pre-treatment the roots were killed and fixed in Carnoy's for at least five minutes. The roots were macerated

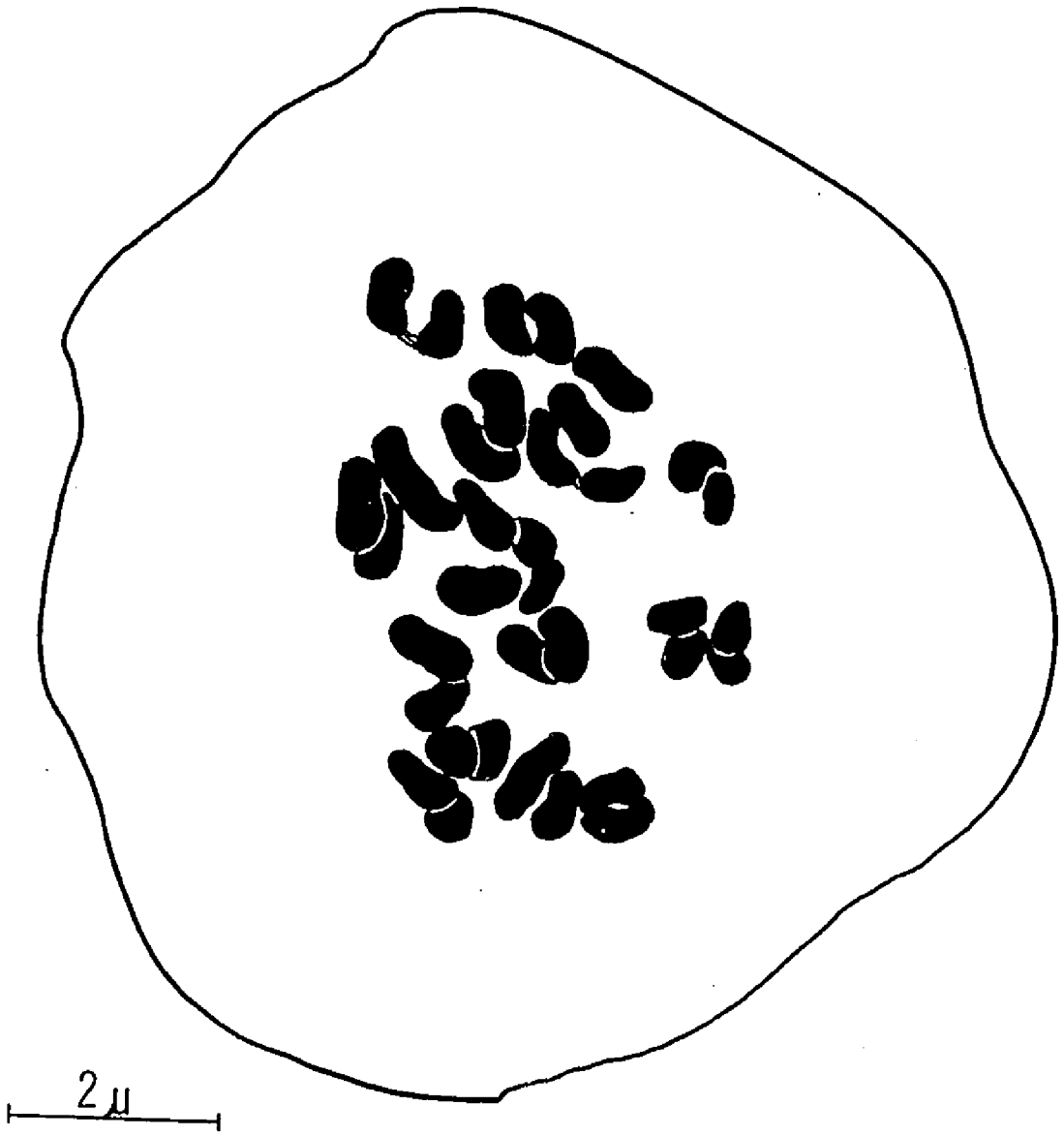


Figure 48. Meiotic Chromosomes of P. mollis at Diakinesis

in a 15 percent solution of hydrochloric acid for not less than 10 minutes. The roots are then washed in ethyl alcohol and stained in aceto-orcein. Such preparations yielded numbers of figures, but chromosomes were so long that counts could not be obtained.

THE MORPHOLOGY OF REPRODUCTION

Although considerable work has been done on genera closely related to Parthenice with regard to reproduction (see Esau 1944, 1946, and Artschwager 1943 on guayule), no reference to the reproductive cycle could be found for Parthenice. Entire capitula of various ages were preserved in Formalin-Aceto-Alcohol made with 50 percent ethyl alcohol. Material was embedded in paraffin and sectioned at 10 microns. Such sections were stained with safranin and fast green.

Reproduction in P. mollis is similar to that of Parthenium (guayule) in many respects. A single ovule occurs at the base of the ovarian cavity (Figure 49). In the initial stages of development the ovule primordium is upright and the megaspore mother cell appears to one side of the single integument. As the ovule matures the divisions concerned with integument formation cause the ovule to become inverted and anatropous. The megaspore mother cell is surrounded by a single jacket layer which is identified as the nucellar epidermis by Esau in Parthenium. Maheshwari (1950, p. 59) refers to this type of nucellus as tenuinucellate.

Megasporogenesis proceeds in the usual way and a linear tetrad of four megaspores is formed. The chalazal megaspore becomes the embryo sac. The embryo sac is of the monosporic type, and at maturity it possesses eight prominent nuclei (Figure 50). Just before fertilization the embryo sac is greatly elongate (130 microns) and narrow (17 microns). The antipodal end is greatly attenuated as Kirkwood (1910) has observed

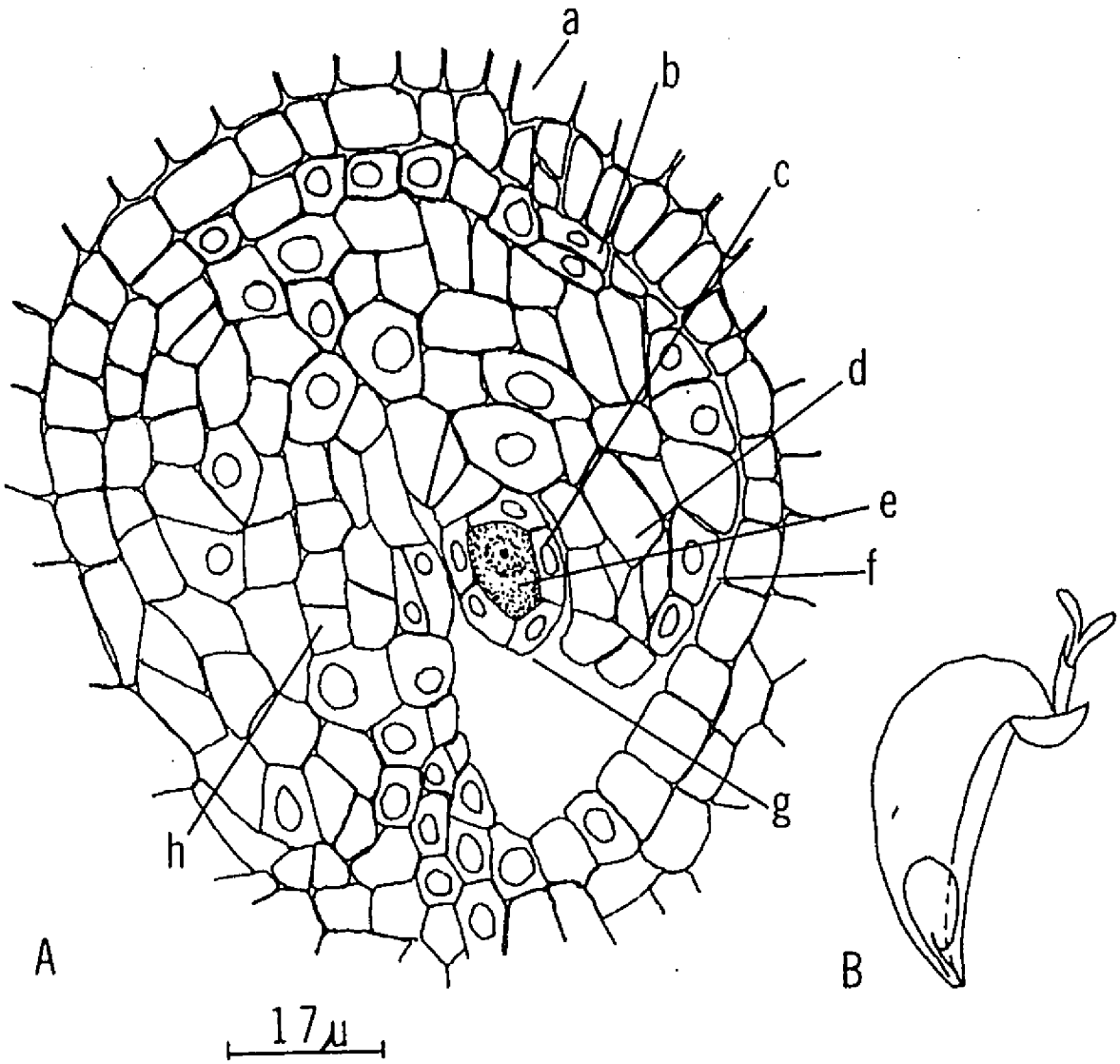


Figure 49. The Developing Ovule of P. mollis

A. a. endocarp; b. epidermis of integument; c. nucellar jacket; d. integument; e. megaspore mother cell; f. ovarian cavity; g. micropyle; h. funiculus. B. Diagram of the achene to show the orientation of the ovule.

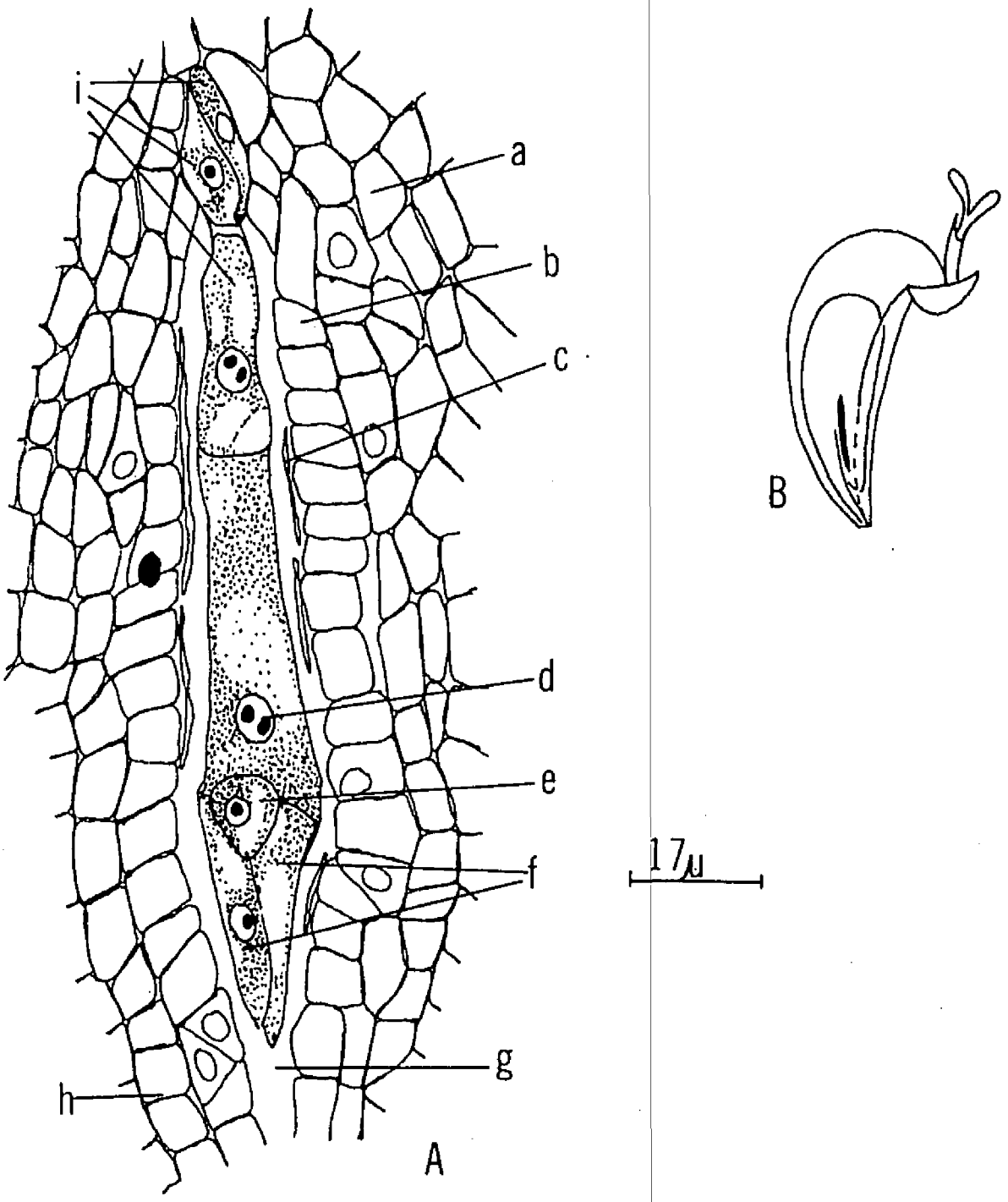


Figure 50. The Mature Embryo Sac as Seen in a Radial Section of the Achene

A. a. integument; b. epidermis of integument; c. collapsed nucellar jacket; d. fused polar nuclei; e. egg. f. syndergids; g. micropyle; h. funiculus; i. antipodals. B. Diagram of the achene to show the orientation of the embryo sac within the ovule.

for Parthenium. Such attenuation renders the antipodals difficult to see in entirety. No more than three antipodals were observed; most often they were not seen at all. Two synergids could be seen associated with the egg, and these appear to be attenuated toward the micropyle. Two polar nuclei contribute to the formation of the primary endosperm nucleus.

Attempts were made to observe the development of the microspore. Pollen was placed in solutions of tap water and sucrose in concentrations of 0.0, 0.5, 10, 15, and 20 percent and allowed to incubate at room temperature and at 90 degrees Fahrenheit. No pollen tubes were observed to form. Two partially germinated grains were found on the stigmas of fresh flowers. Pollen tubes of such grains were only 15 microns long. Subsequently stigmas of fresh flowers were macerated in the solutions described above and incubated both at room temperature and at 90 degrees Fahrenheit. Results were also negative indicating that the requirements for the germination of pollen grains of Parthenice may be somewhat unusual.

Fertilization produces a zygote and a 3n endosperm. The endosperm begins development directly after fertilization, and a cellular rather than a secretory endosperm is formed. The endosperm develops until it nearly fills the embryo sac at which time the first divisions of the zygote occur to give rise to the embryo (Figure 51). The development of the embryo is of the Capsella type: the first division of the proembryo is perpendicular to the divisions which produce the suspensor. A globose embryo is formed in which the basic meristems of the embryo are established (Figure 52). The globose embryo matures into a heart-shaped structure. At the time the seed is shed from the capitulum the embryo is

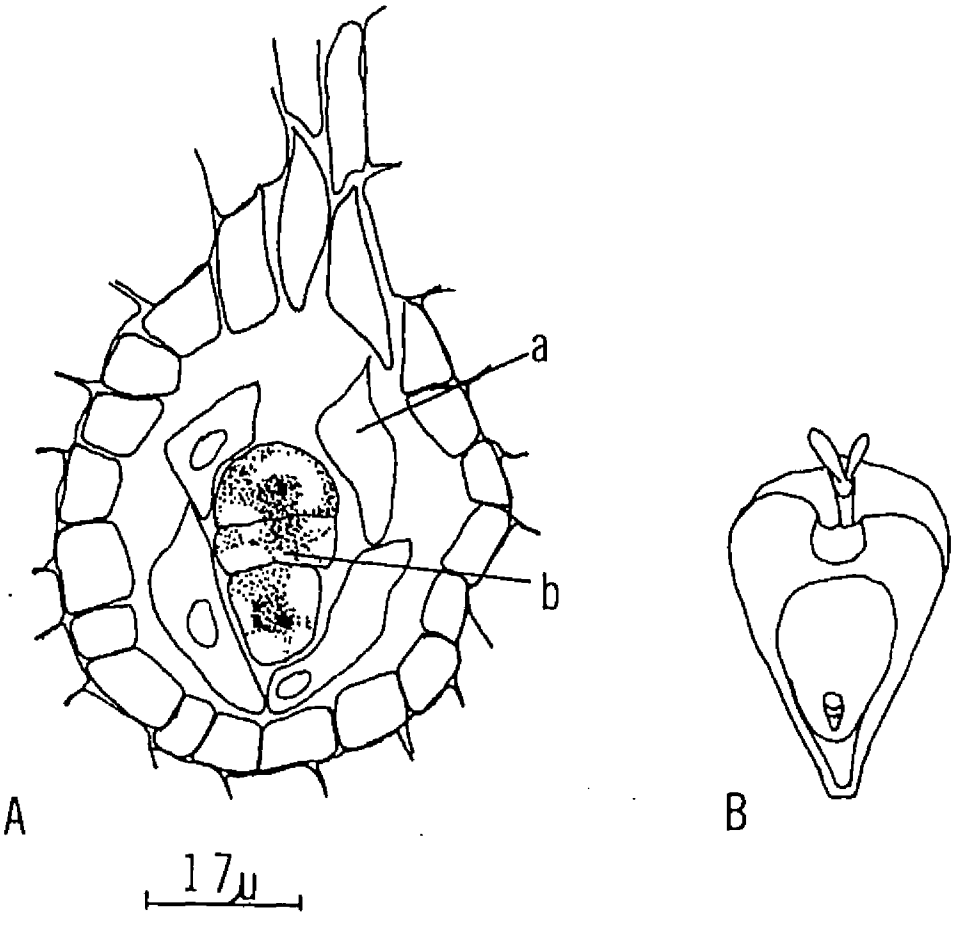


Figure 51. The Proembryo

A. The proembryo as seen in a tangential section of the ovule. a. endosperm; b. proembryo. B. Ventral view of the achene to show orientation of the proembryo in the ovule.

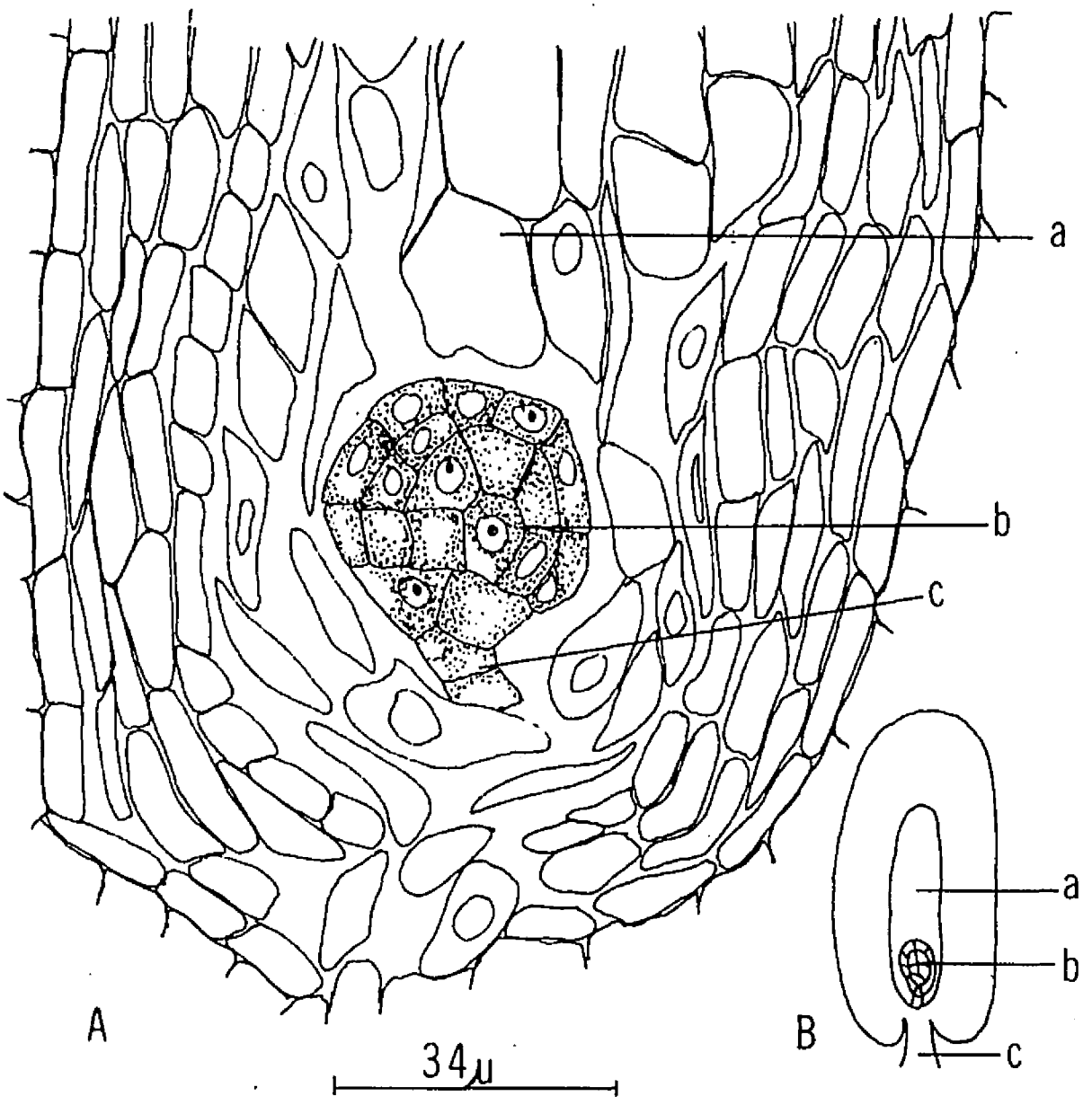


Figure 52. The Young Embryo

A. The young embryo as seen in a tangential section of the ovule. a. endosperm; b. embryo; c. suspensor. B. Diagram of the ovule to show the position of the embryo. a. endosperm; b. embryo; c. funiculus.

mature. It consists of two oval cotyledons, a radicle, and an apical meristem. Endosperm is present in very small amounts.

There appear to be no irregularities in the reproduction of Parthenice. The fact that no irregularities were observed correlates well with data regarding the number of normal embryos produced. The author examined 100 achenes which had been soaked in water for 12 hours and found 98 of them to contain normal, healthy embryos. The remaining two possessed embryos which appeared to have been attacked by fungi. Reproduction in Parthenice is completely sexual there being no form of asexual reproduction.

PATHOGENS

Few pathogenic microorganisms were observed to infect P. mollis and these seem not to produce very conspicuous effects. A rust, which is not completely known, Puccinia parthenoides Jackson, is found only on P. mollis. Telio and uredial stages were found on the leaves of specimens collected by Thornber (#1029) and Goodding (#43). A new collection of the fungus, made by the author, was identified by Dr. Robert L. Gilbertson, The University of Arizona. Examples of the fungus have not been seen in material from Baja California. The only other fungus present was a member of the genus Rhabdospora (Fungi Imperfecti). Infections of Rhabdospora are relatively common in Parthenice. Such infections were observed in collections from Baja California.

Although the leaves of P. mollis frequently appear to be badly chewed, especially toward the end of the summer, the most conspicuous insects observed were ants and aphids. Small, dark brown, conelike projections which appear to have small white caps were identified by Dr. George P. Wene to be injuries due to lace bugs (Stephanitis).

CHEMICAL ANALYSES

Few modern taxonomic studies (except those primarily biochemical in conception) include even the simplest data on the chemical constituents of the taxa in question. This is probably due to the apparently complex nature of biochemical methods. During the past few years much attention has been given to the problem of detection of biologically active substances in higher plants. Pharmacists, in particular, have developed a series of screening tests which are simple, rapid, and require a minimum amount of paraphernalia and yet give a reasonably accurate indication of the types of compounds present. Many such tests can be performed in the field as well as in the laboratory (Farnsworth 1966).

Various portions of P. mollis were subjected to a variety of pharmaceutical screening tests in order to determine types of compounds present which might be useful for taxonomic purposes. Fresh material was used wherever possible. The methods and results of these studies are described below.

Flavonoids

Flavonoids, which provide the yellow coloration for structures such as petals, may be detected in plant material by the addition of a small piece of magnesium ribbon to an alcoholic solution of plant material. Addition of a drop or two of concentrated hydrochloric acid yields an orange-red color in the solution if flavonoids are present. A positive reaction was obtained in Parthenice for the presence of flavonoids in

the inflorescence, but the test was negative for the root and vegetative leaves.

Phenols

One drop of a nine percent solution of ferric chloride was added to an alcoholic extract of vegetative leaves. A blue-black color was formed indicating the presence of phenols.

pH

A piece of litmus paper was placed in separate aqueous solutions of roots, stems, and leaves which had been soaking for an hour. The indicator showed that the solutions were approximately neutral.

Coumarin

A small amount of moistened leaf material was placed in a test tube which was covered with a piece of filter paper moistened with dilute sodium hydroxide. The test tube was placed in a boiling water bath for several minutes. The distillate collected on the filter paper was exposed to ultraviolet light. A positive test for coumarin is indicated by a yellow-green fluorescence. The test for coumarin in P. mollis was negative.

Saponins

A leaf of P. mollis was crumpled and placed in a small beaker of water for several hours. The solution was then vigorously shaken. A considerable amount of foam, which lasted for nearly two hours, was formed. Saponins are indicated by the presence of such froth. Another property of saponins or steroidal compounds is that they produce characteristic color reactions in the Lieberman-Burchard test for steroids. A

small sample of an alcoholic extract of the inflorescence was treated with five drops of acetic anhydride and then two drops of sulfuric acid which was allowed to trickle down the side of the dish. The color changes (mostly purples) which are characteristic for the presence of steroids occurred.

Alkaloids

A rapid field test for alkaloids, known as a spot test, was performed on P. mollis using Dragendorf's reagent. Juice from fresh plant material was prepared in a mortar with a small amount of tap water. The preparation was transferred to a piece of filter paper which had been impregnated with Dragendorf's reagent and allowed to dry. A known alkaloid sample was used on the filter paper as a control. This sample turned the paper a light orange-red color in a solid area. The extract from Parthenice leaves showed color change only around the periphery of the drop. Since the results of the drop test were inconclusive, a second, more definitive test for alkaloids was employed. A sample of fresh leaf material was extracted with 70 percent ethyl alcohol and dried on a steam bath in a small porcelain dish. Twenty milliliters ammonium hydroxide and 20 milliliters of ether were then added to the sample. The extract was placed in a separatory funnel and gently swirled. A few milliliters of the ether fraction were drawn off and treated with 5 milliliters of 50 percent hydrochloric acid. After a few minutes the solution was tested with Mayer's reagent (a mercuric potassium iodide reagent which indicates the presence of alkaloids by the formation of a precipitate). The addition of Mayer's reagent to the ether fraction from the leaves of Parthenice brought about the formation of a white,

cloudy precipitate. Since a false positive test is sometimes given if the extract has not been sufficiently acidified, more hydrochloric acid was added to the extract. The white precipitate remained visible indicating the presence of a tertiary alkaloid. Tertiary alkaloids are soluble in the ether fraction. The ammonium hydroxide fraction was also tested for the presence of alkaloids with Mayer's reagent, but no precipitate was formed. Quaternary alkaloids are soluble in the ammonium hydroxide fraction.

Resins

According to Tetley (1925), a solution of seven percent aqueous cupric acetate causes a precipitate to be formed if resinous plant pieces are soaked in it. Such a test only indicates that resins are present and it does not distinguish between types of resins. Pieces of Cedrus deodar (known to bear resin) and P. mollis were placed in separate petri dishes with the solution of cupric acetate. A whitish precipitate was formed in about fifteen minutes in the dish with Cedrus, but no precipitate formed in the dish with Parthenice even after several hours. It would appear that Parthenice is not a resin-bearing plant.

Rubber and Gutta

Rubber exists in two basic forms: the cis form (true rubber) and the trans form (gutta). Gutta is much less common than rubber as it occurs primarily in species of the genus Euonymus. P. mollis was tested for the presence of gutta by grinding some fresh plant material and heating it in a five percent solution of sulfuric acid for three or four minutes at just below boiling (Paech and Tracey 1955, p. 315). The yellow color

color which is formed if gutta is present did not appear in the extract of the leaves of Parthenice.

Three tests were performed on Parthenice in an attempt to demonstrate the presence of true rubber. A solution of chlorzinc-iodide will turn rubber-bearing latex a wine red color in sections of fresh plant material. The solution was prepared by dissolving 25 grams of anhydrous zinc chloride and 8 grams of potassium iodide in 8.5 grams of water. Iodine crystals were added until the solution was saturated. The solution was used immediately on samples of stem from Parthenice and Nerium oleander (known to bear rubber). Observations on color changes are seen with the aid of a dissecting microscope. The results were positive with Nerium and negative with Parthenice. It was interesting to note, however, that chlorzinc iodide was excellent for demonstrating the presence of the starch sheath in Parthenice.

The method of Artschwager (1943) for the demonstration of rubber in guayule (Parthenium) was used for Parthenice. Material from the stem was saturated in an alcoholic solution of Sudan III for 10 minutes and then washed in absolute alcohol. The sections were subsequently mounted in glycerin jelly for observation. The orange-staining pattern which Artschwager observed for Parthenium was not present.

Whittenberger's method described by Benedict in Paech and Tracey (1955) was used to detect rubber in Parthenice as this method has proved effective in those plants in which rubber is present in very small amounts. The test was positive for Parthenice resulting in a deep blue stain appearing in the cells surrounding the secretory canals in the stem. Such results are most interesting taxonomically as the genus

Parthenium includes rubber-bearing species. Furthermore, Parthenice had not been listed as a rubber-bearing plant of the Southwest by Buehrer and Benson (1945).

The procedure used to detect rubber in Parthenice was as follows. Hand sections were made of fresh material. These were placed in a 5 percent Clorox solution at room temperature for from 5 to 10 minutes. Then they were transferred to 20 milliliters of a 9 percent solution of potassium hydroxide in 95 percent ethyl alcohol for about one hour at room temperature. After several washings in distilled water with a final washing in 95 percent ethyl alcohol, the sections were stained overnight in a 0.05 percent solution of oil blue NA in 70 percent ethyl alcohol in a closed container. The stained sections were then washed for a few seconds in 50 percent ethyl alcohol, placed in 40 percent glycerin in water for a few minutes to clear, then mounted in glycerin jelly.

TAXONOMIC TREATMENT

Description of the Genus Parthenice

Parthenice is a monotypic genus, therefore the description for the genus is the same as that for the species. The one species P. mollis is described below.

Description of the Species of Parthenice

Parthenice mollis A. Gray, Plantae Wrightianae, II, 85-86. 1853.

Plants aromatic, cinereous-puberulent erect annuals to two meters. Stems normally branched only in the inflorescence. Leaves various, alternate; those below the inflorescence triplinerved, ovate, long petioled, toothed to coarsely crenate, some with the lamina decurrent on the petiole for several centimeters; leaves of the inflorescence somewhat reduced, ovate-lanceolate, toothed to entire, cotyledons small, simple glabrous, ovoid, petioled at maturity. Capitula hemispherical, numerous, panicled, sessile or pedunculate, greenish-white, glandular; phyllaries in two distinct series, the outer series five, ovate, hyaline, closely investing but not fusing with the achene, deciduous. Receptacle convex, paleaceous with two types of pales; those associated with the ray flowers coriaceous, linear, purple-mottled, deciduous and curved at the apex; those associated with the disk flowers minute, conical, hollow, persistent. Ray flowers eight, pistillate, corollas minute, greenish, densely glandular, scarcely ligulate, stigma branched, papillate. Disk flowers staminate, the pistil rudimentary, the corolla

five-toothed, actinomorphic, densely pubescent and glandular at the apex, stamens five, loosely coherent, tipped with a deltoid appendage, stigma of the brush type, unlobed, flower shortly pedicellate, the pedicels remaining attached to the receptacle after the dehiscence of the flower. Pollen tricolpate, echinate, yellowish, oblong when dry. Achenes dorsoventrally flattened, obovate, tuberculate, glabrous, sessile, apiculate, falling away at maturity with the pales of the opposed disk flowers. Pappus none on the disk flowers, occasionally represented by a tooth in the ray flower. Chromosome number 2n = 36. Southern slopes rocky hillsides or along washes. Southern Arizona, Northern Mexico, Southern Baja California.

The single species of Parthenice, P. mollis is treated here as being composed of two varieties. The possibility of such a treatment was first suggested to the present writer several years ago by Miss Annetta Carter who also proposed the specific epithet "peninsularis" for the new form. Numerous collections and measurements have shown that the two varieties of P. mollis may be readily distinguished by the length of the pales which are attached to the achene (Figure 53). In material from Arizona, Sinaloa, Chihuahua, and Sonora the pales are longer than the body of the achene while in material from Baja California they are shorter. The two varieties are further distinguished by their geographical distribution; the form with the short pales being confined to southern Baja California.

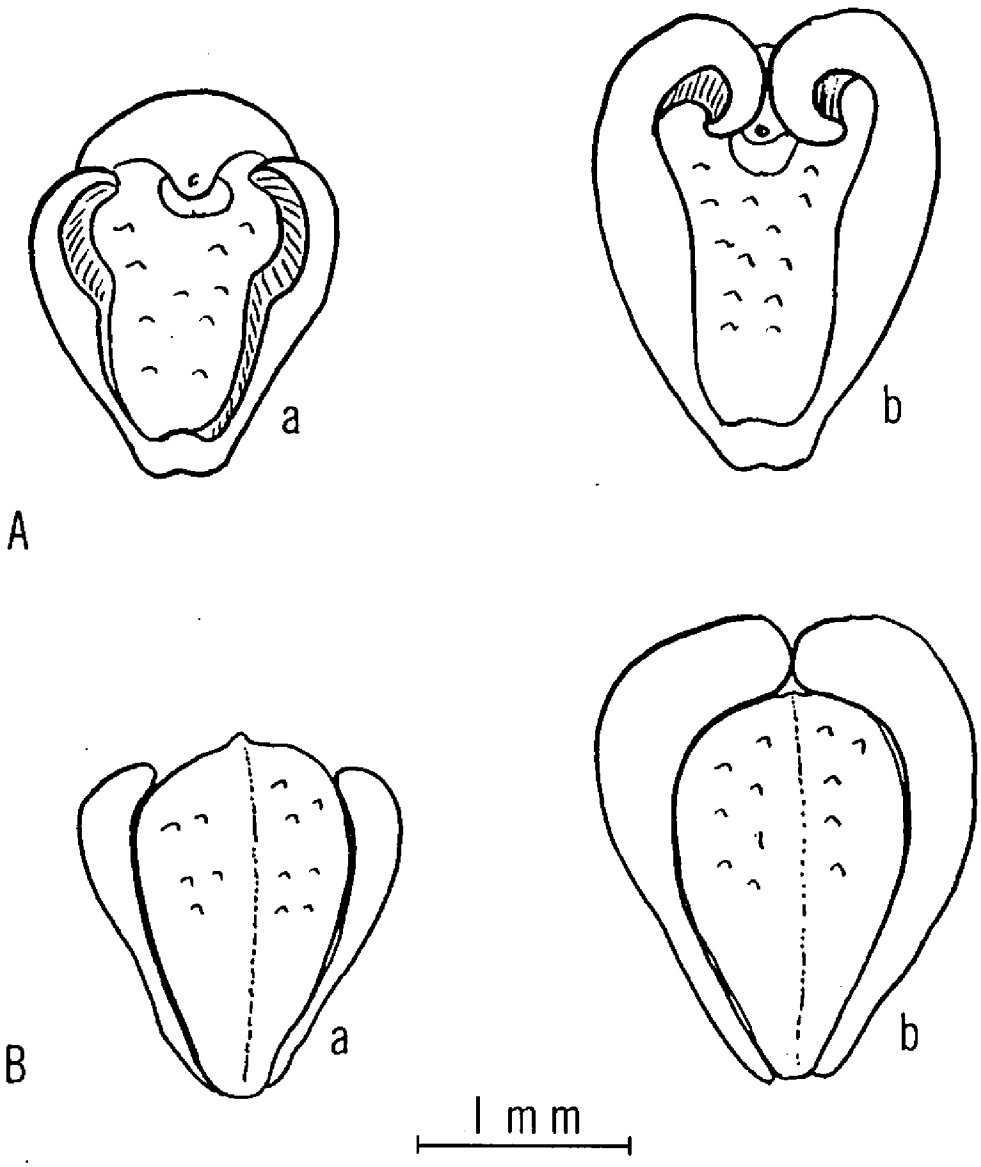


Figure 53. Comparison of Achenes from Baja California with Achenes from Sonora, Mexico and Arizona

A. Ventral view of achene. a. Baja California; b. Arizona. B. Dorsal view of achene. a. Baja California; b. Arizona.

Descriptions of the Varieties of Parthenice mollis

1. Parthenice mollis var. mollis

Wings of the achene longer than the body of the fruit. Plants native in Southern Arizona and Northern Mexico.

Type Locality: Mountain ravine at Santa Cruz, Sonora, Mexico. Charles Wright 1208, September 1851 (Holotype:GH).

Distribution: Sonora, Sinaloa, Chihuahua, Southern Arizona; frequently found along washes or amongst boulders having a distinct southern exposure. In Mexico often found along roadsides in disturbed sites where runoff is available.

Specimens Examined: ARIZONA. Pima County: "Rocky slopes. Box Canyon," Goodding 487-58 (ARIZ); "Stone Cabin Canyon, Santa Rita Mts., elev. 5000 ft." Thornber 130 (ARIZ); "Along edge of dry wash. South end of Coyote Mts," Barr and Goodding 60-385C (ARIZ); "Along lower Alamo Wash Organ Pipe National Monument," Ora M. Clark 11015 (GH); "One mile south of Tubac, Arizona, elev. ca. 3000 ft." Reese 7 (ARIZ); "Toro Canyon, Baboquivari Mts," Harrison 4755 (ARIZ); "Wild Burro Canyon, Tortolita Mts," Reese 12 (ARIZ); "Near Pacing Horse Ranch, Canyon del Oro, Santa Catalina Mts," Reese 171 (ARIZ); "Pontatoc Wash, foothills Santa Catalina Mts," Reese 208 (ARIZ); "Rocky slope, Redington Pass Road, Southern tip of the Santa Catalina Mts.," Reese 3 (ARIZ). Santa Cruz County: "Rocky hillside, road to Lochiel, Patagonia Mts," Reese 8 (ARIZ); "Occasional in canyon bottom, elev 4000 ft., Sycamore Canyon near Ruby," Darrow and Haskell 2079 (ARIZ).

MEXICO. Sonora: "Along road to Ures, elev. 1000 ft.," Reese 176 (ARIZ); "10 miles south of Benjamin hill, along HWY 15," Reese 174 (ARIZ); "Amongst rocks 36 miles west of Cananea," Reese 183 (ARIZ); "Along HWY 15 60 miles south of Guaymas, elev. 50 ft.," Reese 179 (ARIZ); "30 miles south of Hermosillo on HWY 15, elev 700 ft.," Reese 177 (ARIZ); "Puerto de Huepari, nw of Aribabi, Rio Bavispe, elev. 4550," White 2771 (GH); "San Bernardo, Rio Mayo, vernacular 'kotasulu'" Gentry 1622 (ARIZ). Chihuahua: "Rio Aros," LeSueur (s.n.) (GH). Sinaloa: "On hillside roadcut north Culiacan, elev. 830 ft.," Reese 182 (ARIZ); "Maraton, 12 miles west of Culiacan," Gentry 7059 (GH); "Sandy margin of river bottom, Palmar, 50 to 70 miles north of Guamuchil, elev. 1000 ft.," Gentry 6102 (ARIZ); "Plants collected at Ymala, Mexico Aug. 16 to 25, 1891.," Palmer 1430 (ARIZ).

2. Parthenice mollis var. peninsularis

Differt a var. mollis alis achenii fructificatione brevioribus. Plantae limitatae ad Californiam Inferiorem.

Differs from var. mollis in that the wings of the achene are shorter than the body of the fruit. Plants limited to Baja California.

Type Locality: Parkinsonia association; margin of large rain basin, "La Laguna" hills east of La Paz, Baja California, Annetta Carter 2615, 31 March 1949 (Holotype: UC).

Distribution: Moist arroyo margins, hillsides and slopes, dry lake bottoms; Baja California, San Gregorio south to La Paz and Santiago.

Specimens Examined: "Las Cuevitas, below Comondu," Gentry 4233 (UC); "Camp and hillsides near Comondu," Wiggins 5491 (UC); "Pumice slopes and volcanic rocks on southwest side of Tres Virgenes," Wiggins

7927 (UC); "13 miles west of Canipole," Shreve 7112 (ARIZ); "LaPaz," Palmer 66 (GH); "side arroyo heading into Mesa San Alejo, southwest of Rancho El Horno (northeast of San Javier)," Carter and Ferris 3767 (UC); "Broad arroyo north of San Javier," Carter 5050 (UC); "Los Dolores," Bryant (s.n.) (UC); "Santiago," Jones 24626 (UC); "San Gregorio," Brandegee (UC).

SUMMARY

In the introduction to the present paper it was stated that an attempt was being made to characterize the biology of a plant, Parthenice mollis. The purpose of collecting such data was to provide a more adequate basis for the proper classification of the genus Parthenice. During the course of study a new variety of Parthenice mollis was described. Furthermore, a unique stomatal structure was located on the stem and described. Finally, much was added to the distributional data, examples of which are deposited for the most part in the Herbarium of The University of Arizona.

At this time no new conclusions as to the taxonomic position of P. mollis can be offered. Only when sufficient data are available for genera such as Parthenium, Iva, and Ambrosia can proper estimations of relationships be made. The work with Parthenice is just a beginning; much more needs to be done. In place of tenuous speculations on the origin and relations of Parthenice a list of characters which should be worthy of consideration for comparative work is being offered. It is hoped that this approach will be of great value in future studies.

APPENDIX

LIST OF BOTANICAL CHARACTERISTICS OF *PARTHENICE MOLLIS* A. GRAY

I. CHEMISTRY AND PHYSIOLOGY

Character	Description
germination	
time required for	36 to 48 hours
inhibitor	present, water soluble
conditions for	sufficient water
flowering time	Baja California: April or Sept.; Sonora and Arizona: Aug.-Sept.; Greenhouse: any time
chemical analyses	
alkaloids	one tertiary alkaloid
coumarin	absent
flavonoids	present
phenols	present
resins	absent
rubber	present
gutta	absent
saponin	present
pH	neutral
fragrance	aromatic

II. ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

Character	Description
life zone	Upper Sonoran
habitat	
slope exposure	usually southern
soil type	sandy loam high in organic content
most frequent associate	Prosopsis
local distribution	localized, colonial populations
general distribution	Arizona, Sonora, Baja California, Sinaloa, Chihuahua

III. CYTOLOGY AND REPRODUCTION

Character	Description
chromosomes	
size (diakinesis)	1 micron to 1.2 microns
pairing	normal
number	2n = 36
general behavior	normal
compatibility relations	self fertile
megasporogenesis	
spore formation	monosporic
ovule position	anatropous at maturity
endosperm type	cellular
ploidy of endosperm	3n
synergids	two
antipodals	three
polar nuclei	two
shape of mature embryo sac	greatly elongate (17 x 134 microns)
nucellus type	tenuinucellate
number of integuments	one
embryogenesis	
proembryo	*Capsella* type
young embryo	
length	0.1 millimeters
cotyledons	ovoid
mature propagule	ovary of the pistillate flower, seed coat, little endosperm, mature embryo

IV. PATHOGENS

Character	Description
parasitic fungi	*Puccinia parthenoides* *Rhabdospora* sp.
insects	ants, aphids, lace bugs

V. ANATOMY AND MORPHOLOGY

Character	Description
cotyledons	
length of blade	3 mm at maturity
pigmentation	chlorophyllous at maturity
venation	reticulate
longevity	about three weeks
cotyledonary bud	active, may produce a short branch
anatomy	internal differentiation slight
stomata	absent
midrib	present, inconspicuous
foliage leaf	
phyllotaxy	2/5
position	alternate
petiole	
length	absent to 15 cm
number vascular bundles	five
secretory canals	present
blade	
venation	pinnate to palmate
apex	acute
base	acute
margin	coarsely toothed to entire
length	0.5 to 30 cm
width	0.5 to 30 cm
veins (lower surface)	prominent
veins (upper surface)	slightly depressed
areole	
size	about one millimeter square
veins per	2 to 7
shape	extremely variable on any one plant, lanceolate to broadly ovate
palisade parenchyma	adaxial, two storied
spongy parenchyma	abaxial, three to four layers
cell wall (epidermis)	strongly undulate in surface view
secretory canals	present only in main veins
stomata	
position	random and slightly elevated
number on abaxial surface	about 100 per mm square
number on adaxial surface	about 50 per mm square
ratio of stomata of abaxial and adaxial surfaces	1:2
subsidiary cells	none
substomatal chambers	elongate or shallow
length of guard cells	about 30 microns

Character	Description
stem	
branching	unbranched except in inflorescence
height	up to 3 meters
width (widest)	three cm
apex	
shape	broadly hemispherical
tunica	two layered
cortex	
cortical parenchyma	6 to 9 layers
collenchyma	5 to 6 layers
secretory canals	present near phloem
starch sheath	present outside phloem and secretory canals
epidermis	simple, persistent
pith	
color	white at maturity
secretory canals	present near xylem
vascular bundles	up to 30 at any level, collateral
structure of xylem	
vessels	
arrangement	solitary or in groups of 4 to 5, diffuse, porous
pits	oval to elongate
caudae	present or absent
shape	barrel or elongate
widest width	50 microns
longest length	175 microns
number per sq mm	68
perforation plate	horizontal or oblique
fibers	
greatest length	300 microns
greatest width	8 microns
distribution	present in xylem and phloem
phloem	
distribution	extramedullary
sieve plates	15 perforations per plate
root	
basic form	tap root with few lateral branches
hairs	unicellular
radicle	emerges from base of achene
primary xylem	
direction of maturation	exarch
number of protoxylem points	usually two
number of cells in primary xylem	no more than ten
pericycle	produces first formed secondary xylem

Character	Description
root (continued)	
periderm formation	present, begins as the cambium becomes active
endodermis	present, with casparian strips
secretory canals	absent
trichomes	
glandular trichomes	
length	0.2 to 0.4 mm
basic	biseriate, multicellular, differentiated into head and stalk
total cell number	up to 20
origin	single papilla of an epidermal cell
distribution	on all aerial plant parts
behavior	head secretes clear yellowish exudate at maturity
nonglandular trichomes associated with vegetative foliage	
length	1.0 mm
basic structure	multicellular, uniseriate
total cell number	up to 10
origin	single papillate epidermal cell
distribution	found only below inflorescence
terminal cell	
shape	taper pointed
length	up to 150 microns
texture	slightly hispid
nonglandular clothing hair associated with inflorescence	
length	0.5 mm
basic structure	multicellular, uniseriate
total cell number	up to 6
origin	single papillate epidermal cell
distribution	on all parts of inflorescence, flowers, and capitula
terminal cell	
shape	blunt
length	60 to 80 microns
texture	soft, curved, appressed
flowers	
ray flower	
size at maturity	2 mm
attachment	sessile, deciduous
pappus	absent or rudimentary

Character	Description
flowers (continued)	
ray flower (continued)	
stigma	
form	bilobed
vasculation	two bundles which diverge into lobes of stigma
collecting hairs	
shape	elongate, papillate
cell contents	densely staining with conspicuous nuclei present
distribution	restricted to lateral lobes of stigma
corolla	
symmetry	zygomorphic
color	greenish
ligule	minute
vasculation	irregular
persistence	deciduous with stigma
achene (pistil)	
shape	obovate, flattened tangentially
color	dark brown
texture	tuberculate
apex	centripetally curved with bulbous apiculation present
mesocarp	fibrous
exocarp	one or two layers of palisadelike cells
pigmented layer	located between mesocarp and exocarp
nature of mesocarp cells facing pigmented layer	distinctly papillate
vasculation	four veins: one ventral, one dorsal, and two lateral
stamens	absent
disk flower	
length at maturity	1 to 1.2 mm
attachment	pedicellate, deciduous with pedicel remaining attached to receptacle
pappus	none
stigma	unlobed, brush type
corolla	
symmetry	actinomorphic
color	greenish-yellow
lobes	five
veins	five anastomosing a lobe of corolla
persistence	deciduous

Character	Description
flowers (continued)	
disk flower (continued)	
stamens	
number	five
coherence	loose
base	unornamented
apex	hollow deltoid terminal appendage
locules	four: two large and two small
tapetum	single layer
pistil	rudimentary
capitula	
shape	hemispherical
attachment	sessile or pedunculate
arrangement on stem	panicoid branches of cymose clusters
number	numerous
number of ray flower per capitulum	eight
number of disk flowers per capitulum	30 to 40
pales	
disk flower type	
persistence	remains attached to receptacle
form	conical, hollow, hyaline
ray flower type	
persistence	deciduous with achene and attached to it
form	club shaped, solid, coriaceous
receptacle	
shape	convex
texture	paleaceous with two types of pales
anatomy	primarily parenchymatous
secretory canals	absent
phyllaries	
outer phyllaries	
texture	herbaceous
fusion	none
shape	ovate-lanceolate
arrangement	slightly overlapping
persistence	persistent after fall of lowers
secretory canals	present
inner phyllaries	
texture	hyaline
fusion	none
shape	ovate-ovoid
arrangement	definitely overlapping
number	eight
persistence	deciduous with achene but not attached to it
secretory canals	present

Character	Description
peduncle	
length	absent to 2 cm
width	2 mm
secretory canals	present, extramedullary
vasculature	usually 2 or 3 collateral bundles
flowering stem apex	
shape	bulbous
tunica	two layers
pollen	
color	pale yellow
shape when dry	oblong
shape when wet	round
number of pores	three
type of furrows	elongate from pole to pole
spines	present, conical
internal tectum	loosely organized
foramina	absent
foot layer	appressed
columellae	branched
inner aperature	10.6 microns
wall thickness	2.5 microns
development of microspores	simultaneous
state of anthesis	tube and generative nucleus present

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