AN ABSTRACT OF THE THESIS OF

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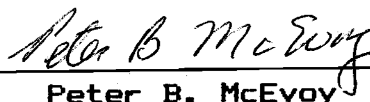
Title: A COMPARATIVE ANATOMICAL STUDY OF GALLS CAUSED BY THE MAJOR CECIDOGENETIC GROUPS, WITH SPECIAL EMPHASIS ON THE NUTRITIVE TISSUE

Abstract approved: 
Peter B. McEvoy

The anatomies of 44 galls are discussed with special attention given to the development, longevity, and tannin content of the nutritive tissues.

Within the main section of the thesis, representative galls from the major cecidogenetic groups, with the exception of bacterial and Australian scale galls, are studied. These include galls caused by fungi, nematodes, mites, moths, sawflys, scales, aphids, adelgids, tephritids, cecidomyiids, and cynipids. Three leaf mines are also described. Observations were taken from thin sections (plastic embedment) with a light microscope.

The galls are arrayed along a continuum of increasing structural complexity, as judged by the degree

of gall tissue differentiation. The sclerenchymatous "protective" zone and nutritive cells are used as indicators of gall complexity and of strength of the gall-former's influence over host plant tissue. Starting with the fungal galls, then moth and sawfly galls, to the thrips, scale, mites, nematode, cecidomyiid, and cynipid galls, one sees greater differentiation of gall tissues, with an increasingly distinct nutritive layer. A sclerenchyma zone develops only in midge and wasp galls.

The longevity of the nutritive tissue varies from gall to gall. Generally, the nutritive tissue is maintained in an enriched state for an extended period only in galls caused by cynipids (and perhaps by nematodes). The mites and midges show enriched nutritive cells only in early gall development. No distinctive nutritive tissue occurs in the aphid galls that were studied.

Generally, nutritive tissue contains less tanniferous material (as detected by the ferrous sulfate stain) than do either peripheral gall tissues or cells of the leaf. Thus, many gall-formers avoid tannins by directing the development of the cells upon which they feed.

The epilogue includes a list of features shared by many galls and by gall-forming organisms. Gall-formers also share several characteristics with other types of

parasites.

The three appendices include 1) an anatomical study of eight galls on shrubs from the drylands of eastern Oregon (mite, cecidomyiid, tephritid, and moth galls), 2) a discussion of fossil galls and leaf mines as indicators of the age and stability of these co-evolutionary relationships. Two galled acorns from the La Brea Tar pits (Los Angeles, California) are described in this section. Lastly, 3) a discussion of economically important galls is provided. This last appendix addresses the question of why there are relatively few gall-forming insect pests, and includes a discussion of the supposed benignity of insect galls.

A Comparative Anatomical Study of Galls Caused by the Major Cecidogenetic Groups, with Special Emphasis on the Nutritive Tissue

by

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DEDICATION

This dissertation is dedicated to my parents, Dr. H. Gordon Larew and Mrs. Mary Jo Larew, and to my two sisters, Jane Larew and Liz Larew. They listen and care.

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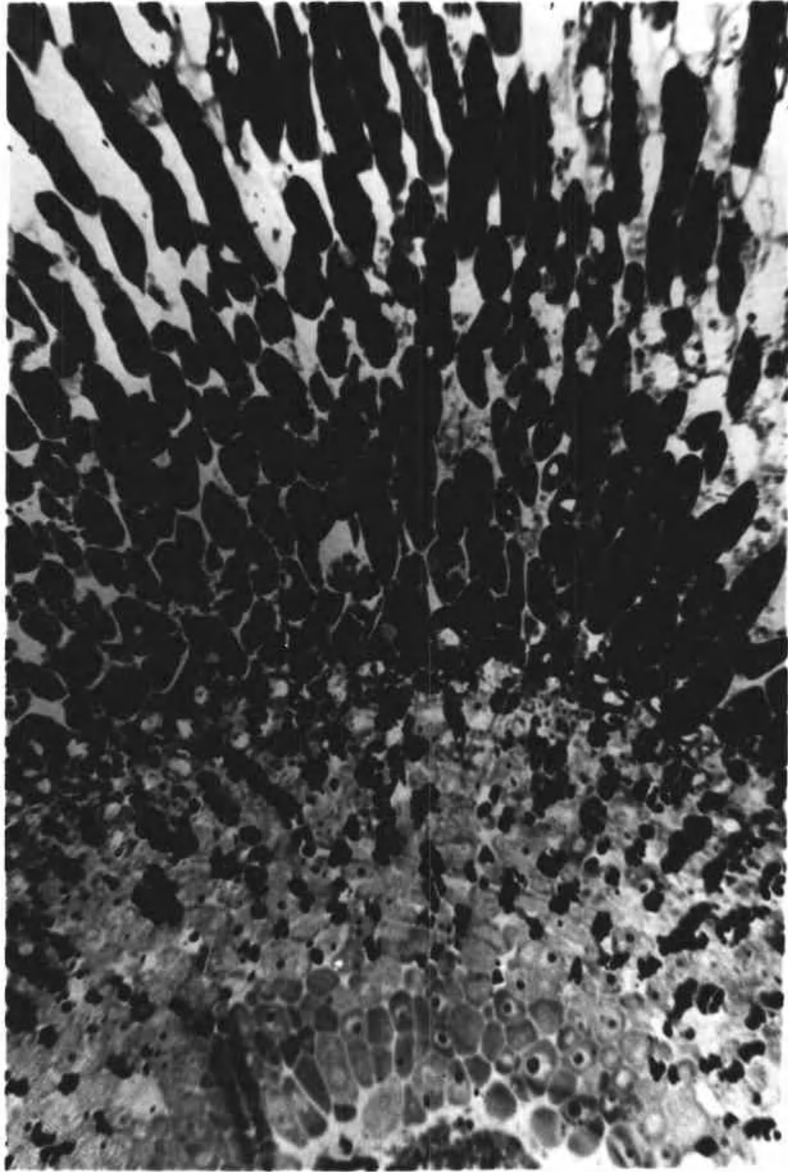
Section through speckled oak apple gall on *Quercus garryana* Dougl. caused by *Besbicus mirabilis* showing larval cavity (at bottom of photograph), larval capsule wall, and radiating fibers (top of photograph). Specimen collected VII/10/80. 730X.



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A COMPARATIVE ANATOMICAL STUDY OF GALLS CAUSED BY THE MAJOR CECIDOGENETIC GROUPS, WITH SPECIAL EMPHASIS ON THE NUTRITIVE TISSUE

INTRODUCTION

This dissertation is a survey of representative plant galls caused by most of the gall-forming groups of organisms. I have observed and studied galls caused by fungi, nematodes, mites, aphids, scales, thrips, cecidomyiids, sawflies, moths, and cynipids for intra- and intergroup patterns in gall morphology. To highlight the unique characteristics of the gall-forming guild I have briefly compared this guild to another endophytophagous group of insects, the leaf miners.

In addition, I have placed special emphasis on studying the diet of the various groups of gall-formers. As first attempts, such descriptions will highlight general trends and suggest future approaches.

The specific objectives are:

1) To assess the degree of tissue reorganization and, thus, the complexity of the galls. In some cases these observations are made over the period of gall development.

2) To study the nutritive cells with the light

microscope. In some cases I record the cytological changes that occur in these cells through time, and in some instances I interpret these changes in light of life-stage changes of the gall-former.

3) To determine the pattern of deposition of tannins in many of the galls, and then to discuss the pattern with the view that tannins are host plant defensive compounds that are best avoided by the gall insects.

By following the development of several galls and pointing to trends in both gall development and nutritive cell characteristics, I hope to contribute to an understanding of the dynamics of gall formation. In so doing, I also suggest novel work of both a specific and general nature which will further that understanding.

LITERATURE REVIEW

This review emphasizes studies that discuss the influence of gall-formers on plant anatomy, with special attention given to studies of nutritive (=food) cells within galls. In toto, few galls have been examined in any detail (Meyer, 1969b). Of the roughly 15,000 types of galls in the world, I estimate that between 100 to 200 have been studied in detail. Certain large floras (e.g. the eucalypt galls) are completely unstudied. With this small sample size in mind, we must make generalizations cautiously.

At the same time, there is no dearth of information. The cecidological literature is a large collection that can trace its beginning to the ancients. It was, however, not until the late 17th and early 18th centuries that the study of galls became active. Malphighi (1686), for example, was the first to clarify that galls were not seeds, but were abnormal plant structures caused by insects. For his insight, he is recognized as the father of cecidology. Both Fockeu (1889) and Plumb (1953) discuss the early history of cecidology.

Most of the significant early studies were made by the Germans and French. The best English summary of these is included in M. S. Mani monograph, "The Ecology

of Plant Galls" (1964). I have drawn on his summaries and upon the original sources or translations of them.

Classification System Based on Host Tissue Disruption

With the increase in number of carefully studied galls came classification schemes based on gall morphology. The authors of these schemes sought to organize the galls into manageable units, and also to highlight the interactive process between gall-former and plant. Because I use gall anatomy to comment upon the interaction, I think it useful to briefly review the schemes.

In his "Pathologische Pflanzenanatomie" (1903) and in his "Die Gallen der Pflanzen" (1911) Kuster divided galls into two major classes.

1) Organoid galls are abnormal modifications of plant organs. "The form, number, or distribution of organs is modified in organoid galls" (Bloch, 1953). The internal anatomy of the attacked organ is not completely disrupted by the gall-former. Usually the attacked organ remains recognizable. For example, flowers and leaves may occur in the wrong place. Fasciations (ribbon-like stems resulting from fusion of

apices), chloranthy (greening of petals) and witches' brooms (many buds developing at one spot) are typical organoid galls.

Bacteria, fungi, mites and aphids are representative agents that cause organoid galls. Recently a virus has also been implicated as the disease agent causing an organoid gall on *Salix* (Westphal, 1977). If the gall-forming agent is an animal, it is generally found in large numbers on the surface of the affected plant part.

Until recently organoid galls were not suspected of showing a distinct enriched nutritive region. Psyllids, for example, that cause chloranthy and brooming of *Juncus articulatus* L. feed on the phloem as do non-gall-forming psyllids (Schmidt, 1966; Schmidt and Meyer, 1966). Westphal (1977) has shown, however, that eriphyoid mites that cause virescence (abnormal flowers) induce the development of a nutritive layer similar to that seen in highly complex cynipid galls.

Generally, organoid galls have been ignored. They are not as eye catching as the more complex galls. They may provide us, however, with a unique opportunity, for if cases exist in which a gall-former is feeding on unaltered plant tissue then we can factor out the nutritional benefits of gall living and instead, focus solely on the other benefits of this life habit. If not

for an enriched diet, why form a gall?

2) <u>Histioid galls</u> are characterized by complex and sometimes novel types and arrangements of internal tissues. Like organoids, hyperplasia and hypertrophy occur in histioid galls, but unlike organoids, some degree of de- and re-differentiation occurs in histioids.

Kuster further subdivided the histioid galls into two groups, the kataplasmas and prosoplasmas. What follows is a review of the characteristics of those two types, and a discussion of the relationship between them.

a) <u>Kataplasmas</u> are histioid galls that possess no regular external form, size, volume or period of development. Usually tissues within these galls are less differentiated (e.g. callus-like parenchyma) than are those in ungalled parts. Cecidogenetic agents that cause kataplasmas (e.g. slime molds, nematodes, mites, bacteria, fungi, homopterans) are not localized in a single spot on the plant organ, but either spread through the tissues or wander and feed over the plant's surface. Thus the field of stimulation and proliferation is large and is a function of the seemingly random wandering of the gall-former. Frequently, if the kataplasma is caused by an animal, both immature and adult life stages live in

and contribute to the maintenance of the kataplasmas. Many of the economically important galls are kataplasmas.

Although numerous distinct tissue layers are not present in kataplasmas, these galls may possess a well defined nutritive tissue. Root knots caused by nematodes, for example, are mostly hypertrophied parenchyma. Surrounding the nematode's head, however, are multinucleate nurse cells that share many of the characteristics of nutritive cells found in insect-caused galls. In another example, the mite-caused gall of vegetative buds on Corylus avellana is listed by Kuster as a kataplasma. Two reports (Westphal, 1977; Larew, 1977) have described the epidermal nutritive cells from this gall. Similarly, nutritive cells or tissues from coccid (Parr, 1940), from aphid (Rohfritsch, 1976) and from adelgid (Plumb, 1953) kataplasmas have been described.

Whether other kataplasmas, such as those caused by bacteria and fungi, contain enriched nutritive cells is unclear. Root cells invaded by Rhizobium may show an enrichment (Newcomb, et al, 1979). Plant cells invaded by the fungus, Gymnosporangium juniperi-virginianae, displays a

large vacuole, a conspicuous nucleus..., ribosomes,

> chloroplasts, mitochondria, dictyosomes, lipid bodies, and strands of endoplasmic reticulum...We did not detect any morphological abnormalities in any host organelles. (Mims and Glidewell, 1978)

This statement and the published plates suggest that the invaded cells possess some of the features of "typical" nutritive cells.

b) The second group of histioid galls are the prosoplasmas. These are structurally complex, and are caused primarily by cecidomyiids and cynipids. Prosoplasmas have a definite size, shape, and brief period of development as well as distinctively oriented tissue layers. Differentiation as great as, but often different from, that in the normal host organs occurs in prosoplasmas. Although arguments have been made that cell-types and tissues never seen before in the host plant arise in prosoplasmas (Mani, 1964), it is now believed that what is novel is not the cell types but their arrangement (J. Shorthouse, personal communication).

The animals that cause prosoplasmas are usually sedentary. Thus the field of stimulation and control of gall morphogenesis is localized (Kuster, 1903). Usually only the larval life stages of the gall-former live in and cause prosoplasmas.

c) The relationship between kataplasmas and prosoplasmas was discussed by Kuster (1903). He pointed out that galls exist which show characteristics of both kataplasmas and prosoplasmas. It was Wells (1921), however, who argued that the prosoplasmic form evolved from the kataplasmic form. The strongest of his arguments is stated as follows:

> All prosoplasmas in their ontogeny recapitulate the kataplasma stage....kataplasmic development progresses, through a process of increasing inhibition of host characters, from the normal host differentiation to complete homogeneity, upon the attainment of which prosoplasmic development may commence the construction of new differentiations and new forms.

Thus according to Wells, kataplasmas are galls in which only dedifferentiation occurs. The prosoplasmas, on the other hand, pass through de- and then re-differentiation. Furthermore, he envisions a continuum in which, through evolutionary time, simple kataplasmas were followed by complex kataplasmas, which were followed by simple and then complex prosoplasmas. The terms simple and complex are subjective, but generally denote the degree to which differentiation and tissue reorganization has occurred in the gall.

Interestingly, neither in Wells' time nor since has the phylogeny of a group of gall-formers (e.g. the

cynipids) been compared to Well's phylogeny of the galls. In fact, Kuster (1903) commented that the "the systematic position of the gall animal...can determine no regular connection between the form and structure of the galls produced by them." This should be tested. Malyshev's treatment of the Hymenoptera (1968) and Mamaev's work (1968) on cecidomyiids are evolutionary in approach, but neither correlates the complexity of the gall structure with the evolutionary position of the cecidozoan. Kinsey's work with the cynipids (1930) comes the closest to providing such correlations in that he considers gross gall morphology, but anatomy is not coupled with his phylogenetic schemes for the wasps. Smith (1970) finds that sawflies that gall primitive willows form primitive galls. His assessments of gall structure, however, are based on naked eye study. The anatomy of the galls should be examined.

Two additional points made by Wells should be mentioned. He dismisses the difference between organoid and histioid galls by saying that organoid galls are simply very primitive kataplasmas. His argument is strengthened by the discovery of nutritive cells in organoids. Without doubt, a continuum exists between organoids and histioids.

Secondly Wells uses the presence or absence of a

sclerenchyma layer in the gall as a principle feature that distinguishes prosoplasmas from kataplasmas:

> The presence in all of them (psyllid prosoplasmas) of specific sclerenchyma layers, together with other highly defined tissue form characters, makes them striking examples of prosoplasmas.

The reasoning here is that a sclerenchyma layer represents an advanced state of differentiation. Thus any gall showing a sclerenchyma layer is more complex than one without such a layer.

Classification System Based on Cecidozoan/Plant Interaction

Kuster (1903) devised another system of classification that is based on the position of the gall-former in the gall, and on the type of covering that develops over the cecidozoan. Because these types are used in the literature, as well as in this dissertation, I review them here. There are six major types:

1) Filzgalls are dense patches of hair on the surface of plant parts (usually leaves). The gall-maker lives on the plant's external surface and is covered only by hairs. Filzgalls are simple kataplasmas to simple

prosoplasmas (very little to moderate differentiation), and they are usually caused by eriophyoid mites. Many mites (all life stages) occur in a single filzgall. The hairs of some filzgalls contain a rich cytoplasm and, the mites feed at the base of these nutritive hairs (Westphal, 1977; Kant and Arya, 1971).

2) Fold galls and roll galls on leaves are caused by uneven growth of the leaf's cell layers. Except in the case of endophytic fungi, the gall-former occurs externally. The attacked leaf either curls at its margin or the leaf blade folds up at the midrib. In both cases the gall-former is enclosed by hypertrophied leaf tissue. According to Kuster (1903) these types of galls can be either kataplasmas or simple prosoplasmas -- they are prosoplasmas if they are "set off absolutely sharply from the healthy part of the leaf" or if "all galls produced by the same species are of the same size" and if they "show a peculiar tissue differentiation." Fold and roll galls can be formed by mites, thrips, aphids, psyllids, cecidomyiids, wasps, and fungi.

3) Pouch or sac galls are formed when gall animals that live on the leaf epidermis force the leaf blade or petiole to invaginate or "out pocket." The gall-former

"sinks" into the newly formed pocket. A wide to narrow ostiole usually occurs where fusion of the lips of the gall is incomplete. Prosoplasmic sac galls are deemed primitive because of their incomplete closure, their lack of predictable form, and their simple internal tissue (Küster, 1903). Mites, aphids, and cecidomyiids form pouch and sac galls. One to several animals can occur in such galls.

4) Covering galls are also formed by gall-formers that live on the epidermis. In this case, however, the cecidozoan induces leaf, petiole, or stem tissue to grow up and over it (the process of "umwallung"). The tissue usually fuses over the gall-former so that no ostiole, or only a minute one, is observed. Mites, aphids, adelgids, cecidomyiids, and cynipids cause these complex kataplasmas or simple prosoplasmas.

Kuster points out that numerous galls share characteristics of both the sac and covering types. In these cases the gall-former is first covered by umwallung, and then the entire gall bulges out from the leaf surface. Common covering galls include the *Pemphigus* galls on poplar petioles (see the Results section).

5) Cynipids commonly cause lysenchyme galls. These are initiated when an egg that is laid on the surface of a plant organ lyses the plant tissue under it (Bronner, 1973). The egg sinks into its excavation. Proliferation occurs in the area neighboring the cavity and tissue fusion closes the cavity. Generally lysenchyme galls include distinct sclerid and nutritive zones, and are thus counted as prosoplasmas.

6) Mark galls (Mani, 1964; Kuster's "cambial" galls) are those in which the egg is deposited into plant tissue by it mother. Ovipositional fluid and/or larval saliva induce gall growth. The galls range from simple prosoplasmas (*Pontania* galls on *Salix*) to complex prosoplasmas (various cecidomyiid and cynipid galls), based on degree of sclerenchyma and nutritive tissue development. Mark galls may erupt through their overlying tissue in which case they are called free mark galls. If, on the other hand, the overlying tissue remains unruptured the gall is termed an enclosed mark gall. One must observe the very early events in gall formation to confidently distinguish between lysenchyme and mark galls.

Other Classification Systems

Thomas (1877) distinguished between two basic types of stem galls. Acrocecidia are those formed at the growing tip of the main axis, while pleurocecidia develop at points on the stem other than at the apex. Houard (1903) further subdivided the pleurocecidia into four groups based on the position of the cecidozoan on or in the stem (external, in cortex, in vascular bundle, or within the pith). Largely because of Houard's use of this system, one still finds mention of it in the literature.

Weidner (1961) suggested that galls be divided into two groups -- those caused by chewing insects, and those caused by sucking insects. This system has not been widely accepted, but this thesis points out that the distinction is useful.

Gall Anatomy and Morphogenesis

In this section, a brief review of gall anatomy is followed by a discussion of the chemical diffusion theory -- a theory that has been offered to explain the pattern of tissue organization that is freqently seen in galls.

1) Gall Anatomy

At least two distinct tissue layers occur in most of the advanced kataplasmas and in all of the prosoplasmas. The layer which surrounds the gall-former, upon which the cecidozoan feeds, and over which the cecidozoan has most direct control is the nutritive layer. More will be said below about this tissue.

Moving out from this layer in a kataplasma, one finds relatively homogenous parenchyma making up the remaining bulk of the gall. In a prosoplasma, however, the layer just outside of the nutritive tissue is the so-called protective layer which is composed of thick-walled sclerenchyma (Kuster, 1903).

Once formed, this layer may protect the gall-former from attack by parasites or predators, but before it develops, many parasitic insects attack the gall. "One can contest its efficacy, since the lignified envelope far from totally protects the cynipid larvae against attack by secondary parasites" (Maresquelle and Meyer, 1965). Most authors now agree that this layer is important for the structural support it provides. It may also play a role in gall dehiscence. In some prosoplasmas it may make up a large part of the gall, or it may occur in two separate layers.

Beyond the protective layer lies the cortical parenchyma and outer epidermis of the gall. In many

prosoplasmas the cortical layer makes up the bulk of the gall.

The vascular system within a gall may range from a disorganized arrangement of elements (in many kataplasmas) to a well-organized system that envelops the nutritive layer (prosoplasmas) (Bloch, 1953; Meyer, 1969a). It is connected to the vascular system of the host plant. In at least one gall, the system ends at the nutritive layer as phloem elements (Docters van Leeuwen and D. van Leeuwen-Reijnvaan, 1909).

2) Gall Morphogenesis: The Chemical Gradient Theory

This popular theory holds that a gradient of stimulation diffuses out from the gall-former. The further a plant cell is from the gall-former, the less affected it is by the stimulant. The nature of the stimulant is unknown; the saliva or ovipostional fluid contains either a plant hormone analogue that directly stimulates plant cells, or a compound that indirectly affects cell growth by triggering hormone production. (See Mani, 1964, for a review of attempts to determine the identity of cecidogenetic agents.)

The existence of a chemical gradient has been most thoroughly discussed by Garrigues (1951). He offered his theory to explain the ordered, concentric arrangement of

hyperplastic and hypertrophied layers in galls. He believed that hyperplasia, observed most dramatically in the nutritive zone, results from high concentrations of the stimulant. Interestingly, in some instances there is an inhibition of growth close to the cecidozoan. In these cases a high concentration of stimulant dampens plant cell growth responses. We do not understand how high or low concentrations of stimulants lead to very different plant cell responses.

As the stimulant diffuses out from the source, and is thus diluted, one sees cellular hypertrophy. Additionally, as the gall ages and the stimulation becomes weaker or the plant cells less receptive, one sees hypertrophy of the nutritive cells.

The protective layer is believed by some to represent the zone in which the stimulant is neutralized (Mani, 1964). This speculation, however, does not explain the hypertrophy that commonly occurs beyond the mechanical layer in the cortical gall tissues.

Boysen-Jensen (1948) suggested that by injecting compounds at scattered spots over the surface of an organ, the cecidozoan could affect the design of the gall. If this is the case, then the rambling behavior of a cecidozoan may be reflected in the design of its gall. This may be particularly true for galls caused by animals

that move about on the plant's surface.

Little is known, however, about the movement of seemingly sedentary gall-larvae submerged within gall tissues (e.g. cecidomyiids, sawflies, and cynipids). The extent of movement of the enclosed larva should be indicated by the location of ruptured nutritive tissue, but I am unaware of studies that have mapped this area through time. Since gall morphology is determined by the young instars, it is their feeding patterns that should be followed. Their size and endophytic habit, however, makes this difficult.

Characteristics of the Nutritive Tissue

The nutritive tissue has often been spotlighted. This is the layer over which the gall-former has strictest control and, thus, is a logical point of focus for studies of the interaction between gall insect and plant tissue. In this section reports which describe characteristics of the nutritive cells will be summarized in the following seven sections.

1) Definition

There is some confusion in the literature about the definition of nutritive tissue. The trouble stems from

our fondness for the complex prosoplasma. Kuster (1903) offers the broadest definition:

> Those gall tissues which are devoured by their inhabitants, or the contents of which at least are of benefit to them may be termed nutritive tissue.

He goes on to say that "no gall is without nutritive tissue." Thus, according to Kuster, any gall by virtue of the fact that it provides food, contains nutritive tissue. The same author, however, never discusses nutritive tissue in kataplasmas. Instead, he states that "the histology of kataplasmas needs no detailed description."

In contrast, he goes to some length to describe the nutritive tissue in prosoplasmas. He begins his discussion with the following comment.

> In prosoplasmas, the division of labor among gall tissues produces definite zones....Especially in the highly organized cynipid and diptera galls, the layers of the nutritive tissue are extraordinarily sharply set off....the cells of which serve exclusively for the storage of carbo-hydrates or of food stuffs containing nitrogen.

The cytology of nutritive cells in complex prosoplasmas is known from several examples. Nutritive tissues in the kataplasmas and lower prosoplasmas, however, are so poorly known (with the exception of Westphal's study of eriophyid galls; 1977) that their features are rarely listed or compared to those of

nutritive tissues in higher prosoplasmas. The following review retains the bias. For a thorough understanding of galls we must study all types of nutritive tissues, not just the most densely cytoplasmic.

2) <u>Development of Nutritive Tissue</u>

Nutritive tissue may develop as a single-layered nutritive epidermis, as a patch of nutritive epidermal hairs, or as many cell layers (a nutritive parenchyma) (Kuster, 1903). Meyer (1952a), in his description of nutritive tissue development, coined the term "metaplasia." During metaplasy, meristematic and slightly differentiated cells cease to differentiate and remain in or return to a meristematic state. They then differentiate to become nutritive cells. Presumably cells of a certain maturity can no longer undergo metaplasy, but we know little about this "point of no return." The point has practical implications: Are there periods of maximum host plant susceptibility to gall formation, and if so, how long are these periods? According to Thomas (1872) "gall formation is only possible while the affected plant is still in the developmental stage." Yet, according to Maresquelle and Meyer (1965), "tissue differentiation does not prevent cecidogenetic hyperplasia. Differentiated palisade

tissue can show hyperplasia when under the influence of certain aphids." It may be that the amount of control and reorganization exerted by the gall-former is simply a function of the age of attacked tissue. The younger the tissue, the greater the control.

This question of the differentiation state of the attacked host plant cell is also of critical importance to the individual who is interested in characterizing the diet of gall-formers. Important questions are: How much feeding occurs before the nutritive tissue develops, where does that feeding occur, and what is the nutritional compostion of that early food? Does the gall insect contend with host plant defensive compounds in differentiated cells before development of the nutritive tissue?

In at least one example, the answer to such questions have been provided. In the lysenchyme gall caused by Rhodites rosae L. on Rosa sp., cellular hypertrophy and metaplasia occur around the unhatched egg -- a "cytologie nourriciere" develops in the cells surrounding the egg. Thus, before the larva begins to feed, a nutritive tissue develops (Maresquelle and Meyer, 1965).

3) Replacement and Maintenance of Nutritive Tissue

In the few observed cases, nutritive tissue replaced as it is eaten. In the _Rhodites_ _rosae_ gall, a secondary nutritive tissue develops from a generative layer ("assise generatrice") that lies just outside the nutritive tissue. It proliferates towards the larval cavity (Maresquelle and Meyer, 1965). More frequently, however, there is no such generative layer in galls. Instead, the nutritive cells themselves divide rather regularly and thus give rise to new nutritive tissue.

The continual presence of the gall-former is required for the maintenance of the nutritive tissue. Experiments have shown that when the cecidozoan is artifically removed, the nutritive tissue becomes enlarged and vacuolate. Under such conditions, "the nutritive tissue takes on the cytological aspects of a normal parenchymatous cell" (Rohfritsch, 1975).

Natural ablation occurs when the gall-former is killed by a parasite. Shorthouse (1975), for example, showed that when parasitic members of the genus _Periclistus_ killed gall-forming _Diplolepis_ sp., the nutritive tissue became "parenchymatous in appearance." Interestingly, however, when the larvae of the parasites began to feed in the gall, new nutritive cells appeared.

Meyer (1952a) observed that the fundatrix female of _Eriophyes_ _macrorhynchus_ Nal. formed nutritive epidermis

on the leaves of Acer psuedoplatanus L. when she fed. Between the time the female died and eggs hatched, however, the nutritive tissue lost its typical appearance and eventually died. Once the eggs hatched and the progeny began to feed, the cell layers under the former nutritive epidermis assumed the characteristics of a nutritive layer. "...Couplings exists between the life cycle of the cecidozoan and the reactions of its host, which are clearly seen in the development of the nutritive tissue."

4) Are Nutritive Cells Meristematic?

There is some confusion about this. Meyer (1969), for example, states that "nutritive tissue, at the light microscope level, resembles to a certain extent a meristem with an intense physiological activity." The nutritive cells have been called "pseudomeristematic" (Bronner and Meyer, 1976).

In other papers, however, the differences between meristematic and nutritive tissues are stressed. The nutritive tissue "is different from a meristem, both by its cellular, nuclear, and nucleolar hypertrophy and by the excessive richness of the mitochondria" (Maresquelle and Meyer, 1965).

The studies that address this question most

thoroughly are by Jauffret (1972, 1973), Jauffret and Westphal (1974) and Jauffret et al (1970). In these papers, acrocecidia are examined in which the nutritive tissue is directly derived from apical meristem cells. Based on ultrastructural and functional differences between these two cell types, the authors conclude that nutritive cells are differentiated, specialized cells. The fact that many nutritive cells store lipids and starch distinguish them from meristematic cells (Jauffret, 1972).

> The transformation of the apex to nutritive tissue with a definite loss of meristematic activity shows that these cells have acquired a new state of differentiation. The cytological similarities (cytoplsamic density, richness of RNA, nuclear appearance) which exists between the nutritive tissue and meristematic tissue are only characteristics common to young or hyperactive tissues. (Jauffret, et al, 1970)

From another article: "Nutritive cells, far from conserving the totipotentiality of meristematic cells, are on a course which rapidly leads to degenerance and death once they fulfill their role." (Jauffret, 1973).

Bronner and Meyer (1976) note the cytological similarities between nutritive tissue, secretory tissue (in nectar glands), storage cells in grain cotyledons, and companion cells. All of these cells show a strong metabolic activity, and are non-meristematic. The

observation, however, that the nutritive cells in some galls divide throughout gall development argues for the meristematic nature of these cells.

5) Absence of Nutritive Cells

The literature contains descriptions of interesting galls that do not have nutritive tissues. For example, many members of the cecidomyiid tribes Oligotrophini and Cecidomyiini form galls with larval cavities that are lined with a fungal growth. The midge larvae feed on the mycelial material rather than on plant tissue. The galls show no nutritive cells (Meyer, 1952b). Mamaev (1968) believes that these galls represent the transitional stage between fungivorous and phytophagous midges.

Additionally, the absence of nutritive cells in galls of three cecidomyiid species was correlated with the close proximity of vascular bundles to the larval cavity wall (Bronner and Meyer, 1972). "It is not impossible that the larva takes its nourishment directly from the sap conveyed by the conducting elements that abut the cavity." Fockeu (1897) observed the absence of nutritive tissue in leaf galls on Populus euphratica caused by a homopteran or midge, but does not suggest what the insects are feeding on. Seed galls should be checked for the presence of nutritive cells. The

richness of this host tissue may obviate the need for further enrichment. The only anatomical study of seed galls (Shorthouse, 1977a,b), however, has shown that enriched nutritive cells occur around the larvae.

6) How Do Gall-Formers Feed?

The details of the feeding process "are still poorly known" (Maresquelle and Meyer, 1965). What is known is based on very few observations. Gall-forming cynipids and cecidomyiids take a liquid diet. Neither defecate in the gall until pupation. Cecidomyiid larvae are thought to strike the nutritive cells, rupture them, and feed on the leaking cell sap (see Summary of cecidomyiid galls). Cynipid larvae tear the nutritive cells with their mandibles and suck up the cell sap. Larval gall sawflies use their strong mandibles to tear through the plant tissue, and they feed on both solid and liquid plant tissue. These larvae produce fecal matter while in the gall. Presumably larvae of gall-forming Coleoptera and Lepidoptera feed like sawflies.

Questions remain about the diet of stylet-bearing gall-forming organisms (e.g. aphids, coccids, adelgids, thrips, eriophyoids). Rohfritsch (1976) showed that the fundatrix of *Chermes* (=*Adelges*) *abietis* L. and *C. strobilobius* Kalt produced a stylet sheath that could be

traced into the nutritive cells at the base of a modified bud. She does not indicate what food is taken by the progeny. Saigo (1968) observed that twig-galling *Adelges piceae* Ratz (undetermined lifestage) cause giant cell formation in the host plant, and these are probably the cells upon which some of the adelgids feed.

Sterling (1952) observed that *Phylloxera* leaf galls on grape develop an enriched nutritive zone that enlarges as the gall grows. Presumably the enlargement reflects a change in feeding depth. Maillet (1957) and Buchner (1965) suggested that the reason *Phylloxera* contains no gut symbionts is that unlike other phloem sap-feeding aphids, they feed on a more complete diet of cell cytoplasm. Whether root-galling *Phylloxera* feed on nutritive cells is not clear (Cornu, 1878).

The gall-forming coccid, *Asterolecanium variolosum*, feeds "while the stylets are being inserted and as they pass through each cell" of a young twig (Parr, 1940). Once the coccid has settled, the plant cells at the end of the stylets develop a rather heavy cytoplasmic content. Unlike other coccids, this species presumably feeds on nutritive cells rather than on phloem sap. The only gall caused by an Australian coccid that has been studied in this regard shows a platform, a modified meristem at which the scale feeds (Gullan, 1978).

Patches of epidermal nutritive cells have been observed in a few thrips galls (A. Raman, personal communication). Presumably these insects use their stylets to suck the contents of the cells.

Eriophyoid mites puncture individual epidermal cells with their stylets and suck the cellular contents. Interestingly, however, the fed-upon cell is not emptied, nor does it die immediately. Instead, the wound site is plugged with callose (Westphal, 1977).

Gall-forming root knot nematodes (*Meloidogyne* sp.) use their stylets to puncture and feed upon giant cells in the root galls (Bird, 1961).

7) Cytological Characteristics of Nutritive Cells

(Bronner and Meyer, 1976; Bronner, 1976)

- cytoplasmic richness and a vacuolar fragmentation
- nuclear and nucleolar hypertrophy
- richness in ribosomes, often grouped in polysomes
- weak differentiation of the plastids
- strong development of dictyosomes
- presence of autophagic vacuoles
- accumulation of nuclear and ribosomal RNA
- strong concentration of soluble proteins that are continually replenished
- strong hydrolase activity (acid phosphatase,

amino-peptidase, invertase)

-absence of starch in the nutritive cells nearest

the gall insect.

MATERIALS AND METHODS

Unless otherwise stated I collected gall specimens from spring to fall, 1980 in MacDonald Forest, Benton County, Oregon (5 miles northwest of Corvallis). Starting at the Oak Creek entrance and walking north along Oak Creek, I was able to find an abundance and variety of galls on trees and shrubs.

Rather than collect individual galls or galled leaves, I clipped entire branches and immediately enclosed the material in a plastic bag. This harvesting method minimized wilt. In the lab I separated the gall material, wrapped it in moist tissue paper, returned it to plastic bags and refrigerated it until it was processed. I fixed all material for microscopy within 24 hours of collection, and most was processed within 3 hours. Processing included photographing the material and preparing it for sectioning. Considering the amount of material that I handled, the above procedure assured the quickest processing with no wilt.

Photography -- Photographs (both macro and micro) were taken both with black and white film (ASA 32) and color slide film (ASA 40, color-corrected for tungsten light source). I took macrophotographs using 1) a

reversed 55 or 35 mm lens on a 35 mm single lens reflex camera, 2) bellows extension with the above lenses (unreversed) and camera, or 3) Bausch and Lomb - Zeiss tessar microscope objectives (32 and 48 mm microaplanats with iris diaphragm in the objective). The last set-up is well suited for work that requires dissecting scope magnification, high resolution and controlled depth of field. The tessars were used on a classroom microscope with a 10X eyepiece (without the eyepiece, a light ring appeared in each exposure).

Sample preparation for sectioning -- All tissue that was embedded was parasite-free. The only possible exception to this was cynipid gall material in which larval parasites were difficult to identify. I prepared all tissue for embedding in paraffin and in methacrylate plastic. (I also prepared material for electron microscopy, and this material awaits study.)

Paraffin embedment and staining followed Johansen's (1940) procedure. The material to be embedded was vacuum infiltrated and fixed with either FAA or CRAF. It was dehydrated in tertiary butyl alchol and embedded in paraffin. I sectioned with a cold steel knife on a rotary microtome at thicknesses betwen 4-10 microns, and I stained paraffin-embedded sections with fast green and safranin.

I embedded the majority of specimens with plastic and followed the methods of Ruddell (1967) and Feder and O'Brien (1968). I sliced the fresh material so that no block of tissue exceeded 3 mm in any dimension. When possible, the slicing was done under fixative. I then vacuum-infiltrated and fixed the tissue block with fresh, cold Karnovsky's (1965), a fixative used routinely in electron microscopy.

After fixation the tissue was dehydrated in passes through methyl cellusolve, pure ethanol, isopropanol and n-butanol. I introduced the plastic to the tissue in increasing concentrations of n-butanol. Before being used, the plastic was charcoal-cleaned -- a procedure I used only late in the study, and which minimizes background staining.

After hardening the plastic by catalysis, I glued the blocks of plastic with embedded tissue to pegs for sectioning. I used a manual ultramicrotome to cut the sections on a dry glass knife that had been aged. (I noticed that freshly broken glass knives chipped more quickly than did those allowed to age a week before use). Sections were cut on a dry knife at 2-4 microns, and were then floated out on a drops of water on a glass slide, dried on a hot plate, and stained in a 0.05% solution of Toluidine Blue buffered at pH 4.4.

<u>Stain for tannins</u> -- I used Johansen's (1940) procedure for this stain. Tissue was vacuum-infiltrated and fixed in a solution of 2% ferrous sulfate in 10% formalin solution. After 24 hours of fixation the material was dehydrated as in the paraffin embedding procedure. I embedded the tissue in paraffin and sectioned it at 7-12 microns. Two passes through xylene were used to de-paraffinize the sections which were then mounted in "Permount" for observation under the microscope.

Reeve (1951) noted that in addition to staining polyphenols dark (black, brown), this stain also formed dark precipitates with pectins in the middle lamella. Thus a positive reaction associated with the outer cells wall cannot be interpreted as indicating the presence of tannins.

The advantage of the Johansen's tannin test is that it allows for preservation and for thin section observation of the material. Reeve's nitroso technique for tannin identification requires fresh sectioned material, and the stain is not permanent. I used the nitroso reaction for a short time, but settled on the Johansen stain primarily because it allowed for bulk processing, and at-leisure observation.

RESULTS

I have grouped the galls according to the type of cecidozoan. At the end of each group (the aphid galls, for example), I summarize the results from that group. Comparisons between groups are made in the Discussion.

Each account of a gall includes comments on its external morphology, its developmental anatomy (if the gall was collected more than once), nutritive tissue characteristics and, finally, the pattern of tannin deposition.

LEAF MINES

Three leaf mines were studied both to focus on some of the characteristics of this guild of insects, and to open a brief discussion on the comparison between this guild and the gall-formers.

Mine 1) Leaf Mine on Fringe Cup

The small, early (January 19) leaves of the host, *Tellima grandiflorum* (Pursh) Dougl., were the most freqently attacked. The plant was found along creek banks. It leafed out beginning in December and flowered

in mid-May. By mid-spring mined leaves frequently were matted beneath the plant and were decomposing.

The mine was a simple, meandering ophionome (linear mine) (Hering, 1951). It was caused by an undescribed species of the agromyzid genus, Phytomyza. The adult fly is shown in Plate 1, Figure 3, and the diagnostic atrophied ventral branch of the larva's tined pharyngeal skeleton is seen in Plate 1, Figure 2. The mine did not resemble any known mine on saxifrages (Frost, 1924; Hering, 1951).

During early instars the larva mined the one-cell thick palisade layer. Pupation, however, occurred in the spongy mesophyll (Pl. 1, Fig. 1), and some late instar feeding perhaps also occurred in this tissue. The larva used the pharyngeal skeleton as a sickle to slice through cells, and the contents were taken up by the larva. Frass was deposited along the edge of the mine.

In order to characterize the diet of this miner one would need to determine if and when the larva stopped feeding on the palisade and began in the spongy mesophyll. In many plant species the palisade is cytoplasmically richer and less vacuolate than the spongy layers. It may provide the richer diet for young instars.

Mine 2) Leaf Mine on Salal

This blotch mine (stigmatonome) occurred in leaves of *Gaultheria shallon* Pursh. (Pl. 1, Fig. 6). It was collected at Seal Rock Wayside, Highway 101, Lincoln Co., Oregon on May 27, 1980. Up to 13 larvae were found in each mine. The mine-former was a gracilariid moth in the genus *Lithocolletis*, and was probably *L. gaultheriella* Walshm. (Needham et al, 1928). The dorso-ventrally flattened larvae fed side by side in a circle so that the blotch was roughly circular and on average, 1.5 cm in diameter. Up to twelve mines occurred per leaf usually in the angle between the midvein and a secondary vein. Almost every leaf was mined on some shrubs. The mines were easily visible on the foliage because of the cream-pink color of the upper blotch surface. Frass was deposited in the center of the mine.

Feeding occurred only in the palisade layer (Pl. 1, Fig. 5). The presence of cell wall remnants of the sliced cells suggested that the palisade cells were cut at their mid-section and that some of the cell wall was left intact.

The mouthparts of *Lithocolletis* larvae were distinct in that the labrum was bilobed and enlarged (Pl. 1, Fig. 4). Presumably the labrum supported the circular saw-like mandibles that, with their toothed edges, sliced

through the cell walls (See Needham et al, 1928, Fig. 23-E, for diagram of mandibles). According to some sources, early instar larvae of this genus usually are sap-feeders, meaning that only fluid cellular contents are taken, while later instars feed on cellular contents and cell walls (Hering, 1951).

Mine 3) Leaf Mine on Black Cottonwood

This linear tortuous mine in the leaves of *Populus trichocarpa* T. and G. looked like a slime trail over the surface of the leaf. Only the upper epidermis was mined (Pl. 1, Fig. 7), and the separated epidermis gave a silvery sheen to the mine. The mine began on the petiole and then proceeded along the major veins or leaf edge. The epidermal cells in many plant genera, including *Populus*, have a large central vacuole that is often tannin-rich. Presumably then, the quality of this miner's diet was poor.

The mining larva was of the gracilariid (or lyonetid; Needham et al, 1928) genus *Phyllocnistis* and perhaps was the species *P. populiella*, a common member of the genus (Needham et al, 1928). Species of *Phyllocnistis* "represent the only miners which throughout their life live as sap-feeders solely in the relatively flat cells of the epidermis" (Hering, 1951). These

miners also have an enlarged labrum which covers the serrated mandibles and presumably prevents the mandibles from accidently rupturing the epidermis -- an accident that, according to Hering, would be fatal.

Summary of Leaf Mines

The major feature which distinguished these leaf miners from gall-formers was that the miners moved through the tissue and fed on the contents of unaltered plant cells. They controlled the quality of their diet by selecting the cells upon which they fed. Gall-formers, as will be seen, induce the formation of their food.

GALLS

Fungal Galls

Fungal Gall 1) Gall on Larkspur

This gall was collected on *Delphinium trolliifolium* Gray. Infected plants were found only in April. The galls occurred on only a few plants in a dense patch of larkspur. Leaves and stems were galled, and were easily found because of the pigmented uredospores and uredia that ruptured the host plant epidermis. From a distance, the galled organ looked as if it was covered with a bright orange powder.

The causative fungus was a species of the rust, *Puccinia* (Basidiomycetae: Uredinales), and was *P. delphinii*, *P. recondita*, or *P. rubigo-vera* (Pirone et al, 1960). It is a simple basidiomycete -- it has no basidiocarp.

The fungus caused considerable hypertrophy. A transverse section of an infected stem (Pl. 2, Fig. 1, 2) showed that cortical cells in the infected region were three to four times as large as comparable cells in the uninfected cortex. The enlarged host plant cells did not

possess a dense, rich cytoplasm. Even those cells directly beneath the uredium that might service spore development did not show a dense cytoplasm.

The distinction between the palisade and spongy mesophyll layers was lost in infected leaves. Instead, the mesophyll of an infected leaf was composed of large, isodiametric cells with little intercellular space. Epidermal cells of the infected area also were hypertrophied.

Vascular bundles were larger on the infected side of the stem. More phloem and xylem cells occurred in these enlarged bundles than in normal bundles, and the xylem cells, particularly the metaxylem, were about twice the diameter of those found in the normal vascular bundle.

It was not clear from the collected material how and where this intercellular fungus derived its food. Perhaps the collected galls were old enough that host cells that had previously been parasitized via haustorial invasion were now empty. Harvesting tissue earlier, before maturation of the fungal fruiting structures, might provide a better idea of host cell reaction to haustorial invasion.

Fungal Gall 2) Azalea Gall

Specimens of this gall were collected on the Oregon

State University campus. It was a common leaf and flower bud gall on azaleas (Rhododendron sub-genus Azalea). It was caused by the simple basidiomycete Exobasidium discoideum (Basidiomycetae: Exobasidiales). The leaves became thick and fleshy, and turned pale green or whitish (Pl. 2, Fig. 3). As the fungus matured (May 21) the free basidia occurred in a dense accumulation (hymenium) over both surfaces of the leaf so that to the naked eye the leaf had a white powdery bloom.

A galled leaf from April 1 (Pl. 2, Fig. 5) was at least twice as thick as an ungalled leaf (Pl. 2, Fig. 4) due to the excessive hypertrophy of the mesophyll cells. The distinction between palisade and spongy layers was lost. Instead, the mesophyll was filled with large, tightly packed, vacuolate isodiametric cells that did not possess a dense cytoplasm. The lower epidermal cells retained much of their size, shape, and orientation, but the upper epidermal cells became enlarged. Before and during sporulation, both epidermises became filled with a deeply stained deposit that was not common in the epidermal cells of ungalled leaves. Stomates were absent in the lower epidermis of the galled leaf. The fungus appeared to travel intercellularly (Pl. 2, Fig. 6).

The vascular strands in galled leaves showed both an increase in number and size of elements, and the

arrangement of elements also was disrupted. This disruption was most apparent in the midvein. In galled leaves, the xylem cells of the midvein radiated out in all directions in irregular rows, and were surrounded by a ring of phloem. In the healthy leaf, however, phloem elements occurred in the lower side of the bundle and the xylem cells formed rows on the adaxial side of the bundle.

As in the _Puccinia_ gall, it was not clear where the fungus derived its food. Graafland (1960) stated that infection by _E. japonicum_ on _Azalea_ was first observed in the youngest leaves of the unfolding buds, and suspected that leaves were probably susceptible to attack until they were about 1 cm long.

Thus it might be that very early in the infection process, the young cells contained a richer, denser cytoplasm which served as food for the fungus. If such a food supply was not replenished by the host plant but instead was exhausted by the fungus, then one might expect to see what I observed: namely, that attacked host plant cells in older galls were devoid of dense cytoplasm. The early stages of infection should be studied further.

Fungal Gall 3) Black Cottonwood Gall

This gall was formed on the leaves of *Populus trichocarpa* T. and G. by *Taphrina aurea* (Pers.) Fr. (Ascomycetae: Exoascales), a simple ascomycete (i.e. one that produces no ascocarp). The lower surface of the leaf showed oval depressions (Pl. 2, Fig. 7) that were 1-2 cm long, 1 cm wide, and 0.5 cm deep. The undersurface of the depression remained light green until sporulation, at which time it took on a yellow, powdery appearance. The gall was expressed as an oval chlorotic bulge on the upper leaf surface.

In transverse section, the leaf tissue that formed the depression was thicker than was the adjacent ungalled tissue (Pl. 2, Figs. 8,9). Hypertrophy occurred particularly in the epidermal and spongy mesophyll cells. This, coupled with hyperplasia, resulted in a dense spongy mesophyll.

The palisade parenchyma in the healthy leaf was 2 cell layers thick and was characterized by a large quantity of darkly stained substance in almost all of the cells (probably tannins; see Pl. 18, Fig. 1). The same tissue was recognizable in the gall, but it was disorganized -- the rows of cells were not as neatly aligned in palisade fashion as in the healthy leaf. The darkly stained material did not occur as regularly in the palisade cells of the gall as in the healthy palisade.

Vascular bundles in the galled tissue were generally larger (primarily due to the increased number of xylem cells), but this difference was not especially marked.

Asci occurred on the lower surface of the leaf (Pl. 2, Fig. 10) and their hyphal bases occurred intercellularly in the epidermis and subepidermal layers. Other than in this region, it was difficult to find hyphal strands. Graafland (1960) states that the fungus moves intercellularly. It is not clear which host cells the fungus parasitized.

Summary of Fungal Galls

There was a continuum in the amount of disruption of host tissue caused by these gall-forming fungi. For example, *Taphrina*-attacked poplar leaves retained some of the characteristics of the two mesophyll layers, while *Exobasidium*-attacked leaves underwent complete homogenization of the mesophyll. Such a continuum reflected the variation in ability of fungi to control host tissue organization.

All three fungal galls showed cellular hypertrophy as well as a lack of distinct tissue layers -- they were true kataplasmas. They also showed augmented vascular systems -- a fact that suggested that the galls were acting as sinks.

Nematode Gall

Nematode Gall 1) Root Knot on Tomato

Root galls caused by *Meloidogyne* hapla on greenhouse-grown Rutgers tomatoes were harvested in spring. Infested roots were stubby (Pl. 1, Fig. 8). The developing females (many per root) were completely embedded in the cortex of the root (Pl. 1, Fig. 9). At the head of each female, and near the stele, was a sphere of at least 5 very large cells (Pl. 1, Fig. 10). These giant cells, upon which the nematode fed, possessed enlarged nuclei and a dense cytoplasm.

The cells that surrounded the giant cells had been displaced slightly, were smaller than healthy cortical cells, and also possessed a dense cytoplasm. They probably serviced the giant cells.

Cellular hypertrophy was not noted in the galled root (the giant cells were formed by merger of neighboring cells, not by enlargement of a single cell; Bird, 1975). Instead, the galls were caused primarily by hyperplasia of stelar and some cortical cells. Disruption of the stele was evident, and probably contributed to the damage caused by the nematodes. Root

anatomy was most disrupted near the nematode's head. The cortex and epidermis, and the stele slightly above and below the giant cells were undisturbed. No sclerid zone was formed. Healthy and galled roots were free of tannins.

Summary of Nematode Gall

In this example, a sedentary gall-forming nematode manipulated the development of host plant cells that surrounded its head so that the cells became cytoplasmically enriched. The gall was a kataplasma with a well-defined nutritive tissue.

Eriophyoid Mite Galls

Eriophyoid Gall 1) Willow Leaf Gall

The gall occurred on *Salix* sp. (perhaps *S. piperi* Bebb) and was caused by an eriophyid (Pl. 3, Fig 3). It was found on only a few leaves on an isolated group of meter high saplings. Felt (1965) says that "a number of undescribed capsule or pocket galls are produced (on *Salix* sp.) by undescribed species of *Eriophyes*." He suggests that some of these mites should tentatively be assigned to *Eriophyes oenigma* Walsh.

On May 20 the galls (Pl. 3, Fig. 1) were small sub-spherical blisters (2-3 mm in diameter) that were red on the upper leaf surface (surrounded by a chlorotic area) and were covered with a white tomentum on the lower leaf surface. They occurred in no regular arrangement over the leaf surface.

When the upper surface of the gall was cut away (Pl. 3, Fig. 2) one could see that the internal gall cavity was incompletely partitioned by 2-3 enations that arose from the gall walls. A few hairs also grew out from the gall wall, particularly from the tips of the enations. An average of 12 mites occurred per gall by early June.

The gall completely disrupted the cellular arrangement of the mesophyll in healthy leaves (Pl. 3, Fig. 4, 5), but derivation of gall wall tissues was easy to trace through the transition zone. The upper wall of the gall was evenly thick, contained large vascular strands, and contained cells that in their staining properties resembled both mesophyll and palisade cells. These observations suggested that this wall was derived from minimally proliferated leaf tissue. The lower wall, however, was derived from "umwallung" of the spongy mesophyll region. The shape of the mature gall and its lack of an aperture suggested that it was a covering gall. The gall was a complex kataplasma; distinct, cytoplasmically rich nutritive cells were present, but the mature gall wall was otherwise parenchymatous in composition.

Nutritive cells were present in young galls (May 27) (Pl. 3, Figs. 5, 6, 7). They lined the gall cavity in layers two to four cells thick, and showed a rich cytoplasm and a prominent nucleus and nucleolus. Nutritive cells on June 5 continued to show a cytoplasmic richness. As the gall aged, however, the nutritive tissues became thicker in some spots (5-10 cells thick) (Pl. 3, Fig 8)) and thinner in others (one cell thick) (Pl. 3, Fig. 9). The increase in thickness was due to

cell division, and the decrease to incorporation of tannins into the outer layers. There was a deposit of unknown material lining the cavity (Pl. 3, Fig. 8). This was perhaps ruptured nutritive cell contents, or the ruptured contents of mites.

In a dying gall that contained mites (August 19), the nutritive cells had little cytoplasm, either because they had been heavily fed upon, and/or because they were no longer being serviced from the surrounding tissue (Pl. 3, Fig. 10). On this same day I observed new galls on young leaves.

The nutritive cells stained lightly for the presence of tannins (Pl. 4, Fig. 1) in galls collected on June 5, 1980. These cells contained less tannins than did most of the cells forming the gall wall, and less than many of the cells in healthy leaves. In fact, there was a gradient of decreasing amounts of tannins from the outer gall wall to the nutritive cells.

<u>Eriophyoid Gall 2)</u> Alder Bead Gall

This gall occurred on <u>Alnus</u> <u>rubra</u> Bong.. Russo (1979) described a gall on <u>A.</u> <u>rubra</u> caused by the sierraphytoptid, <u>Phytopus</u> <u>laevis</u> Nal., that resembled the mite gall in MacDonald Forest. He stated that the mites induced "round, yellow to green bead galls on the upper

surfaces of the leaves.... There is an opening on the underside." Shevtchenko (1957) studied the life history of this mite.

The galls that I collected were yellow or red when young, were roughly spherical (about 2 mm in diameter) (Pl. 4, Fig. 5), and occurred toward the leaf edge (Pl. 4, Fig. 2). The gall projected both above and below the leaf surface.

Until the middle of June, only a single orange mite, probably the deutogyne (=overwintering female), occurred in the gall (Pl. 4, Fig. 3) and was responsible for gall formation. Her eggs were laid in the galls beginning in the middle of May, but eclosion apparently did not occur immediately because the first white nymphs were not observed until June 25. By mid-August many mites occurred in each gall. At this time, orange mites were present along with white forms (Pl. 4, Fig. 4) (males and protogynes (=summer females)).

When one cut a mature gall longitudinally (Pl. 4, Fig. 5), one saw that there was usually a large unpartitioned central cavity. Additionally, the upper surface of the gall was flat while the lower surface was more V-shaped. The internal cavity was occasionally partitioned (Pl. 4, Fig. 6).

A longitudinal thin section of a young (April 22)

(Pl.4, Fig. 7) gall indicated that the founding mite had settled on the upper leaf surface and that "umwallung" growth of the leaf surface arched over the mite. The aperture had not yet closed. Eventually it did, and for this reason, the gall was a covering gall (Pl. 4, Fig. 9, Pl. 5, Fig. 3). The nutritive cells on April 22 had dense, slightly stained cytoplasms (Pl. 4, Fig. 8).

The organization of the healthy leaf (Pl. 5, Fig. 1) was disrupted in the gall. At the transition zone, the palisade cells lost their shape and orientation, while the spongy mesophyll cells enlarged and divided.

In slightly older galls (April 29) many of the cells of the wall, particularly those lining the gall cavity, were cytoplasmically rich and were dividing. The gall was still growing and yet, some of the nutritive cells contained a darkly stained deposit. When checked for the presence of tannins, the gall stained more lightly than did the healthy leaf. Some of the nutritive cells, however, stained yellow-brown, a reaction that indicated the presence of a small amount of tannins.

As the gall matured (May 13) (Pl. 4, Fig. 9) the cells in the wall lost their meristematic appearance. The nutritive cells enlarged and showed a deeply stained deposit. These same cells showed a fairly positive (light brown) reaction for the presence of tannins (Pl.

5, Fig. 5). Up to this point, only the founding mite was present in the gall. Plate 4, Figure 10 shows the extremely enlarged nutritive cells that were present as eggs began to appear in the gall. These cells were multinucleate and possessed a very dense cytoplasm with many small vacuoles. Many dark deposits occurred in the lightly stained granular cytoplasm of these cells. The cells that underlaid the nutritive cells contained similar deposits.

By July 16 (Pl. 5, Fig. 3) several mites were found in each mature gall. According to Jeppson et al (1975) up to 400 mites may occur per gall. Many of the nutritive cells were flat and no longer bulged into the gall cavity. Some were empty while others showed cytoplasms that, with the exception of many small non-staining vacuoles, stained deeply (Pl. 5, Fig. 4). The same stained positively for the presence of tannins (deep yellow-brown) (Pl. 5, Fig. 6). By September 21, many of the galls had begun to die (Pl. 5, Fig. 2).

Thus, fully developed nutritive cells occurred in these complex kataplasmas before they were heavily populated. With the exception of very young galls, the nutritive cells contained compounds that stained positively for the presence of tannins (yellow-brown), although not to the same extent as did the palisade cells

of ungalled leaves (black).

Eriophyoid Gall 3) Linden Leaf Gall

This is commonly called the cerateon gall on Tilia spp. According to Felt (1965) it is "presumably" incited by the eriophyid Eriophyes abnormis Garm.. The galls were collected from T. europaea, or some cultivar of this species, near the Oregon State University campus in Corvallis. They sometimes occurred singly or a few per leaf, but most often many occurred per leaf in no apparent arrangement.

The very young gall appeared as a small blister on the upper surface of the leaf. It grew and elongated so that when mature (May 22), it was cylindrical, tapered, and sometimes curved at the tip. It was widest at slightly lower than its midpoint, and tapered at both ends (Pl. 5, Fig. 7). The lower leaf surface showed few if any signs of the gall.

I have no photograph of the mites that caused this gall. Instead, the mite that is shown in Plate 5, Figure 8 was taken from a linden leaf gall brought from New York state (Pl. 7, Fig. 9) that, according to Felt, is also caused by E. abnormis.

Until the middle of May most galls held only a single mite. Fully grown galls (May 20) contained eggs

and a few mites. A single founding mite was undoubtedly responsible for forming the gall. Only when the gall was nearly mature did progeny appear.

A young gall (late April) in longitudinal section (Pl. 5, Fig. 10) showed that it was a pouch gall that was formed when the founding mite attacked the lower leaf surface. The leaf surface bulged up, and a lipped portal that was plugged with hairs remained on the gall's undersurface. The region of transition between leaf and gall wall was sharp (Pl. 5, Fig. 13). The palisade and mesophyll layers lost distinction in the thick gall wall.

The nutritive cells in these young galls (Pl. 5, Figs. 11,12) were in a palisade-like arrangement, had dense, granular cytoplasms, and prominent nuclei. They thus formed a distinct layer that lined the cavity. Many of the portal hairs also had a dense cytoplasm.

As the gall matured (May 6) the nutritive layer became even more distinctly set off from underlying cells; the nutritive cells retained their dense cytoplasm while underlying cells became vacuolate. The nutritive cells retained their palisade arrangement in the lower part of the cavity, but were more randomly arranged in the upper part.

By May 20, when egg and progeny began to appear in the gall, the nutritive cells in the upper half of the

cavity were vacuolate (Pl. 6, Fig. 2). Cytoplasmically rich, palisade nutritive cells were most common in enations (=surface outgrowths) along the cavity wall (see Pl.6, Fig. 3). At the portal, the nutritive cells showed no particular arrangement, and many were without dense cytoplasms (Pl. 6, Fig. 1).

By July 24 almost all of the cells lining the gall cavity were vacuolated (Pl. 6, Fig. 3) and some had collapsed. Occasionally, a multinucleate, cytoplasmically rich cell was seen in the enations. Most of the portal hairs had developed thick walls, and showed little if any cytoplasm.

The mature gall wall contained large canals or ducts (Pl. 6, Fig. 3) that were filled with an amorphous darkly stained material (not tannins). The derivation of the ducts was not clear in that they resembled nothing seen in the healthy leaf (Pl. 5, Fig. 9).

Tannins were present in only a few scattered palisade cells in the ungalled leaf. In walls of mature (July 24) galls, the outer epidermis and subepidermal layers stained positively for tannins. A few cells scattered throughout the gall wall also contained tannins, but the nutritive cells did not.

The E. abnormis pouch gall collected in New York state (by G. Nielsen) on May 26, 1980 was similar in

design to the Corvallis galls, but had a wrinkled external surface. Internally the gall was filled with hairs (Pl. 7, Fig. 10) that arose from enations (Pl. 7, Fig. 10). Some of the cells that formed the enations showed a dense, active cytoplasm. Most cells that lined the cavity, however, were vacuolate.

Eriophyoid Gall 4) Erineum on Garry Oak

This filzgall was found occasionally on leaves of Quercus garryana Dougl.. It perhaps was caused by the eriophyid, Eriophyes mackiei K., but was caused more likely by an undescribed species (Jeppson et al, 1975).

Interestingly, both leaf surfaces showed dense patches of hairs. On the underside of the leaf (Pl. 6, Fig. 4) the hairs formed a white patch, while the upper surface erinea were usually pink to red in young, or yellowish green when old. Mites were found in both upper and lower surface erinea. One such mite pulled from the upper surface erineum is shown in Plate 6, Figure 5.

The upper-surface erinea collected on May 20 showed little disruption of leaf tissues (Pl. 6, Fig. 6,7) and only slight thickening of the lamina. The palisade layer maintained its arrangement, but the cells became more densely cytoplasmic. The intercellular space between

many spongy mesophyll cells was decreased. Cells of both epidermises were vacuolate, and remained much as they were in ungalled areas of the leaf.

The unicellular erineal hairs appeared to be of epidermal or subepidermal origin; their bases were placed deeply in the epidermis. The hairs were thick-walled and vacuolate.

A stain for tannins at this time (Pl. 6, Figs, 9, 10) indicated that the epidermal and sub-epidermal layers of the erineum contained rich deposits of tannins (black stain) as did the bundle sheath cells. The palisade layer, both in the erineum and healthy leaf, stained positively. The spongy mesophyll region of the erineum stained poorly, and the erineal hairs stained lightly brown.

Older galls collected on July 24 (Pl 6, Fig. 8) showed a leaf mesophyll with palisade cells of shorter, broader shape than normal and a dense spongy mesophyll. Most of the mesophyll cells stained very lightly if at all, and were vacuolate. The cells of the lower epidermis stained very deeply with a deposit that was most likely tanniferous.

The mites probably fed on the epidermal cells and not on the thick walled hairs, but this was not established. If they did feed on epidermal cells, then

tannins were included in their diet. Westphal (1977) observed that in erinea on other plant genera, mites fed on the hairs or at the hair bases. The hairs of the oak erineum, however, were not densely cytoplasmic, i.e. they were not enriched nutritive hairs.

Eriophyoid Gall 5) Ash Leaflet Gall

These galls were collected from *Fraxinus latifolia* Benth.. The causal agent may have been the eriophyid *Eriophyes fraxini* Garm., but was most likely undescribed (Felt, 1965).

The galls were usually associated with one of the major veins (Pl. 7, Figs. 1, 2). On May 13 the galls were about 1 mm in diameter. Each gall emerged from both sides of a leaflet, and was red above, and greenish-pink and pubescent below. Later the galls turned yellowish green. Until June 25 only a single orange mite (Pl. 7, Fig. 4) was found in each gall. On June 25, the gall contained an orange mite, eggs, and in a few cases, white mites. On August 12, there were many mites (orange and white) in most of the galls. The leaflets on this late date were beginning to yellow and brown, but the galls were green or yellow-green. The galls were frequently chambered (Pl. 7, Fig. 3), but the chambers are usually interconnected.

Initiation of the covering gall occurred when the mite attacked the lower surface of the leaflet and caused both a thickening of the leaf lamina and an "umwallung" from the lower leaflet surface (Pl. 7, Fig. 6). A small, hair-filled aperture was present in galls on the lower side of the gall.

There was complete homogenization of leaflet tissue layers (Pl. 7, Fig. 5,6) in the gall wall. With the exception of the one-cell thick nutritive layer, the cells of the wall were parenchymatous, enlarged, and vacuolate.

Plate 7, Figures 7 and 8 show the nutritive cells (and a few hairs) in galls collected on May 13. The cells were cytoplasmically dense and had prominent nuclei. They were not arranged in palisade fashion. By June 5 the nutritive cells had become vacuolated, although they still possessed a denser cytoplasm than of any other cells in the gall. By the time the progeny were present (August 12), the nutritive cells were indistinguishable from the other vacuolate cells in the gall.

Only the upper epidermis of the gall stained slightly (yellow-brown) for tannins. All other gall tissues did not stain. The palisade layer of the ungalled leaflet stained very lightly brown. Otherwise,

the leaflet was tannin-poor.

Eriophyoid Gall 6) Poison Oak Leaflet Gall

This gall was collected in Finley Wildlife Refuge (5 miles south of Corvallis) on May 31, 1980. It also occurred in MacDonald Forest. It was found on the leaflets (Pl. 8, Fig. 1) of *Rhus diversiloba* T. and G., and it was caused by the eriophyid *Aculops toxicophagus* Ewing (Pl. 8, Fig. 3). The mite caused "raised, pubescent, bead galls on the upper and lower surfaces of the leaves in late spring" (Russo, 1979). The galls occurred singly or in clusters and were usually red.

Transverse sections of this leaflet pouch gall (Pl. 8, Figs. 4, 6) showed that it was primarily caused by hypertrophy of the lower epidermal cells. All other leaf tissues layers remained almost unaffected (see section of ungalled leaf; Pl. 8, Fig. 5). The transition between normal epidermal and gall epidermal (=nutritive) cells took place over about ten cells. The normal epidermis was vacuolated with only peripheral, granular cytoplasm while the nutritive cells contained a homogenous granular cytoplasm with few if any vacuoles. Nuclei in the nutritive cells, interestingly, were not prominent. Epidermal hairs arose from the gall epidermis and were thick walled and void of cytoplasm. The gall was not

stained for tannins.

I also found poison oak flowers that had been galled by eriophyoids (perhaps *A. toxicophagus*) (Pl. 8, Fig. 2). The galls were pubescent convolutions of the flower spray. Flowers were completely disrupted and non-functional. These mites have not been used in poison oak control programs.

Eriophyoid Gall 7) Leaf Gall on Trembling Aspen

This filzgall was collected from *Populus tremuloides* Michx. on June 1, 1980 one mile west of Sisters, Oregon (Deschutes Co.) on Highway 20 in the Pilot Butte State Park. It was caused by an undescribed species of eriophyoid mite (Pl. 8, Fig. 8). According to Felt (1965) there are many erinea produced by unnamed species of mites on poplars.

The gall occurred on the lower leaf surface as a circular to oblong spot (4-5 mm in diameter) (Pl. 8, Fig. 7). Many fleshy, finger-like enations (Pl. 8, Fig. 9) arose from the leaf surface and the mites lived on, between, and at the base of the enations. The upper leaf surface at the gall was yellow and bulged slightly.

The upper epidermis and palisade layers of the leaf retained their orientation in the gall (compared to ungalled leaf, Pl. 8, Fig. 10), but the spongy mesophyll

became densely packed with cells. The cells in the enations resembled those in the spongy layer. The lower epidermis covered the enations, and its cells were enlarged and vacuolate. Thus, the gall showed no tissue that resembled an enriched nutritive layer. The enations superficially resembled those seen in the filbert bud gall (Pl. 9, Fig. 9). As will be seen, however, the lack of an enriched palisade-like nutritive enatial epidermis in this poplar leaf gall distinguished it from the bud gall.

It may be that the gall was collected too late to observe enriched nutritive cells. The mites, however, were present, active, and presumably feeding in the collected specimens. The gall was not stained for tannins.

Eriophyoid Gall 8) Leaf Gall on Choke Cherry

This gall was collected on *Prunus virginiana* L. on June 15, 1980 in Ironside, Oregon (Malheur Co.) at the southern foot of the Blue Mountains. It is most likely the plum finger gall caused by the eriophyid *Phytoptus emarginatae* (K.) (which may be synomymous with *P. padi*; Jeppson et al, 1975).

The gall was visible on the upper surface of the leaf as a short, yellow, finger-like pouch (Pl. 9, Figs.

2, 5). Like the linden gall, it was a tubular out-pocketing of the leaf surface (Pl. 9, Fig. 4). Most of the galls contained a single orange mite (Pl. 9, Fig. 3), but a few contained eggs and white mites as well.

The cells of the leaf's upper epidermis became flat, elongate and filled with deeply stained deposits as they formed the gall's outer epidermis. The leaf mesophyll (Pl. 9, Fig. 6) layers underwent complete homogenization as the gall was approached. Compared to the cells of the palisade and spongy layers, the cells in the gall wall were enlarged and elongated with the long axis parallel to the long axis of the gall. Most of the cells of the gall wall were vacuolate, and droplets in the thin peripheral cytoplasm stained deeply. In some cases the cells were filled with this deposit (Pl. 9, Fig. 7).

The nutritive cells (Pl. 9, Fig. 7) were large, occasionally bulging into the cavity. Some contained a lightly stained cytoplasm with a prominent nucleus and nucleolus, and many small vacuoles. Others contained deeply stained droplets around the nucleus. This gall was not stained for the presence of tannins.

<u>Eriophyoid Gall 9</u>) Big Bud of Filbert

This gall, caused by the sierraphytoptid <u>Phytoptus avellanae</u> Nal. (Pl. 10, Fig. 5) was collected in

Corvallis, Oregon from <u>Corylus avellana</u> (Cultivar, 'Daviana') throughout 1976. It was discussed in detail elsewhere (Larew, 1977; Westphal, 1977). The galls were swollen stunted buds (Pl 9, Fig. 8). The enlargment of bud parts primarily was due to the presence of many multicellular enations which covered the surface of all bud parts (Pl. 9, Fig. 9). The mites lived on, between, and at the bases of the enations. The surface of an enation was covered with a nutritive layer that was generally one cell thick (Pl. 10, Fig. 1) and was palisade-like in arrangement.

Electron micrographs of the nutritive cells (Pl. 10, Fig. 2) showed that the cytoplasmic density observed with the light microscope primarily was due to an accumulation of rough endoplasmic reticula and of mitochondria (Pl 10, Fig. 3). The large nucleus and nucleolus also were apparent in these micrographs.

When tested for tannins, the nutritive cells stained poorly, while the cells immediately beneath them stained positively (Pl. 10, Fig. 4). Epidermal cells of ungalled filbert bud scales and leaves also stained positively.

<u>Summary of Eriophyoid Galls</u>

1) <u>Classification</u>. Those galls which possessed no distinctive nutritive layer (oak erineum, trembling aspen

gall) and/or those that retained much of the organization of the healthy leaf (oak erineum, poison oak gall and trembling aspen gall) were simple kataplasmas. The anatomical evidence suggested that the mites in these cases caused relatively little disruption. Whether amount of disruption indicated amount of damage to the host plant was unclear.

The remaining eriophyoid galls possessed a distinctive nutritive layer at least during the early stages of gall development. Additionally, the disruption (homogenization) of the mesophyll layer was seen in all of them. These two characteristics indicated that the mites influenced the host plant tissue to a significant extent, and thus their galls were categorized as complex kataplasmas. None of the mite galls was a prosoplasma primarily because they lacked a sclerid zone. Instead, the gall wall was usually composed of hypertrophied, homogenous parenchyma.

Within the group of complex kataplasmas one might sub-categorize the galls based on features such as thickness of nutritive layer at gall maturity, or alignment of nutritive cells and general type of nutritive cell. For example, the mature willow leaf gall had a nutritive layer that was 2-5 cells thick while all the other galls generally possessed a one-cell thick

nutritive layer. If amount of nutritive tissue was indicative of damage to the host plant, such anatomical information might be useful in planning biological control programs (Shorthouse, 1977a,b).

A palisade arrangement of nutritive cells was seen in the willow gall, and the filbert bud gall. A more random arrangement of globular nutritive cells was seen in the alder bead gall and the choke cherry gall. The ash leaflet gall had a few nutritive cells arranged as a palisade, but most were small and randomly aligned. The linden gall was an interesting case, for when the gall was mature there were both cytoplasmically rich palisade-like nutritive cells and vacuolate, randomly arranged cells lining the gall cavity. I know of no discussion of the significance of different shapes and arrangements of nutritive cells in mite (or any other) galls.

2) Nutritive layer dynamics. The mite galls on willow, alder, linden, and ash showed an enriched nutritive layer before they were inhabited by a large population of mites. By the time the progeny were present, most of the nutritive cells in the linden and ash galls were vacuolate, and in the alder gall, these cells were collapsed and stained heavily for the presence

of tannins. In the willow gall, nutritive cell collapse was coincident with an increase in the number of mites.

In at least one known example (Meyer, 1952a), a nutritive layer reappeared once the progeny began feeding. This was not observed in the alder and ash galls. Instead, the results indicated that the deutogyne elicited and enjoyed a rich diet while poorer food cells were available to her progeny. The filbert bud gall, on the other hand, showed active nutritive cells when the bud was filled with mites. Short of gall death, there was no period during infestation that this gall did not show rich nutritive tissues in at least some portion of the gall. The willow gall provided a good example of nutritive tissue that was enriched and available for the progeny. Once used by the progeny, it was not rejuvenated. Both the choke cherry and poison oak galls showed enriched nutritive tissues in young galls. The aspen gall, however, showed no enriched nutritive tissue even though mites were present.

The phenomenon of a single founding mother preparing the gall for her progeny was also seen in some of the gall aphids and sawflies. See the discussions of these galls for comparisons of the quality of the diet that was passed on to the progeny.

According to Jeppson et al (1975), "urgency to

abandon (mite) galls only comes when the plant prepares to shed its leaves at the end of the season." Before this study, I would have disagreed, and suspected that deterioration of the nutritive tissue (an event that often occurred well before abscission) was the primary factor forcing mites to abandon their galls. Apparently this was not the case in that mites were often found in galls with collapsed nutritive cells. Eriophyoids have stylets of 15-35 um in length. As the nutritive cells deteriorated and collapsed, the mites perhaps tapped underlying unenriched cells, and waited almost until abscission before leaving the galls.

3) Tannins. Those mite galls that were stained for the presence of tannins gave varying results. For example, gall and leaflet tissues of ash stained poorly for tannins. Regardless of where a mite chose to feed on an ash leaflet, in or out of a gall, it would avoid tannins.

The galls on willow and filbert showed many tanniferous cells in their walls, but the nutritive layers stained poorly for tannins. In these two cases the mites probably avoided tannins that accumulated nearby.

As the alder gall matured its nutritive tissue accumulated tannins. Early inhabitants probably

contended with fewer dietary tannins than did later inhabitants. Such observations emphasized the dynamic nature of the nutritive tissue.

The possibility that mites in mature oak erinea were feeding on slightly transformed, tannin-rich cells is worth additional study. This gall may be an interesting exception to the proposal that gall-formers avoid tannins throughout gall development.

Lepidopteran Gall

Lepidopteran Gall 1) Stem Gall on Peck's Penstemon

This gall was collected by Dr. Andrew Moldenke at Camp Sherman (Jefferson County) Oregon near Sisters. It occurs on *Penstemon peckii* Pennell and is caused by the microlepidopterous gracillariid, *Caloptilia murtfeltella* (Bsk.) (identified by Dr. Don Davis, Smithsonian Institution) (Pl. 13, Fig. 1). (In the summer of 1981, Dr. Moldenke collected a similar stem gall caused by a lepidopteran from *P. procerus* Dougl. on Lookout Mountain (6200 ft elevation) in the Andrews Forest, Lane Co., Oregon.) Young instar larvae were found in the galls on June 6. By July 31, old instars and pupae were found in the galls, and adults emerged in the lab on August 13 (from July 31 material). The larva chewed a window in the gall wall (outer epidermis was left intact) (Pl. 11, Fig. 5) before pupating in a silken cocoon on the gall wall just beneath the window. The adult broke through the window.

The spindle-shaped gall was formed directly beneath the apex of this herbaceous perennial (Pl. 11, Fig. 5) and was thus an acrocecidium (Houard, 1904). The single larva found in each gall (Pl. 11, Fig. 6) uses strongly

dentate mandibles (Pl. 13, Fig. 4) to cut through the nutritive tissue.

In tranverse section, the open pith of an ungalled stem was partially filled with isodiametric parenchymatous cells that increased in diameter toward the center. A ring of radially arranged xylem elements surrounded the pith that was in turn surrounded by a compact ring of phloem. The cortical cells were similar in appearance to the pith cells, but there were smaller intercellular spaces in the cortex (Pl. 11, Fig. 7).

On June 6 cortical cells were almost twice as large in diameter in the gall wall as they were in the ungalled stem, and in the gall, air spaces between these cells were prevalent. The vascular system was disrupted; instead of solid rings, the tissues occurred intermittently around the stem in large to small bundles. The xylem cells lost their radial alignment and, on the average, were smaller in diameter than those in the ungalled stem.

Only remnants of pith cells remained in the gall. This suggested that most of the pith was eaten by the larva soon after the stem was attacked. The first instar larva probably bored from the stem apex into the pith of the young stem. As the pith (and occasionally, xylem) was consumed, new, smaller parenchymatous cells arose

near the vascular cambium (Pl. 11, Fig. 8). Thus, the pith cells and the derivatives of the vascular cambium were the nutritive cells in this gall. Both of these were unenriched and vacuolate with only a minimal peripheral cytoplasm and an unenlarged nucleus (Pl. 11, Fig. 9). Staining indicated that only the epidermal cells of the healthy stem and of the gall contained tannin deposits.

Summary of Lepidopteran Gall

This gall was a simple kataplasma. A sclerid zone was not formed. The stem's cortex, although hypertrophied in the gall, was recognizable, and the nutritive tissue was of a low level of differentiation and was unenriched.

Sawfly Galls

Sawfly Gall 1) Gall on Snowberry

This gall was collected from *Symphoricarpos albus* var. *laevigatus* Fern.. The gall was caused by an undescribed tenthredinid (Felt, 1965). Each gall contained a single larva. Because the earliest collected galls (April 29) contained larvae, it was not known if a colleterial (=ovipositional) fluid was responsible for early gall development as it was in other sawfly galls. The larvae used sclerotized mandibles to chew through the nutritive tissue (Pl. 12, Fig. 2).

The galls were small capsule-like structures (Pl. 12, Fig. 1) at the twig terminal. These were probably bud galls, but their derivation was unclear. Each of the two terminal buds was replaced by a gall, and often the pairs shared a common wall. The gall walls were thick (2-3 mm), and deep green.

A transverse section of a young (April 29) gall wall (Pl. 12, Fig. 3) showed that the outer epidermis and the 5-6 subepidermal layers were composed of vacuolate cells. The bulk of the wall, however, was composed of several layers of cells that contained a fairly rich cytoplasm with prominent nuclei and many plastids. This was the nutritive tissue. It was produced as very broad, stubby

enations from the gall wall. The nutritive cells were not arranged in palisade fashion.

As the gall matured (May 6) (Pl. 12, Figs. 4 and 5) the nutritive cells became vacuolate. This occurred from the outer surface of the gall inward. Some of the nutritive cells lining the gall cavity were ruptured, probably from having been fed upon.

Vacuoles continued to enlarge in older nutritve cells (May 13) (Pl. 12, Fig. 6), so that by June 5 (Pl. 12, Fig. 7) only a peripheral cytoplasm with plastids was seen. By July 25 (Pl. 12, Fig. 8) the nutritive cells showed no cytoplasm. Many had been ruptured. Frass was abundant in the gall. At this time, however, the larvae had not eaten all of the gall wall material (i.e. the wall was still thick).

The cells of the gall wall stained lightly yellow-brown when stained for tannins, but there were no tannin-rich cells in the gall.

Sawfly Gall 2) Willow Leaf Gall

This gall occurred on *Salix* sp.. I generally found it on creek bank clumps (clones?) of saplings that showed few of the other types of willow galls. The gall (Pl. 13, Fig. 6) was caused by the tenthredinid, *Pontania* sp. (Pl. 13, Fig. 3). The species was presumed to be *P.*

pacifica (but see Smith, 1970) because lenticels occurred as brown spots on the surface of the galls - a distinctive characteristic of galls caused by this species (Russo, 1979).

This was an unusual gall when compared to most others in that it was initiated by the adult female as she oviposited into the young willow leaf. Thus it was a mark gall. Compounds in the colleterial fluid were responsible for a great deal of gall development (Smith, 1970). Although I collected galls that contained eggs as early as April 26, it was not until May 13 that I collected galls that contained larvae.

The youngest galls that were collected (April 26) (Pl. 13, Fig. 8) were small pubescent bulges on the underside of the leaf (Pl. 13, Fig. 5) that coresponded to shiny reddish spot on the upper surface (Pl. 13, Fig. 2). Galls were frequently adjacent to the midvein. Some of these very young galls showed a small slit on the upper surface of the gall, the tissue on either side of which had turned necrotic. This perhaps was the slit cut by the female sawfly to deposit the egg.

In longitudinal section, the young gall was seen to be produced primarily on the lower leaf surface, and the transition between ungalled leaf and gall was sharp. The leaf midvein occurred on one edge of the gall, and it was

partially split by the gall cavity (Pl. 13, Fig. 11). In fact, much of the gall wall tissue arose from meristematic tissues associated with the differentiating midvein. Although much of the gall at this time was composed of actively dividing, cytoplasmically rich cells, these were most prevalent in the center of the upper (Pl. 13, Fig. 9) and lower (Pl. 13, Fig. 10) gall wall.

Young nutritive cells were slightly larger in diameter than most of the cells in the gall, and they were vacuolate with a thin strip of peripheral cytoplasm. Some of these cells were ruptured. They were probably cut by the ovipositor, and/or lysed by the colleterial fluid.

Throughout the young gall, one finds scattered groups of cells that, although densely cytoplasmic, also contain a deeply stained deposit. This material stains dark reddish brown with ferrous sulfate, i.e. it is tanniferous. Many of the gall epidermal cells, scattered cells throughout the midvein, and the palisade cells in the young ungalled leaf (Pl. 14, Fig. 4) also stained positively (dark brown).

The most noticeable change that occurred in slightly older galls (April 29, and May 6) was that many of the cells of the gall wall lost their meristematic

appearance, and became vacuolate and filled with tannins. The nutritive cells lining the larval cavity remained free of these deposits and, although mostly vacuolate, began to show a dense cytoplasm.

By the time that larvae began to appear and feed in the gall (May 13, and 22; Pl. 13, Fig. 7), both upper and lower gall walls had doubled in thickness since the first collection date. A band of tannin-rich cells encircled the nutritive cells, and was derived from the scattered groups of tannin cells that were seen in younger galls.

At the same time, the nutritive tissue had increased in depth, and its cells, in cytoplasmic density (Pl. 14, Figs. 2, 3). The cells were not arranged in palisade fashion, and small enations grew into the larval cavity. Feeding damage was still not yet extensive (Pl. 13, Fig. 6).

Older galls collected on June 5 showed vacuolate nutritive cells that contained no tannins (Pl. 14, Fig. 6), while many of the cells in the gall wall stained positively for tannins (Pl. 14, Fig. 5). The lower gall wall continued to grow in thickness such that by August 12 it was 2-3 times as thick as in the May specimens. Much of the nutritive tissue had been fed upon and in spots had been eaten to the tannin-rich band of cells. The nutritive cells that had not been fed upon were

vacuolate with only a thin strip of peripheral cytoplasm. Frass was abundant in these galls.

The last galls that were sectioned (September 22) were about 1 cm in diameter. They were yellow with brown lenticels. Those galls that had not been invaded by weevils (probably Anthonomus sp.; see Caltagirone, 1964) and that still contained a sawfly larva displayed a band of vacuolate nutritive cells that was 10-12 cells thick (Pl. 14, Fig. 1). Galls collected on October 16, 1981 were on completely dead leaves that had fallen to the ground. Many of the galls, however, were still succulent and contained a 1 cm long white or purplish sawfly larva.

Caltagirone (1964) mentioned that feeding by late instar larvae of P. pacificus might completely hollow the gall, or might merely tunnel it, depending on the thickness of the gall wall. My own observations indicated that the younger larvae fed on the tannin-poor, cytoplasmically richer nutritive cells, while the older instars consumed both tannin-rich and tannin-poor cells.

Summary of Sawfly Galls

1) Classification. Both sawfly galls were simple kataplasmas. Neither contained sclerid zones, and both showed callus-like nutritive tissue. In complexity, they resembled the gracilariid gall on Peck's penstemon.

2) Nutritive cell dynamics. Both galls showed their most cytoplamically dense cells early in the season. As the season progressed, the proportion of vacuolate to cytoplasmically dense cells increased. The older the instar, the less nutritious was the appearance of its diet.

3) Tannins. In the case of the snowberry gall, the larva fed on tissue that stain relatively poorly for tannins. As the larva in the willow gall matured, on the other hand, it began to feed on tissue containing tannin-charged cells. Thus in the willow gall, the older instars contended with a diet that was probably less nutritious both because of the vacuolation of many cells, and because of the inclusion of tannins in many of those vacuoles. It should be stressed, however, that in the willow gall, the larva was presented with a diet poor in tannins when compared to willow leaf tissues (compare Pl. 14, Figs. 4, 5 and 6).

Thrips Gall

Thrips Gall 1) *Memecylon* Leaf Roll Gall

A preserved leaf gall on *Memecylon* sp. Roxb. (Melastomaceae) caused by *Crotonothrips danahasta* Ramakrishna was shipped to me from India by Dr. A. Raman. The specimen was collected on July 7, 1980 on the campus of Madras Christian College, Chengalpat District, Tamil Nadu, India.

The gall, like many thrips galls, was a leaf edge roll gall. Both edges curled over the leaf's upper surface. The galled leaves were green when picked and were, on average, 2.5 cm in length. No thrips were found in the preserved galls, but a few were found at the bottom of the specimen vial.

The leaves had a speckled appearance because of black circular, thickened areas, 1-1.5 mm in diameter that occurred between the secondary veins. There were approximately 90 of these areas per leaf. Most were discrete, but a few were fused.

The galled leaf showed an abnormal mesophyll layer that was thick and contained enlarged, densely arranged isodiametric cells. In patches the upper epidermis changed from vacuolate, small rectangular cells that had their long axes parallel to the leaf surface, to much

enlarged palisade-like cells with cytoplasms that contained deeply stained deposits (Pl. 17, Fig. 10; Pl. 28, Fig. 10). These last were the nutritive cells, and the nutritive patches in which they occurred corresponded to the black patches on the leaf surface that were seen with the naked eye. They were underlaid by radial rows of small cells. Some of which were empty (dead) while others contained large vacuoles, the contents of which stained lightly and homogenously. The gall was not stained for tannins.

Summary of Thrips Gall

1) Classification. This gall had characteristics of a complex kataplasma in that it showed a fairly distinct nutritive epidermis. It was simple in design and contained no protective layer. As with the eriophyoid galls, I classified this as a complex kataplasma.

2) Nutritive Cells. Thrips feed with stylets (Pl. 17, Fig. 9). According to Ananthakrishnan (1978) in

> the majority of thrips galls, feeding is often locally restricted to the surface layer of a particular portion of the infected organ, where the epidermal cells are densely filled with cytoplasmic contents and are prominently nucleated. These cells and some of the cells of the mesophyll within constitute the feeding zone.

The last statement is supported by measurements I

made of the stylets of mature thrips. The stylets of C. danahasta were, on average, 0.15 mm long. The nutritive cells were 0.07 mm deep. Thus this thrips was able to penetrate beyond the surface nutritive cells. Most interesting is the fact that the nutritive cells in the Memecylon gall occurred in patches. This indicated a limited manipulative ability and a sedentary feeding behavior.

3) Tannins. The presence of dark deposits in the nutritive cells suggested that tannins were present in the cells. In response to an inquiry about this, A. Raman wrote that "tannin deposition is not unusual in mature galls induced by thrips especially in the nutritive cells." The important word here was "mature." Most likely, nutritive cells in thrips galls develop deposits of tannins over time. I infer from this and from the absence of thrips in my specimens that the galls I studied were mature. Young galls should be studied.

Scale Gall

Scale Gall 1) Oak Pit Gall

Although common, this gall was collected only once from *Quercus garryana* Dougls. in Corvallis, Oregon. The gall was caused by a species of Asterolecanium (probably *A. minus* Lindinger - a common scale on west coast deciduous oaks; Koehler, 1964). The galls that were collected (April 2) had been formed the previous spring. Thus the scale insect was either old, dead, or missing.

The pit scales, as they are commonly called, formed galls on the current or previous year's twigs. The galls were unusual in at least one respect - they did not cover or enclose the insect, but instead surrounded the sides of the insect with an incomplete "umwallung" (Pl. 11, Fig. 1). The insect was cradled in the gall (Pl. 11, Fig. 3).

The gall was caused by a proliferation of the phellogen (=bark meristem) which gave rise to the "umwallung". The periphery of the gall wall was composed of elongate, thin-walled cells arranged in radial rows (Pl. 11, Fig. 3). Toward the center of the pit, underlying and couching the insect, were radial rows of elongate sclerids. Under these were small isodiametric cells (probably phelloderm). Cortical cells were under

these cells. There was a slight enlargement of the cortical cells, and former cellular enrichment was indicated by prominent nuclei (Pl. 11, Fig. 4) and granular cytoplasm in a few of the cells. Most, however, were vacuolate. The stem's vascular tissue and pith appeared undisrupted by the gall (Pl. 11, Fig. 2). The gall was not stained for tannins.

Summary of Scale Gall

1) Classification. The presence of a sclerid zone that couched the gall suggested that it was prosoplasmic. The layer, however, did not surround the insect. The facts that the gall did not enclose the insect and that the vascular and pith tissues remained undisturbed by the scale indicated that the gall was a complex kataplasma.

2) Nutritive cells. The collected specimens were too old to allow for a study of the nutritive cells. Other workers have observed enriched cells in this and another scale gall (Parr, 1940, and Houard, 1903, respectively), but more work with younger galls is needed to further characterized these cells.

Aphid and Adelgid Galls

Aphid Gall 1) Poplar Petiole Gall

This gall was collected from saplings and mature *Populus trichocarpa* T. and G.. It was caused by an undescribed species of *Pemphigus* (Aphididae: Subfamily Eriosomatinae). Stem mother measurements did not match any of those given by Palmer (1952) for species that occurred in the Rocky Mountains. The gall involved both a thickening of the petiole (Pl. 15, Figs. 2 and 4) and an overgrowth of the lamina at the petiole-leaf junction. It was a covering gall.

One of the earliest signs of galling (April 15; Pl. 15, Fig. 1) was a sligtly swollen and bent petiole, and a twisted leaf lamina at the leaf base. By April 26 the gall had formed a curled and swollen structure at the leaf base (Pl. 15, Figs. 2 and 4). When the gall was forcibly opened, one saw a gall chamber formed by the flared petiole and enlarged leaf base (Pl. 15, Fig. 5). The aphids lived in this chamber on the modified lower leaf surface. The gall continued to grow until it reached full size in late June at which time it resembles a subspherical pouch (Pl. 15, Fig. 3).

Until May 20, the galls contained only a single stem

mother that molted at least twice in the gall before producing progeny. Thus this female incited gall development and prepared a large gall cavity for her progeny. As a young (April 15) gall was approached, the mesophyll underwent complete homogenization. Different amounts of cell division in the mesophyll layers caused the lamina portion of the wall to arch up and curl partially around the petiole.

At the gall, the lower surface of the petiole thickened due to proliferation of the vacuolate, parenchymatous cells underlying the vascular bundle. The petiole lost its circular shape and became oblong in transverse section with the long edge forming part of the gall wall (Pl. 15, Fig. 5). Comparison with ungalled petioles indicated that there was little disruption in the organization of the vascular bundle in the galled petiole.

At the top of the cavity and on the petiole side of the gall, the cavity epidermal cells (these were probably not nutritive cells; see below) were palisade-like and, although partially vacuolate, showed a fairly dense cytoplasm and prominent nucleus.

By April 29, most of the cavity epidermal cells were vacuolate (Pl. 15, Fig. 6). There was, however, a small area of cytoplasmically dense epidermal cells in the

arched gall wall (Pl. 15, Fig. 7). These cells were not arranged in a palisade-like fashion, and a few formed unicellular hairs.

The meristematic cells of the vascular bundles were cytoplasmically rich and were 8-15 cell layers in from the gall cavity. Frequently there was a large intercellular cavity in the center of the bundles. At the same time, the outer surface of the leafy gall wall was uneven in thickness due to ridges on the outer gall surface (Pl. 15, Fig. 8).

Specimens collected May 6 still showed large groups of densely cytoplasmic cells in the vascular bundles of the leafy gall wall. The bundles were larger and more widely separated than previously.

Specimens from May 13 showed a cavity epidermis composed of cells that were either densely cytoplasmic (on petiole gall wall) or vacuolate (on leafy gall wall). The leafy gall wall continued to contain bundles of cytoplasmically dense cells (Pl. 15, Fig. 9) that were 5-10 cells beneath the gall cavity's epidermis.

The June 5 specimens contained progeny and were larger than earlier, mainly due to growth of the leaf gall wall (Pl. 15, Fig. 5). The epidermal cells lining the gall cavity at this time were generally vacuolate but a few along the leafy gall wall possessed a rich

cytoplasm. The band of densely cytoplasmic elongate vascular cells were still present in the gall wall (Pl. 16, Fig. 1), and in some spots, passed within 4 cells of the cavity's epidermis. Frequently xylem cells on the periphery of the band showed spiral secondary wall thickening.

On August 12 many of the galls were dying. The specimens contained no living aphids. The cells of the cavity epidermis were vacuolate and the cells of the densely cytoplasmic vascular band had either vacuolated and taken on deeply stained deposits or had differentiated into vascular elements (Pl. 16, Fig. 2). The cells of the leafy gall wall had begun to collapse and die (Pl. 16, Fig. 3).

Some of the galls collected May 6 were stained for tannins. Cells scattered on either side of the vascular strands contained deposits of tannins (light to dark brown) as did randomly scattered cells throughout the gall wall. The cavity epidermis stained very lightly brown, while the subepidermal layer, in some cases stained dark brown (Pl. 16, Fig. 4).

The most important unanswered question concerning the poplar petiole gall was: Where do the stem mother and progeny feed? A gall collected on May 13 showed 20-30 collapsed, neighboring cavity epidermal and

subepidermal cells. Some of the cells beneath these showed dense cytoplasms. This may have been a feeding site, but no stylet tracks were seen in the area.

A few cells of the cavity epidermis retained cytoplasmic density from April through June, and one wonders if these were the nutritive cells. The stylets, however, undoubtedly penetrated beyond this layer. On May 20, for example, the stem mother's rostrum on the average measured 0.5-0.6 mm in length. (Rostral length should slightly underestimate stylet length.) Young progeny had rostrums 0.45 mm long. The gall wall on the same day was 0.95 mm thick. Thus the aphids, regardless of life stage, were capable of feeding well beyond the epidermal layer.

Although they did not resemble in shape or position the nutritive cells found in mite, midge, and wasp galls, the densely cytoplasmic cells of the vascular bundles may have been a primary food for the stem mother and her progeny. Their candidacy as a possible food source was strengthened by the fact that they were present in relatively large numbers, in fairly close proximity to the aphids (0.37 mm under the cavity epidermis), and in an enriched state for a long period of time.

Another possibility is that the aphids fed on vascular sap. Suggestive observations included the

occurrence of liquid balls in galls beginning on May 20.

Aphid Gall 2) Poplar Marginal Leaf Gall

This gall was collected from Populus trichocarpa T. and G., and was caused by Thecabius populi monilis (Riley) (Aphididae: Subfamily Eriosomatinae). Palmer (1952) described the galls in abbreviated form as follows:

> The fundatrix gall contains a solitary fundatrix, consists of a pocket-like gall on upperside of a leaf at the base of the new growth, gall opening on underside, her young migrating soon after birth and locating separately near the margins on the underside of new leaves, forming a row of pocket-like or bead-like galls...each containing a solitary aphid apterous or alate.

Her description fits well with what I observed. The stem mother (Pl. 17, Fig. 4) and her pouch gall were first seen on young leaves that were not fully expanded. She attacked the lower leaf surface and caused an outpocketing of the lamina along a straight line for at least 1 cm (Pl. 17, Figs. 1 and 2). The gall usually occurred slightly in from the leaf's edge with the long axis parallel to that of the leaf. It was red when young.

Up until May 20 only the stem mother was found in the gall. On this collecion date, however, progeny were

present in the gall. On June 25, all of the galls were empty and many of the new poplar leaves (a late flush) bore rows of new pouch galls (1 cm long and 1 cm in diameter at widest point) formed by the progeny (=the fundatrigeniae) (Pl. 17, Fig. 3). The rows ran the length of the leaf and there were usually 2-3 rows per leaf. Each row contains 5-8 bead-like galls arranged end to end. The rows resemble linked sausage. These galls, like the stem mother galls, were produced when the aphids attacked the underside of the leaf and caused outpocketing. Each cavity was separated by a septum formed of pinched lamina.

An apterae fundatrigeniae is seen in Plate 17, Figure 5. Only a single aphid occurred per fundatrigeniae gall on June 25, but on July 15, some contained 3-4 aphids--most apterae, a few alatae. Liquid droplets also were common in these galls. On the last collection date, August 12, the galls were empty, but many were still green and succulent.

In transverse section the young (April 15) stem mother gall appeared as in Plate 17, Figure 6. The mesophyll layers (Pl. 17, Fig. 7) lost their distinctiveness as the gall was approached so that its apex, the gall wall was composed of tightly packed isodiametric cells (Pl. 17, Fig. 8). The cells in the

periphery of the gall wall were larger than those near the gall cavity -- a difference that caused the curved outpocketing.

The cavity epidermis in this young stem mother gall was made up of vacuolate cells. Densely cytoplasmic cells made up much of the center of the gall wall.

By April 29 the gall was closed and the transition zone between ungalled leaf and gall wall was sharp. The cavity was nearly circular in transverse section. The cavity epidermis cells were small and vacuolate. The majority of cells in the gall wall were also vacuolate.

Several vascular bundles ran the length of the gall. They contained many cytoplasmically dense xylem and phloem parenchyma cells that were both small and dividing. The bundles were 3-4 cells in from the cavity epidermis (Pl. 18, Fig. 2) and were partially surrounded by vascular bundle cells that contained deeply stained deposits.

On May 13, the stem mother was still alone in the galls. The cavity epidermal cells in some areas were collapsed, and in other areas were uncollapsed and vacuolate (Pl. 18. Fig. 4). Vascular cells on the inside of the bundle (phloem parenchyma) were cytoplasmically dense. The healthy leaf by this time has matured, and many of its palisade parenchyma cells contain deeply

stained deposits (Pl. 18, Fig. 1).

By May 20 the gall had reached full size. The cavity was about 3 mm in diameter in transverse section. The cavity epidermis contained groups of collapsed and uncollapsed cells. The vascular bundles, still with densely cytoplasmic cells, contained more elements and were broader under the collapsed cells.

By June 5, progeny were present in the stem mother galls. As before, the cavity epidermis was collapsed in spots and those spots were underlaid by 4-5 layers of cells filled with deeply stained deposits (Pl. 18, Fig. 3). Cells in the vascular bundles were now vacuolate and many had collapsed. Short segments of stylet sheath tracks (stained purple with toluidine blue) extended out to the external epidermis.

On August 16 empty fundatrigeniae galls were larger than the mature stem mother galls, and the gall cavity was 3-4 mm in diameter in transverse section. With respect to anatomy, however, these galls were like the stem mother gall. The cavity epidermal and subepidermal layers in many areas were collapsed. Numerous vascular bundles ran the length of the gall wall and these contained a few cytoplasmically dense, small cells in the phloem of the bundle. The bulk of the gall wall was made up of enlarged vacuolate parenchyma. Scattered cells

throughout the gall wall contained deeply stained deposits, and a few contained stellate crystals. Stylet tracks were not seen in sections of these galls.

When a young (April 29) stem mother gall was stained for tannins, scattered cells throughout the wall stained positively (light to dark brown). The cavity epidermis and the vascular tissue were free of tannins (Pl. 18, Fig. 5).

As with the previous aphid gall, the location of feeding sites in both the stem mother and fundatrigeniae galls was not clear. The densely cytoplasmic vascular cells may be the primary feeding site, rather than the vacuolate epidermal cells that line the cavity. The occurrence of stylet sheaths deep within the gall wall, however, suggested that the older stem mothers fed in the wall parenchyma.

The wall of a mature stem mother gall was on average between 0.6 and 0.9 mm thick. The vascular bundles were 0.2–0.3 mm beneath the cavity epidermis. A mature stem mother's rostrum was about 0.6 mm long. Her young's rostrums were 0.3–0.6 mm long. Thus in a stem mother or fundatrigeniae gall, even considering a winding intercellular stylet path, the aphids could penetrate into the gall wall beyond the vascular tissue.

Aphid Gall 3) Midvein Gall on Poplar Leaves

This gall (Pl. 18, Fig. 6) was collected on *Populus trichocarpa* T. and G.. There was some question about the identity of the gall-former (Palmer, 1952; Grigarick and Lange, 1962). It was most likely either *Pemphigus balsamiferae* or *P. populivenae*.

According to Palmer (1952), both of these species overwinter on poplar and the stem mothers form galls on the young leaves in spring. The stem mothers produce alate progeny (fundatrigeniae) in the gall and, in mid-spring to mid-summer, the alates leave the gall and settle on the crowns of herbs such as sugar beets. Their progeny in turn attack but do not gall the roots of these herbs. Alates returns to poplars.

The gall cavity was formed by the out-pocketing of the leaf lamina. The midvein, which was turned on its side by the galling, formed a portion of the gall wall (Pl. 18, Fig. 7). The transition between ungalled leaf and gall wall was sharp and, as in many other galls, occurred at a vascular bundle. On the ungalled side of the bundle the two distinct mesophyll layers were seen while on the galled side there was an homogenization of the two layers.

The wall of a young gall (May 6) and its cavity epidermis were primarily made up of vacuolate, enlarged

parenchyma cells. Many of the cavity epidermal cells elongated and divided to form short hairs (2-3 cell). Small cells rich in cytoplasm occurred 2-5 cell layers under the cavity epidermis in the vascular strand. Some of these had differentiated into metaxylem with spiralled secondary wall thickenings.

One week later (May 13) the stem mother was still the only gall inhabitant. All of the cells in the gall wall other than those in the vascular bundle showed very thin peripheral strips of cytoplasm. Many of the elongate cells of the vascular strand still contained a dense cytoplasm although vacuoles were present (Pl. 18, Fig. 8).

The galls on May 20 looked much like those of the week before. These galls, however, contained the stem mother and her progeny. As in previous aphid galls, the identity of the food tissue was unknown, but enriched vascular bundle cells were likely candidates.

Aphid Gall 4) Leaf Gall on Bearberry

This gall was collected from *Arctostaphylos uva ursi* (L.) Spreng. in Corvallis, Oregon (Oregon State University Campus) and from *A. glutinosa* in Tuolumne County, California (Pl. 19, Fig. 1). The causative aphid was *Tamalia coweni* (Cockerell) (Aphididae: Subfamily

Aphinae). The galls were leaf rolls. The margin of the leaf swelled and curled under the lower leaf surface. Curling formed the gall cavity. On May 8 most of the galls contained a single stem mother and two caste skins, but a few contained 2 aphids. All galls that were checked on May 20 contained a single stem mother. By August 20, progeny were present in the gall (Pl. 19, Fig. 2).

When the young (May 8) gall was cut transversely (Pl. 19, Fig. 4) one saw that the transition zone between ungalled and galled lamina was either long (Pl. 19; Fig. 5), or abrupt (Pl. 19, Fig. 7). The palisade cell derivatives were easily identified in the gall wall because of their staining characteristics (dark, granular material) and their alignment (Pl. 19, Fig. 6). Some of the intercellular space in the leaf mesophyll layer was retained in the wall and, the gall mesophyll cells were vacuolate much like spongy mesophyll cells (compare Pl. 19, Figs. 5 and 6).

The cavity epidermis and subepidermis were made of small, deeply stained cells with long axes tangent to the cavity surface. Cells with granular contents made up the bulk of the wall and showed a peripheral nucleus. In addition to the midvein, there were about 10 vascular bundles that ran the length of the gall. Each was 2-3

times as large in transverse section as its counterpart in the ungalled side of the leaf. The bundles were 4-5 cell layers under the cavity epidermis, and all contained several small cytoplasmically dense cells.

The galls collected May 20 showed further thickening of the gall. The vascular bundles contained fewer meristematic cells, and the cavity epidermis cells remained flat and darkly stained (Pl. 19, Fig 8).

With the exception of the epidermal, vascular, and a few spongy mesophyll cells (Pl. 20, Fig. 1) in an ungalled leaf collected on May 20, cytoplasms stain positively (black) for the presence of tannins. In the gall, the contents of the cavity epidermal cells and the granular contents of many of the gall wall cells stained positively (black) (Pl. 19, Fig 9).

The stylets of the young stem mothers in the gall on May 8 were about 0.2 mm long (Pl. 19, Fig. 3). The gall wall at this time was 0.5 mm wide. The aphids could penetrate beyond the vascular tissue.

No nutritive tissue such as found in cynipid galls was found in this gall. If the aphids fed upon the contents of the large, parenchymatous wall cells, then they encountered tannins.

<u>Aphid Gall 5)</u> Leaf Gall on Witch Hazel

This gall was collected on <u>Hamamelis</u> <u>virginica</u> L. in New York State by Gary Nielsen on May 26, 1980. It was caused by the aphid <u>Hormaphis</u> <u>hamamelidis</u> Fitch. Each gall contained a single stem mother. The life cycle of this aphid has been studied by Pergande (1901) and by Morgan and Shull (1910).

The galls were cone-shaped outpocketings of the lamina and were produced on the upper leaf surface. They had a lipped aperture on the lower leaf surface (Pl. 20, Fig. 2). The transition zone between ungalled leaf and gall wall was sharp (Pl. 20, Fig. 3). The cells of the cavity epidermis and the subepidermal layer were vacuolate (Pl. 20, Figs. 4,5) and were of various sizes, shapes and alignments.

The vascular bundles that ran up the sides of the gall wall contained many cytoplasmically enriched cells. The bundles were 3-4 cells layers (0.15 mm) beneath the cavity epidermis. Although my observations did not suggest a feeding site, Pergande (1901) observed liquid balls in older (mid-May) galls in which stem mother and progeny occurred -- an observation that suggested that vascular saps were tapped at this time.

<u>Adelgid Gall 1)</u> Anasas Gall on Engelmann Spruce

The gall was collected in Oakridge, Oregon (Lane

Co.) on July 5, 1980. It was taken from a 1 m sapling of _Picea engelmannii_ Parry and was caused by _Adelges cooleyi_ (Gillette) (Adelgidae=Chermidae). The gall resembled a small pineapple (Pl. 16, Fig. 5) and was formed by swollen needle bases.

According to Plumb (1953) the stem mother of another adelgid, _A. abieis_ "preconditions" vegetative buds of _P. abies_ for her progeny by causing them to swell. Both mother and progeny are required for gall formation, but only the gallicolae (the progeny) are found in the gall chambers. The same scenario is assumed to be true for the collected gall. Four to eight small wax-covered adelgids (Pl. 16, Fig.7) were seen in each gall cavity at the time of collection (Pl. 16, Fig. 6).

A longitudinal section through a gall cavity showed that the cavity epidermis was made of large, unaligned, isodiametric cells that were either vacuolate or filled with a granular material (Pl. 16, Fig. 8). These cells rested upon 3-4 rows of cells that were also filled with granular material. Under these were cells filled with large refractive grains (probably starch). These last cells formed a band about 10 cells thick. The vascular tissue was under this band.

The stylet length of the collected gallicolae was about 0.36 mm. The granular layer surrounding the gall

cavity was, on average, 0.44 mm thick, while the presumptive starch layer beyond was 0.88 mm thick. Thus, the gallicolae were most likely tapping the cellular contents of the granular layer. No stylet tracks were found in these sections. Increased stylet length might allow growing gallicolae to tap the deeper starch layers and vascular system. The lack of liquid balls in the collected galls suggested that the vascular tissue was not being tapped at the time of collection. Perhaps the stem mother fed on nutritive cells much like those in cynipid galls (Rohfritsch, 1976) while the gallicolae fed on a starch storage tissue.

Summary of Aphid and Adelgid Galls

1) Classification. My observations did not allow for identification or characterization of the nutritive tissue in aphid and adelgid galls. Characters other than those of the nutritive tissue, however, indicate that these were simple kataplasmas in which no protective layer occurred. The leaf mesophyll was disrupted in the gall wall but the derivation of the cells could be quickly discerned. The galls were relatively simple in design. An aperture, although often pinched closed, occurred in all of the galls.

2) Diet. These homopterans possessed stylets of

lengths that allowed for penetration beyond the cavity epidermis. Thus, unlike most other gall insects (with the possible exception of the gall-forming coccids), the aphids and adelgids probably tapped the contents of cells that were layers beneath the cavity epidermis. The epidermal cells perhaps were fed upon in passing, but most feeding undoubtedly occurred deep in the gall wall.

The fact that the cavity epidermal cells became vacuolate early in gall development (such as the poplar petiole gall), the fact that they were generally some of the smallest in the gall, and the fact that they generally showed no ordered alignment suggested that the epidermal cells nor the subepidermal cells were the food tissues. In all but the adelgid gall, the vascular bundles were within reach of all but the shortest (youngest) stylets. The bundles were abundant in the galls and contained elements that remained cytoplasmically rich longer than any other cells in the gall. Whether the cytoplasms of these constituted a nutritive material was not clear. The presence of liquid balls in some of the galls suggested that excess fluids were taken up by the aphid, as would occur if phloem sap was tapped.

In the poplar midvein gall stylet paths were found well beyond the vascular tissue. In this case, the

enlarged vacuolate, unenriched cells that made up the bulk of the gall wall were possible food cells.

All of the aphid and adelgid galls described were formed or initiated by a single stem mother. In the poplar petiole, poplar midvein, and bearberry galls the progeny developed in the stem mother gall. There was, however, no rejuvenation of wall tissue with the appearance of the progeny. On the contrary, the cells of the gall wall continued to deteriorate through the season. To the human eye, the dietary quality of cytoplasm appeared to decrease with time.

The fact that _Thecabius populi monilis_ fundatrigeniae left the stem mother galls and hazarded dangers of migration to form new marginal leaf galls on poplar suggested that the stem mother gall provided an inadequate diet. Rather than rejuvenating tissues in an old gall, the aphids moved to new tissue. In fact, it was interesting that not more gall-forming poplar aphids used this late season resource. Instead, many moved to a completely different host plant species.

From Rohfritich's (1976) work we know that the stem mother adelgids fed on cytoplasmically enriched nutritive cells. My own observations suggested that the progeny fed on a much different storage-like tissue.

3) _Tannins_. Without knowing where feeding occurred

it was not possible for me to say if tannins were ingested. If, however, cell contents were taken randomly throughout any of the galls, then tannins would be ingested. This would be particularly true in the bearberry gall where the wall was composed of tannin-charged cells. At the same time, the proportion of tannin-rich to tannin-poor cells in poplar galls was less than in leaves. Regardless of their feeding site, these aphids suppress the development of the normal tannin content.

Cecidomyiid Galls

Cecidomyiid Gall 1) Hawthorn Leaf Gall

This gall was caused by an undescribed cecidomyiid on *Crataegus* *douglasii* var. *suksdorfii* Sarg.. Larvae caused a leaf fold along the length of the midvein (Pl. 20, Figs. 6,7). The lamina adjacent to and on both sides of the midvein swelled and formed the thick walls of the gall. Where the two sides met over the cavity, they remained unfused, but pinched together. There were about 10 larvae in the single long, tube-like larval cavity.

Ungalled leaves on May 13 showed a spongy mesophyll with large intercellular spaces (Pl. 21, Fig. 2). The palisade cells were irregular in alignment, shape, and spacing.

Galls collected on May 13 were already fairly mature. In transverse section (Pl. 20, Fig. 8) the gall walls were 3-4 times as thick as the ungalled lamina. The transition zone between leaf and gall wall occurred abruptly at a vascular bundle (Pl. 21, Fig. 1). The gall wall was made up of enlarged vacuolate cells with very little intercellular space (Pl. 21, Fig. 4).

The nutritive cells lined the cavity wall and were the smallest cells in the gall. They were usually sub-circular to elongate, and some showed a nucleus and

prominent nucleolus. Those near the neck of the gall were vacuolate. Those in the neck of the gall produced cytoplasmically rich, single-celled hairs. Many nutritive cells at the bottom of the cavity also had rich cytoplasms.

The bulk of this young gall wall was made up of about 14 layers of elongate cells with their long axes perpendicular to the cavity's surface. These large cells were vacuolate. A few showed a nucleus and some were filled with dark deposits.

The leaf midvein at the base of the gall contained metaxylem elements and phloem and xylem parenchyma that were still densely cytoplasmic. In addition to the midvein there were 7 enlarged bundles that were several cell layers under the nutritive cells.

By June 5, nutritive cells at the bottom of the gall still contained more cytoplasm than did those at the neck, but vacuoles were more prominent than previously. A few groups of collapsed nutritive cells on the side of the cavity wall were seen at this time. Nuclei and nucleoli were still present in these cells, and the neighboring and underlying cells were not affected.

On August 12, the larvae were 0.84 mm long and show no sternal spatula (=a T-shaped sclerite on the anterior ventral surface of older instar cecidomyiid larvae). The

nutritive cells both at the bottom and neck of the gall were vacuolate by August and many contained dark droplets. The same was true of the cells in the 3-4 underlying layers. As in earlier material, groups of neighboring nutritive cells on the side wall and bottom of the cavity were collapsed. The collapsed cells contained cytoplasmic remnants and some showed nuclei and nucleoli.

The very large cells that made up the gall wall remained vacuolate (some with deeply stained droplets), and showed nuclei. Their cell walls at this time were very thick and perforated. Perforations were seen in earlier (May 13) material, but had become more evident in the August 12 material. The walls of the cells directly beneath the nutritive cells also showed these pits.

Galls collected on September 22 had a gall cavity only slightly larger in diameter (1.5 mm) than the same on May 13 (1.0 mm). Similarily, the gall wall was only slightly thicker. The larvae had grown (Pl. 20, Fig. 9) so that they were 5.2 mm in length and filled the gall cavity. Each showed a prominent sternal spatula.

Extensive areas of the nutritive layer were collapsed and necrotic on September 22. Where uncollapsed these cells contained dark droplets and many were thick walled (Pl. 21, Fig. 5). A few of the

nutritive cells near the neck region continued to have a fairly rich cytoplasm. The large, pitted, thick-walled cells of the gall wall were filled with unstained crystalline deposits (perhaps starch). As of September 22 no extensive sclerid layer had developed in this gall. A thin band of sclerids occurred under the midvein, but did not extend up the sides of the gall.

When stained for tannins, a young ungalled leaf (May 13) showed deposits (dark brown to black) in the palisade parenchyma cells and in the spongy mesophyll. The same was true for older leaves (June 5 and September 22). From May 13 to September 22, cells associated with the vascular bundles stained positively (Pl. 21, Fig. 3) as did several cells scattered through the gall wall.

Through the season the cells of the nutritive layer and 3-4 subepidermal layers stained light to dark brown (droplets). Collapsed nutritive cells (September 22) stained more deeply for tannins (darker brown).

Cecidomyiid Gall 2) Leaf Roll Gall on Snowberry

This gall occurred on *Symphoricarpos albus* var. *laevigatus* Fern.. It was frequently collected on the same plants as were the previously described sawfly snowberry galls. The gall was caused by an undescribed cecidomyiid (Felt, 1914).

The gall was formed when the leaf edge became thick and rolled up across the leaf's upper surface to the midrib. When both edges were galled, as often happens, the lamina looked like a scroll. The gall usually occurred on leaves at the tip of the branch. Many larvae occurred in the gall cavity at the center of the leaf curl (Pl. 21, Figs. 6,7).

On May 6 the larvae were 0.56 mm long and showed no sternal spatula. The young ungalled leaf had well differentiated palisade and spongy mesophyll layers (Pl. 21, Fig. 8). The midrib was about twice as large in diameter on a galled leaf as on an ungalled leaf. The transition between galled and ungalled lamina often occurred at the enlarged midvein. For a short distance on the galled side of the midvein, the lamina was only slightly thickened (Pl. 21, Fig. 9), but showed no distinct mesophyll layer.

In the thick gall wall, there were 12-14 irregular cell layers as compared to 6-7 in the ungalled leaf. The vacuolate cells in the gall wall were 3-4 times the diameter of the cells in the adjacent lamina and contained numerous (starch-storing?) plastids.

In this young gall the nutritive cells were transformed epidermal cells of the upper leaf surface (Pl. 21, Fig. 10). They showed no special alignment and

were half the diameter of the enlarged gall wall cells. Most were vacuolate with a peripheral nucleus, nucleolus and some cytoplasm.

In transverse section, the gall cavity was teardrop-shaped and was 0.45 mm long and 0.21 mm wide at its widest point. The cavity spiralled out as a thin space between rolled leaf surfaces. Thus, in May the gall was not completely closed.

There were about as many vascular bundles in the gall wall as there were in the ungalled lamina, but those in the wall were 2-4 times larger and were about 8 cell layers beneath the cavity epidermis.

On May 20 the curled leaf surfaces were pressed against one another, i.e. the cavity was closed. In transverse section the cavity was 0.53 mm in length and 0.34 mm at its widest point. The gall cavity was partially surrounded by a strip of thick-walled sclerids. Nothing similar to these was seen in the ungalled leaf, or in the outer curls of the gall wall.

Many nutritive cells in late May were partially collapsed and rich in cytoplasm with a prominent nucleus and nucleolus. Some had pitted walls that were shared with the underlying cells.

By June 5 a larva was 1.33 mm long and had a shallowly forked sternal spatula. In transverse section

the gall cavity was 0.84 mm long and 0.52 mm wide at the widest point. The band of sclerids (3-4 cell layers thick) formed an overlapping spiral around the gall cavity. Most nutritive cells were partially collapsed. Some still contained a nucleus and dense cytoplasm, but many were vacuolate and anucleate.

On July 24 an average larva remained 1.33 mm long. The gall cavity was almost circular and was 1.6 mm in diameter. The band of sclerids had increased in width (6 cell layers) so that most cells that were beyond the vascular tissue were sclerids.

Many nutritive cells at this time were uncollapsed, elongate and vacuolate with a peripheral cytoplasm (Pl. 22, Fig. 1). Nuclei were rarely present. The wall pits were still present.

By October 9 a larva was 3.92 mm long and the sternal spatula was deeply cleft. On October 16, galled leaves were the only ones remaining on the plant. The dry, brown, and slightly uncurled galls contained larvae.

When a young gall (May 6) was stained for tannins, scattered cells throughout the gall wall stained brown (Pl. 22, Fig. 2). Most gall cells, however, did not stain positively. The same held for galls collected on June 5 and July 24. Only the palisade cells of a young (May 6) ungalled leaf stained slightly (light brown) for

tannins.

<u>Cecidomyiid Gall 3)</u> Leaf Gall on Serviceberry.

This gall was collected on <u>Amelanchier</u> <u>alnifolia</u> Nutt.. It was caused by the cecidomyiid <u>Trishormomyia canadensis</u> Felt or a closely related species. One larva occurred in each gall.

The gall was a pouch gall of complex design. It usually occurred to the side of the midrib (Pl. 22, Fig. 6) and was often found in clusters. The gall's ostiole protruded slightly above the leaf's upper surface and was at the upper end of a neck. The central chamber was at the bottom of the neck. This chamber, for much of the season, was distinct and separated from the larval cavity.

Below the leaf surface, one saw the gall's tomentose U-shaped pouch with two broad, flat sides (Pl. 22 Fig. 3). When cut longitudinally through its narrow width (Pl. 22, Fig. 4), the gall showed a tunnel that ran along its bottom. This tube-like cavity ran half way up both sides of the pouch where it tapered to an end. This was the larval cavity. Wall outgrowths separated it from the open central chamber mentioned above.

On April 15 the ungalled leaf lamina (Pl. 23. Fig. 1) was actively growing. Although distinct, the palisade

and spongy layers were meristematic and relatively rich in cytoplasm. At this time the transition from healthy to galled lamina was abrupt (Pl. 23, Fig. 2). The gall's upper neck region was built primarily of enlarged, vacuolate palisade derivatives. The lower neck, however, and much of the wall at the bottom of the gall were derived from the spongy mesophyll layer. Vascular bundles with meristematic undifferentiated elements ran down the middle of the gall wall.

In this young gall the central cavity and larval cavity were interconnected (Pl. 22, Fig. 6) and both were lined with cells derived from upper epidermal cells of the leaf. Along the wall of the central cavity these cells were vacuolate. At the bottom of the larval cavity, however, several layers were actively meristematic, with cytoplasmically rich cells (Pl. 22, Figs. 7 and 8). The galls at this stage were 1.4 mm long, and 0.9 mm wide (on edge). The larval cavity was about 0.52 mm long, and 0.21 mm wide.

On April 22 an orange larva from a gall was 0.59 mm long. By May 6 the healthy leaf showed a non-meristematic palisade and spongy layer (Pl. 23, Fig. 3). Close to the gall, the palisade cells were filled with plastids. In early May the central cavity was closed off from the larval cavity. The larval cavity was

lined by vacuolate, anucleate nutritive cells that contained dark deposits (Pl. 23, Fig. 4). The cells of the 2-3 layers under the nutritive layer resembled the nutritive cells.

Many small vascular bundles occurred 6-8 cell layers beneath the nutritive layer. Several layers of sclerids occurred beneath the bundles and around the bottom of the gall.

By May 20 the gall was difficult to slice through because of sclerid development. It is 4.9 mm long. The nutritive cells were vacuolate with peripheral cytoplasm and dark deposits.

On June 5 the gall was 5.0 mm long. The nutritive cells were vacuolate and thick-walled. A few were collapsed. The cell walls between nutritive and subepidermal cells were pitted.

On June 25 a larva was 0.98 mm long and was without a distinct sternal spatula. On August 12 the larva was 1.68 mm long and the sternal spatula was present (Pl. 22, Fig. 5). On August 12 the band of sclerids had developed around the entire periphery of the gall, and a band also lined the central empty gall cavity. Thus the gall wall and the gall's central core were re-inforced by these cells. In transverse section (Pl. 23, Fig. 5), there was a striking difference between the sclerids lining the

central cavity and the slightly larger, vacuolate nutritive cells (Pl. 23, Fig. 6). The nutritive cells showed numerous large pit connections with the underlying cells. Several of the underlying cells had fairly rich cytoplasms.

On September 20 a larva was 4.48 mm long. Thus, most larval growth occurred between August 12 and September 20. The gall was 4-5 mm long. The nutritive cells contained dark deposits (Pl. 23, Fig. 7), as did most of the cells of the gall wall. There was no indication of collapse or rupturing of the nutritive cells, but many were covered on their exposed surface with material that resembled ruptured cell contents (Pl. 23, Fig. 7).

By October 16, galls on the few leaves remaining on shrubs were dry and the two chambers in the gall were no longer separated by constrictions. The larva, however, remained in the bottom of the gall.

The stain for tannins indicated that the cells of the upper epidermis of a young (May 20) ungalled leaf were filled with tannins (brown stain), and that the palisade cells contained dark brown droplets. Vascular bundles also were surrounded by cells with large dark droplets. At this time the gall was mostly free of tannins. The nutritive cells, however, contained

numerous small brown droplets in the cytoplasm (Pl. 23, Fig. 9).

On June 5 the tannin deposits in the palisade layer of the ungalled leaf had become larger (Pl. 23, Fig. 8). Some of the nutritive cells contained small brown droplets.

On September 20 the ungalled leaf had palisade cells filled with tannins (dark brown). Most of the gall wall was tannin-free. The nutritive cells and subepidermal cells contained dark brown droplets. The debris on the surface of the nutritive cells contained numerous small dark brown droplets.

Cecidomyiid Gall 4) Poplar Bud Gall

The gall was collected from *Populus trichocarpa* T. and G.. It was an abnormally enlarged terminal or side bud (Pl. 24, Fig. 1), and was common on mature trees. Several gall midge larvae lived between the bud scales (Pl. 24, Fig. 2), and were immersed in a yellow resin that bathed the bud parts. The gall was caused by an undescribed cecidomyiid (Felt, 1965).

The earliest (May 6) indications of galling were slightly swollen buds that had exuded a yellow resin from between the bud scales. The brown necrotic, swollen buds from last year's infestation also occurred on the same

tree or same branch as the young galls.

When cut transversely a galled bud collected on May 13 showed the whorled arrangement of bud parts (Pl. 24, Fig. 4). All of the inner bud parts at this time were composed almost entirely of meristematic, densely cytoplasmic cells with prominent nuclei and nucleoli. The midge larvae occurred between the surfaces of adjacent bud parts (Pl. 24, Fig. 4). Thus, both the outer and inner epidermises of bud parts were potential nutritive cell layers.

In May these epidermal cells were arranged in palisade fashion and were cytoplasmically rich (Pl. 24, Fig. 5). All showed a prominent nucleus and nucleolus.

By August 12 the galled bud was 1.7 cm long and 1.0 cm in diameter at its widest point while an ungalled bud was 1.1 cm long and 0.3 cm in diameter. The galled bud was dark green externally while the internal tissues were yellow to white. At this time an outer scale from a galled bud was 0.91 mm thick (approximately 47 cell layers thick) (Pl. 24, Fig. 6). The outer (abaxial), palisade-like nutritive layer of the scale had a thick cuticle. Most of the nutritive cells were vacuolate and contained dark deposits. The bulk of the scale was composed of isodiametric, vacuolate cells. Vascular bundles were about 13 cell layers under the inner

(adaxial) nutritive layer. The inner nutritive layer was heterogenous. In extended patches (roughly 200 cells), the cells were palisade-like and were completely filled with dark deposits. Plate 24, Figure 8 shows the area of transition between these cells and the neighboring nutritive cells that had rich cytoplasms and no dark deposits. In still other patches, lightly stained, vacuolate, round cells were seen (Pl. 24, Fig. 7). Occasionally a few small (10 cells in section) enations arose from the scale's inner surface and were covered with the palisade-like nutritive cells.

On September 22 (Pl. 24, Fig. 9) a scale from an ungalled bud was 0.30 mm wide (19 cell layers thick). Its abaxial epidermis was covered with a thick cuticle and the small bead-like cells of this surface contained dark deposits. The bulk of the ungalled scale was made up of lightly stained, richly cytoplasmic, isodiametric cells. Each vascular bundle contained 2-6 vessels. The cells of the adaxial surface were palisade-like in arrangement toward the middle of the scale, and bead-like on either end. Dark deposits occurred in these cells.

A scale from a galled bud collected on the same day was 0.98 mm wide (46 cell layers thick). The scale resembled the specimen from August 12 with two exceptions. The September scale showed an inner

epidermis with all cells filled with dark deposits. Secondly, through the middle of the scale, one saw circular groups of 7-12 sclerids. Whether the groups eventually formed a continuous band was unknown.

On October 16 the galls still contained several white larvae most of which were at the bud's center. Resin was abundant but had dried to a gum. Many of the bud scales showed brown, dead areas near the midges. On December 20, many large larvae were found under the outermost scales.

When stained for tannins on June 5, the nutritive cells from the adaxial surface of a galled bud stained positively (brown). The further from the center of the bud, i.e. the older the scale, the darker the brown. The lumen of the abaxial surface cells stained brown.

On May 6 a larva was 0.77 mm long with no sternal spatula. On September 22 a larva was 3.5 mm long and showed a sternal spatula (not seen in Pl. 24, Fig. 3).

Cecidomyiid Gall 5) Willow Stem Beaked Gall

This gall was collected from *Salix* sp.. It was caused by *Phytophaga rigidae* O. S. (Pl. 26, Fig. 1). This stem tip gall (acrocecidia) killed the terminal bud. Side shoots from the base or on the side of the gall frequently developed as new terminals.

The earliest collected specimens (April 8) were empty, necrotic galls from the previous year. A longitudinal internal view of the old gall (Pl. 25, Fig. 5) showed the larval cavity and exit portal. A transverse section (Pl. 25, Fig. 6) demonstrated the woody nature of the thick gall wall. Thin sections indicated that the nutritive tissue (see below) that lined the abandoned larval cavity was inactive, i.e. was made up of cells that were filled with dark deposits.

Young galls were collected on May 13. A larva in these galls was 1.47 mm long and showed an unforked sternal spatula (Pl. 25, Fig. 9). The galls were 2 cm long and 3 mm wide (Pl. 25, Fig. 1) and were green both externally and internally. An ungalled stem of comparable age was 1.4 mm wide (Pl. 26, Fig. 2).

In transverse section the young ungalled stem showed small bead-like epidermal cells and isodiametric cortical cells. The vascular tissue formed an almost continuous ring within the stem. Metaxylem vessels were arranged in radial rows, as were the phloem elements. The pith cells were large, isodiametric and vacuolate.

Transverse section of a May 13 gall showed a circular larval cavity 1.54 mm in diameter. The gall wall was about 0.5 mm thick although this varied because of bulges in the gall wall caused by the presence of 5-6

large vascular bundles in the cortex. These bundles were leaf traces, a fact made clear by the presence of smaller vascular bundles nearer the cavity (Pl. 26, Fig. 3).

The cuticle, epidermis, and cortex in the gall wall were similar to their counterparts in ungalled stems. The vascular tissue, however, was dispersed as small circular bundles. The pith was hollow in the gall. The cells lining the larval cavity were undamaged. This suggested that the cavity was not the result of burrowing. The nutritive cells were pith cell derivatives and contained dark deposits (Pl. 26, Fig.4). There were, however, lightly stained vacuolate nutritive cells in small patches (Pl. 26, Fig. 5).

On June 5 the gall was 2.5 cm long and 4.5 mm wide. The vascular bundles had increased in width such that the interfasicular spaces (i.e. spaces between bundles) were only 4-12 cells wide. The bundles were no longer circular, but were strips or very shallow semicircles with radial rows of elements. The bundles were about 23 cell layers (0.7 mm) in from the cavity epidermis. Fifteen layers of cortical-like cells that were large, vacuolate, and lightly stained occurred between the bundles and the cavity.

The nutritive cells resembled those cells in the 4-5 underlying layers. All were vacuolate with peripheral

cytoplasms, a large nucleus and nucleolus. Many of these cells contained dark deposits. There were patches, however, of deposit-free nutritive cells (Pl. 26, Fig. 6).

By July 15 the gall was 3.5 cm long and 0.7 cm wide (Pl. 25, Fig. 2). It had become woody. A gall from July 24, when cut transversely, showed a larval cavity that was 2.3 mm in diameter. The gall wall was 1.82 mm wide. A larva at this time was 1.89 mm long and had an unforked sternal spatula.

On July 24 half of the gall cortical cells were filled with dark deposits. The vascular ring was continous around the gall (Pl. 26, Fig. 7), and radial files of secondary xylem contributed 0.3 mm to the wall width. Inside the ring of vascular tissue were 12-16 layers of sclerids. To the inside of the sclerids were 3-4 layers of cells that contained dark deposits. Resting on these cells were the fairly large, lightly stained nutritive cells (Pl. 26, Fig. 8), each of which showed a nucleus, nucleolus and many small vacuoles in a granular cytoplasm. The lightly stained nutritive layer was continuous around the cavity -- it was not found in patches as previously observed.

On August 12 a larva was 2.1 mm long and showed an unforked sternal spatula. The gall wall was 2.94 mm wide

of which about 1.26 mm was secondary xylem (Pl. 26, Fig. 9). Air pockets had developed in the cortex and most all of the cortical cells contained dark deposits. The cells of the 4-5 layers encircling the larval cavity had become unusual in appearance (Pl. 27, Fig. 2). Many were partially filled with a lightly stained amorphous (non-granular) material. This material frequently accumulated on the larval cavity side of the cell. The nutritive cells resembled those underlying them. A few patches of 4-5 collapsed nutritive cells were seen.

On August 19 the gall's "beak" (distal end) had begun to turn yellow (Pl. 25, Fig. 3), and the larva was noticeably larger (Pl. 25, Figs. 7 and 8).

By September 21 a larva was 5.6 mm long and had a forked sternal spatula. By September 21 the gall's beak had turned brown (Pl. 25, Fig. 4). The nutritive cells were either empty, contained dark deposits (Pl. 27, Fig. 1), or in some spots, contained a small amount of granular cytoplasm and a nucleus and nucleolus.

Many galls were green on October 16 and contained a 3 mm long larva. The tissue lining the larval cavity was yellow-green.

When an ungalled stem from May 13 was stained for tannins (Pl. 27, Fig. 3) one saw dark brown deposits in the epdiermal cells, in some cortical cells, in some of

the vascular elements, and in scattered pith cells.

Tannins in galls (May 13 and June 5) occurred in scattered cortical cells. Some nutritive cells also stained positively, but there were patches that stained negatively (corresponding to the patches of lighter cells in Toluidine Blue stained material) (Pl. 27, Fig. 4).

Most nutritive cells in late July had brown deposits. On September 21 the amorphous deposit material in the nutritive cells did not stain as tannins, but several nutritive cells did contain tannins (Pl. 27, Fig. 5).

Summary of Cecidomyiid Galls

1) Classification. The midge galls were of different complexities. The poplar bud gall and hawthorn fold gall showed abbreviated sclerid zones. Because both showed enriched nutritive cells for at least a short period, I classified them as simple prosoplasmas. The other midge galls were complex prosoplasmas primarily because of their extensive sclerid zones.

The leaf gall on serviceberry with its false central chamber caused more reorganization and disruption of host plant tissues, and showed a more complex design than did any of the other midge galls. In this respect it was comparable to cynipid galls (see next section).

2) Nutritive layer dynamics and tannins. With the exception of the willow gall (see below), the nutritive cells in these galls were cytoplasmically richest when the galls were very young. By the time the larva was half to fully grown, the cells upon which it fed were vacuolate and contained tannins. Generally, however, the tannins in gall tissues were not as prevalent as in the cells of the ungalled leaf. If cytoplasmic richness was positively correlated with nutritional quality, then I conclude that the best diet was available to the early instars. The larvae did not maintain the cytoplasmically rich diet through time.

The number of collapsed nutritive cells tended to increase in the midge galls as the season progressed. This was most likely due to damage by the larvae. Never, however, was there evidence of torn cells. Apparently the larvae crushed but did not tear or cut through the tissue as they fed. On the other hand, the following observations suggested that the larvae subsisted partially on nutritive cell secretions: The presence of debris on the surface of nutritive cells in older serviceberry galls, the pitted walls of the nutritive cells in mature hawthorn leaf galls and snowberry leaf roll galls, the abundance of resins in the poplar bud gall, and the accumulation toward the cavity of amorphous

material in the willow stem beaked gall nutritive cells. These observations suggested that nutritive cells produced and secreted materials, or simply facilitated the passage of materials through the wall to the larvae.

The willow gall was interesting in that as the gall matured, the patches of lightly stained nutritive cells increased in size. Galls in late summer (August 21) also showed nutritive tissues with large amorphous deposits in many of the cells. The deposited material was not tanniferous. It perhaps was nutritious (i.e. carbohydrates, lipids). Given these observations one would suggest that the nutritive cells in the willow gall improved as the season progressed.

Cynipid Galls

Cynipid Gall 1) Stem Gall on Cat's Ear

I collected this gall (Pl. 27, Fig. 6) from the herbaceous perennial, Hypochaeris radicata L.. According to Weld (1957) the gall is "widely distributed in western Oregon and Washington where it helps to check the spread of its introduced (European) host plant." Inspite of Weld's assessment, its impact on the host plant is not known. The fact that flowers are produced on galled stems indicates that plant reproduction is not eliminated. The wasp's potential as a biological control agent should be checked.

The gall was caused by the cynipid, Aulax (=Aylax; see Weld, 1957 and Felt, 1965) hypochaeridis Kieff. (Pl. 27, Fig. 7). The larva fed with lightly sclerotized mandibles (Pl. 27, Fig. 9). This was probably a mark gall, but early gall events were not observed.

Galls collected on August 12 (Pl. 27, Fig. 6) were 2-4 cm long and 7 mm in diameter at the widest point. The galls were yellowing. A white spongy pith tissue made up their bulk. The larval cavities (several occurred in each gall with 1 larva per cavity) were scattered throughout the enlarged pith (Pl. 27, Fig. 8). There was no sclerid zone (the gall was easily cut

through). The tissue immediately surrounding the larva was green -- not white pith tissue.

A thin section cut transversely through the August gall showed a very thin (6 cell layers) cortex. The bundle caps were extensive with numerous sclerids. The phloem was concentrated in a solid mass while the xylem contained radial rows of both vessels and parenchyma.

The pith cells were very large, thin walled and vacuolate. The larval cavity was about 1.4 mm in from the outer epidermis and was 0.5 mm in diameter. Near the cavity, cytoplasms became denser (Pl. 28, Fig. 1). Nuclei and nucleoli (1 each per cell) became apparent in the cells, at first peripherally, and then centrally in the midst of a dense, granular cytoplasm (Pl. 27, Fig. 10).

Some of the nutritive cells were collapsed. Those that were not were the same size and shape as the vacuolate pith cells. The gall was not stained for tannins.

Houård (1903) studied this gall in France on the same host plant species. The galls he collected in November showed a sclerid layer surrounding the nutritive tissue.

<u>Cynipid Gall 2)</u> Small Leaf Gall on Garry Oak

The gall (Pl. 28, fig. 2) was collected on young leaves of _Quercus garryana_ Dougl. It was found only once (May 6). The gall occurred on the upper surface of very young leaves. It was red and spherical with a nipple at its top. It was not associated with a major vein, and was 2.38 mm in diameter. The gall was caused by an undescribed cynipid.

The oak leaf that bore the gall showed a meristematic mesophyll. In longitudinal section the gall was set deeply in the young spongy layer, but the lower leaf surface remained undisturbed by the gall. The leaf veins ran from the ungalled lamina to the base of the gall, but no vascular strands were seen in the gall wall. The wall was 0.63 mm wide and anatomically was divided into an outer and inner gall wall. The outer wall was 0.21 mm wide (7 cell layers) and was made up of thin walled, tangentially elongate, vacuolate cells primarily derived from palisade parenchyma. The outer and inner gall walls were separated at the base of the gall by a single cell layer of pitted, densely cytoplasmic cells.

The inner wall was made up of 7 cell layers (Pl. 28, Fig. 3). The most peripheral were relatively small, half vacuolate, half densely cytoplasmic. Each contained a small nucleus and nucleolus and many crystalline granules. Nearer the cavity, the cells and their nuclei

and nucleoli became larger (the cells were uninucleate and the nuclei were uninucleolate) (Pl. 28. Fig. 4). The cytoplasms become avacuolate, and densely granular (Pl. 28, Fig. 5).

The nucleolus in the nutritive cells that lined the cavity were either very large or dispersed, and the nuclei showed many finger-like projections. The long axes of the nutritive cells were perpendicular to the gall surface, but the cells were not regularly palisade-like in alignment. Collapsed or vacuolate nutritive cells occurred in patches. The larval cavity was 1.26 mm in diameter. The gall was not stained for tannins.

Cynipid Gall 3) Bullet Gall on Garry Oak

This gall was collected from *Quercus garryana* Dougl. and was caused by *Andricus spongiolus* Gill. (according to Houard (1940) the wasp was *A. quercus-californicus* var. *spongiolus* Gill.) (Pl. 28, Fig. 9). Felt (1965) described the gall as "globose, clustered, many-cells, buff colored, diameter 1 to 3 inches on Oregon oak, gall wasp." Houard (1940) gave a more complete description of the external and internal appearance of the gall (see his page 121).

This is one of the largest insect-caused galls in

North America. Although diameters as small as 1.5 cm were common, these small galls were frequently in clusters with galls that were 9 cm long and 6.5 cm wide. Regardless of size, the galls resembled small to large green apples. They were yellowish green when young and turned brown to black with age. When sliced through, young galls showed a white, pulpy internal tissue. The galls were detachable stem galls, and the stem swelled at the point of attachment (Pl. 28, Fig. 6).

Free-hand sections suggested that the gall arose from the cambial region of the stem and ruptured the cortex and epidermis of the stem. Thus, this was most likely a mark gall. Several larval cavities occurred in each gall (1 larva per cavity) (Pl. 28, Fig. 7) and the cavities were grouped into what became a hardened mass at the center of the gall (Pl. 28, Fig. 8).

On May 6 the gall was small (1.7 cm long, and 1 cm in diameter at the widest point). The circular larval cavity was 0.38 mm in diameter. A larva was 0.40 mm in diameter.

The cells that made up the white pulp in the gall were large, vacuolate and parenchymatous. They contained a prominent nucleus and nucleolus in a peripheral band of granular cytoplasm. The pulpy tissue was traversed by provascular strands that showed small, elongate, densely

cytoplasmic, undifferentiated cells.

Near the larval cavity the pulp cells became smaller, and had fewer large vacuoles. The enriched nutritive tissue was several cells thick. These cells were filled with a lightly stained cytoplasm and had a greatly enlarged nucleolus (Pl. 29, Fig. 3). Many were elongate with their long axis perpendicular to the cavity (Pl. 29, Fig. 2). The cells that actually lined the larval cavity showed a similar cytoplasm but had no nucleus or nucleolus.

A week later (May 13,) the larval cavity was 0.91 mm in diameter. The pulp cells were larger than earlier. The further from the larval cavity, the larger were the cells (some were 0.15 mm long). The amount of peripheral cytoplasm had decreased, and the central vacuole had enlarged. The vascular strands remained mostly undifferentiated.

In July, most all of the cells in the nutritive region, including those that lined the cavity, had developed vacuoles (Pl. 29, Fig. 4). The cytoplasm in the nutritive cells stained lightly, was of fine-grain consistency, and held large nuclei (1 per cell, sometimes lobed) with very large nucleoli. The nucleoli frequently contained small to large vacuole-like spaces in their centers. Occasionally very small "satellite" nucleoli

occurred in the nuclei.

A layer of lightly stained fine-grained material covered the surface of the nutritive cells that lined the cavity. The presence of recognizable cell parts in this material (e.g. an intact nucleolus) indicates that it was in part the ruptured contents of the nutritive cells.

At this time, the midgut of a larva was filled with a very lightly stained material (more lightly stained than nutritive cell cytoplasm) with dark droplets scattered throughout. No solid cell material (wall, nucleoli) was seen in the gut.

By June 16 a larval cavity was 2.7 mm in diameter. Larvae were about 2.5 mm in diameter. Hand dissections of the gall indicated that the larval cavities were embedded in woody tissue that was very difficult to slice through. The pulp of the gall showed macroscopic air spaces throughout. By July 15 the galls were yellowish green and were 4-6 cm in diameter, 6-9 cm long (Pl. 28, Fig. 6). The fibers that ran from the stem to the hardened mass of capsules were seen in an older gall that was collected October 9 (Pl. 28, Fig. 8).

A small gall collected on July 24 that contained larval cavities with diameters of 0.5-0.7 mm was stained for tannins. The cells in the nutritive region (May 6) stained poorly, while those of the pulp contained

peripheral contents and centrally placed droplets that stained dark brown or black (Pl. 29, Fig. 5). The ruptured cell contents on the surface of the nutritive cells stained darkly (Pl. 29, Fig. 7). A transverse section of the larval gut also showed dark droplets in an unstained matrix.

Cynipid Gall 4) Rose Tip Gall

This acrocecidium was collected by Dr. Andrew Moldenke in Corvallis, Oregon from *Rosa nutkana* Presl.. Of the galls on *R. nutkana*, those of *Diplolepis oregonensis* (Beut.) (holotype from Corvallis) most closely resembled the collected specimens (Weld, 1957). This was a bud gall (Felt, 1965), and was probably formed as a mark gall.

On August 12 the gall was mature (2 cm long, 1.4 cm in diameter at widest point). The gall was spindle-shaped with its tapered point at the distal end of the gall (Pl. 29, Fig. 6). The gall surface showed 2 to 4 overlapping expanded stipular bases with an axillary bud at the apex of each.

The gall contained several larvae, each in a separate cavity. Some of the galls showed browning of the tissue surrounding the larval cavities. A cavity was 0.9 mm in diameter (Pl. 29, Fig. 8). Most of the cells

of the gall were enlarged, completely vacuolate and with thick walls. A band of sclerids (5-8 cell thick) encircled scattered vascular bundles. The nutritive tissue occurred between the bundles and the cavity. The amount of granular cytoplasm increased in cells near the cavity (Pl. 29, Fig. 9). The nutritive cells showed no pattern of alignment. The nucleus and nucleolus were enlarged in the nutritive cells. There was only one nucleus per cell, but there were often more than one nucleolus per nucleus. The nucleus was occasionally lobed. Cellular remnants (walls and contents) lined the cavity and were most likely the result of larval feeding. The gall was not stained for tannins.

Cynipid Gall 5) Spherical Stem Gall on Garry Oak

This gall was collected on *Quercus garryana* Dougl. It was caused by *Disholcaspis washingtonensis* (Gill.) (= *Callirhytis washingtonensis* Gill. (see Felt, 1965, and Weld, 1957). Russo (1979) briefly discussed the gall and wasp.

The gall was spherical and was frequently found in clusters on 1-3 year old stems. When mature (Pl. 30, Fig. 1) the galls were 7-8 mm in diameter and each rested upon a very short neck. When cut open, the gall showed a single large larval cavity in the center of the gall that

was inhabited by a single larva. The cavity was much larger than the larva (Pl. 30, Fig. 2).

On April 25 the gall had ruptured through the stem and was 3 mm in diameter and the larval cavity was 0.77 mm in diameter. The gall wall was 1.32 mm wide. The gall arose from the stem's vascular cambium. The embedded neck was composed of elongate, heavily pitted cells.

At this time, with the exception of the neck, the outer gall wall was made up of parenchymatous, vacuolate, isodiametric cells (Pl. 30, Fig. 3). Peripheral nuclei with nucleoli occurred in these cells. Otherwise, they contain very little cytoplasm. Vascular bundles occurred well beneath the gall epidermis, and were cut both longitudinally and transversely when the gall was cut longitudinally. Cells become smaller and more cytoplasmically dense near the nutritive region.

The nutritive tissue (10 cell layers deep) showed no organized alignment. The nutritive cells were distinguished from those of the outer wall by their lightly stained, dense cytoplasms. Vacuoles were present, but were generally small. The cytoplasm was coarse- to fine-grained, and the nuclei and nucleoli increased in size near the larval cavity. Many of the cells lining the cavity were covered with remains of

ruptured nutritive cells.

On June 5 the larval cavity was 2.8 mm in diameter, and the gall wall was 1.4 mm thick (Pl. 30, Fig. 4). The cells immediately outside the nutritive region had developed porous, thick secondary walls.

The cells of the nutritive region were vacuolated with a strip of cytoplasm peripherally. Nuclei with nucleoli were present in some of the cells, but were not as prevalent as earlier. The nutritive cells lining the cavity were covered with a thin layer of amorphous material.

On May 20 the nutritive cells did not contain tannins. Most of the cells of the outer gall wall had peripheral tannin deposits (black stain). The same description held for material from June 5 with the exception that the ruptured contents of the nutritive cells stained positively.

Cynipid Gall 6) Mossy Rose Gall

This gall was collected from the introduced *Rosa eglanteria* L. My observations indicated that females oviposited in buds that had opened only slightly in mid-spring. The galls generally arose from a twig, but small galls were observed on sepals, petals, and leaflet midveins and petioles. Apparently most organs in a young

bud were subject to galling. The moss-like covering was the gall's most distinctive external feature (Pl. 30, Figs. 5 and 6). The gall was caused by Diplolepis (=Rhodites) rosae L. (Pl. 30, Fig. 7) (but see Weld (1957)).

Numerous larvae, each in a separate cavity, lived in a gall (Pl. 30, Fig. 8). The larvae used sclerotized mandibles to feed on the plant tissue (Pl. 30, Fig. 9). This was either a mark or lysenchyme gall.

On July 7 the multicellular "moss" fibers were well developed, each with its own vascular system. The fibers were still growing.

The cells that made up the solid wall of the gall were enlarged and vacuolate. Vascular strands ran throughout the gall wall. Near the larval cavity, the cells were smaller, but retained a large vacuole. The larval cavity was surrounded by 1-3 layers of enlarged, densely cytoplasmic, avacuolate nutritive cells that contained prominent, centrally located nuclei (1 or 2 per cell) with enlarged nucleoli (1 or 2 per nucleus). A thin band of amorphous material covered the surface of the nutritive cells that bordered the larval cavity. At this time a larval cavity was 0.25 mm in diameter.

On July 24 a larval cavity was 0.52 mm in diameter (Pl. 31, Fig. 1). The gall wall was similar to that in

July 7 material (Pl. 31, Fig. 2). The cells were mostly vacuolate, but as the nutritive cells were approached a rich cytoplasm took the place of a large central vacuole, and the cells began to enlarge and bulge toward the cavity (Pl. 31, Fig. 3).

At this time the nutritive cells were avacuolate or contained only small vacuoles. The nucleus was lobed and the nucleoli were enlarged.

By August 12 the larval cavity was 1.33 mm in diameter. The galls themselves were 2-4 cm in diameter. The "moss" fibers were mature. Near the nutritive tissue (Pl. 31, Fig. 4), cells showed a thick band of peripheral cytoplasm. The lobed nucleus with enlarged nucleolus also increased in size near the larval cavity. The cells bordering the cavity were cytoplasmically dense (Pl. 31, Fig. 5) and contained few vacuoles. The nucleus in these cells was dispersed and frequently had no nucleolus. The nutritive cells show no particular alignment or shape.

On September 21 the "moss" was brownish green. On average the galls were 2-3 cm in diameter. A larval cavity was 1.96 mm in diameter. A band of sclerids (4-5 cells thick) occurred 5 cell layers in from the solid surface. The band encircled the larval cavity and ran through, or on either side of the vasuclar bundles.

As in younger galls, the cytoplasmic density

increased near the larval cavity (Pl. 31, Fig. 6). The nutritive tissue was made up of enlarged, elongate cells that contained numerous small vacuoles in an otherwise lightly stained granular cytoplasm (Pl. 31, Fig. 7). Nuclei were present, and nucleoli (frequently 2 per nucleus) were prominent, but were not as enlarged as earlier. Some of the cells bordering the cavity contained no nucleus. There was a thick film of ruptured contents over the surface of the nutritive cells that lined the cavity.

On October 9 the galls were difficult to slice through. Large white larvae were still present in the cavities. The wall of the larval cavity was woody and cream-colored. Galls collected on December 20 still contained larvae.

Galls from July 7 that were stained for tannins showed that many of the cells in the "moss" fibers were tannin-rich (black cytoplasmic stain), as were many cells in the outer gall wall. The cells near the nutritive tissue were free of tannins. The nutritive cells contained some tannins (stain light brown).

A similar pattern occurred in galls from July 24 (Pl. 31, Fig. 8), August 12 (Pl. 32, Fig. 1) and September 21 (Pl. 32, Fig. 2). The older the gall, the more common were tannin-rich cells in the outer gall wall

and mossy fibers, and the less darkly stained were the nutritive cells.

A larva on July 7 was 0.77 mm long. By August 12 a larva was 4.34 mm long. Many of the September larvae (lactophenol-cleared, and mounted in Hoyer's) show dark granules in the mid gut that were not seen in larvae collected earlier in the season.

Cynipid Gall 7) Speckled Oak Apple on Garry Oak

This gall (Pl. 32, Fig. 4) was collected from *Quercus garryana* Dougl.. It was caused by agamic (=asexual) females of *Besbicus* (=*Cynips*) *mirabilis* var. *mirabilis* (Kinsey) Weld (Pl. 32, Fig. 7). According to Kinsey (1930), pupae occur in mid-September in the galls, and adults emerge in October - November. Kinsey (1930) also described the external and internal macroscopic appearance of the gall.

This was a mark gall that ruptured the cortex and epidermis of one of the major veins (most frequently the midvein) on the underside of the leaf (Pl. 32, Fig. 3). Each gall contained a single centrally placed larval cavity that held a single larva. The cavity was within a capsule (see below). The spherical gall showed a short neck at the leaf - gall junction. Very young galls were covered with a dense pile of white hairs. As the gall

grew this pile was lost and was replaced by fuzz that in turn fell off so that mature galls were glabrous and shiny.

The young gall was solid, but as the gall matured the outer gall wall became separated from the centrally-placed larval capsule. The outer wall or shell of a mature gall was thin (the flexibility of stiff wax paper -- if the wall was very fragile, the gall had probably been invaded by an inquiline). The central capsule was suspended in the center of the gall by fibers that radiated from it to the outer gall wall. There was a concentrated group of these fibers that rans from the capsule to the point of gall attachment on the leaf (Pl. 32, Fig. 5). The larva lived within the central capsules (Pl. 32, Fig. 6) and fed with lightly sclerotized mandibles (Pl. 32, Fig. 8).

On May 31 the young gall was 1.54 mm in diameter. The gall wall was solid and was 0.56 mm thick. The larval cavity was 0.36 mm in diameter. The neck of the gall was deeply embedded within the midvein (Pl. 33, Fig. 1). The gall arose from elements near the vascular cambium (Pl. 33, Fig. 3). Vascular strands occurred along both sides of the neck and up through the outer gall wall, and most cells within these strands were densely cytoplasmic.

At this time, the outer gall wall, was made up of vacuolate cells. Nuclei were visible in these cells. Toward the center of the gall was a band of thick walled cells (6-7 cells thick) that encircled the nutritive tissue and constituted an early "protective" zone.

Most of the nutritive cells were arranged in radial rows around the cavity. The cells were recent products of cell division. Only those lining the cavity were enlarged and densely cytoplasmic. These showed a prominent nucleus and nucleolus, and a dense granular cytoplasm (no vacuoles). The nutritive cells that lined the cavity were covered with amorphous material.

On June 3 and 11 the galls were still pubescent and red to pink. They were solid, with a light brown capsule at their center. Green succulent tissue surrounded the capsule.

By June 17 the pink gall was 1.96 mm in diameter, the larval cavity was 0.31 mm in diameter, and the gall wall was 0.87 mm thick. Many of the cells of the outer gall wall were elongate and radiated out from the central gall capsule. These were the forerunners of the fibers that suspended the capsule in a mature gall. As yet, they had not separated.

The radiating cells abutted the "protective" zone (Pl. 33, Fig. 4). The nutritive tissue was inside this

zone and the transition between the two was abrupt. The nutritive cells closest to the "protective" zone (furthest from the larva) were small, flat, and densely cytoplasmic with few vacuoles (Pl. 33 Fig. 5). Near the cavity the cells swelled, and showed larger nuclei and nucleoli (usually one of each per cell).

By June 25 the gall was 3.72 mm in diameter. It was covered with a white pubescence. The larval cavity was 0.49 mm in diameter, and the gall wall was 1.40 mm thick. The internal fibers had begun to separate so that the gall wall had a spongy consistency. The outer gall wall (the shell) was 9-10 cell layers thick.

On July 10 the galls were about 1 cm in diameter. The central capsule was 1 mm in diameter. The larval cavity was 0.30 mm in diameter (Frontispiece). The fibers were long and separated. Interestingly, lightly stained cytoplasm (the same color as in the nutritive cells) occurred between some of these "protective" cells. Apparently there was an invasive growth of protoplast-like nutritive cells into the "protective" zone.

With the exception of some of the large nutritive cells bordering the cavity, all showed a prominent nucleus (usually unlobed) and nucleolus (larger nearer the cavity). Many of the largest cells contained

numerous small vacuoles.

By August 12 the galls were yellowish green and were 2-3 cm in diameter. The outer shell was firm, but still fleshy. The larval cavity was 0.30 mm in diameter. The long fibers had reached their full length (Pl. 33, Fig. 6). The cells of the "protective" zone were being replaced by thin-walled densely cytoplasmic cells that contained numerous small vacuoles, but otherwise resembled the nutritive cells. Cell wall remnants of the early protective zone were lodged between these new metabolically active cells. Because of this invasive growth, the nutritive tissue had almost doubled in thickness since the previous collection.

Nutritive cells nearer the cavity showed lobed, enlarged nuclei and enlarged nucleoli. Many bordering the cavity showed a dispersed nucleus with no nucleolus or nucleus (Pl. 33, Fig. 7).

On September 22 some of the largest galls were brown. The central capsule was suspended on brown fibers, and could be separated easily from the gall and fibers. The larval cavity was 3.78 mm in diameter. A band of thick walled cells (3 cell layers) occurred between the nutritive region and constituted the sclerid zone (not the same as the early "protective" zone).

The nutritive cells in older galls showed numerous

vacuoles and a granular cytoplasm. Remnants of thick walls from the old "protective" zone pin-pointed the new nutritive cells derived from the invasive growth. These cells were as large but more vacuolate than the older nutritive cells.

The nuclei in the older nutritive cells were very large, dispersed, and granular (Pl. 35, Fig. 7), while most nucleoli had broken down completely (Pl 33, Fig. 8). Many of the cells neighboring the cavity had been torn, and it was probably their contents that formed a film on the surface of intact cells.

On June 3, June 17, June 25, and August 25 the deposition of tannins was the same: The radiating fibers were filled with a deep reddish brown deposit. Most gall wall cells stained lightly, and the nutritive cells did not stain. The material on their surfaces (Pl. 35, Fig. 8) stained slighly.

On September 12, 1980 I collected mature leaves with small spherical galls in clusters on the leaf's underside at the midvein (Pl. 33, Fig. 2). They were 3-5 mm in diameter and were succulent within. A single larva was in a single central cavity in each gall. According to Kinsey (1930) these were stunted _B_. _mirabilis_ galls, but he states that "I have no explanation for the stunted development of so many of the growths." Instead of being

hollow with radiating fibers, the gall was solid.

Summary of Cynipid Galls

1) Classification. The cynipid galls I studied were complex prosoplasmas because they possessed sclerid zones (usually late in gall development), because they were closed, and because they showed distinctly enriched and multiple layers of nutritive cells. Most were complex in design.

2) Nutritive tissue and its dynamics. As mentioned earlier, when we think of nutritive cells in galls, the tendency is to consider only cells in cynipid galls. Although this bias has led to confusion, the association is understandable; cytological characteristics of these nutritive cells immediately set them apart (and some would say, above) all others in any gall. Their abundance is noteworthy. For example, at least half of the substance of the small leaf gall on Garry oak was nutritive tissue. The nuclear and nucleolar hypertrophy in the nutritive cells of all 7 cynipid gall were striking and most likely indicated an active metabolism. From the herbaceous Cat's Ear, to the shrubby wild roses, to the arborescent oaks -- regardless of genus or growth form, the host plants produced very similar nutritive cells around the larva.

Was the cytoplasmic richness of the nutritive cells maintained through the season? In the two examples where this was followed (mossy rose gall, and speckled oak gall) the nutritive cells contained rich cytoplasm through the last sampling. Vacuoles appeared in older cells, but they did not completely replace the granular cytoplasm.

Most interesting was the occurrence of the invasive nutritive tissue in the spotted oak gall that replaced the early "protective" zone. Although the larval cavity remained about the same size (0.3-0.4 mm) throughout the summer, in mid-summer the nutritive cell doubled in thickness. The larval cavity remained about the same size (0.3-0.4 mm) throughout the summer. Whether the larva fed on the new nutritive tissue later in the season was unknown.

3) Sclerid zone. The sclerid zone usually developed late in gall development. The speckled oak gall provided an interesting variation. In this gall 2 layers of thick walled cells developed. One developed after the other had broken down. The nature of the early "protective" layer should be examined more closely; even when encircled by thick walled cells through most of its development, the gall-former was heavily parasitized (Ken West, personal communication).

4) <u>Tannins</u>. The nutritive tissue in the galls that were appropriately stained was usually tannin-poor. Peripheral gall tissues were tannin-rich. Young nutritive cells in the mossy rose gall stained slightly positively for tannins but as they matured, they stained more lightly.

The material that covered the surface of the nutritive cells in many of the cynipid galls stained fairly positively for tannins. This material may have been ruptured cell contents and/or nutritive cell secretions. Whether it was larval food was unknown. The observation that larval midguts (oak bullet gall) contained tannin droplets suggested that some tannins were ingested.

TABLE Su-1

Summary Table: Reorganization of Host Plant Tissues,

and Nutritive Cell Characteristics in the Studied Galls

Gall-Former	Reorganization	Nutritive Cells
(Leaf Miners)	(No reorganization of tissues.)	(Nutritive cells do not develop; but see Hering, 1951.)
Fungi	Parenchymatous. No distinct tissue layers. Derivation of cells easy to trace.	No long-lived, enriched cells; but see Erlich and Erlich, 1971.
Moth	Simple proliferation of parenchyma into mined pith. Peripheral stem tissues are mostly unaffected.	Callus-like. Not enriched.
Sawflies	Galls with simple (parenchymatous) walls. Reorganization moderate. Derivation of cells in wall not quickly traced.	Callus-like enations. Some short-term enrichment.
Nematode	Structurally simple root swelling. Little reorganization of root other than in immediate vicinity of giant cells.	Enriched synctial nutritive cells. Long-term enrichment (Bird, 1975).
Aphids	Simple leaf curls or pouch galls with parenchymatous walls. Derivation of cells in wall easy to trace.	No obvious, enriched nutritive tissue.
Thrips	Simple parenchymatous leaf curl.	Patches of palisade-like enriched cells.
Scale	Moderate reorganization. Distinct layers in gall. Incomplete sclerid zone.	No obvious, enriched nutritive cells, but see Parr; 1940.
Adelgid	Much reorganization of needle tissue. Gall wall parenchymatous.	Storage-like nutritive cells.
Eriophyoids	Leaf epidermal cells strongly reorganized. Mesophyll cells much less so. Parenchymatous wall.	Palisade-like or enlarged epidermal nutritive cells. Enriched when young.
Cecidomyiids	Moderate to considerable reorganization and structural complexity. Sclerid zone in mature galls.	Usually briefly enriched when young. Apparent rapid deterioration, collapse. Sometimes heavily pitted.
Cynipids	Considerable reorganization of leaf or stem tissue. Derivation of cells difficult to trace. Sclerid zone in mature galls.	Enriched through much of gall development. Usually multi-layered.

DISCUSSION - CONCLUSIONS

In this section I discuss four patterns that have emerged from the results. The first two patterns are summarized in Table Su-1.

PATTERNS

1) Degree of Reorganization. There is a continuum in the degree of disruption and the amount of reorganization of host plant tissues caused by gall-formers. My assessment of reorganization is based upon three types of observations. First, a completely parenchymatous, layer-less gall wall indicates little reorganization. If a distinct nutritive or sclerid zone is present, then the gall-former has caused noticeable reorganization. Second, the more difficult it is to trace the derivation of cells in the gall, the greater the reorganization. Third, the more complex the disign of the gall, the greater the reorganization.

In contrast to the gall-formers, most leaf miners cause no reorganization as they wander and feed through the leaf. There are, however, mines in which callus-like enlarged cells partially fill the tunnel (Hering, 1951). Pith flecks in wood caused by cambial miners provide an excellent example of this phenomenon (Greene, 1914). In

some instances the miners return to feed on these cells and thus, by definition, these could be called (slightly enriched) nutritive cells. In some mines, then, we see a generalized host wound response to insect attack that is initiated by, but is not further influenced by, the insect. The wound response, while only infrequently used by miners, is capitalized on by many gall-formers.

The fungal galls I studied show minor reorganization. All internal cell layers are made up of enlarged mesophyll cells. No differentiation occurs beyond the parenchymatous state. Mechanical disruption is minimal and instead, the fungus relies on chemical disruption to elicit host cell responses. Invaded host cell cytoplasm may be enriched in some cases (Erlich and Erlich, 1971).

Galls caused by moths are glorified mines. A moth larva bores from the apex (site of oviposition) into the stem, and feeds on pith as it goes. The larva, however, limits the length of the mine. The attacked host plant produces callus-like tissue from the vascular cambium -- a response probably elicited both by mechanical damage and salivary constituents. The older instar larva feeds on this new nutritive tissue, and continues to elicit the host's callus response. Thus the gall-forming moth larva shows a dependence on, and control over, callus

development. Interestingly, the gracilariids and gelechiids, two families that contain most of the gall-forming moths, also contain numerous leaf-mining members. Wangberg (1976) has observed tephritid flies that are both stem miners and gall-formers.

The sawfly galls are not merely swellings of healthy organs, but instead, are detachable structures that show some reorganization of host tissues. The disruption may be great enough that the gall's derivation is not clear (snowberry gall). The gall wall is homogenously parenchymatous. No sclerid zone is produced. Sawfly galls show nutritive cells that are more cytoplasmically enriched than are those in moth galls -- an observation that indicates that sawfly larvae influence the plant's response to a slightly greater extent than do gall moths. Nutritive tissue in sawfly galls consists of callus-like enations.

The root-knot nematode (as well as the cyst nematode, Heterodera sp.) behaves like a miner as it tunnels into a root, but instead of wandering, it settles and causes dramatic enrichment of the cells surrounding its head. Thus the nematode strongly influences cells in closest proximity to its mouth. The degree of cellular alteration decreases greatly outside of the giant cells zone. There is some hypertrophy and hyperplasia in a few

cell layers surrounding the giant cells, but there is little differentiation beyond the parenchymatous state. The disruption of the stele is primarily of a mechanical nature (i.e. elements crushed or pushed aside by giant cells). Thus, the arena of strict control in a nematode gall appears to be fairly restricted.

Bird (1975) has stated that the giant cells "undergo a cycle of growth that is directly related to the physiological age of the nematode." The metabolic activity of the syncytium peaks "around the time the nematode has started to lay eggs" and then decline sets in. This is the best indication we have that maintenance of the nutritive cells is tightly linked to the physiology of the gall-former.

Cecidogenetic stylet-bearing insects (scales, thrips, aphids, adelgids) possess the power to disrupt host tissue, but the disruptions are simple parenchymatous swellings, leaf curls, or out-pocketings. In only the scale gall is there differentiation of a scerid zone, and it is incomplete. The thrips gall is the only one that shows an enriched, but discontinuous, nutritive epidermis. The adelgid gall show considerable reorganization of needle tissue and a storage-like nutritive zone. The aphid galls show no readily distinguishable nutritive zone. No sclerid zone is

produced. These organisms do not shape host tissue responses to the same extent as do the midges and wasps.

The mite galls also show only a parenchymatous cell wall. These galls, however, have a continuous layer of enriched epidermal nutritive cells for at least a short time. Thus, somewhat like the nematode galls, the mites cause marked metabolic disruption in the cells with which they are in intimate contact, but the impact and influence drops off quickly with distance from the mites.

Cecidomyiid galls have a sclerid zone in the wall that encircles the larva(e) -- a zone that is not found in the ungalled leaf. With the possible exception of the cecid galls on dryland shrubs (Appendix 1), however, the nutritive cells in the galls do not remain enriched through larval maturation. Additionally some of these galls cause only moderate disruptions of the host organ (leaf curl, swollen bud, leaf fold), while others (e.g. dryland shrub cecid galls and the service berry gall) show considerable tissue realignment in the leaf and stem. All in all, the influence exerted by midge larvae (as indicated by the depth and degree of disruption) is second only to that exerted by cynipids. The tephritid gall on rabbitbrush (Appendix 1) is similar in complexity to the midge galls.

The complex structure of most cynipid galls is

undoubtedly the product of strong, continuous influence by the larva. All show a definite sclerid zone, and the nutritive tissue is always heavily enriched through much of the life of the gall.

It should be stressed that a gall-former's ability to produce a complex or simple gall has little bearing on the success of the gall-former. Gall-forming nematodes and crowngall bacteria, for example, occur globally and show numerous races, i.e. are successful, but cause structurally simple galls. We also know little about the relationship between complexity of the structure and intimacy of the interactants. The relationship between the crown gall bacterium and its host cell, for example, appears to be very intimate (a matter of gene splicing), and yet, as already said, this is a structurally simple gall.

2) Nutritive Cells. In many instances the diet of gall-forming arthropods apparently deteriorates (as indicated by vacuolization) before or during periods of greatest consumption. There is no rejuvenation of the feeding cells in these galls. In sawfly and mite galls the nutritive tissue is formed by the mother before progeny begin to feed. The deutogyne (mites) or young instar (sawflies) enjoys a better diet than do the mid-

to late-season gall inhabitants. There are exceptions to this pattern. The big bud gall of filbert, for example, shows cytoplasmically rich nutritive cells for some time after progeny are produced. More exceptions may come to light as more types of gall are studied.

Most midge galls also display a deterioration of the nutritive region through the season. The early instars enjoy the cytoplasmically richest diet. The beaked willow gall may provide an exception in that changes in the nutritive tissue fairly late in the season suggest an enrichment.

The cynipid galls that were followed through much of the season also showed a deterioration of the nutritive tissue. The process, however, appeared slower than in other types of galls. Even the last samples taken showed nutritive cells with considerable granular cytoplasm. The results indicate that cynipids can maintain their diet in an active state for longer than most other gall-forming arthropods.

The degree of enrichment and the longevity of the nutritive cells in various galls are summarized in Table Su-1. Generally there is a positive correlation between the amount of reorganization and the enrichment and longevity of nutritive tissues. The nematode and some cecidomyiid galls, however, run against the trend.

Nematode galls show little reorganization but have enriched, long-live nutritive cells, while some cecidomyiid galls (e.g. the hawthorn, snowberry, poplar, and service berry galls) show only briefly enriched nutritive cells but a distinct sclerid zone.

The discussion of diet highlights an important point: cynipids are not the representative gall-formers they are freqently assumed to be. To be sure, they are, to the human eye, consummate cecidozoans, and their abilities distinguish them from most other groups. In fact, however, no single gall-forming group encompasses all cecidogenetic methods and results. There are common features of many galls and gall-formers (Epilogue), but the uniqueness of each should also be appreciated.

Lastly, I suggest that the deterioration of diet seen in many galls as they mature may in part be compensated for by improved protection. As many galls mature their walls thicken and, in many instances, are reinforced. This undoubtedly provides protection.

3) The Aphid Galls. The aphids and their galls are problematic. In no instances was I able to determine precisely in which cells the stem mother or her progeny feed. In no instance did I find cells in the gall wall that were clearly nutritive. The fact that aphid stylets

allow for sub-epidermal foraging, coupled with the fact that the depth of foraging most likely increases through instars, indicates that a wide variety of cell types found throughout the gall wall are potential food. The potential feeding area is further increased by the aphid's movement within the gall.

Based on these possibilities, if an enriched nutritive area were to occur in an aphid gall, one would expect it to encircle the gall chamber, to lie well within the gall wall, and to consist of numerous cell layers. Nothing exactly like this is seen in the galls. The closest match to the prediction is the vascular tissue which lies within the gall wall, and which retains cytoplasmically dense members throughout the season. Its candidacy as a food tissue is unconfirmed because stylet tracks to it were never observed. Additionally, stylet length was often well in excess of that needed to penetrate the vascular tissue.

Interestingly, the known examples of nutritive cells in homopteran galls occur in instances in which the gall-former is sedentary (e.g. adelgid stem mother and oak pit scale). Meandering may shape the gall (sensu Boysen-Jensen, 1948), but at the same time it may prevent (or obviate the need for) establishment and maintenance of enriched nutritive cells.

This dissertation points out the uniqueness of aphid and scale galls. They deserve the thorough study that midge and wasp galls have received.

4) Tannins. The galls that were appropriately stained showed generally low levels of tannins in the nutritive cells. Younger galls usually contained lower amounts of tannins. In some cases, particularly in the cynipid galls, even older galls showed very low levels of tannins in the nutritive cells.

Even when tannins occur in the food tissue, they appear to occur in lower quantities than found in the ungalled leaf. Thus the development of a nutritive layer, regardless of degree of enrichment or longevity, assures the gall-forming arthropods of a diet that, in terms of tannin content, is superior to a leafy diet.

Frequently the tannin-poor nutritive tissue is surrounded by a tannin-rich gall wall. This is particularly true of the cynipid galls. D. H. Janzen (personal communication) proposes that tannins in the gall's periphery protect the cecidozoan and the nutritive layer from exploiters. Such an interpretation, however, fails to explain the high rates of invasion experienced by so many galls -- particularly by the cynipid galls.

EPILOGUE: CHARACTERISTICS OF THE GALL-FORMING HABIT

Gall-formers are internal plant parasites. Viewed in this way they can be compared to other internal plant parasites (e.g. leaf miners) and, interestingly enough, to internal parasites of animals. A thorough comparison will not be made here, but as gall-forming features are discussed, occasional comparison to other life habits will be made. Not far behind any discussion of parasitism come questions about host defense. These will be considered briefly in closing.

As internal plant parasites, gall-formers show the following features:

1) Host Plant Specificity. The physiological tracking of host plant response and biochemistry required for formation of a gall undoubtedly forces a strict monophagous habit upon the gall-former, i.e. the gall-former attacks a single host plant genus, or frequently, a single species. In fact in some instances I suspect that demes of gall-formers become restricted to individual long-lived host plants, much like scale insects on conifer needles (Edmunds and Alstad, 1978).

I take as indicative of specificity the occurrence

of numerous species or strains of a gall-former. In many cases strains have been detected, but their specificity is unknown. For example, the taxonomy of crown gall bacteria is "confused" and numerous strains are known to exist (Lippincott and Lippincott, 1975). The degree to which such strains are host specific, however, is not clear. The study of host specificity within the genus Rhizobium (a genus very closely related to Agrobacterium) has also focused on bacterial strains and cross-inoculation groups of plants. In this case each nodulating strain is considered host specific particularly "when one takes account of effectiveness of the association" (Vincent, 1974).

According to Brian (1976), "Plasmodiophora brassicae,...and most of the rusts, powdery mildews, and downy mildews" (all with gall-forming members) show the strictest host specificity among the plant pathogenic fungi. Later he states, "...the pathogen species...may consist of physiologic races each restricted to a few genotypes of a host species, as, for instance, in the well studied case of Puccinia graminis f. sp. tritici on wheat."

Nematodes in the genus Meloidogyne also show races, each with a restricted host range. In fact, host susceptibility has historically been used to determine

identity of the root-knot nematode (Jenkins and Taylor, 1967).

Arthropod gall-formers are generally very host specific, and in those instances in which a gall-former is suspected of being oligophagous or polyphagous, the possibility of cecidozoic races should be considered. As biochemical coupling or intimacy between host and parasite increases, so should specificity.

Thus, the gall-formers resemble other monophagous groups all of which are parasitic. "A very large proportion of miners are monophagous" (Hering, 1951). The parasitic insects (fleas, lice, wasps) include some highly host specific members (Price, 1980) as do the zooparasitic helminths (Cameron, 1964; Whitfield, 1979), and the entomoparasitic fungi (e.g. the Laboulbeniales; Madelin, 1966).

2) Morphological Modifications of the Gall-Former. From the fungi (naked fruiting bodies in some gall-forming groups), to the cecidogenetic mites (reduction in appendages), to the gall-forming insects (reduction in appendages in cecidomyiid larvae (Mamaev, 1975) and cynipid larvae), there is a pattern of reduction in parts. Do root-knot nematodes, crown gall bacteria, and gall-forming homopterans show a similar

reduction?

The reductions seem to occur as the gall-former becomes more sedentary and the gall more confining. Only Mamaev (1975) has traced the reductions through a group of gall-formers, and he states that they are specializations (advancements). Interestingly, it is often implied that the gall-forming fungi are primitive.

The leaf miners have also shown a general reduction in appendages (Hering, 1951) as have the parasitic fleas and lice (Rothschild and Clay, 1952). Many of the ectoparasitic insects and zooparasitic helminths, however, have developed elaborate mechanisms for holding on to the moving hosts.

There are also internal modifications in many gall organisms. For example, the midgut of cynipids and root-knot nematodes is blind. According to Mamaev (1975) the gut of gall-forming cecids is open, but simplified (few if any blind side sacs), and in some cases excretion only occurs before pupation. The eriophyoids, although presumably equipped with an open digestive tract, do not produce visible quantities of feces, and the suggestion has been made that excreta is stored within the hemolymph or used in eggshell construction (Jeppson et al, 1975).

The "biological harmfulness of contamination of the gall by excretion" (Mani, 1964) is given as the possible

reason for closed gut characteristics. In this regard it is of interest to note that gall aphids actively push liquid droplets out of galls, and that sawflies cut holes in their galls through which they eject feces. Despite these efforts, however, most aphid, moth, sawfly, and beetle galls frequently contain solid or fluid excretions.

Most leaf miners leave a fecal trail behind them. Many parasitic helminths are gut-less and absorb nutrients through the body wall. I have never seen this mode of nutrient uptake suggested for the metazoan gall-formers, but Mamaev remarked upon a thin cuticle in some gall-forming midge larvae. I do not know when excretion occurs in helminths.

Apparently then, storage of excreta occurs frequently in sedentary or confined parasites. Mamaev points out that the phenomenon of stored excreta may simply indicate that very little excreta is produced, i.e. that assimilation efficiency and diet quality are very high. This suggests that gall-forming moths, sawflys, and aphids, as well as most miners are poor assimilators and/or take a low quality diet much of which is unassimilable.

3) Gall Invaders.

A) Parasitoids and predators. Most all gall-forming insects are attacked by parasitoids and/or predators (Mani, 1964; Caltagirone, 1964). A possible exception: according to A. F. Bird (personal communication) "the gall probably does protect the nematode." One wonders if this protection occurs under uncultivated conditions? The below-ground habit of most nematodes may explain the lack of insect parasitoids (do above-ground gall-forming nematodes show parasites?), but subterraneanism should not prevent below-ground parasites (helminths, bacteria, fungi) from attacking the nematodes.

Predators are common in or on the periphery of some eriphyoid galls (Jeppson et al, 1975). I have never read of bacterial or fungal diseases (parasites) of gall-forming arthropods, but one suspects that numerous individuals, frequently in a single chamber, would provide excellent opportunities for epidemics. I do not know the extent to which gall-forming bacteria, slime molds, and fungi are protected from parasitization (by phages or other bacteria) or from predators.

Like gall-formers, leaf miners are heavily parasitized (Hering, 1951; Needham, et al, 1928). I do not know if by being in their host, parasites of animals gain protection from hyperparasites, although if galls and mines are again considered, hyperparasitoids

(parasitoids of the parasitoids that attack the gall-formers) are common. In this case then, being within the body of a host animal that is within a gall does not afford complete protection. To what extent are fleas and lice parasitized? It would be interesting to compare rates of (hyper)parasitism on endo- and ectoparasites.

Gall insects, like all other organisms, are attacked because they are an available resource. But why are they attacked so heavily? I suggest that in addition to providing food, the gall offers another important attraction. The microclimate of a gall is most likely conducive to growth. Thus a parasite (or predator) attacking and living in a gall feeds on a high protein diet in an ameliorated climate. The same reasoning could be extended one more trophic level to explain the high rates of hyperparasitism in galls.

There are other locations on the plant that combine these features of microclimate and diet. These include the flowers, seeds, or seed heads. It would be interesting to compare rates of invasion in fruits vs. galls.

Based on the above, I would predict that parasitic helminths and ectoparasitic insects would experience parasitization because they are a resource, but not at

the intensity experienced by gall insects. These creatures do not create a habitat with an improved microclimate. Just as importantly, they provide no richer a source of protein than does their animal host. Thus instead of attacking the helminth or flea, a (hyper)parasite would do as well to attack the primary animal host.

B) Inquilines. Inquilines are frequently found in arthropod galls. These are organisms that invade the gall while it is inhabited by the gall-former, but do not directly kill the gall-former. Some inquilines, however, may kill the gall-former indirectly. Thrips, mite, and cynipid galls provide good examples of gall types with a rich inquiline fauna. I am unaware of reports of inquilines in homopteran galls. Only a few inquilines are known from leaf mines, but this may reflect lack of observation (Hering, 1951).

Like parasites, inquilines are most likely attracted by the gall microclimate, but unlike parasites, they are attracted to the plant tissue or insect feces as a food source rather than to the gall-former. Based on their location in the gall, inquilines can be divided into 3 groups: 1) those that live in the gall or larval cavity and feed on the nutritive tissue (or rarely, perhaps on

the gall-former's excreta), 2) those that feed in the gall wall, and 3) those that feed in all tissues of the gall. The last 2 groups, in many galls, feed in tannin-rich tissues. Apparently the advantages of the microclimate more than compensate for efforts expended to contend with tannins.

The only other instance in the insect literature in which inquilinity is mentioned is in discussions of ant nest inhabitants (myrmecophiles). "The number and diversity of myrmecophilous arthropods are almost incredible" (Wheeler, 1910). From the same reference,

> The existence of this great number of myrmecophiles can be accounted for only on the suppositon that ant nests have a strong attraction for terrestrial arthropods. It is not difficult to understand how this can be the case since, in the first place, the nests are usually permanent abodes inhabited for months or years by successive broods of ants. Second, these nests have at all seasons a slightly higher temperature than the surrounding soil. Third, there is usually more or less refuse, food, or offal, pupal exuviae and dead ants, at least in the superficial chambers. Fourth, the living larvae and pupae represent an abundant and highly nutritious food supply for any insect that can elude the watchfulness of the ants.

The extended quote is provided to highlight the similarities between galls and ant colonies. I do not believe that the high incidence of parasitism and inquilinity in these two particular life habits is fortuitous. I suggest that the prerequisites for a high

incidence of invasion is an accumulation of energy and protein sources in an ameliorated microclimate (elevated or buffered temperature, high humidity). The higher rate or incidence of invasion in ant nests (vs. galls) is undoubtedly due to their longevity and to the ants' group defense (the inquiline is also defended), and to the philoprogenetive behaviors that may be deceived and exploited by the myrmecophile -- characteristics not exhibited by galls and gall-formers. Additionally the social insects show greater active control of the microclimate than do the gall insects.

The proposed pattern, however, is immediately called to question by Wheeler's (1910) observation that some colonial insects have fewer inquilines than ants. Colonial wasps, bees, and termites "have their nest mates and parasites. These, however, are far less numerous than the myrmecophiles." Wilson (1971) amends Wheeler's statement by pointing out that the higher termites have a large and complex symbiont (inquiline) fauna. Wilson further explains that colonies of bees and wasps do not host as many guests because only those insects with specializations "for arboreal life and a preference for dark, tight spaces, perhaps together with a tolerance for higher temperatures and lower humidity" become successful guests. He suggests that "opportunities for invasion"

are lower in these above ground colonies. Using his suggestion one would predict higher invasion rates in below-ground galls than above-ground -- a prediction that probably does not hold. I suggest that climate control may not be as great in an arboreal colony and, in part, for this reason, one may find fewer inquilines here than in terrestrial colonies.

Comparisons between invasion of an insect colony and a gall should continue. This is a first attempt. It will require more information on inquilinity in galls, and an appreciation for the difference in definitions (Wilson's inquilinity does not equal Mani's), as well as systems. The chance for a more accurate conceptualization and modelling of inquilinity will result.

4) Site of Attack, and Host Response. Gall-formers attack meristematic regions of the host plant or tissues that have undergone only slightly differentiation. The tissue must be responsive. It must be capable of dedifferentiation to a meristematic state.

As far as I can determine very few other parasites have this requirement or cause similar host reactions of hypertrophy and hyperplasia. Leaf miners frequently mine mature leaves. Callus development, if it occurs in

mines, results from the activity of either meristematic tissue associated with the vascular tissue, or from dedifferentiation of "fully developed tissue" (Hering, 1951).

The only example of a hyperplastic reaction in an animal host to a parasite is provided by Dawes (1963). He observed that "minute cytoplasmic blebs appear on the free surfaces of the epithelial cells of the bile ducts over extensive areas" early in the infection of mice, rats, sheep, and other hosts by the liver fluke, *Fasciola hepatica*. The reaction occurs in the tissues immediately surrounding the parasite. He goes on to say that,

> mitotic figures indicate that (the affected) cells are multiplying. This becomes more evident with the production of minute invaginations of the epithelium, possibly the earliest indications of enormous overdevelopment and folding which ensues.

The epithelium in later stages becomes "folded with numerous crypt-like formations with crowded nuclei." As a result of the inflammation the flukes are provided with a "pasture" of tissue on which to feed. The hyperplastic state lasts from 3-11 years.

The resemblance of the verbal and microphotographic descriptions of this host reaction to that of a host plant attacked by a gall insect is striking. Differences certainly exist between the 2 systems, but the

similarities invite further comparisons. For example, how do the hyperplastic animal cells compare ultrastructurally to nutritive cells?

5) Diet Enhancement. Most gall-forming organisms induce a cytological enrichment of the cells upon which they feed. As seen in this study, the nutritive cells remain enriched for different lengths of time, depending on the gall-former.

Bird (1961) used protein stains and cytophotometry to observe that the giant cell cytoplasm in root knots gave 4 times more extinction (i.e. a greater amount of protein) than did "normal cells". According to Rapp and Kirst (1974) "there is no distinct difference in the content of carbohydrates based on dry weights" between ungalled leaves, galled leaves, and galls of the cecidomyiid, *Mikiola fagi* Htg. on *Fagus silvatica* L.. On a fresh weight basis "the protein content of the gall decreases compared with the quantity of protein in the leaves...(and) two thirds of the soluble proteins are located in the nutritive tissue of the gall."

Rapp and Kirst also showed that a gall collected on July 12 contained nutritive tissue with 1.3 mg soluble protein per gram fresh weight. An ungalled leaf at this time contained 1.4 mg soluble protein per gram fresh

weight. Thus, although there is a concentration of soluble proteins in the nutritive tissue, the larva, in mid summer, was feeding on no better a diet than if it had fed on an ungalled leaf. Perhaps earlier in the season the nutritive tissue was of a higher soluble protein content. How would the soluble protein contents of nutritive tissue in a cynipid, thrips, or eriophyoid gall compare to the same in this cecid gall?

Rapp and Kirst also found that, on a dry weight basis, whole galls between mid-June and early July averaged 9.3 mg total protein per gram of tissue. Leaves averaged 18.7 mg/g. Thus galls were 0.93% protein on dry weight basis and leaves were 1.87%. These last figures are at least an order of magnitude lower than that given by Southwood (1973) as an average percent protein (22%) on a dry weight basis of leaves of eight different (mostly herbaceous) crop species. Insect tissues on average are 50% protein on dry weight basis. Thus if the figures of Rapp and Kirst are correct, there is a very large disparity (a large hurdle, sensu Southwood) between total protein in the gall and total protein in the cecid larva.

In spite of the figures, I predict that the young nutritive tissues of most galls, and the young-to-old nutritive tissues of cynipid galls provide the gall

larva with a diet as rich in protein as any other organ or tissue on or in the host plant. I also predict that nutritive cells will be found comparable in protein content to animal tissues. In this regard it is interesting that there are eurytomid and torymid parasites in cynipid galls that switch from feeding on the host larva to nutritive tissue (Shorthouse, 1975). Apparently nutritive tissue satisfies some of the dietary requirements of these hyperparasites.

As far as I can determine, parasites of animals (with the possible exception of Fasicola hepatica; see above) cause no host response that can be interpreted as an enrichment of food cell cytoplasm. Most animal parasites either feed as they wander through the tissues, settle and feed on gut contents, or feed on blood cells in the vascular system. Enrichment, if it occurs at all, would most likely be seen where a parasite settles to feed in a protein-poor region of the host -- if such regions exist in an animal host.

6) Symbionts. Gut symbionts assist their host in obtaining a full complement of nutrients from a nutrient poor diet. Buchner (1965) has the following to say about the apiomorphine coccids, gall-formers on eucalypts in Australia:

> Apparently the absence of symbionts is connected with the fact that the apiomorphines are the only coccids which live in galls, and it is certainly no accident that in the gall-forming Hymenoptera and Diptera or in most of the insects which mine in leaves and stems, symbionts are always lacking.

Likewise gut symbionts "are not associated with the genus *Meloidogyne*" (A. F. Bird, personal communication). Mamaev (1975) predicts that intracellular symbionts may occur in gall midge larvae. The evidence at the moment suggests that both gall-formers and leaf miners require few if any symbionts. The diet alone satisfies the nutritional needs of larvae. Blood-feeding parasites (lice, fleas, and certain mites) frequently require symbionts for vitamin production even though the diet is protein- and carbohydrate-rich.

7) *Galls as Metabolic Sinks.* Kirst and Rapp (1974) showed that galls of *Mikiola fagi* on leaves of *Fagus silvatica* L. began to accumulate 14C metabolites "3-5 minutes after 14CO2 application to the leaf tissue." Translocation of metabolites to the gall occurred when the host leaf or adjacent leaves were labelled.

Jankiewicz et al (1969) studied the sink properties of oak apple galls on *Quercus robur* L. caused by *Cynips quercus-folii* L.. Results were variable, but when 14CO2 was introduced to certain spots on the underside of a

galled leaf, the gall, regardless of its position with respect to the point of label application, was labelled at 36 hours. Generally the major vein servicing the gall showed heavy labelling. Additionally, the longer the labelled assimilates were allowed to be transported in the leaf (up to 6 days), the greater was the concentration of label in the larva and nutritive tissue.

Both of the above reports used detached leaves or branches. Thus they do not give an indication of how galls would compete for metabolites against natural sinks such as the roots.

Bird and Loveys (unpublished results discussed in Bird, 1975), on the other hand, used whole tomato plants with root knots.

> Infected plants were allowed to photosynthesize in an atmosphere of $^{14}CO_2$ and were left in the glasshouse for periods of time which varied from two hours to five days before being harvested. The uptake of the label into the nematode is slow and not significant over periods of two and four hours. However, over periods of from one to five days, there was a much greater accumulation of translocated photosynthates in the galls than in adjacent tissues. After five days exposure to $^{14}CO_2$ for instance, galls with egg masses contained about six times as much ^{14}C as did adjacent roots and about half of this had become incorporated into the eggs.

This report gives the clearest indication of the sink properties of a gall and gall-former that is

available. Similar work with insect galls (on whole, perhaps herbaceous, plants) should be done.

I have never seen the suggestion that mines are sinks. Other sedentary phytophagous insects, however, establish sinks. For example, various authors have shown that aphids, when feeding in groups on a plant, can influence nutrient flow (Way, 1968; Kennedy and Fosbrooke, 1973).

I do not know if animal parasites are considered sinks to which blood and nutrients are shunted preferentially. Again, sedentary parasites would be the most likely ones to show this phenomenon.

8) Unusual Life Cycles and Reproduction. The cynipids are the only Hymenoptera that show alternation of generations. Both generations usually occur on the same host plant species.

Many gall-forming aphids, like many other aphids, show complex life cycles in which at least two species (or genera) of host plants are attacked by different generations.

Some of the gall-forming eriophyoid mites show summer and winter forms, but these do not switch hosts, nor do they form different galls. Parthenogenesis occurs in the nematode genus *Meloidogyne*, but no host or

gall switching is known. Parthenogenesis is also known in a few gall-forming cecidomyiids.

Parasites of animals frequently show very complex life cycles that involve host switching and parthenogenesis (Whitfield, 1979). The unusual reproductive biologies of parasites are usually interpreted as means of producing numerous offspring that saturate the environment. In this regard, it is unfortunate that there is no comprehensive review of fecundity of gall-formers.

9) Damage to Plant. See Appendix 3 for a discussion of this point.

HOW DOES THE PLANT DEFEND ITSELF AGAINST GALL PARASITES?

Historically some cecidologists have considered the gall itself as a form of plant protection in that it walls off, contains, localizes the damage caused by the insect. Otherwise, the reasoning goes, the insect would cause considerable damage by moving through plant tissues. The anatomy of a plant gall, however, indicates both that the insect controls gall development and that the gall is a drain on the plant. In fact, others have suggested that galls represent a host

defensive response (callusing) that has been usurped by the gall-former. If a gall is viewed as detrimental to the host plant, then one should consider possible defensive plant strategies.

Interestingly, there are no observations available on the percentage of ovipositions or attempted establishment by gall arthropods that fail. Evelyn Westphal has studied host plant resistance to eriophyoid attack, but her results are not yet available. It may well be that plant defense reactions early in attempted gall establishment are an important deterrent to successful attack. In another system, hypersensitive reactions have been observed. The reactions prevent root knot nematodes from parasitizing the host, and occur early in the infection process (Paulson and Webster, 1972).

Gall formation requires meristematic or only partially differentiated cells for successful initiation. Thus a plant might defend itself by making these tissues less available in time, in space, in amounts, or in quality. Whitham (1979) has suggested that prime galling sites on a host are in limited numbers.

Gall formation requires a tight biochemical and physiological coupling between host plant and

gall-former. The host plant species might realize some short term protection by being able to vary the biochemical pathways targeted and usurped by the gall-former from plant to plant. (The crown gall system has the greatest chance of elucidating such a mechanism.) One would expect, however, that variation in the host plant would eventually be tracked by the gall-former.

Lastly, we should consider the possibility that rather than chemical control, host plants may rely on biological control of gall-forming pests. The high incidence of predation and parasitism undoubtedly contributes a great deal to the control of gall-formers. According to Stinner and Abrahamson (1979), parasitism may also reduce the damage that a gall causes its host plant. To be sure, a gall-former, parasitized or not, is a drain on the plant. Damage may be minimized, however, if parasitoids are in some way actively encouraged to attack the gall. In this regard, it is interesting that some cynipid galls on oaks secrete a nectar that attracks ants. It may be that the predaceous ants protect the galls from parasitoids (Tom Seibert, personal communication). (The development of secretory cells in the gall tissues would be interesting to follow.) Thus, by in some way directing the gall

tissues to secrete nectar, the gall-former may have exploited a strategy that compromises any system used by the plant to attrack parasitoids.

PLATE 1

Figure 1. Trans. section through the agromyzid mine in the leaf of _Tellima grandiflorum_ (Pursh) Dougl.. Pupa (arrow) rests in the mine cavity (MC). The cavity has been excavated through the spongy mesophyll. (III/21/80).* 105X.

Figure 2. The pharyngeal skeleton of the agromyzid leaf miner with mouth hooks (upper arrow) and the atrophied ventral branch (lower arrow). (III/21/80). 85X.

Figure 3. The adult agromyzid that attacks _T. grandiflorum_. (IV/8/80). 10X.

Figure 4. Head capsule of _Lithocolletis_ sp. that mines leaves of _Gaultheria shallon_ Pursh.. Note bilobed labrum (arrow). (V/27/80). 55X.

Figure 5. Trans. section through leaf mine on _G. shallon_. The mine cavity (MC) has been excavated through the palisade (arrow). The larva (L) is seen in trans. section. (V/27/80). 70X.

Figure 6. Blotch leaf mine (arrow) on _G. shallon_. (V/27/80). 2.5X.

Figure 7. Trans. section through mine in leaves of _Populus trichocarpa_ T. and G. caused by _Phyllocnistis_ sp.. The mine cavity (MC) is excavated through the upper epidermis (arrow). The larva (L) is seen in trans. section. (V/13/80). 85X.

Figure 8. The stubby root knot gall (arrow) on tomato caused by _Meloidogyne hapla_ Chitw. (Grhse. culture). 6X.

Figure 9. Long. section through galled tomato root showing numerous groups of nurse cells (arrow) near the center of the root. 12X.

Figure 10. A group of nurse cells (left arrow) that are being fed upon by a female root-knot nematode (right arrow) in tomato roots. 290X.

* Date specimen was collected.

PLATE 1

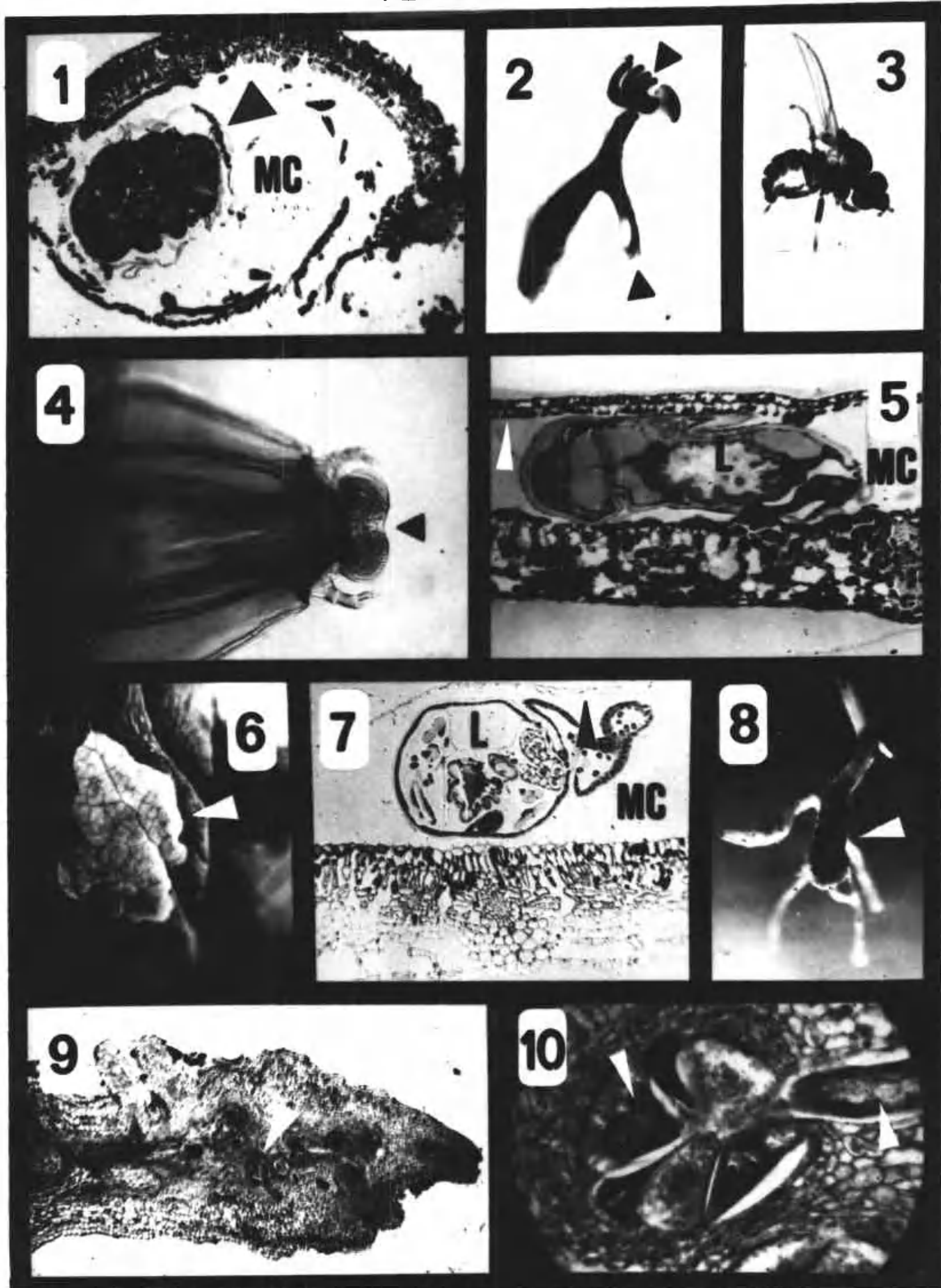


PLATE 2

Figure 1. Trans. section of <u>Delphinium</u> <u>trolliifolium</u> Gray stem galled by <u>Puccinia</u> rust. The uredia, (left arrow) occur on galled side of stem, as does fungal mycelium in the stem's hollow center (right arrow). Note enlargement of vascular bundles on galled side of stem. (IV/8/80). 15X.

Figure 2. An enlargement of the galled region of larkspur stem. Uredia with urediospores (arrow) are apparent. Enlarged vascular bundle (V) is surrounded by enlarged, vacuolate stem cells. (IV/8/80). 55X.

Figure 3. A galled leaf (arrow) of azalea attacked by <u>Exobasidium</u> <u>discoideum</u>. Note chlorotic condition. (V/1/80). 2X.

Figure 4. Trans. section through an ungalled azalea leaf. Palisade parenchyma (arrow) and spongy mesophyll layers are distinct. (V/1/80). 200X.

Figure 5. Trans. section through a galled leaf of azalea. Fruiting structures seen on both surfaces (arrows). (V/1/80). 130X.

Figure 6. The free basidia (upper arrow) on the surface of a galled azalea leaf. Lower arrow points to intercellular mycelium. (V/1/80). 320X.

Figure 7. Leaves of <u>Populus</u> <u>trichocarpa</u> galled by <u>Taphrina</u> <u>aurea</u> on upper (left arrow) and lower (right arrow) leaf surface. (VIII/12/80). Cm scale.

Figure 8. Trans. section through an ungalled poplar leaf. Palisade (arrow) and spongy mesophyll layers are distinct. (VIII/12/80). 100X.

Figure 9. Trans. section through a galled poplar leaf. Palisade layer (arrow) is recognizable. (VIII/12/80). 100X.

PLATE 2 (Cont.)

Figure 10. Lower leaf epidermis in poplar gall. Asci (arrow) with spores are seen. (VIII/12/80). 275X.

PLATE 2

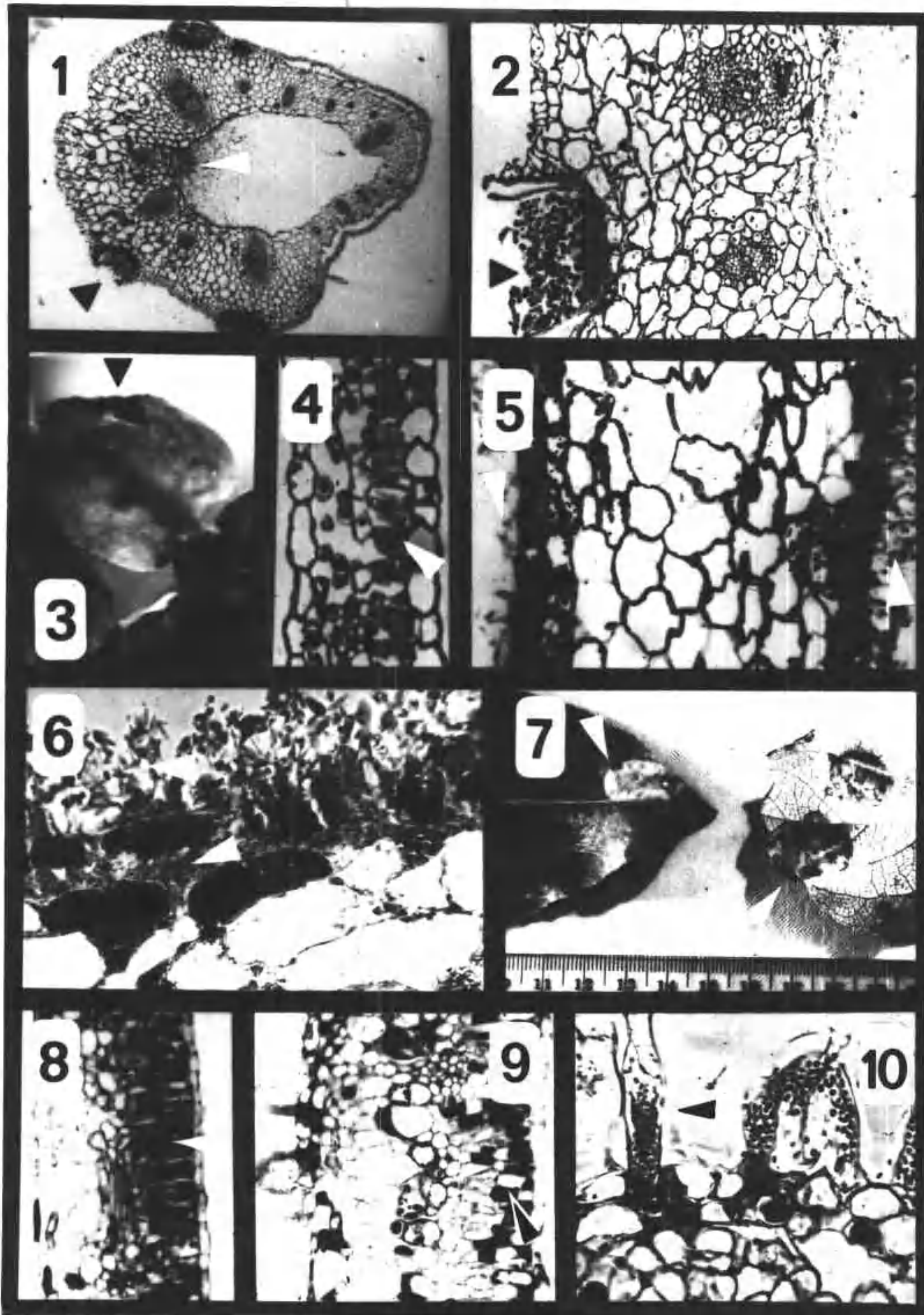


PLATE 3

Figure 1. Upper surface of willow leaf gall (arrow) caused by an eriophyoid mite. Note chlorotic halo surrounding red gall. (V/20/80). 7.5X.

Figure 2. Willow leaf galls with upper surface cut away. Note interconnecting chambers (arrow). (V/20/80). 7.5X.

Figure 3. Eriophyoid in willow leaf gall (star at anterior end). (VI/6/80). 230X.

Figure 4. Trans. section of ungalled willow leaf. Palisade layer (arrow) is evident. Spongy layer is tightly packed with cells (V/27/80). 190X.

Figure 5. Long. section through willow leaf gall with upper surface to right. Two gall cavities (G). Note vascular strand (upper arrow) that passes through the top of the gall. Nutritive tissue (lower arrow) lines the cavities. (V/27/80). 40X.

Figure 6. Long. section through gall cavities (G) of willow leaf gall with lower surface in lower left corner of photograph. Nut-ritive tissue (arrows) lines cavity. (V/27/80). 100X.

Figure 7. Nutritive cells (arrow) lining cavity (G) of willow leaf gall. (V/27/80). 350X.

Figure 8. Long. section through older willow leaf gall with top of gall in upper portion of photograph. A deposit (arow) lines the cavity (G), on the surface of the nutritive cells. (VIII/19/80). 45X.

Figure 9. Cavity (G) of willow leaf gall lined with nutritive cells (arrow). (VIII/19/80). 200X.

PLATE 3 (Cont.)

Figure 10. Cavity (G) of necrotic willow leaf gall with vacuolate nutritive cells (arrow). (VIII/19/80). 185X.

PLATE 3

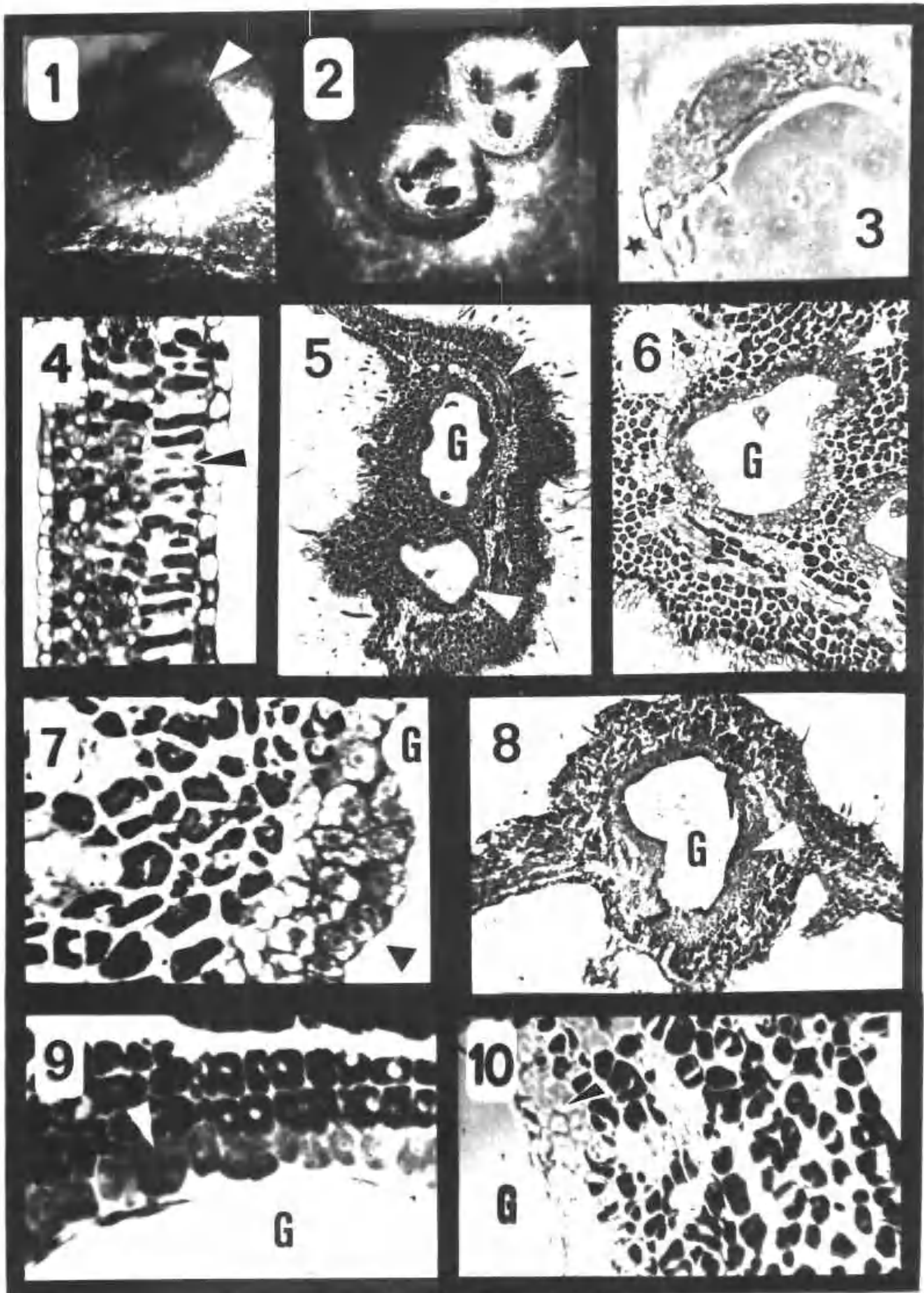


PLATE 4

Figure 1. Wall of willow leaf gall stained for tannins. The gall cavity (G) is lined by lightly stained nutritive cells (arrow). (VI/5/80). 250X.

Figure 2. Upper surface of leaf of Alnus rubra Bong. galled by Phytoptus laevis Nal. The arrow points to a single bead gall (VII/15/80). Scale in mm.

Figure 3. Deutogyne taken from alder bead gall. Star at anterior end. (V/6/80). 270X.

Figure 4. Mite taken from alder bead gall. Star at anterior end. (VIII/12/80). 270X.

Figure 5. Long. cut-away view of alder bead gall with upper surface to the left. Large, single gall cavity is seen (arrow). (VIII/12/80). 30X.

Figure 6. Trans. cut-away view of alder bead gall with cavity at arrow. Note cavity partition in upper gall. (V/20/80). 15X.

Figure 7. Long. section of young alder bead gall with central gall cavity (G). (IV/22/80). 60X.

Figure 8. Nutritive cells (arrow) of young alder bead gall. (IV/22/80). 265X.

Figure 9. Cavity of alder bead gall with large, prominent nutritive cells (arrow). (V/13/80). 100X.

Figure 10. Nutritive cells (arrows) that line the cavity of the alder bead gall. (VI/5/80). 175X.

PLATE 4

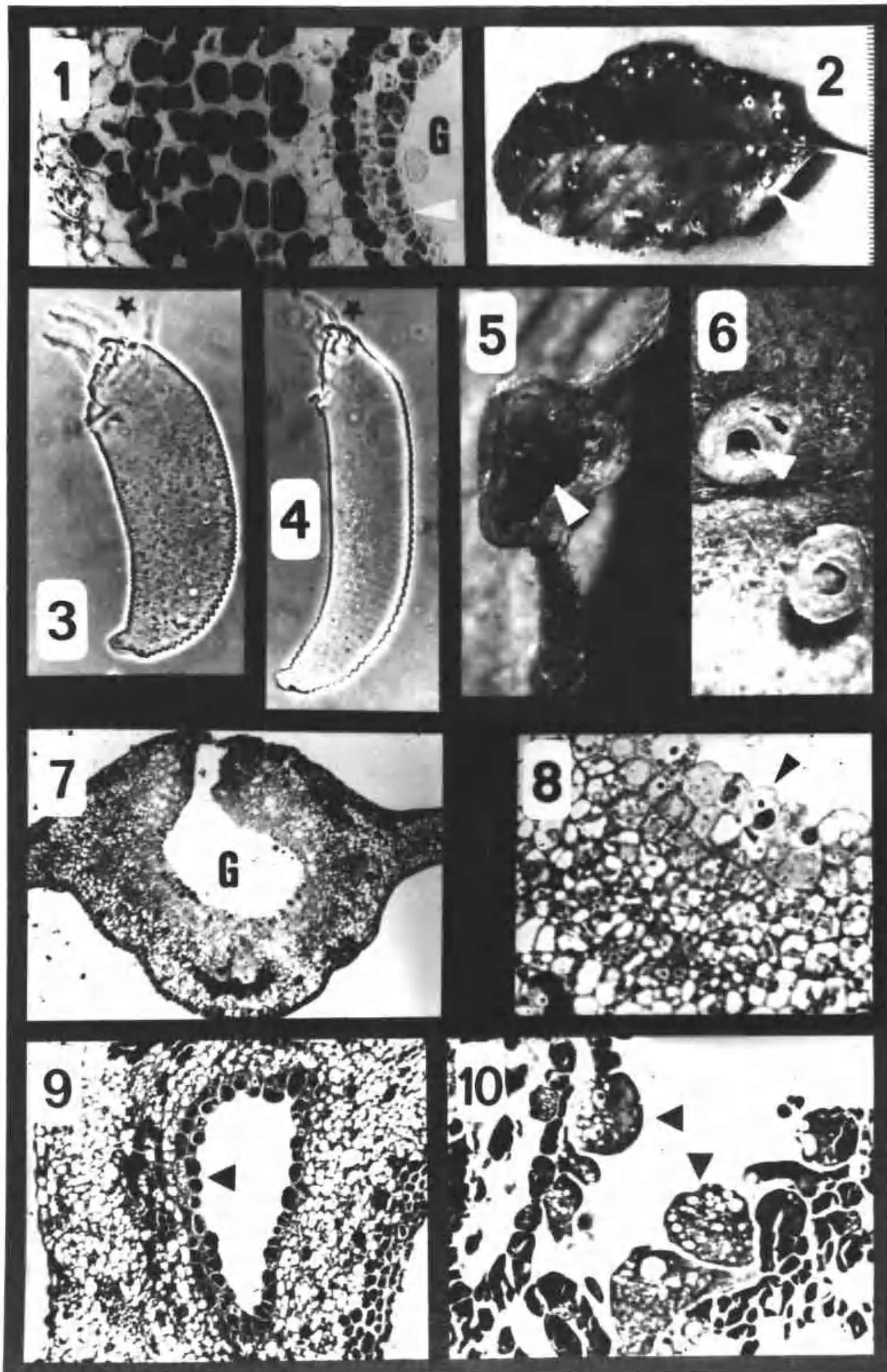


PLATE 5

Figure 1. Trans. section through an ungalled alder leaf. Palisade (arrow) and spongy layers are distinct. (IV/22/80). 250X.

Figure 2. Older alder leaf with necrotic bead galls (arrow). (IX/21/80). Cm scale.

Figure 3. Long. section of mature alder bead gall with large central cavity. Nutritive cells (some collapsed) line the cavity (arrow). (VII/16/80). 25X.

Figure 4. Wall of alder bead gall showing partially collapsed nutritive cells (arrow). (VII/16/80). 140X.

Figure 5. Wall of alder bead gall stained for tannins. Nutritive cells (arrow) stain fairly positively. (V/20/80). 160X.

Figure 6. Wall of alder bead gall stained for tannins. Nutritive cells (arrow) stain very positively. (VII/24/80). 150X.

Figure 7. Leaf gall on *Tilia* caused by an eriophyoid. (V/20/80). 4.5X.

PLATE 5 (Cont.)

Figure 8. Eriophyoid mite from New York *Tilia* leaf gall. Star at anterior end. (V/26/80). 250X.

Figure 9. Trans. section of ungalled *Tilia* leaf. Palisade (arrow) and spongy mesophyll layers are distinct. (IV/30/80). 325X.

Figure 10. Long. section through young *Tilia* gall showing central cavity (G) and portal hairs (arrow). (IV/7/79). 40X.

Figure 11. Wall of *Tilia* gall with nutritive cells (arrow) lining gall cavity. (IV/30/80). 250X.

Figure 12. Close-up of nutritive cells in very young *Tilia* gall. (IV/7/79). 550X.

Figure 13. Transition zone between ungalled *Tilia* leaf (to lower left of lower arrow) and gall wall (to upper right of lower arrow). Palisade layer is indicated by upper arrow. (IV/30/80). 200X.

PLATE 5

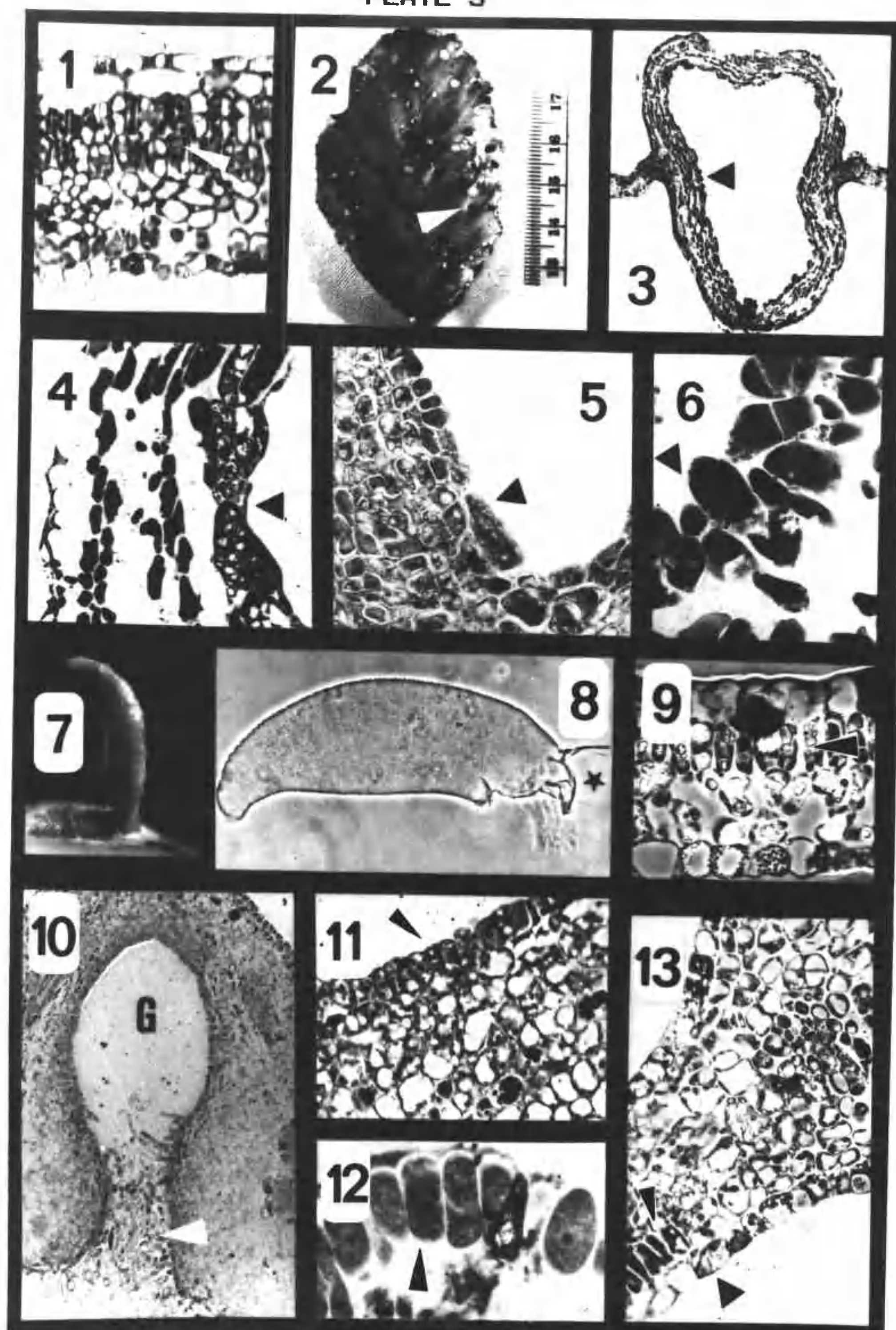


PLATE 6

Figure 1. Portal region of *Tilia* gall with numerous hairs (arrow). The gall cavity is to the right, outside of the photograph. (V/20/80). 75X.

Figure 2. Wall of *Tilia* gall. Arrow points towards cavity and at vacuolate nutritive cells. (V/20/80). 130X.

Figure 3. Wall of *Tilia* gall. Upper arrow lies within cavity and points to base of cavity hairs. Large dark-filled ducts are seen (lower arrow). (VII/24/80). 130X.

Figure 4. Erineum gall (arrow) on the underside of Garry oak leaf. (V/20/80). 25X.

Figure 5. Eriophyoid mite taken from oak erineum. Star at anterior end. (VII/24/80). 260X.

Figure 6. Trans. section of young oak leaf showing palisade (arrow) and spongy mesophyll. (V/20/80). 175X.

Figure 7. Transition zone of oak erineum. At left of bundle, the leaf is ungalled, while to the right (arrow) of the bundle, the spongy mesophyll is denser, and hairs develop from both epidermises. (V/20/80). 140X.

Figure 8. Trans. sect through oak erineum showing darkly stained lower epidermal cells (arrow) and hairs arising from lower epidermis. (VII/24/80). 125X.

Figure 9. Transition zone of oak erineum stained for tannins. Epidermal layers to the right of the vascular bundle (arrow) stain deeply. The hairs do not. (V/20/80). 70X.

Figure 10. Tannin stain of oak erineum. Upper epidermal cells (arrow) stain very deeply. (V/20/80). 285X.

PLATE 6

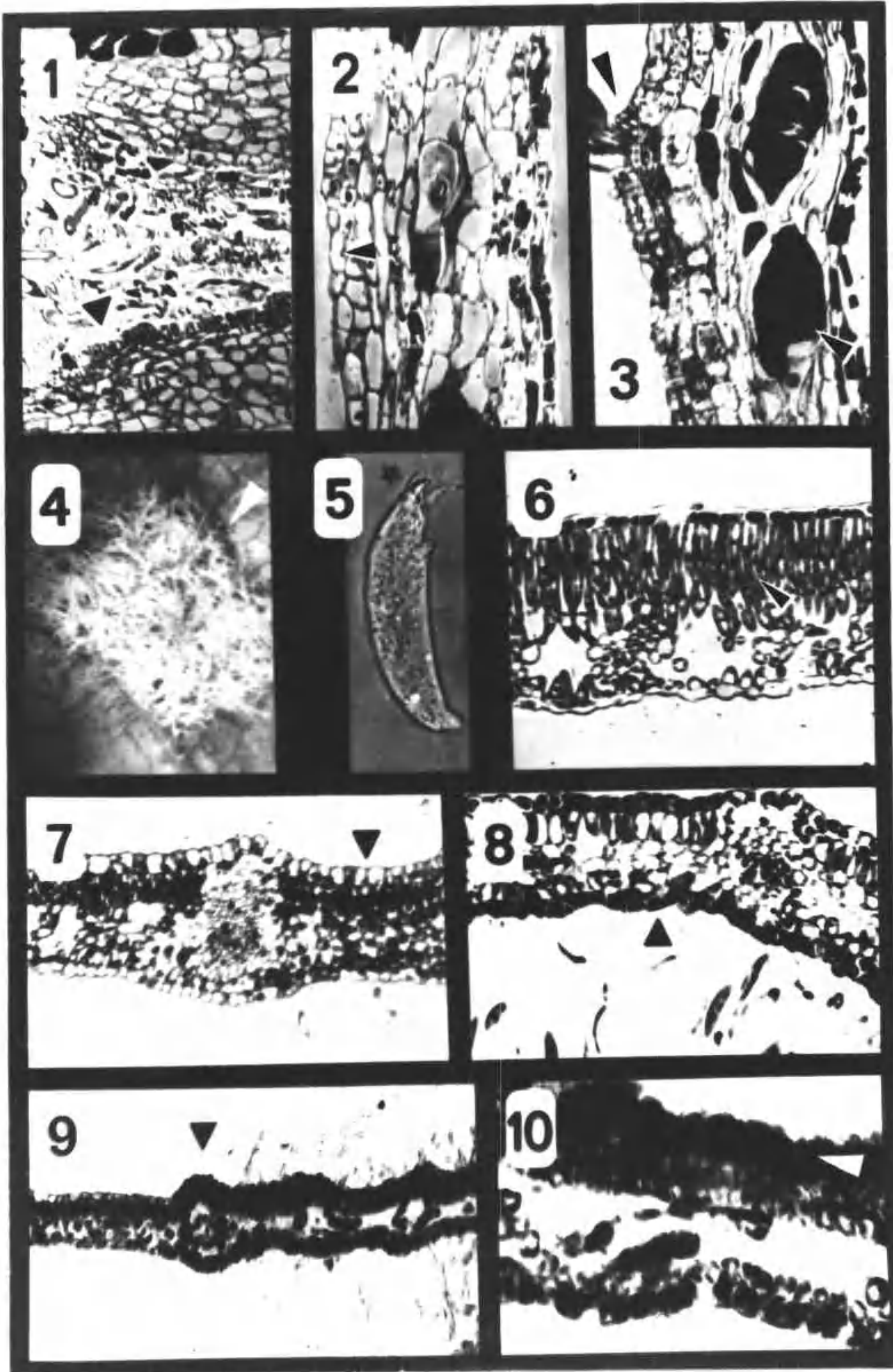


PLATE 7

Figure 1. Upper surface of eriophyoid gall (arrow) on leaflets of *Fraxinus latifolia* Benth.. Several galls occur on each leaflet. (VIII/12/80). 0.6X.

Figure 2. View of ash leaflet galls (arrow) from under-surface of leaflet. (V/13/80). Scale in mm.

Figure 3. Long section through ash leaflet gall that has been built over a large vein (arrow). Gall cavity (G) is seen. (VIII/12/80). 20X.

Figure 4. Deutogyne from ash leaflet gall. Star at anterior end. (V/20/80). 260X.

Figure 5. Trans. section of ungalled ash leaflet. Palisade (arrow) and spongy layers are distinct. (V/13/80). 220X.

Figure 6. Long. section through ash gall showing transition zone (lower arrow), gall cavity (G), and nutritive cells lining cavity (upper arrow). (V/13/80). 70X.

Figure 7. Section through gall cavity of ash gall showing nutritive cells (arrow) lining the gall cavity. (V/13/80). 190X.

Figure 8. Section through older cavity of ash gall (lower right corner) showing nutritive cells (arrow) lining the gall cavity. (V/13/80). 295X.

Figure 9. Eriophyoid gall on *Tilia* sp. from New York. Cut away to show hairy interior. Leaf surface at arrow. (V/26/80). 13X.

Figure 10. Long. section of New York *Tilia* gall showing cavity (star) and enation (arrow). (V/26/80). 110X.

PLATE 7

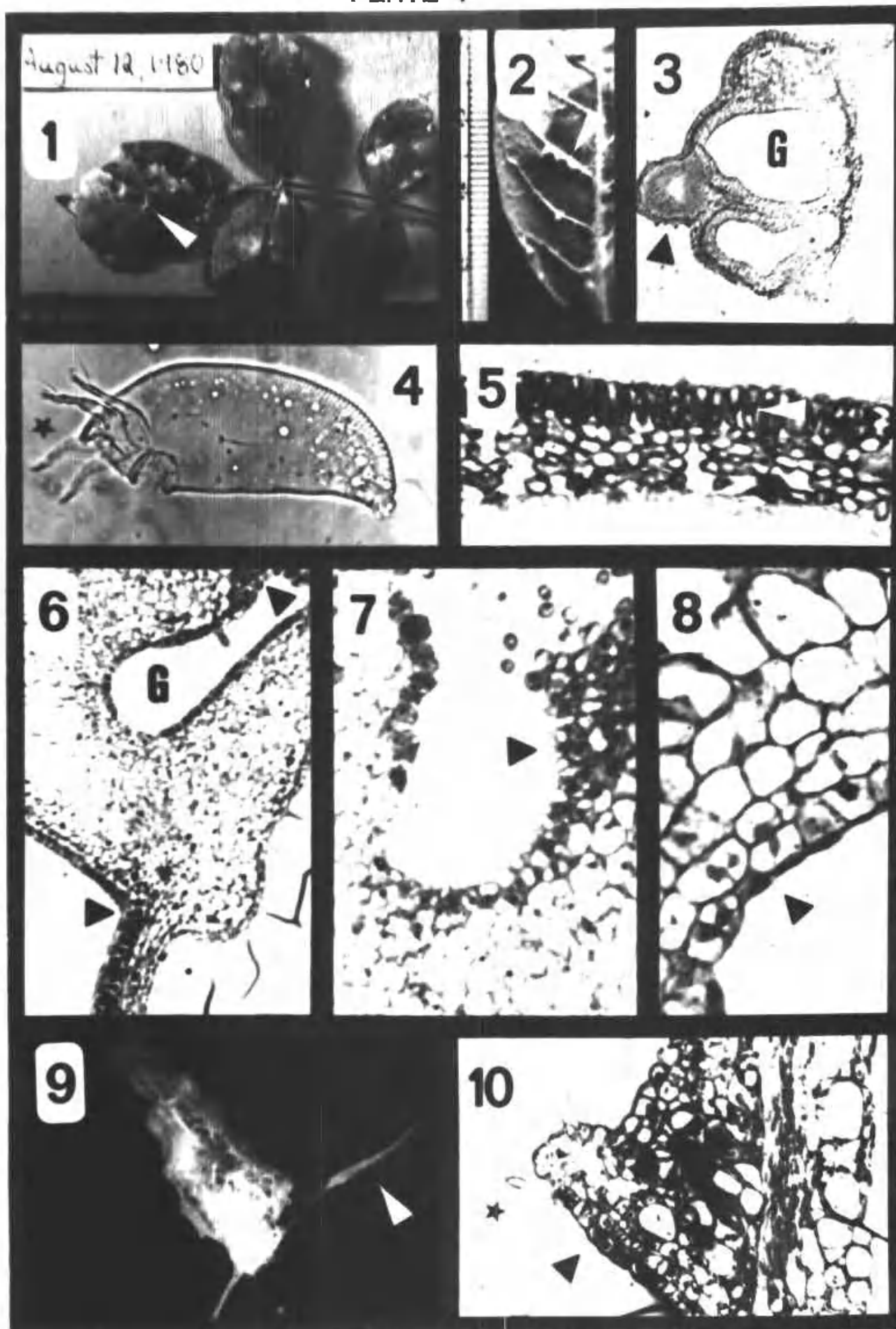


PLATE 8

Figure 1. Eriophyoid gall on _Rhus_ _diversiloba_ T. and G.. A group of galls (arrow) is seen on the upper leaflet surface. (V/31/80). 4X.

Figure 2. Eriophyoid gall (arrow) on poison oak flowers. (VI/25/80). 4X.

Figure 3. Eriophyoid mite taken from poison oak gall on leaflets. (V/30/80). 250X.

Figure 4. Section through poison oak leaflet gall showing transition between ungalled leaflet (bottom arrow) and gall (upper arrow). Most change occurs at large vein (middle arrow). (V/31/80). 13X.

Figure 5. Trans. section through ungalled poison oak leaflet. Palisade (arrow) and spongy mesophyll layers are distinct. (V/31/80). 150X.

Figure 6. Trans. section. of poison oak leaflet gall showing enlarged nutritive cells on lower leaflet surface (upper arrow), and recognizable palisade (lower arrow) and spongy mesophyll layers. (V/31/80). 350X.

Figure 7. Eriophyoid leaf gall of _Populus_ _tremuloides_ Michx. on underside of the leaf (right arrow). (VI/15/80). 0.4X.

Figure 8. Eriophyoid mite taken from the leaf gall on trembling aspen. Star at anterior end. (VI/15/80). 260X.

Figure 9. Close up of trembling aspen leaf gall. Gall is the circular, enated area (arrow) on underside of leaf. (VI/15/80). 15X.

Figure 10. Trans. section of ungalled trembling aspen leaf. Palisade (arrow) and spongy mesophyll layers are distinct. (VI/15/80). 200X.

PLATE 8

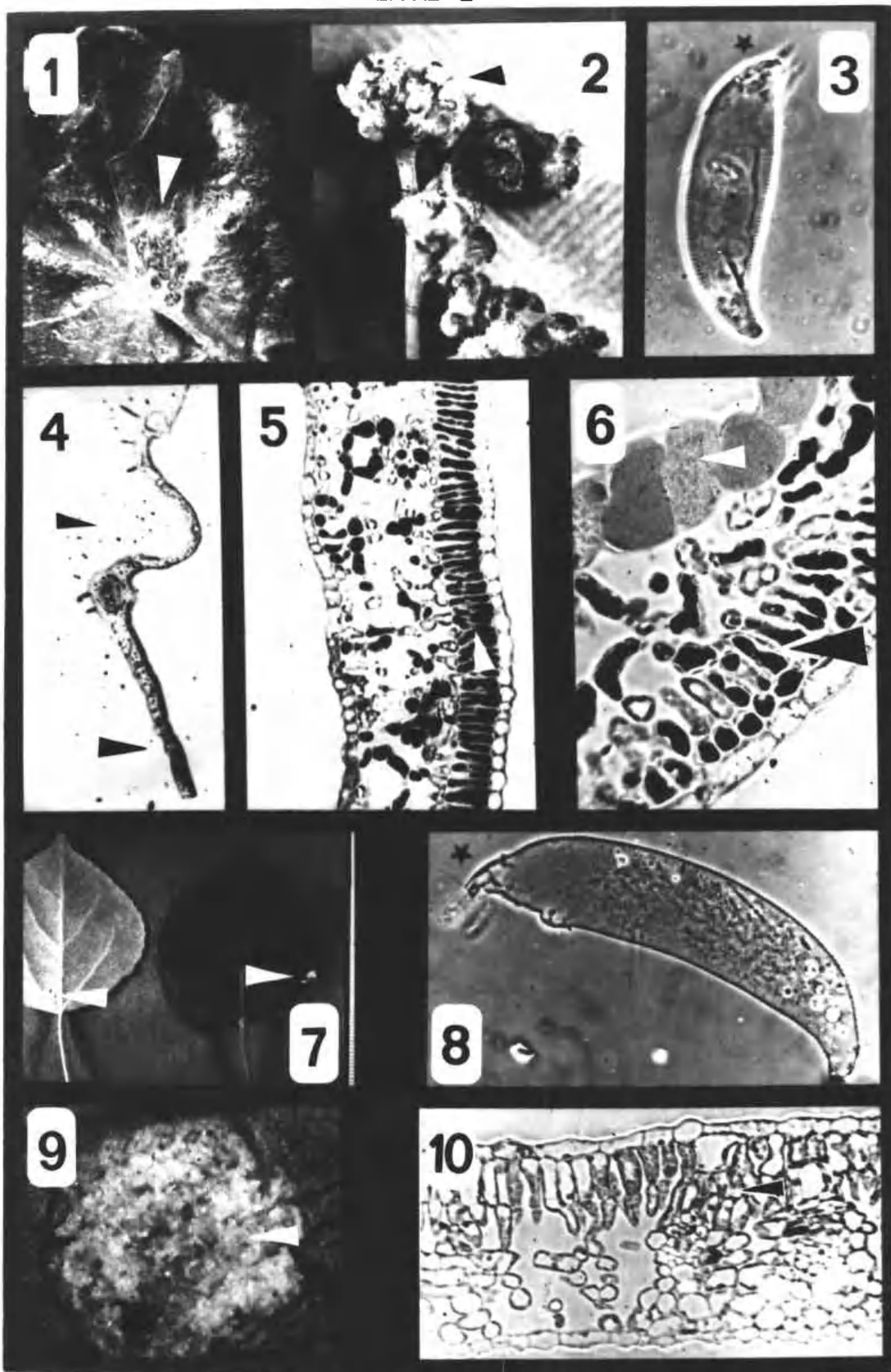


PLATE 9

Figure 1. Section through enated region of trembling aspen leaf. Enation (upper arrow) arises from spongy mesophyll region. The palisade parenchyma (lower arrow) remains distinct. (VI/15/80). 85X.

Figure 2. Eriophyoid leaf gall (arrow) on Prunus virginiana L. as seen on the upper leaf surface. (VI/15/80). 2.5X.

Figure 3. Long. section through choke cherry leaf gall with central cavity (G) and leaf surface (arrow) apparent. (VI/15/80). 16X.

Figure 4. Eriophyoid mite taken from choke cherry gall. Star at anterior end. (VI/15/80). 260X.

Figure 5. Choke cherry leaf gall cut-away partially to show cavity (upper arrow). Leaf at lower arrow. (VI/15/80). 20X.

Figure 6. Trans. section through ungalled choke cherry leaf showing distinct palisade (arrow) and spongy mesophyll layers. (VI/15/80). 120X.

Figure 7. Nutritive cells (white arrow) lining cavity (star) in choke cherry leaf gall. Black arrow points to dark, circular nucleolus. (VI/15/80). 280X.

Figure 8. A galled bud of Corylus avellana L. caused by Phytoptus avellanae Nal. (Winter, 1976). 2X.

Figure 9. Scanning micrograph of enated bud scale from filbert big bud. Enations (upper arrow) occur on inner surface of scale (middle arrow). Hairs (lower arrow) cover the outer surface of the scale. (Winter, 1976). 50X.

PLATE 9

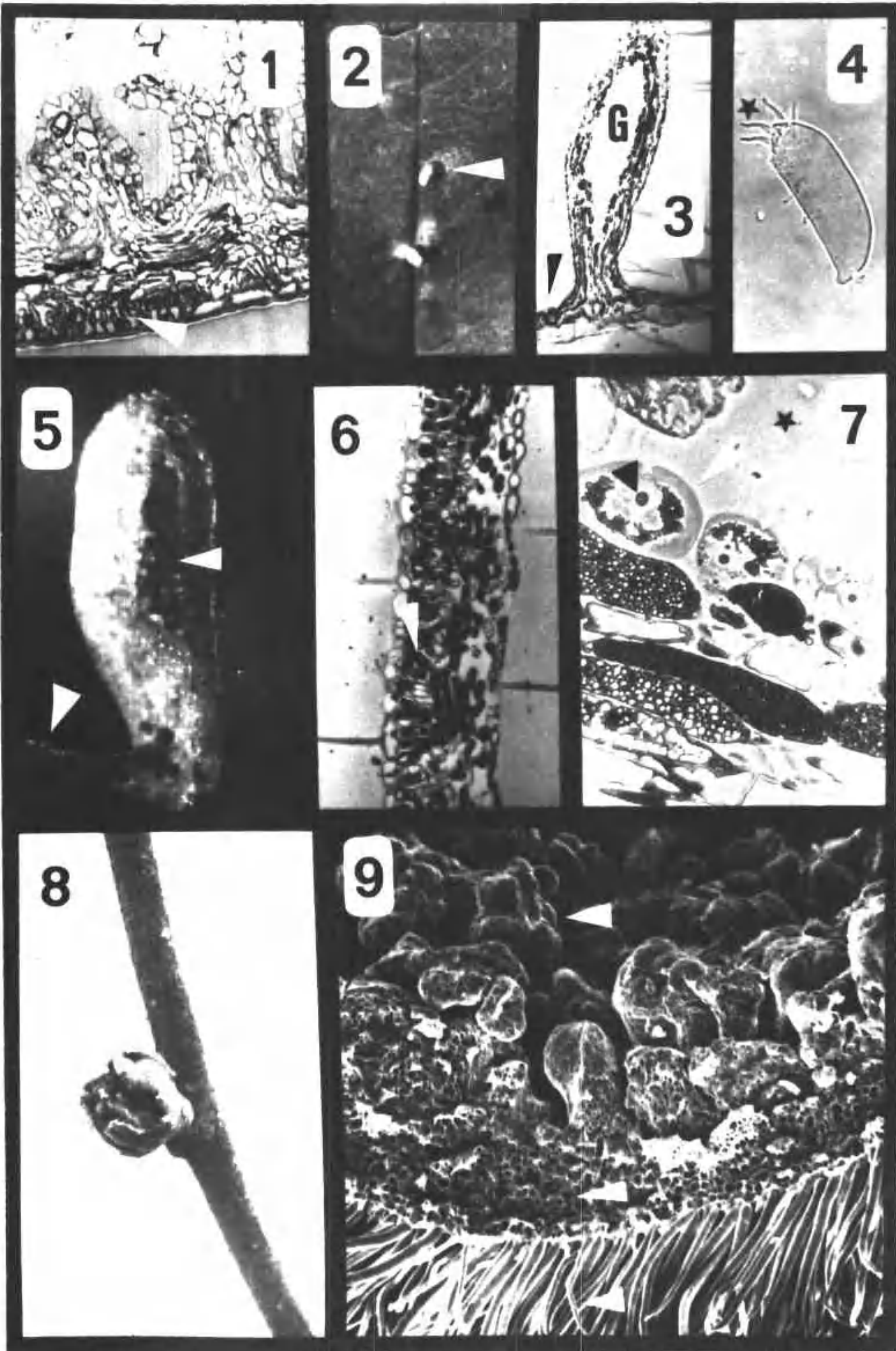


PLATE 10

Figure 1. Trans. section through enated big bud scale. Base of enation is seen at far left (left arrow). Nutritive cells (left, middle arrows) cover surface of enation. At far right (right arrow), epidermal cells are not nutritive, but are undergoing transition to nutritive state. Mite (m) lies on scale surface. (Spring, 1976). 175X.

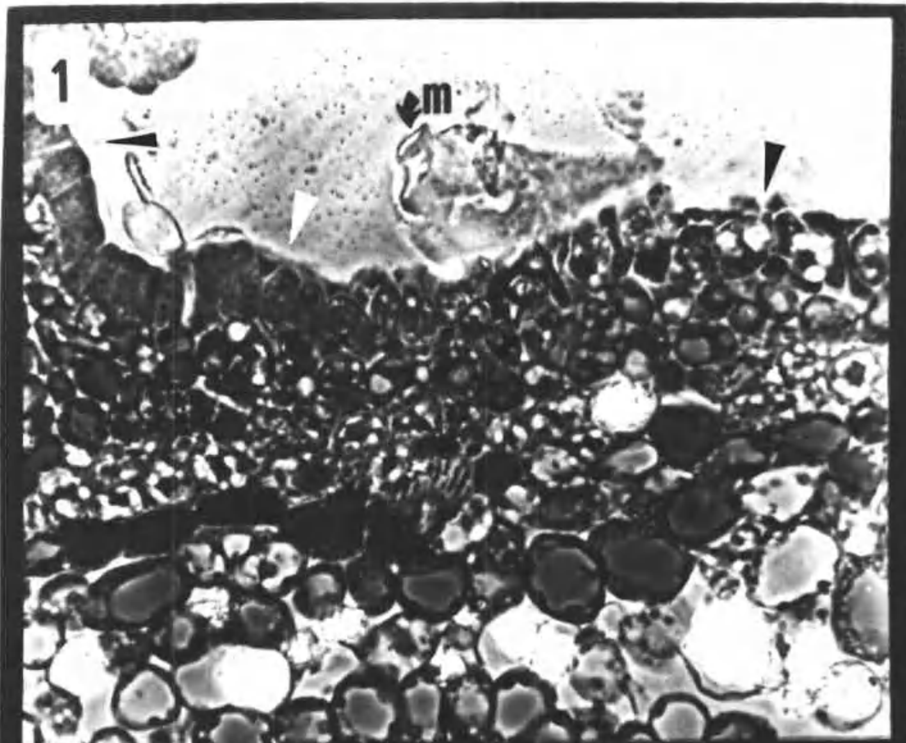
Figure 2. Nutritive cell from filbert big bud with prominent nucleus (Nc) and nucleolus (Nu). (Spring, 1976). 2000X.

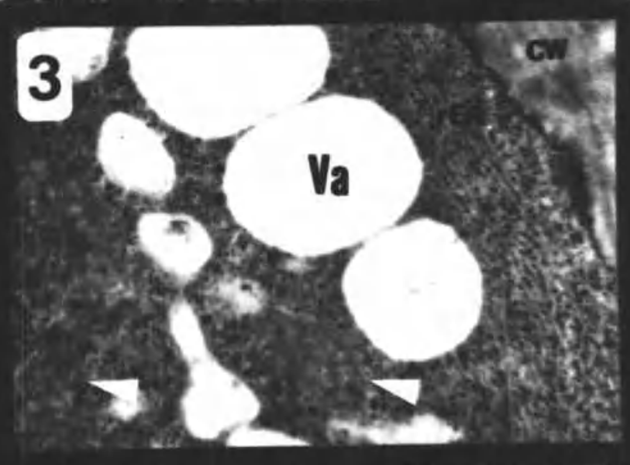
Figure 3. Cytoplasm of nutritive cell from filbert big bud showing vacuoles (Va), rough endoplasmic reticulum (rER), mitochondria (arrows) and cell wall (CW). (Spring, 1976). 8700X.

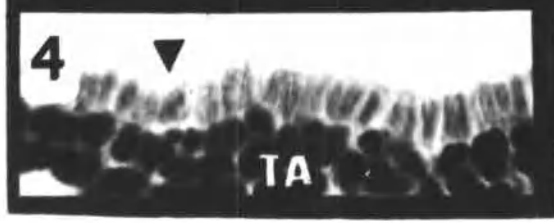
Figure 4. Enation in filbert big bud stained for tannins. Nutritive layer (arrow) stains poorly while subsurface layers (TA) stain positively. (Spring, 1976). 160X.

Figure 5. Phytoptus avellana Nal.. Star at anterior end. (Spring, 1976). 260X.

PLATE 10







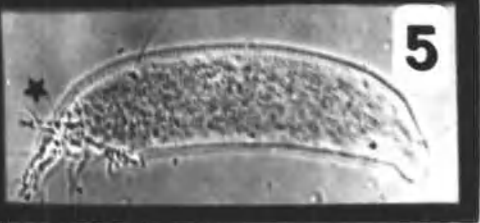


PLATE 11

Figure 1. Galls (arrows) on *Quercus garryana* caused by *Asterolecanium* sp.. (IV/2/80). 3X.

Figure 2. Trans. section of oak stem with pit scale. Proliferation of gall tissue is at arrow. (IV/2/80). 20X.

Figure 3. Trans. section through oak pit gall, and through scale insect (black arrow). The sclerenchyma tissue that underlies the insect is seen at the white arrow. (IV/2/80). 55X.

Figure 4. Trans. section through oak pit scale gall showing insect (left arrow), sclerenchyma (right arrow), and the cortical tissue underlying the insect. (IV/2/80). 85X.

Figure 5. Stem gall on *Penstemon peckii* Pennell caused by *Caloptilia murtfeltella* (Bsk.). Note the exit window (arrow). (VIII/28/80). Scale in mm.

Figure 6. *C. murtfeltella* larva. (VI/6/80). 6X.

Figure 7. Trans. section of ungalled stem of Peck's penstemon showing pith (P), vascular tissue (V), and cortex (C). (VI/6/80). 100X.

Figure 8. Trans. section through a galled stem of Peck's penstemon showing nutritive tissue (arrow) that lines the larval cavity (star). Vascular tissue (V) is also seen. (VI/6/80). 75X.

Figure 9. Trans. section through nutritive tissue of Peck's penstemon (lower arrow) that lines the larval cavity (star). Vascular tissue (upper arrow) is also seen. (VI/6/80). 140X.

PLATE 11

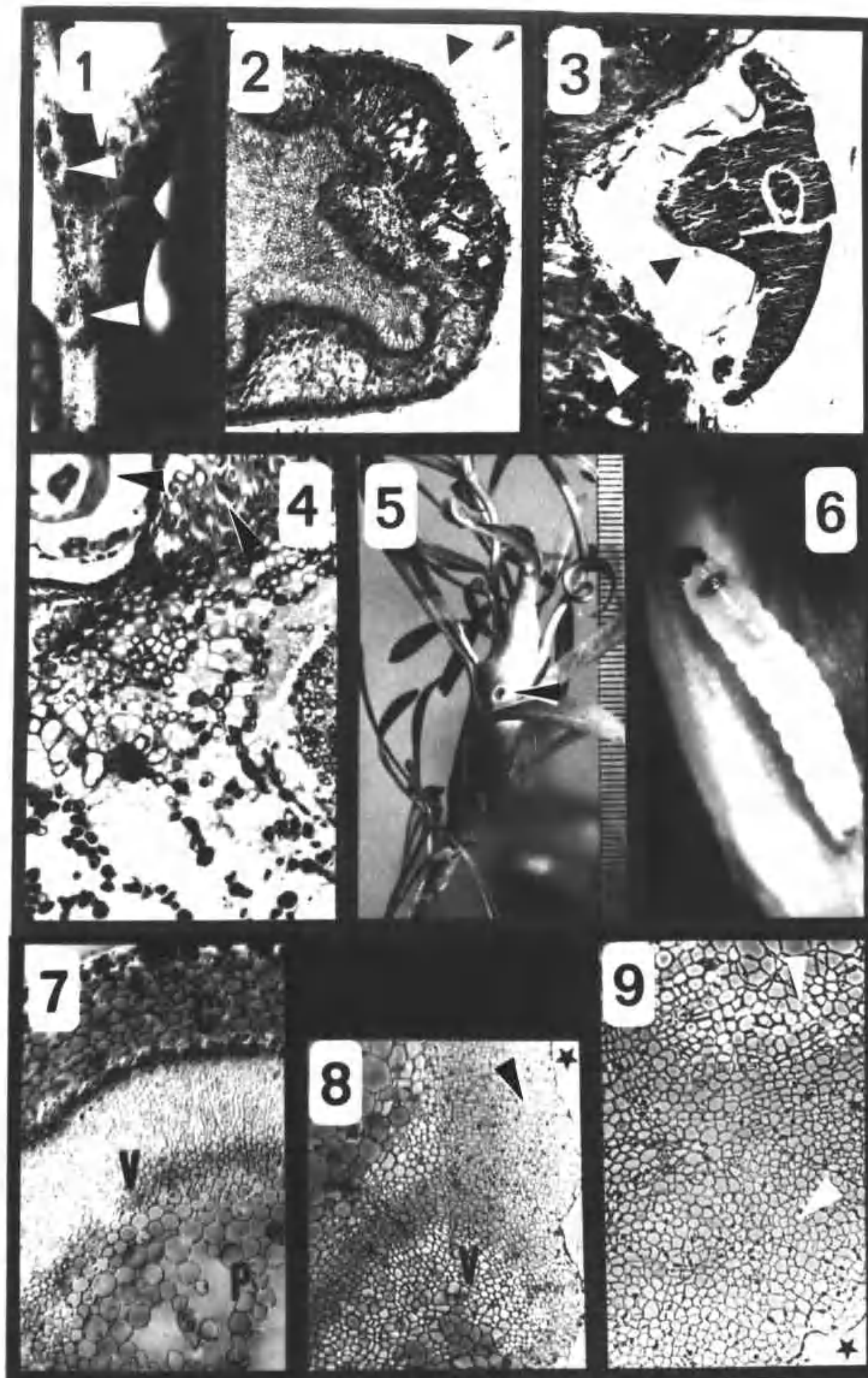


PLATE 12

Figure 1. Sawfly gall (arrow) on *Symphoricarpos albus* var. *laevigatus* Fern.. (V/6/80). 1.5X.

Figure 2. Head capsule of sawfly larva taken from snowberry gall. Sclerotized mandibles (arrow) are seen. (IV/25/80). 60X.

Figure 3. Trans. section through wall of snowberry gall showing enatial-like development of nutritive tissue (arrow) that lines the larval cavity (G). (IV/29/80). 80X.

Figure 4. Close up of nutritive tissue of snowberry gall. (V/6/80). 300X.

Figure 5. Trans. section through wall of snowberry gall showing nutritive tissue that has been fed upon (arrow), and that borders the larval cavity (G). (V/6/80). 60X.

Figure 6. Trans. section through wall of snowberry gall showing nutritive tissue (arrow) and cavity (G). (V/13/80). 100X.

Figure 7. Close up of nutritive tissue (arrow) that lines the gall cavity (G) in the snowberry gall. (VI/5/80). 200X.

Figure 8. Trans. section through old snowberry gall showing nutritive tissue (left arrow), gall cavity (G), and frass pellet (right arrow). (VI/25/80). 50X.

PLATE 12

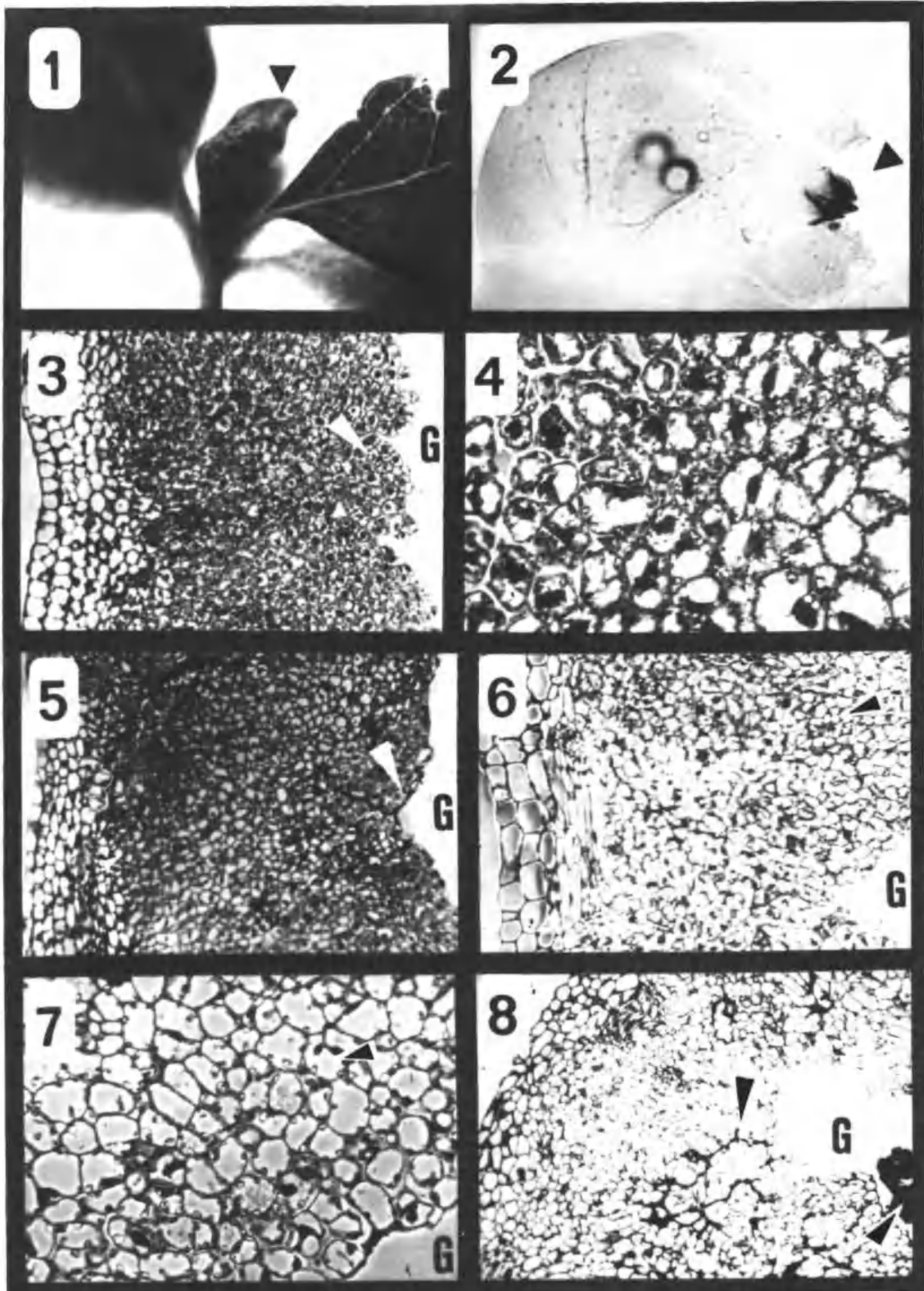


PLATE 13

Figure 1. Adult *Caloptilia murfeltella* (Bsk.). (VII/31/80). 4.5X.

Figure 2. Very young willow leaf gall (arrow) caused by *Pontania* sp.. Upper leaf surface. (IV/26/80). Scale in mm.

Figure 3. Adult *Pontania* sp. (From OSU Insect Collection).

Figure 4. Manidibles of *C. murfeltella* larva. (VII/31/80). Scale in mm.

Figure 5. Very young willow leaf gall (arrow) caused by *Pontania* sp.. Lower leaf surface. (IV/26/80). 200X.

Figure 6. Mature willow leaf gall (arrow) on underside of leaf (VII/10/80). Scale in mm.

PLATE 13 (Cont.)

Figure 7. Cut-away view of willow leaf gall showing larval cavity (G) and larva (arrow). (V/22/80). 8X.

Figure 8. Section through young willow leaf gall showing leaf (star), upper gall wall (upper arrow), lower gall wall (lower arrow), and gall cavity (G). (IV/26/80). 25X.

Figure 9. Upper wall of young willow leaf gall showing nutritive tissue (arrow) that lines the gall cavity (G). (IV/26/80). 150X.

Figure 10. Lower wall of young willow leaf gall showing nutritive tissue (arrow) that lines the gall cavity (G). (IV/26/80). 100X.

Figure 11. Section showing the junction between a willow leaf (star) and the willow leaf gall (middle arrow). The leaf midvein (upper arrow) and gall cavity (lower arrow) are also seen. (IV/26/80). 50X.

Figure 12. Section trough willow leaf gall showing gall cavity (G) and nutritive tissue (star). The lower surface of the gall is indicated by the arrow. (IX/22/80). 10X.

PLATE 13

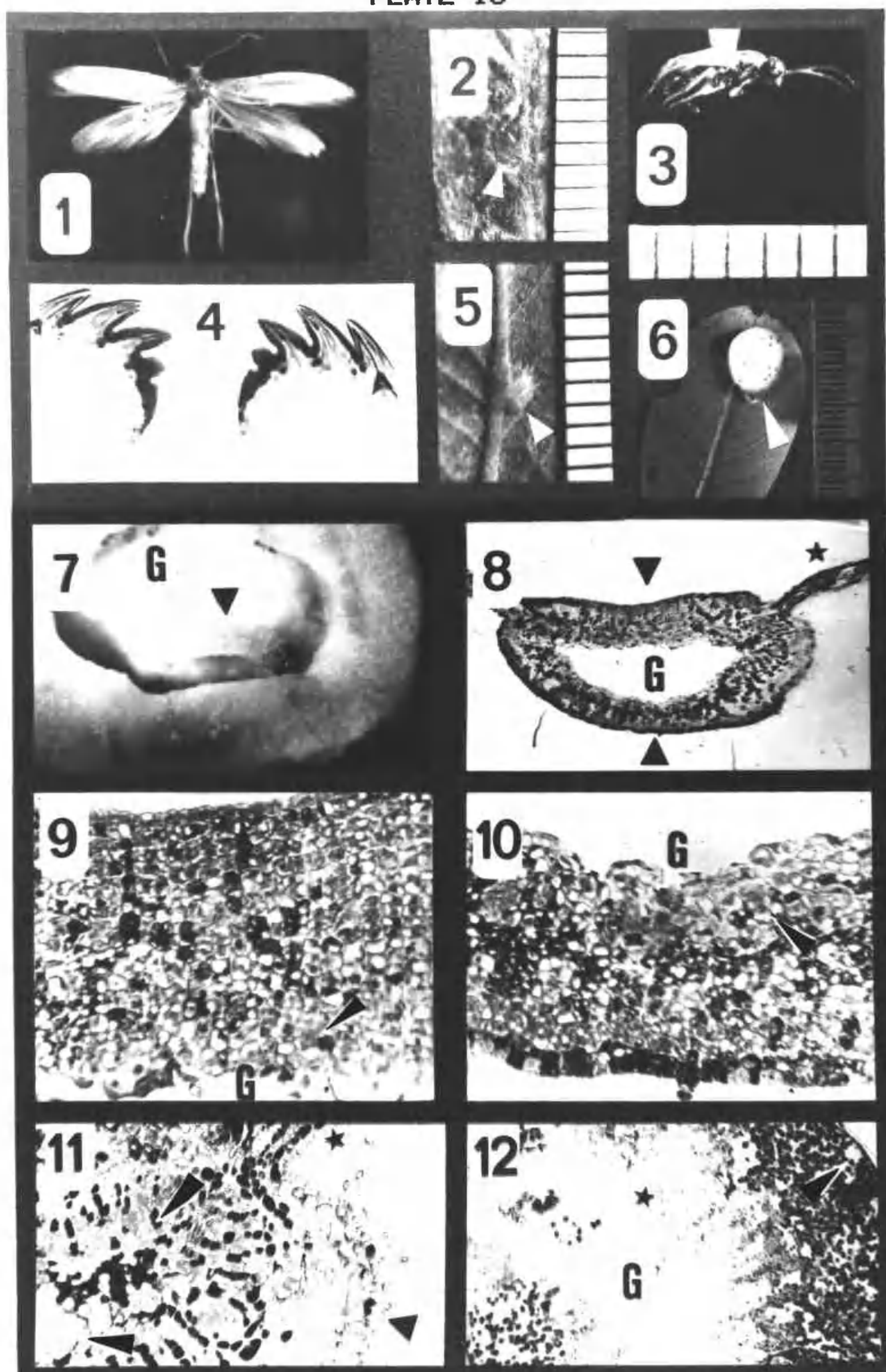


PLATE 14

Figure 1. Section through wall of willow leaf gall showing gall cavity (G), nutritive tissue (upper arrow), outer wall cells (middle arrow) and outer epidermis (lower arrow). (IX/22/80). 175X.

Figure 2. Section through willow leaf gall wall showing enatial-like growth of nutritive tissue (right arrow), darkly stained underlying cells (left arrow), and gall cavity (star). (V/13/80). 85X.

Figure 3. Nutritive cells (arrow) in willow leaf gall that line gall cavity (star). (V/13/80). 215X.

Figure 4. Trans. section of willow leaf stained for tannins showing positively stained palisade layer (arrow). (IV/26/80). 70X.

Figure 5. Willow leaf gall stained for tannins showing cells in outer wall that contain positively stained material (arrow). (VI/5/80). 65X.

Figure 6. Willow leaf gall nutritive tissue (arrow) stained for tannins. Negative results. Star in gall cavity. (VI/5/80. 150X.

PLATE 14

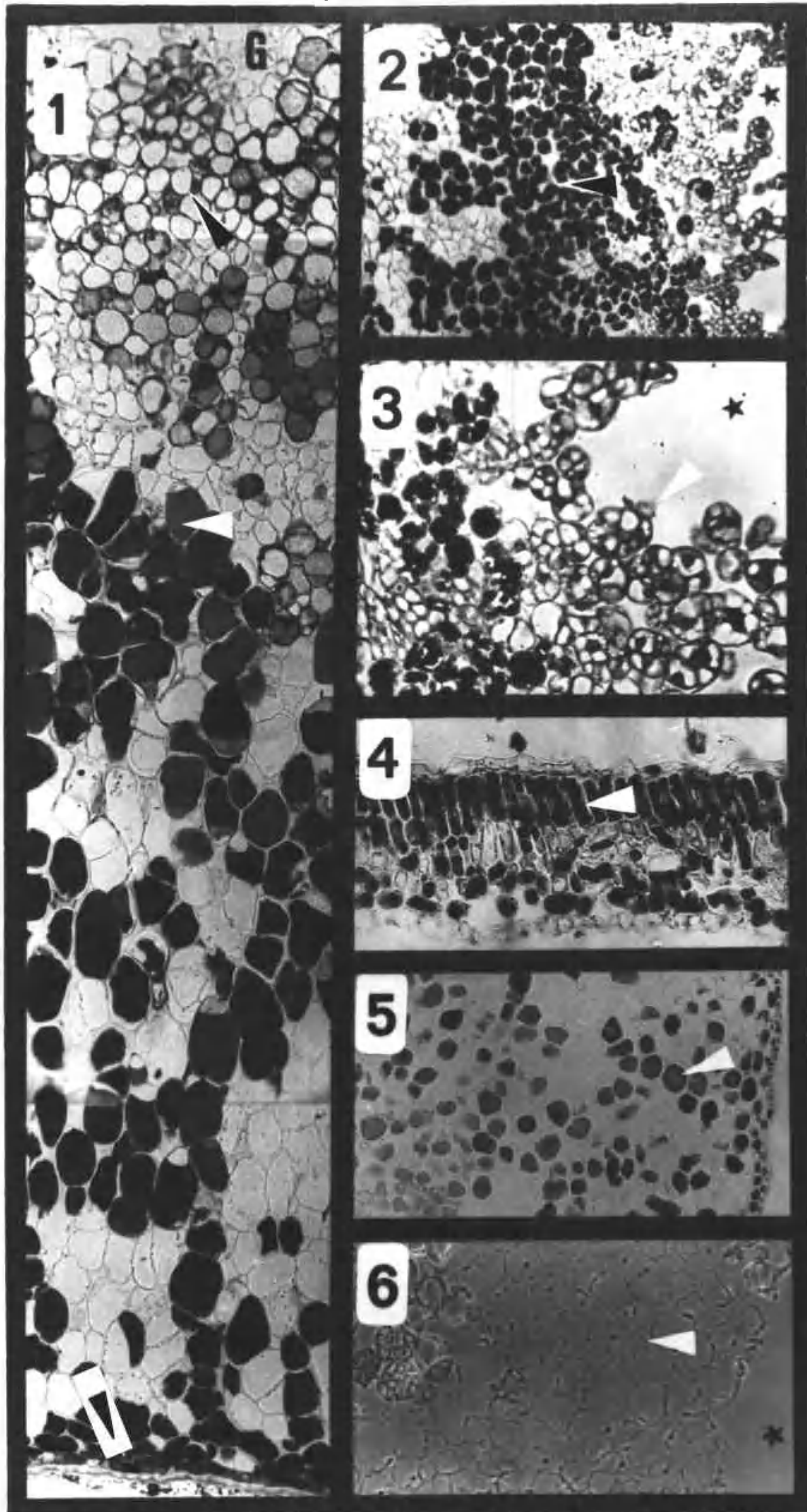


PLATE 15

Figure 1. Young petiole gall (arrow) on *Populus trichocarpa* T. and G. caused by *Pemphigus* sp. as viewed from upper leaf surface. (IV/15/80). 3X. (For view from underside see Pl. 39, Fig. 1).

Figure 2. Popular petiole gall (arrow). Note curled petiole. (IV/30/80). 2.5X. (For another view of same aged gall see Pl. 39, Fig. 2.). Scale in mm.

Figure 3. Mature poplar petiole galls (arrows). (VIII/12/80). Scale in mm.

Figure 4. Poplar petiole gall viewed from undersurface of leaf. (IV/30/80). 2.5X.

Figure 5. Section through poplar petiole gall showing gall cavity (G), and curled leaf lamina (left arrow). (VI/5/80). 15X.

Figure 6. Section through poplar petiole gall wall showing cavity (G) and groups of cytoplasmically dense vascular cells (arrow). (IV/29/80). 50X.

Figure 7. Sections through poplar petiole gall showing cavity (G) and cells lining cavity (arrow). (IV/29/80). 215X.

Figure 8. Section through poplar petiole gall wall showing ridges (arrow) in outer gall wall, and cavity (G). (V/20/80). 53X.

Figure 9. Section through poplar petiole gall wall showing gall cavity (G) and cytoplasmically dense vascular tissue (arrow). (V/13/80). 270X.

PLATE 15

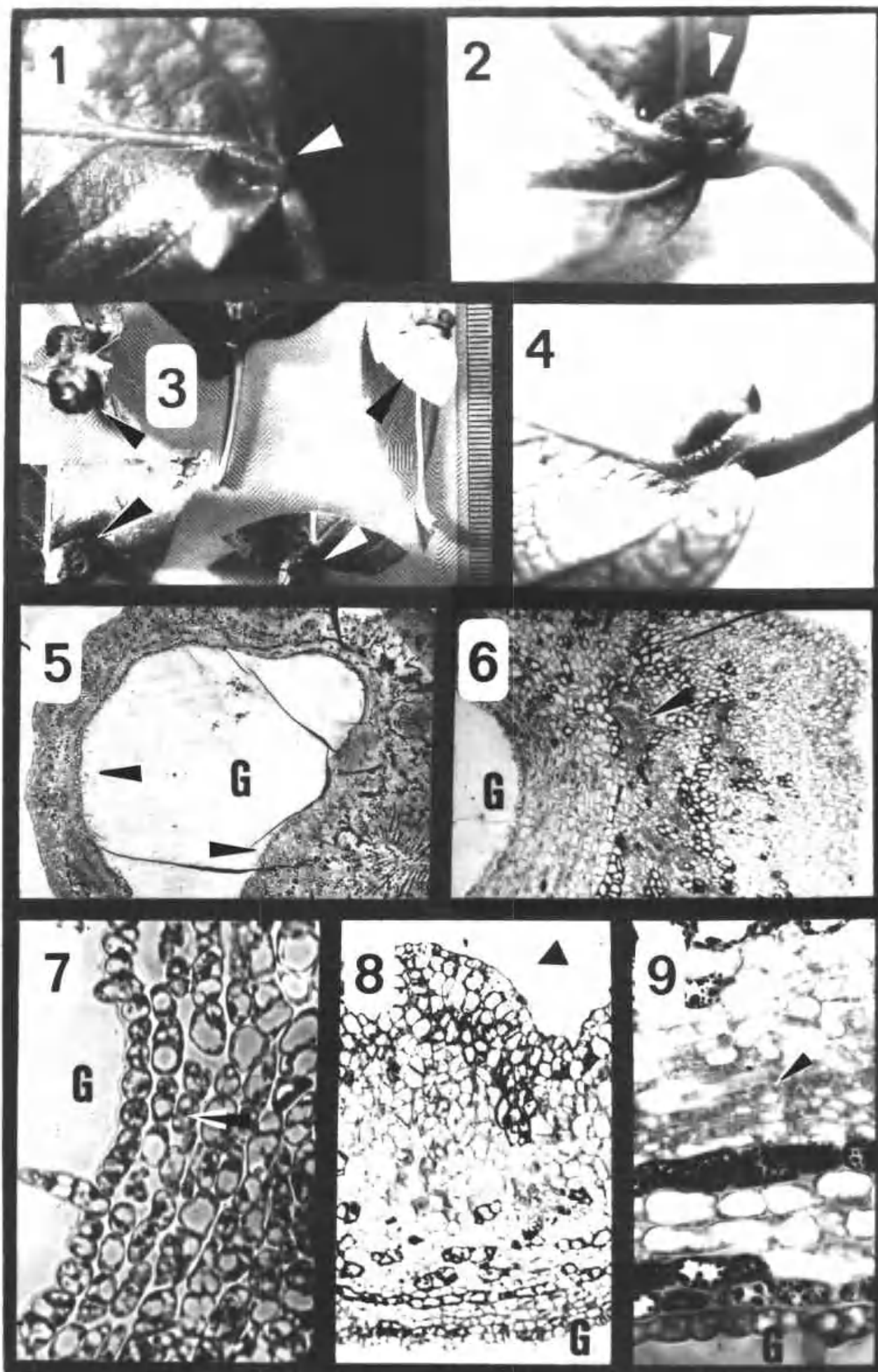


PLATE 16

Figure 1. Section through poplar petiole gall wall showing cavity (G) and strand of cytoplasmically dense vascular cells (arrow). (VI/5/80). 100X.

Figure 2. Section through poplar petiole gall wall showing gall cavity (G) and vascular strand (arrow). (VIII/12/80). 85X.

Figure 3. Section through poplar petiole gall wall showing gall cavity (G) and collapsed, necrotic region (arrow). (VII/12/80). 55X.

Figure 4. Section through poplar petiole gall wall stained for tannins showing cavity (G). (V/6/80). 65X.

Figure 5. Anasas gall (arrow) on *Picea engelmannii* Parry caused by *Adelges cooleyi* (Gill.). (VII/5/80). Scale in mm.

Figure 6. Cut-away view of anasas gall showing adelgids (arrows) in gall cavity. (VII/5/80). 12X.

Figure 7. *Adelges cooleyi*. Arrow at stylet. (VII/5/80). 85X.

Figure 8. Section through gall cavity (G) of anasas gall. Arrow at cells lining cavity. (VII/5/80). 70X.

PLATE 16

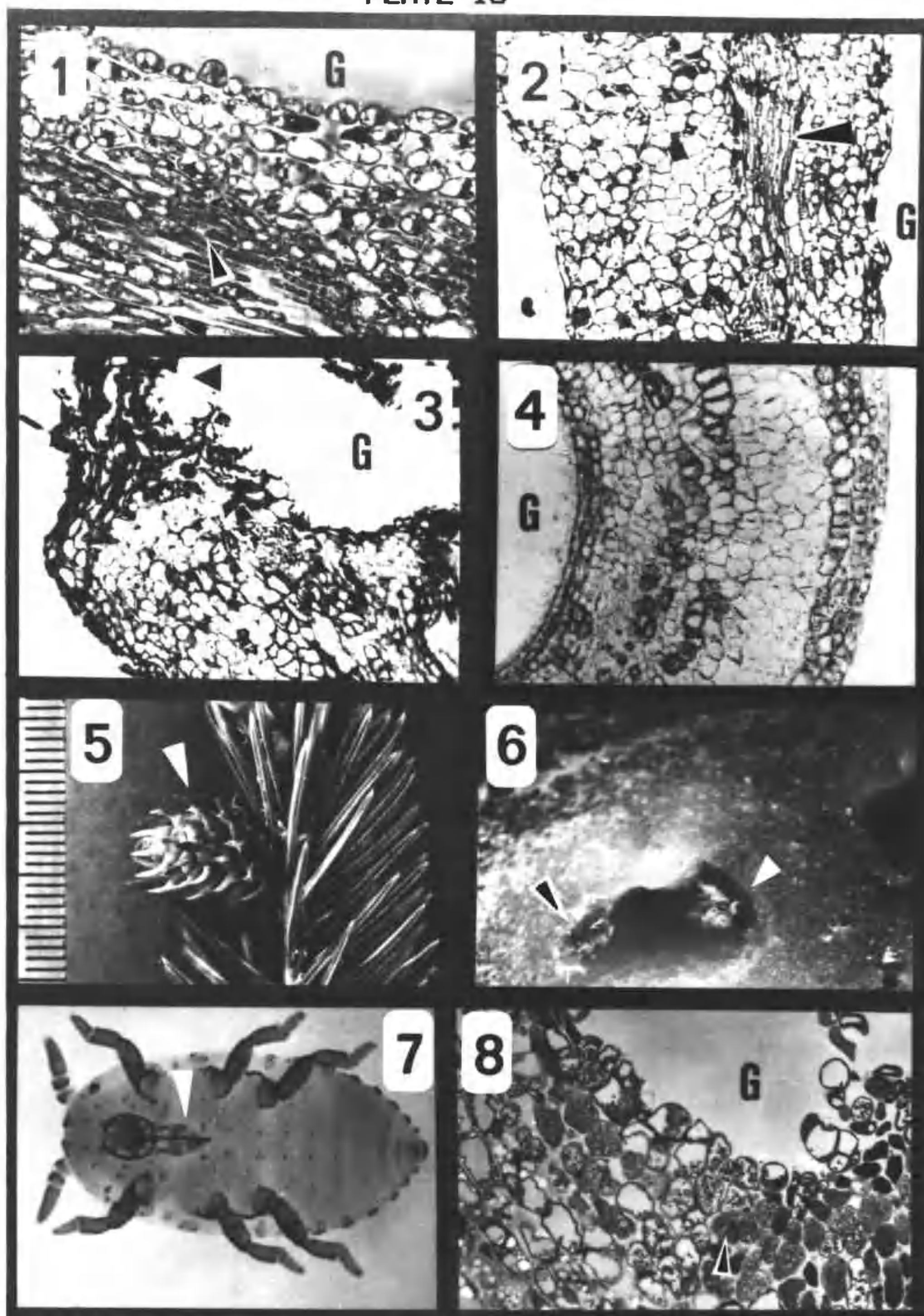


PLATE 17

Figure 1. Marginal leaf gall (arrow) on *Populus trichocarpa* T. and G. caused by *Thecabius populi monilis* (Riley) as seen from upper leaf surface. (IV/15/80). 4X.

Figure 2. Marginal leaf gall (arrow) as seen from lower lear surface (IV/15/80). 4X.

Figure 3. Secondary galls (arrow) on *P. trichocarpa* caused by fundatrigeniae of *T. populi monilis*. (VIII/12/80). Scale in mm.

Figure 4. *T. populi monilis* stem mother. (V/22/80). 20X.

Figure 5. *T. populi monilis* apterous fundatrigeniae. (VIII/12/80). 65X.

Figure 6. Section through marginal leaf gall caused by stem mother. Cavity (arrow) is seen. (IV/15/80). 20X.

Figure 7. Trans. section through ungalled poplar leaf. Palisade (arrow) and spongy mesophyll layers are distinct. (IV/15/80). 170X.

Figure 8. Transition zone from ungalled leaf to marginal leaf gall caused by stem mother. Spongy mesophyll (left arrow) of ungalled portion becomes more densely packed (right arrow) beyond area of transition (middle arrow). (IV/15/80). 130X.

Figure 9. Head of *Crotonothrips danahasta* Ram. that causes a leaf roll gall on *Memecylon* sp.. Arrow points to stylet. (VII/7/80). 200X.

Figure 10. Section through thrips leaf roll gall showing gall cavity (star) and patch of darkly stained nutritive cells (arrow). (VII/7/80). 100X.

PLATE 17

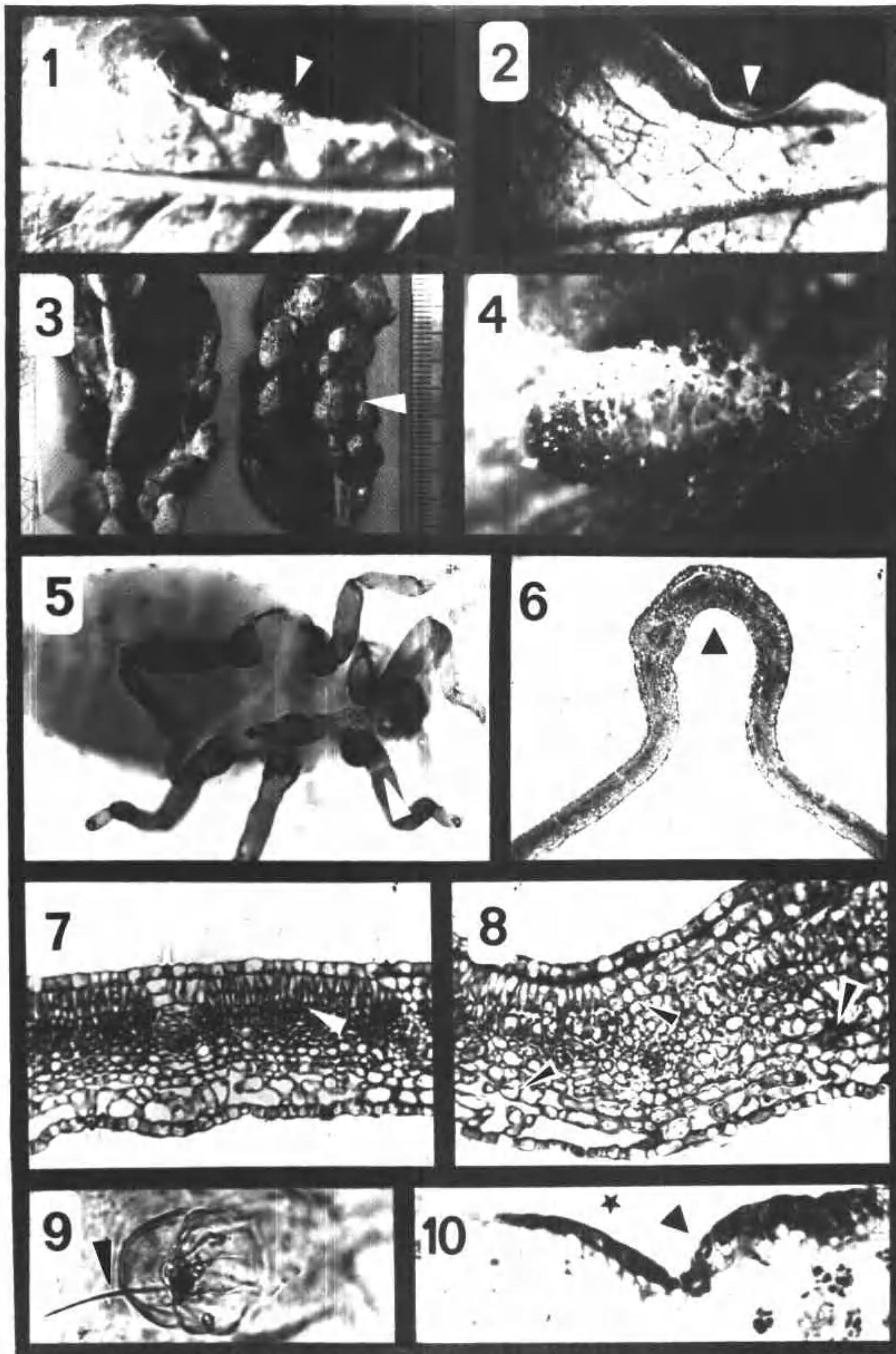


PLATE 18

Figure 1. Trans. section of mature, ungalled poplar leaf. Palisade (arrow) and spongy layers are distinct. (V/8/80). 100X.

Figure 2. Trans. section through wall of marginal leaf gall caused by stem mother. Gall cavity (G) and cytoplasmically dense vascular cells (arrow) are seen. (IV/29/80). 110X.

Figure 3. Trans. section through wall of stem mother marginal leaf gall, showing gall cavity (G) and vascular bundles (arrow). (VI/5/80). 75X.

Figure 4. Section through wall of stem mother marginal leaf gall, showing gall cavity (G) and vascular bundle (arrow). (V/13/80). 200X.

Figure 5. Section through wall of stem mother marginal leaf gall stained for tannins. Only cells in outer region of wall stain positively. Those near gall cavity (G) do not. (IV/29/80). 105X.

Figure 6. Midvein gall (arrow) on leaves of _Populus trichocarpa_ T. and G. caused by _Pemphigus_ sp. as viewed from underside of leaf. (IV/22/80). 4X.

Figure 7. Section through poplar midvein gall showing midvein (arrow) and gall cavity (star). (V/6/80). 10X.

Figure 8. Section through wall of poplar midvein gall showing gall cavity (G) and strand of cytoplasmically dense vascular cells (arrow). (V/13/80). 250X.

PLATE 18

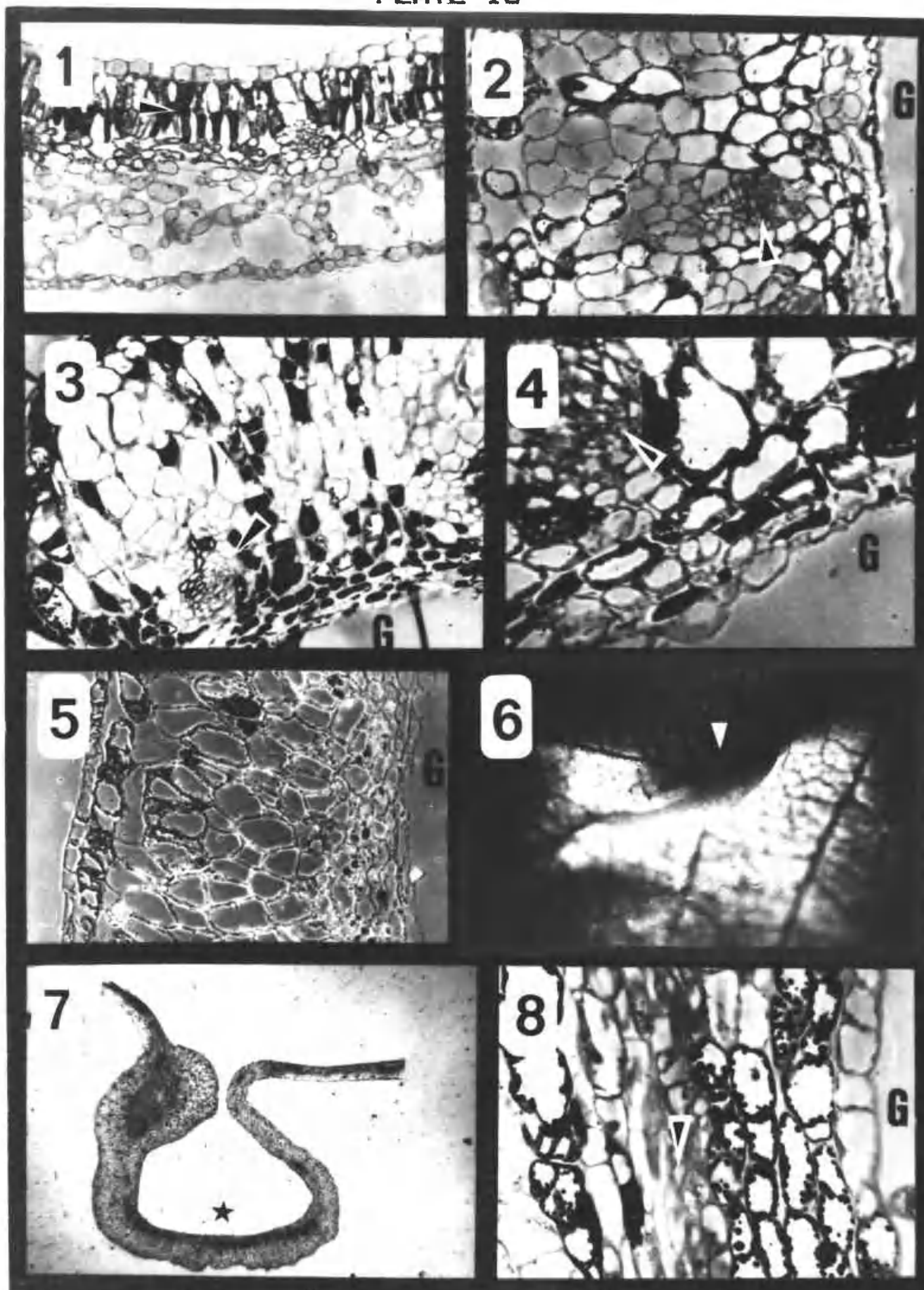


PLATE 19

Figure 1. Leaf gall (arrow) on *Arctostaphylos glutinosa* caused by *Tamalia coweni* (Cock.). (X/6/80). Scale in mm.

Figure 2. Cut-away view of leaf gall on *A. uva-ursi* L. showing aphids (arrow) inside gall cavity. (VII/20/80). 8X.

Figure 3. Anterior end of *T. coweni* showing stylet (arrow). (V/8/80). 170X.

Figure 4. Trans. section through galled bearberry leaf showing ungalled portion of leaf (arrow) and galled leaf curled around gall cavity (G). (V/8/80). 18X.

Figure 5. Ungalled bearberry leaf showing distinct palisade (arrow) and spongy mesophyll layer. (V/8/80). 140X.

Figure 6. Galled bearberry leaf showing recognizable palisade (arrow) and dense spongy mesophyll layer. Gall cavity indicated by star. (V/8/80). 85X.

Figure 7. Transition zone between ungalled bearberry leaf (lower arrow) and galled leaf (upper arrow). (V/20/80). 55X.

Figure 8. Section of bearberry gall wall showing gall cavity (G) and cells lining cavity. (V/20/80). 200X.

Figure 9. Wall of bearberry gall stained for tannins with gall cavity (G) indicated. (V/20/80). 40X.

PLATE 19

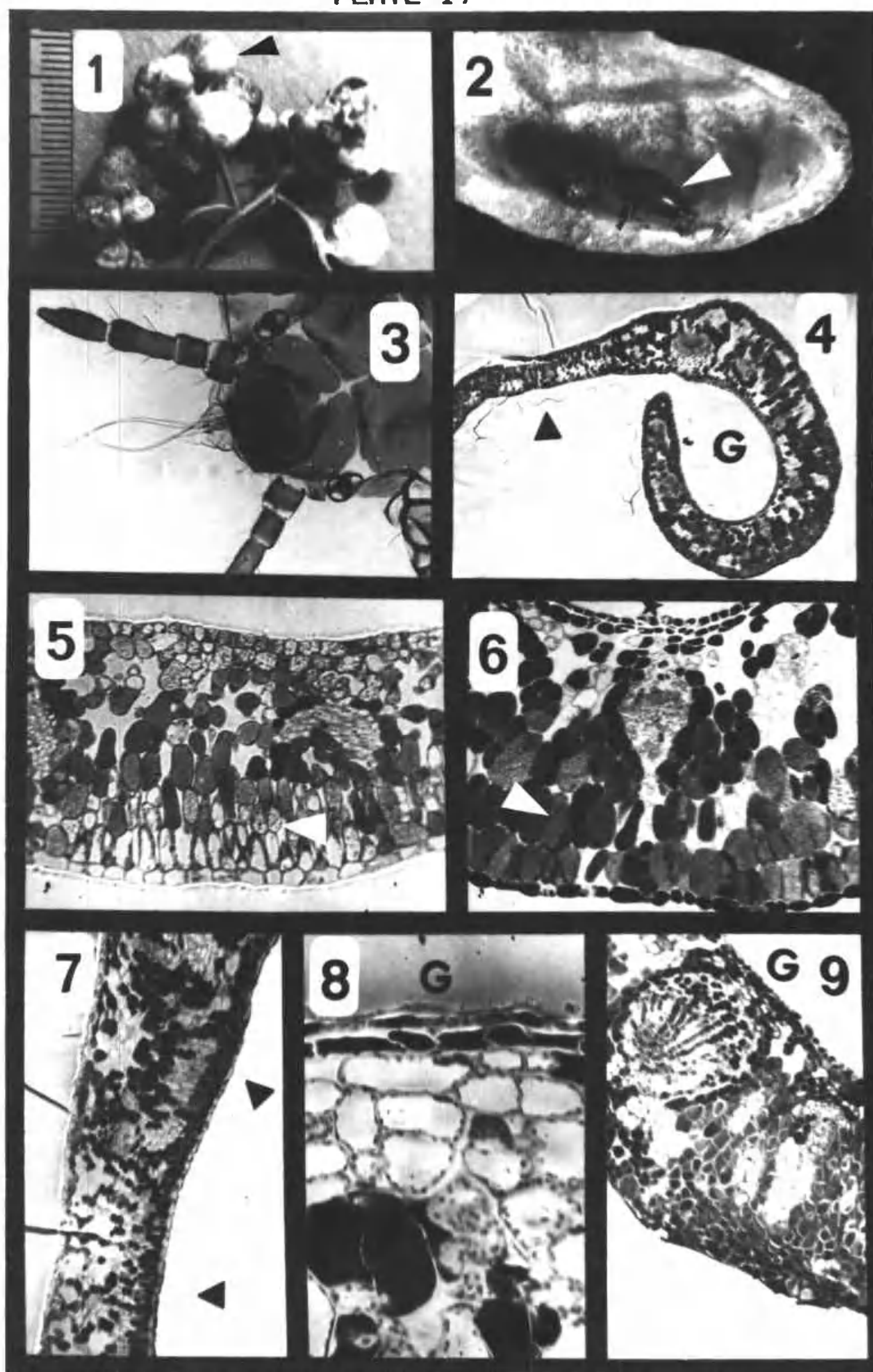


PLATE 20

Figure 1. Trans. section through ungalled bearberry leaf stained for tannins, showing distinct palisade (arrow) and spongy mesophyll layers. (V/20/80). 55X.

Figure 2. Long. section of *Hormaphis hamamelidis* Fitch on *Hamamelis virginica* L. showing the large gall cavity at the base of which is a portal (arrow). Ungalled leaf surface is indicated by stars. (V/26/80). 8.5X.

Figure 3. Ungalled witch hazel leaf showing distinct palisade (arrow) and spongy mesophyll cells. (V/26/80). 80X.

Figure 4. Long. section through wall of witch hazel leaf gall, showing the gall cavity (G) and the cells that line the cavity (arrow). (V/26/80). 80X.

Figure 5. Section through wall of witch hazel leaf gall showing gall cavity (immediately to the left of the G) and the cells lining the cavity (arrow). (V/26/80). 290X.

Figure 6. The leaf gall (arrows) on *Crataegus douglasii* var. *suksdorfii* Sarg. caused by a cecidomyiid. Ungalled leaf is in lower right corner. Hand cut trans. sections through gall are seen in upper right corner. (VIII/12/80). Scale in mm.

Figure 7. Cut-away hawthorn leaf gall showing young cecid larva (arrow). (V/22/80). 75X.

Figure 8. Trans. section through hawthorn leaf gall showing cavity (G), portal with hairs (arrow) and ungalled leaf (arrow). (V/13/80). 15X.

Figure 9. Older instar cecid larvae in hawthorn leaf gall. Forked sternal spatula (arrow) is visible in one larva. (IX/22/80). 20X.

PLATE 20

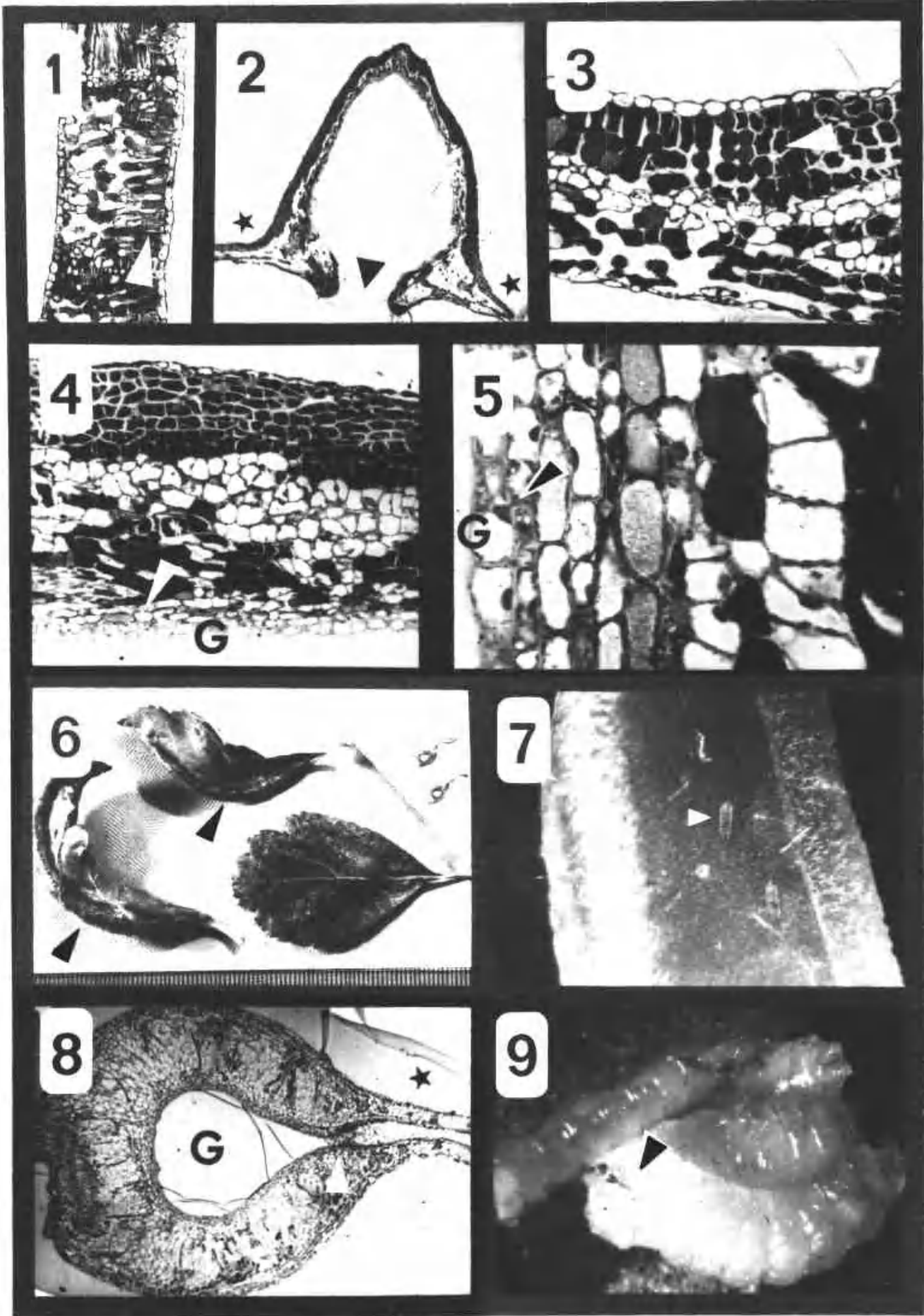


PLATE 21

Figure 1. Transition region of hawthorn leaf gall. At right the already altered leaf becomes thicker and more densely packed with cells as the gall is approached (to the left). The remnants of the palisade layer (arrow) are still apparent. (V/13/80). 130X.

Figure 2. Trans. section of ungalled hawthorn leaf showing distinct palisade (arrow) and spongy mesophyll layer. (V/13/80). 150X.

Figure 3. Wall of hawthorn leaf gall stained for tannins. Cells lining the larval cavity (arrow) contain some positively stained material. (V/13/80). 150X.

Figure 4. Section through wall of hawthorn leaf gall showing larval cavity (G) and cells lining the cavity (arrow). (V/13/80). 150X.

Figure 5. Section through wall of hawthorn leaf gall showing larval cavity (star) and cells lining the cavity (arrow). (IX/22/80). 190X.

Figure 6. Cut-away view of leaf roll gall on Symphoricarpos albus var laevigatus Fern. caused by a cecidomyiid. Larvae are at upper arrow, larval cavity at lower arrow. (V/20/80). 7X.

Figure 7. Anterior end of cecidomyiid larva taken from leaf roll gall on snowberry. Head capsule at arrow. (X/20/80). 110X.

Figure 8. Trans. section through ungalled snowberry leaf showing palisade (arrow) and spongy mesophyll layers. (V/6/80). 55X.

Figure 9. Transition zone from ungalled snowberry leaf (lower arrow) to slightly swollen lamina showing no palisade or spongy layers (upper arrow). Edge of swollen gall wall is seen at left (middle arrow). (V/6/80). 55X.

PLATE 21 (Cont.)

Figure 10. Trans. section through central larval cavity (G) of snowberry leaf roll gall, showing cells that line the cavity (arrow). (V/6/80). 80X.

PLATE 21

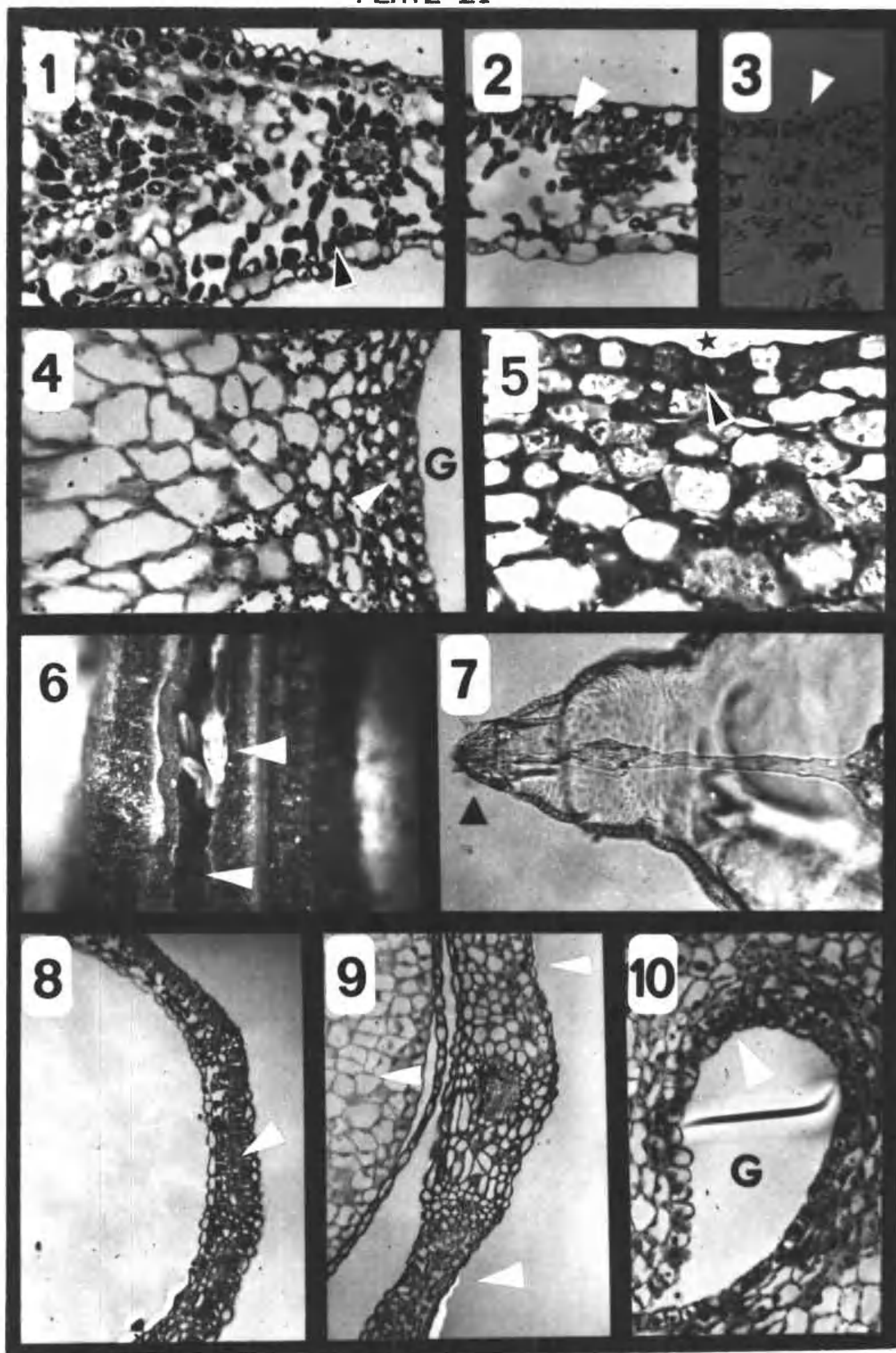


PLATE 22

Figure 1. Trans. section through wall of snowberry leaf roll gall showing larval cavity (G) and cells lining the cavity (arrow). (VII/24/80). 130X.

Figure 2. Trans. section through snowberry leaf roll gall stained for tannins, showing central larval cavity (G). (V/6/80). 6X.

Figure 3. Leaf gall on <u>Amelanchier</u> <u>alnifolia</u>. Nutt. caused by a cecidomyiid, as seen from the upper leaf surface (left arrow) and the lower leaf surface (right arrow). Two galls that have been pulled from the leaf are shown broadside in the upper right corner. (VII/12/80). Scale in mm.

Figure 4. Cut-away view of serviceberry leaf gall showing larval cavity (right white arrow), outgrowth that separates larval cavity from central cavity (left white arrow), and ostiole (black arrow). (V/20/80). 3.5X.

Figure 5. Anterior end of cecidomyiid larva taken from serviceberry gall. Head capsule indicated by right arrow, and out-of-focus sternal breastbone by left arrow. (VIII/12/80). 150X.

Figure 6. Long. section through young leaf gall on serviceberry with midvein (black arrow), gall cavity (white arrow), and ungalled leaf (star) indicated. (IV/15/80). 13X.

Figure 7. Long. section through larval cavity (G) of serviceberry leaf gall with larva (arrow). (IV/15/80). 100X.

Figure 8. Section through wall of leaf gall on serviceberry with larval cavity (G) and cells lining the cavity (arrow). (IV/15/80). 330X.

PLATE 22

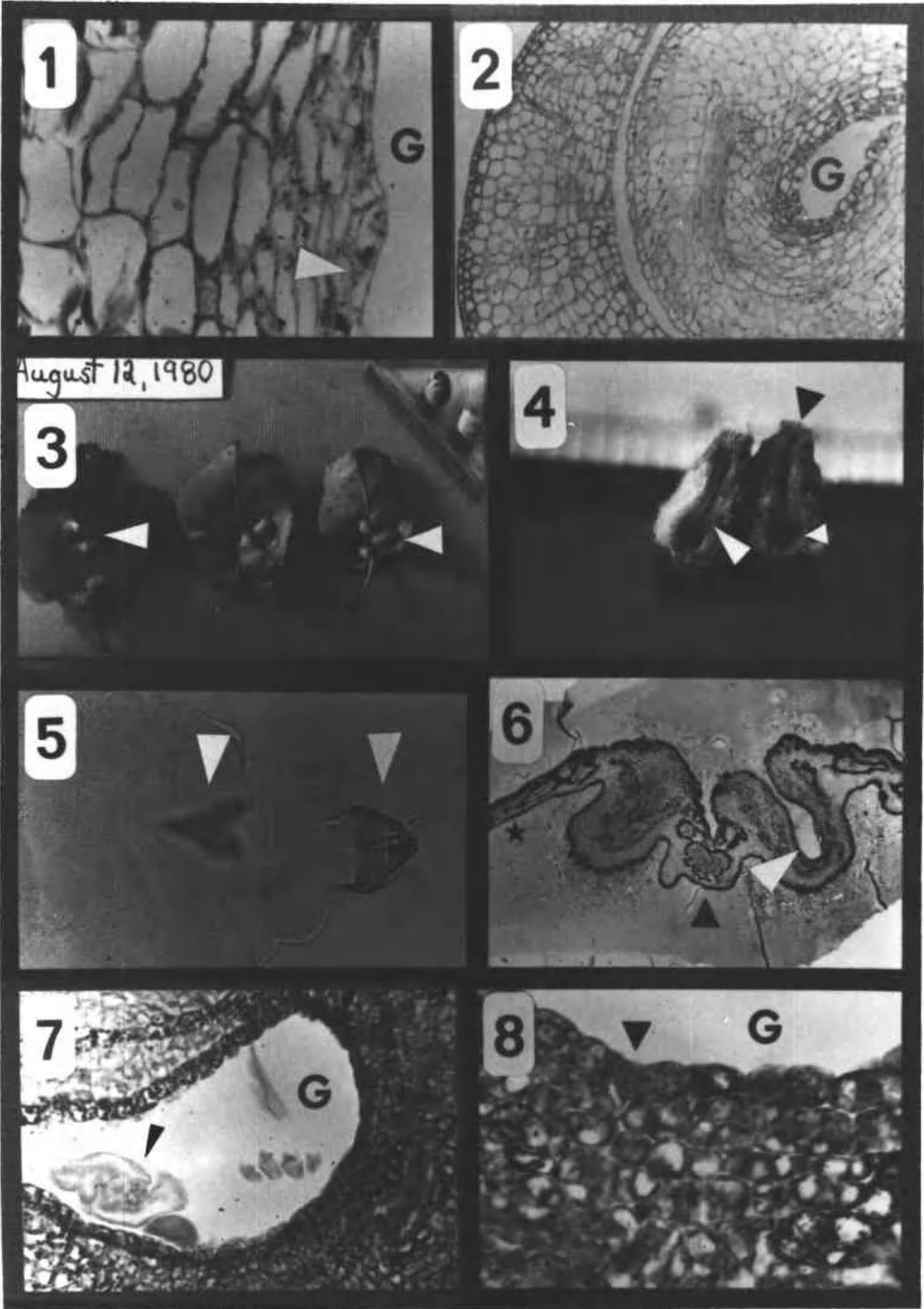


PLATE 23

Figure 1. Trans. section through ungalled serviceberry leaf showing palisade (arrow) and spongy mesophyll layers. (IV/15/80). 160X.

Figure 2. Trans. section through transition zone showing ungalled serviceberry leaf at right and thickened lamina left. Altered palisade cells are seen at arrow. (IV/15/80). 140X.

Figure 3. Trans. section through ungalled serviceberry leaf showing palisade (arrow) and spongy mesophyll layers (V/6/80). 130X.

Figure 4. Section through larval cavity (G) of serviceberry leaf gall showing cells lining the cavity (arrow). (V/6/80). 290X.

Figure 5. Trans. section through serviceberry leaf gall showing larval cavity (G), central cavity (star) and sclerid layer (S). (VIII/12/80). 14X.

Figure 6. Trans. section through serviceberry gall showing cells (arrow) lining the larval cavity (G), and sclerids that line the central cavity (star). (VIII/12/80). 55x.

Figure 7. Trans. section through larval cavity (G) of serviceberry gall showing cells lining cavity (arrow). (IX/20/80). 240X.

Figure 8. Trans. section through ungalled serviceberry leaf stained for tannins showing lightly stained palisade layer (arrow). (VI/5/80). 190X.

Figure 9. Long. section through serviceberry gall stained for tannins showing the larval cavity (G), cells lining the larval cavity (arrow), and the central cavity (star). (V/20/80). 65X.

PLATE 23

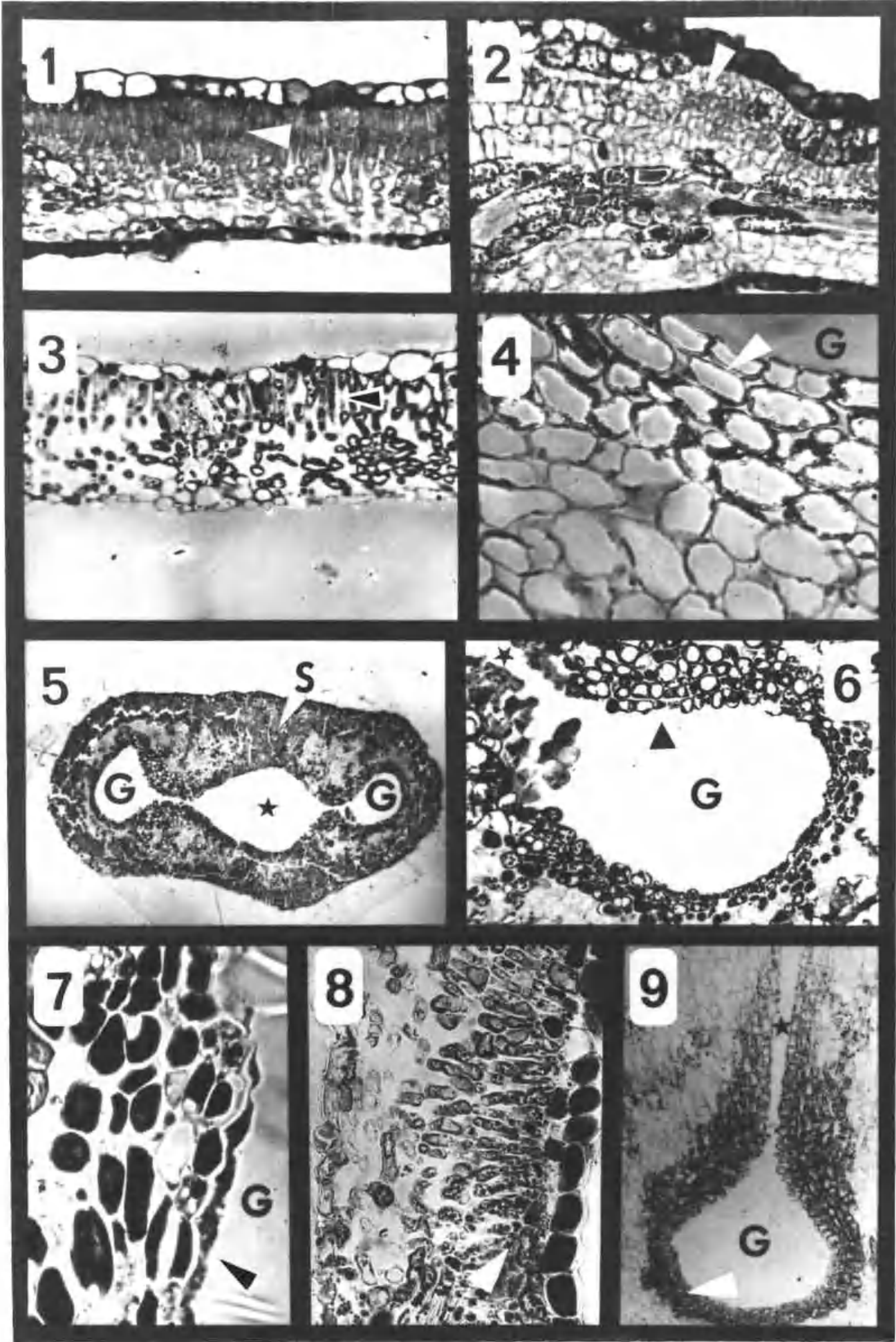


PLATE 24

Figure 1. Bud gall of _Populus trichocarpa_ T. and G. (far left arrow) caused by a cecidomyiid. Ungalled bud of same age shown to right (middle left arrow) of galled bud. Hand cut trans. section through galled (far right arrow) and ungalled (middle right arrow) bud are shown. (VIII/12/80). 1.2X.

Figure 2. Trans. cut-away view of poplar bud gall. Larvae (arrow) present between bud scales but are difficult to see. (VIII/19/80). 12X.

Figure 3. Anterior end of cecidomyiid larva taken from poplar bud gall. Head capsule is indicated by arrow. (IX/22/80). 280X.

Figure 4. Trans. section through galled poplar bud showing overlapping bud scales. Center of bud is indicated by star, and midge larva by arrow. (V/13/80). 12X.

Figure 5. Trans. section through galled poplar bud showing cells on surface of bud scale (right arrow), and larva (left arrow). (V/13/80). 400X.

Figure 6. Trans. section through bud scale from poplar bud gall showing inner (adaxial) surface (right arrow) and outer (abaxial) surface (left arrow). (VIII/12/80). 90X.

Figure 7. Trans. section through scale from poplar bud gall showing inner surface (arrow). (VIII/12/80). 350X.

Figure 8. Trans. section through bud scale from poplar bud gall showing inner surface with change in surface cells at arrow. (VIII/12/80). 350X.

Figure 9. Trans. section through bud scale from poplar bud gall showing inner (upper arrow) and outer (lower arrow) surfaces. (IX/22/80). 180X.

PLATE 24

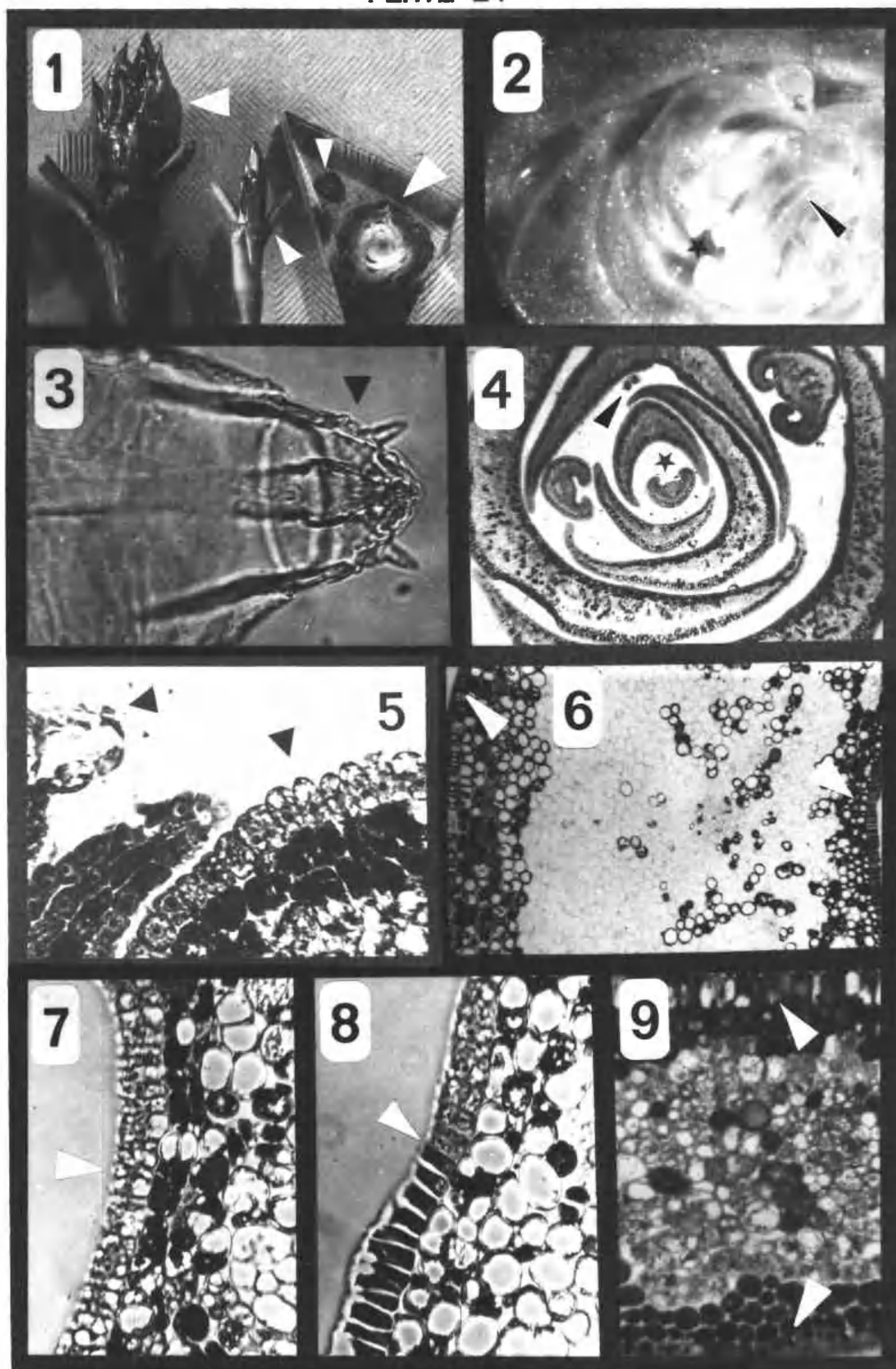


PLATE 25

Figure 1. Stem beaked gall (arrow) on Salix sp. caused by Phytophaga rigidae O. S. (V/13/80). Cm scale.

Figure 2. Willow stem gall (arrow). (VII/15/80). Cm scale.

Figure 3. Willow stem gall showing yellow "beak" (arrow). (VIII/19/80). Scale in mm.

Figure 4. Willow stem galls showing necrotic "beak" (arrow). (IX/21/80). Cm scale.

Figure 5. Long. cut-away view of willow stem gall showing larval cavity (left arrow) and exit portal through beak (right arrow). (IV/8/80). 3X.

Figure 6. Trans. cut-away view of willow stem gall showing larval cavity (arrow). (IV/8/80). 3X.

Figure 7. Long. cut-away view of willow stem gall showing larva (arrow) in larval cavity. (VIII/19/80). 8X.

Figure 8. Large cecidomyiid larva in willow stem gall. (VIII/19/80). 12X.

Figure 9. Anterior end of larva from willow stem gall showing head capsule (right arrow) and sternal spatula (left arrow). (V/13/80). 170X.

PLATE 25

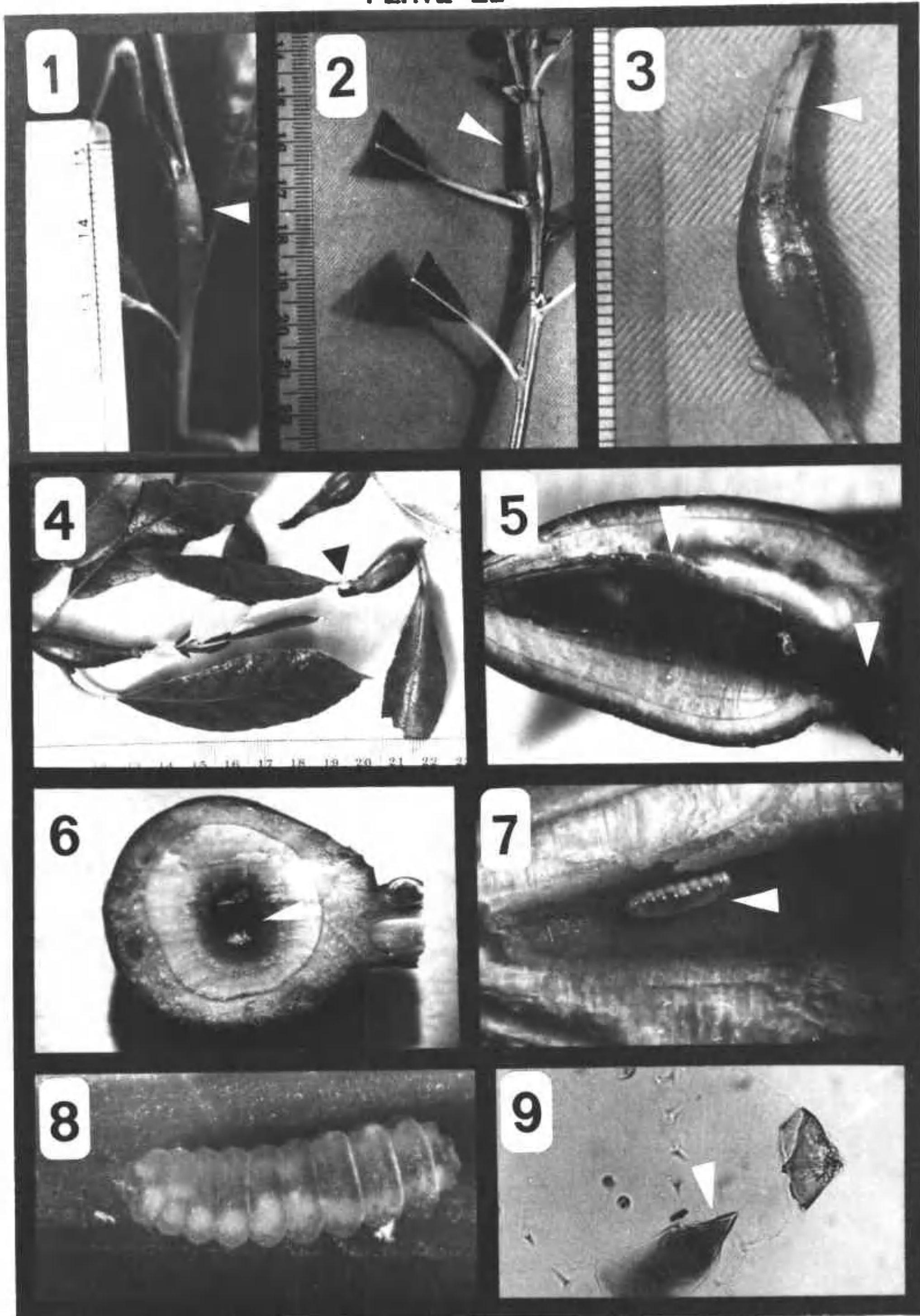


PLATE 26

Figure 1. *Phytophaga rigidae* adult. (OSU Insect Collection). Scale in mm.

Figure 2. Trans. section of ungalled willow stem showing pith (P), vascular tissue (V), and cortex (C). (V/13/80). 35X.

Figure 3. Trans. section through young willow stem gall showing larval cavity (G) and inner and outer vascular bundles (upper and lower arrows, respectively). (V/13/80). 13X.

Figure 4. Trans. section through young willow stem gall showing larval cavity (G) and cells lining the cavity (arrow). (V/13/80). 50X.

Figure 5. Trans. section through young willow stem gall showing larval cavity (G) and cells lining the cavity (arrow). (V/13/80). 140X.

Figure 6. Trans. section through willow stem gall showing larval cavity (G) and cells lining the cavity (arrow). (VI/5/80). 240X.

Figure 7. Trans. section through wall of willow stem gall showing larval cavity (G), scelerid zone (S), and secondary xylem (V). (VII/24/80). 30X.

Figure 8. Trans. section through wall of willow stem gall showing larval cavity (G), cells lining cavity (arrow) and sclerenchyma zone (S). (VII/24/80). 200X.

Figure 9. Trans. section through wall of willow stem gall showing gall cavity (G) and secondary xylem (V). (VIII/12/80). 17X.

PLATE 26

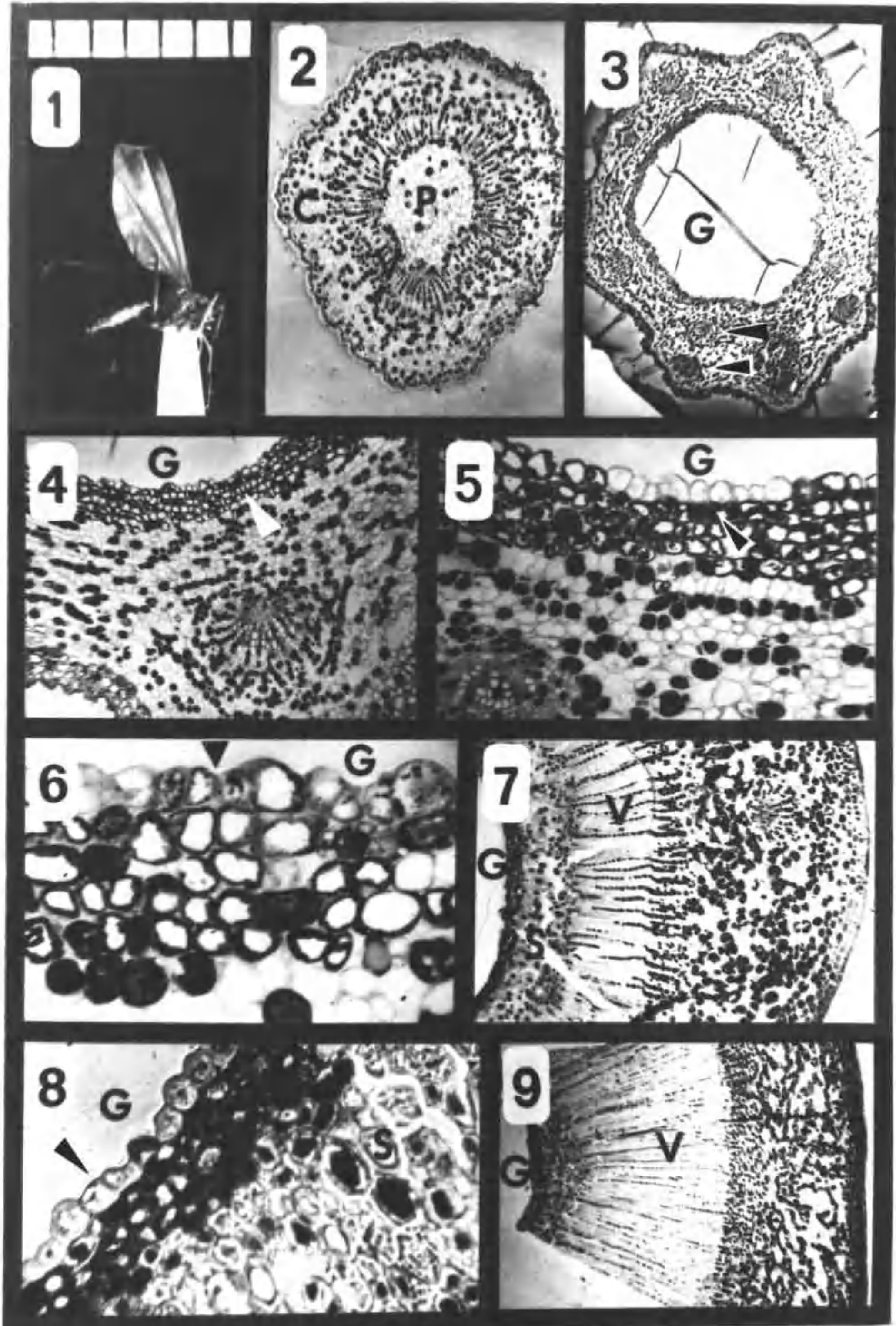


PLATE 27

Figure 1. Trans. section through wall of willow stem galls showing larval cavity (G), cells lining the cavity (arrow) and sclerenchyma zone (S). (IX/21/80). 200X.

Figure 2. Trans. through wall of willow stem gall showing larval cavity (G) and cells lining cavity (arrow). (VIII/12/80). 200X.

Figure 3. Trans. section through ungalled willow stem stained for tannins, showing cortical cells and epidermal cells (upper, lower arrow, respectively). (V/13/80). 40X.

Figure 4. Trans. section through willow stem gall stained for tannins showing larval cavity (star) and cells lining the cavity (arrow). (VI/5/80). 100X.

Figure 5. Trans. section through willow stem gall stained for tannins showing larval cavity (star) and cells lining the cavity (arrow). (IX/21/80). 100X.

Figure 6. Stem gall (arrow) on _Hypochaeris radicata_ L. caused by _Aulax hypochaeridis_ kieff. (VIII/12/80). Cm scale.

Figure 7. _Aulax hyopchaeridis_ adult. (OSU Insect Collection). Scale in mm.

Figure 8. Wasp larva (arrow) in larval cavity of Cat's Ear stem gall. (VIII/12/80). 35X.

Figure 9. Mandible of wasp larva taken from Cat's Ear stem gall. (VI/11/80). 170X.

Figure 10. Section through larval cavity (G) of Cat's Ear stem gall. Cells lining the cavity (arrow) are indicated. (VIII/12/80). 120X.

PLATE 27

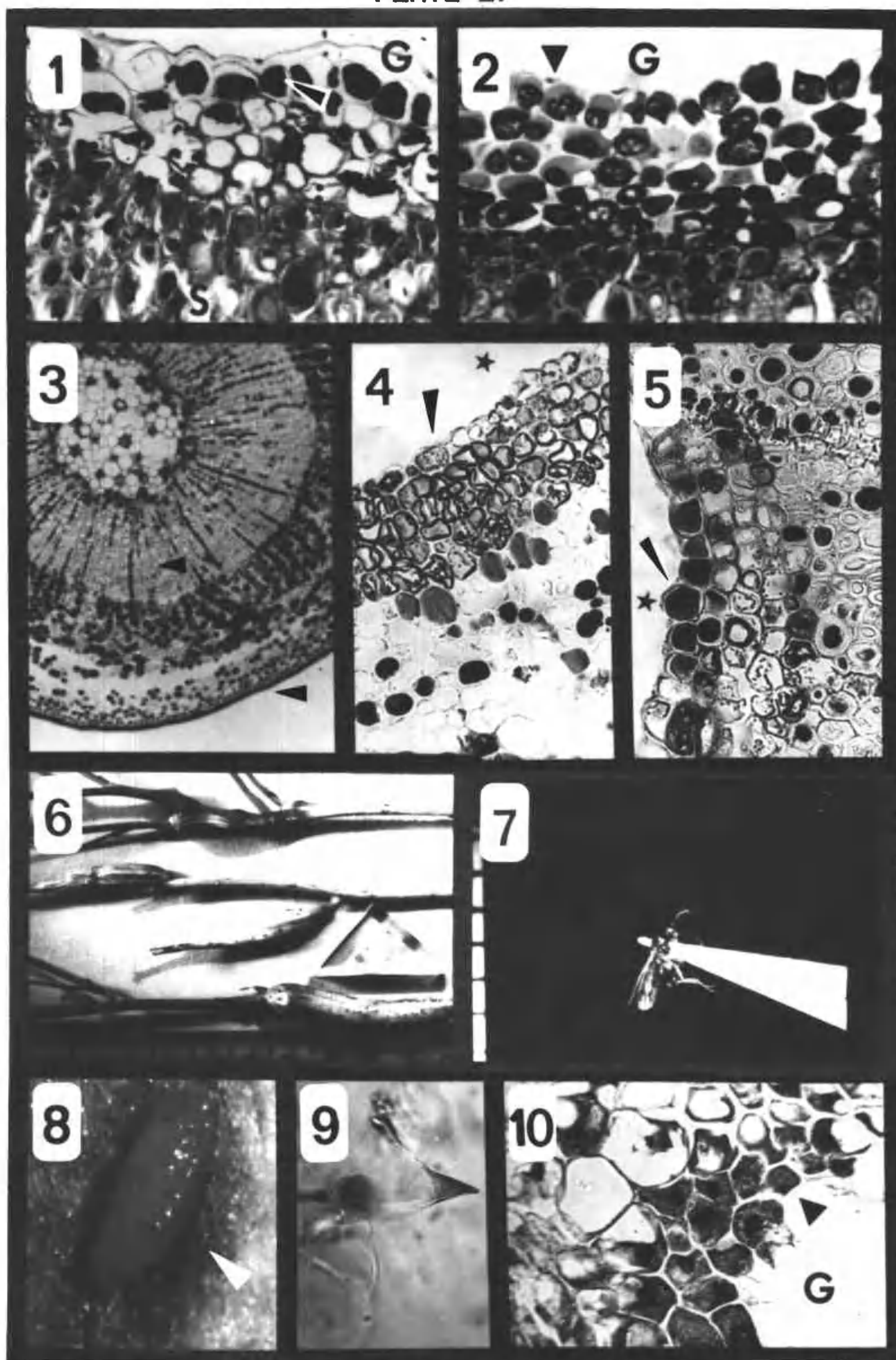


PLATE 28

Figure 1. Trans. section through larval cavity (star) of stem gall on Cat's Ear. Area of nutritive cells is indicated (arrow). (VIII/12/80). 17X.

Figure 2. Small gall (arrow) on young leaf of Quercus garryana Dougl. caused by a cynipid. (V/6/80). 4X.

Figure 3. Section through wall of small leaf gall on Garry oak showing larval cavity (G), nutritive region (left arrow), and outer region of gall wall (right arrow). (V/6/80). 80X.

Figure 4. Section through nutritive region of small leaf gall on Garry oak showing larval cavity (star) and nutritive cells with prominent nucleoli (arrow). (V/6/80). 180X.

Figure 5. Section through nutritive cells of small leaf gall on Garry oak showing nucleus (Nc) and nucleolus (Nu). (V/6/80). 300X.

Figure 6. Oak bullet gall on Quercus garryana Dougl. caused by Andricus spongiolus Gill.. Note swollen stem at point of attachment (arrow). (VII/15/80). Cm scale.

Figure 7. Cut-away view of oak bullet gall showing opened larval cavity (arrow) and larva (star).

(VIII/18/80). 10X.

Figure 8. Cut-away view of old oak bullet gall showing point of attachment (upper arrow), connective strands (middle arrow), and hardened sphere of larval capsules (lower arrow). (X/9/80). Cm scale.

Figure 9. Adult Andricus spongiolus. (OSU Insect Collection). Scale in mm.

Figure 10. Section through thrips leaf roll gall showing gall cavity (left arrow) and nutritive region (right arrow). (VII/7/80). 200X.

PLATE 28

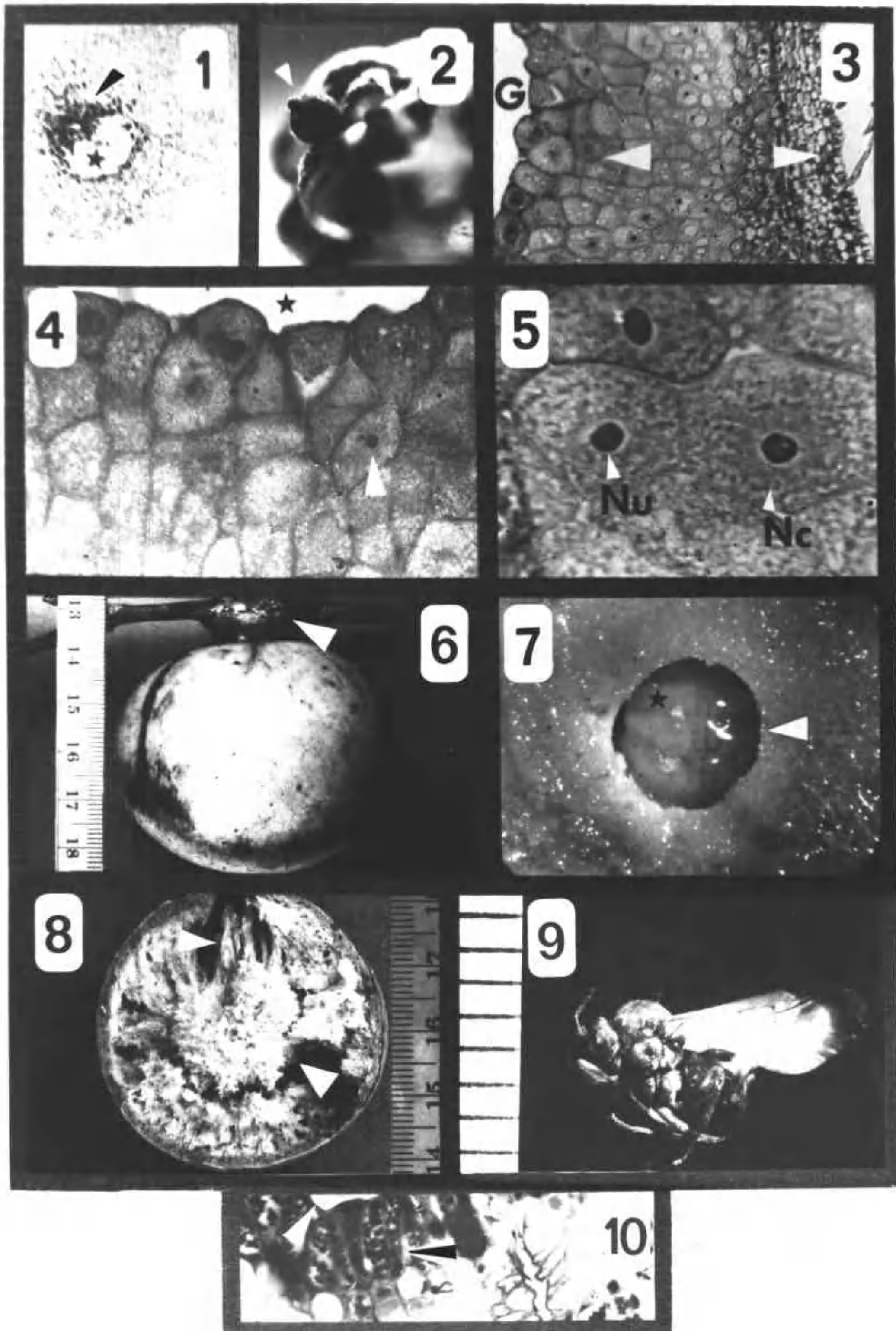


PLATE 29

Figure 1. Section through oak bullet gall showing larval cavity (arrow). (V/6/80). 20X.

Figure 2. Section through larval cavity (G) of oak bullet gall showing nutritive cells that line the cavity. (V/6/80). 150X.

Figure 3. Nutritive cells of oak bullet gall showing prominent nucleoli (right arrow). Larval cavity (G) is to the upper left (arrow). (V/6/80). 280X.

Figure 4. Section through larval cavity (G) of oak bullet gall showing nutritive cells that line the cavity (arrow). (VII/15/80). 75x.

Figure 5. Section through oak bullet gall stained for tannins. Cells lining larval cavity (right arrow) stain poorly, while those in surrounding area (left arrow) stain positively. (V/6/80). 16X.

Figure 6. Tip gall (arrow) on <u>Rosa nutkana</u> Presl. caused by cynipids. (VIII/12/80). Scale in mm.

Figure 7. Section through oak bullet larval cavity (G) stained for tannins showing poorly stained nutritive cells (left arrow) and deeply stained material that covers nutritive cells (right arrow). (VII/24/80). 80X.

Figure 8. Section through rose tip gall showing larval cavity (G) and nutritive region lining the cavity (arrow). (VIII/12/80). 20X.

Figure 9. Section through nutritive region of rose tip gall showing nutritive cells with prominent nucleolus (lower arrow). Larval cavity (G) is toward upper right corner (upper arrow). (VIII/12/80). 160X.

PLATE 29

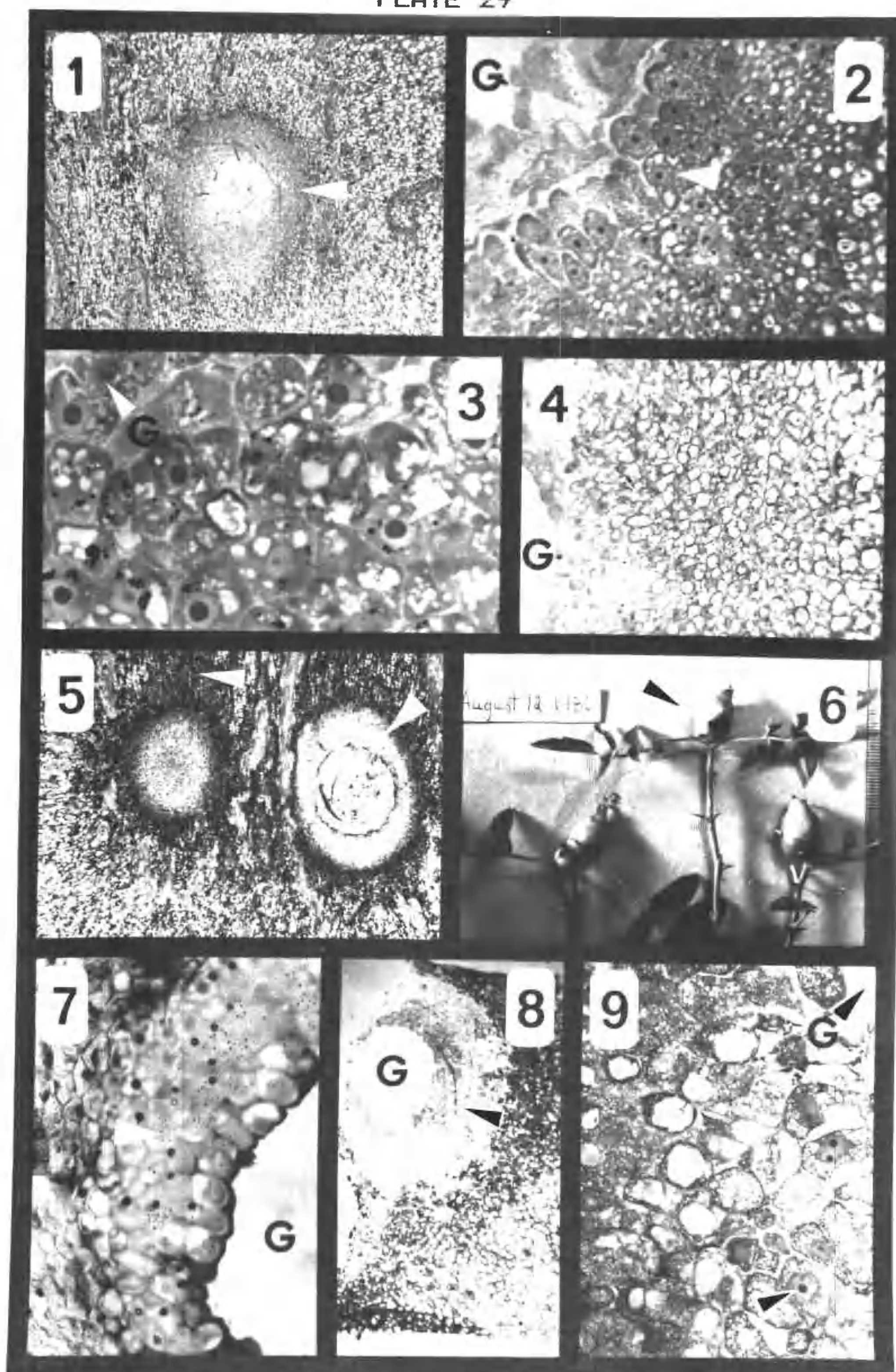


PLATE 30

Figure 1. Spherical stem gall (arrow) on *Quercus garryana* Dougl. caused by *Disholcaspis washingtonensis* (Gill.). (IV/20/80). 1.5X.

Figure 2. Cut-away view of larval cavity of spherical stem gall on Garry oak with larva (arrow). (V/22/80). 16X.

Figure 3. Section through wall of spherical stem gall on Garry oak showing outer gall wall (left arrow) and nutritive region (right arrow). The larval cavity is to the right of "G". (IV/25/79). 30X.

Figure 4. Section through wall of spherical stem gall on Garry oak showing outer gall wall (left arrow), nutritive region (right arrow) and larval cavity (G). (VI/5/80). 30X.

Figure 5. Mossy gall (arrow) on leaflets of *Rosa eglanteria* L. caused by *Diplolepis rosae* L.. (VIII/12/80). 0.6X.

Figure 6. Mossy rose gall. (VIII/12/80). Scale in mm.

Figure 7. *Diplolepis rosae* adult. (II/8/79). Scale in mm.

Figure 8. Cut-away view of larval cavity (arrow) in mossy rose gall. (VIII/18/80). 8X.

Figure 9. Mandible of larva taken from mossy rose gall. (IX/24/80). 110X.

PLATE 30

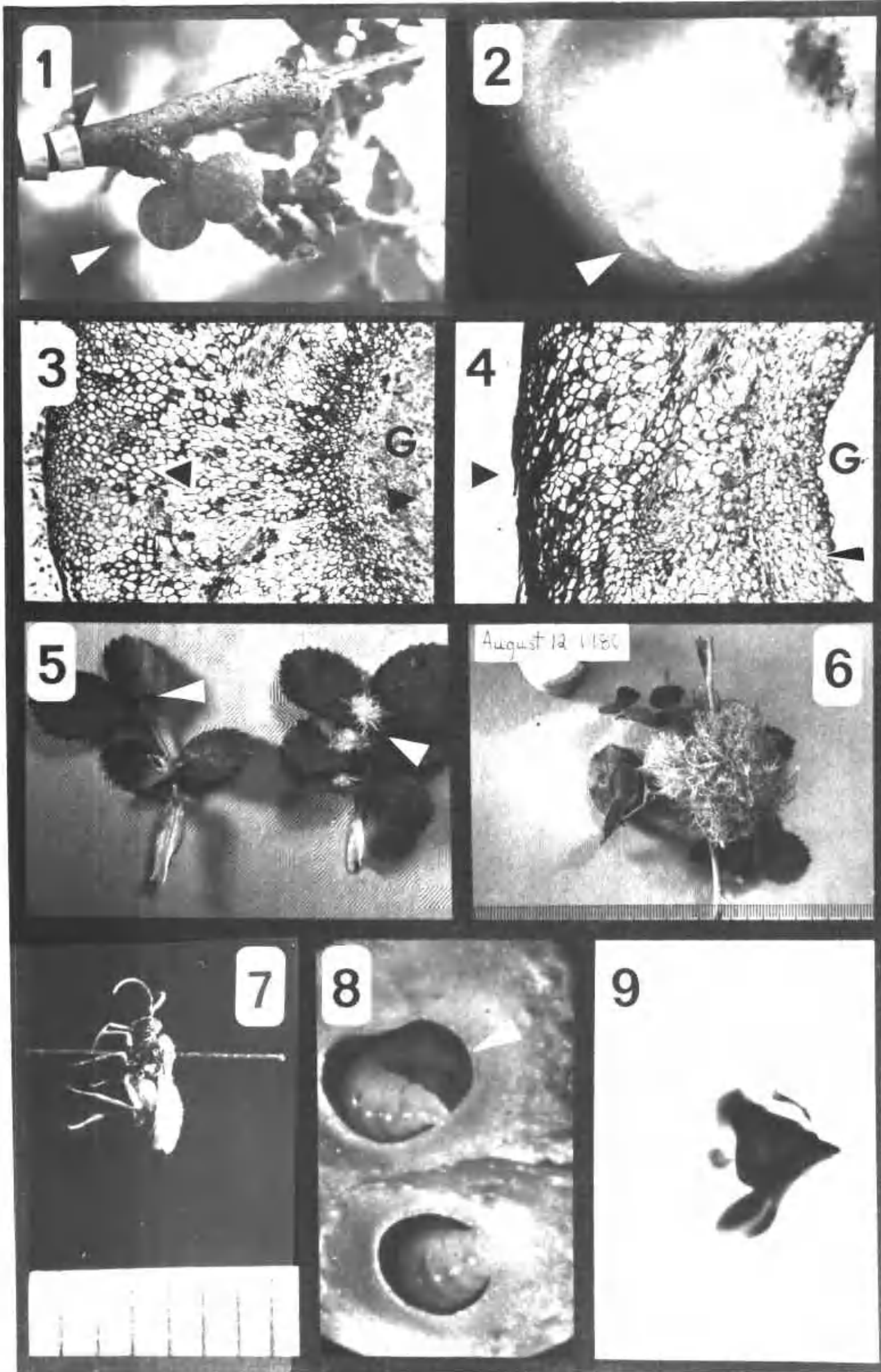


PLATE 31

Figure 1. Section through larval cavity (G) of mossy rose gall showing nutritive region (left arrow) and "mossy" fibers (right arrow). (VII/24/80). 30X.

Figure 2. Section through larval cavity (G) of mossy rose gall showing nutritive region (arrow). (VII/24/80). 50X.

Figure 3. Section through larval cavity (G) of mossy rose gall showing nutritive region (arrow). (VII/24/80). 130X.

Figure 4. Section through larval cavity (G) of mossy rose gall showing nutritive region (arrow). (VIII/12/80). 80X.

Figure 5. Nutritive cells in mossy rose gall showing prominent nucleolus (right arrow) and gall cavity (G) above upper edge of photograph (arrow). (VIII/12/80). 270X.

Figure 6. Section through gall cavity (G) of mossy rose gall showing nutritive region (arrow). (VIII/21/80). 100X.

Figure 7. Section through gall cavity (G) of mossy rose gall showing nutritive region (arrow). (VIII/21/80). 160X.

Figure 8. Section through larval cavity (star) of mossy rose gall stained for tannins. Nutritive tissues (arrow) stains fairly lightly. (VII/24/80). 18X.

PLATE 31

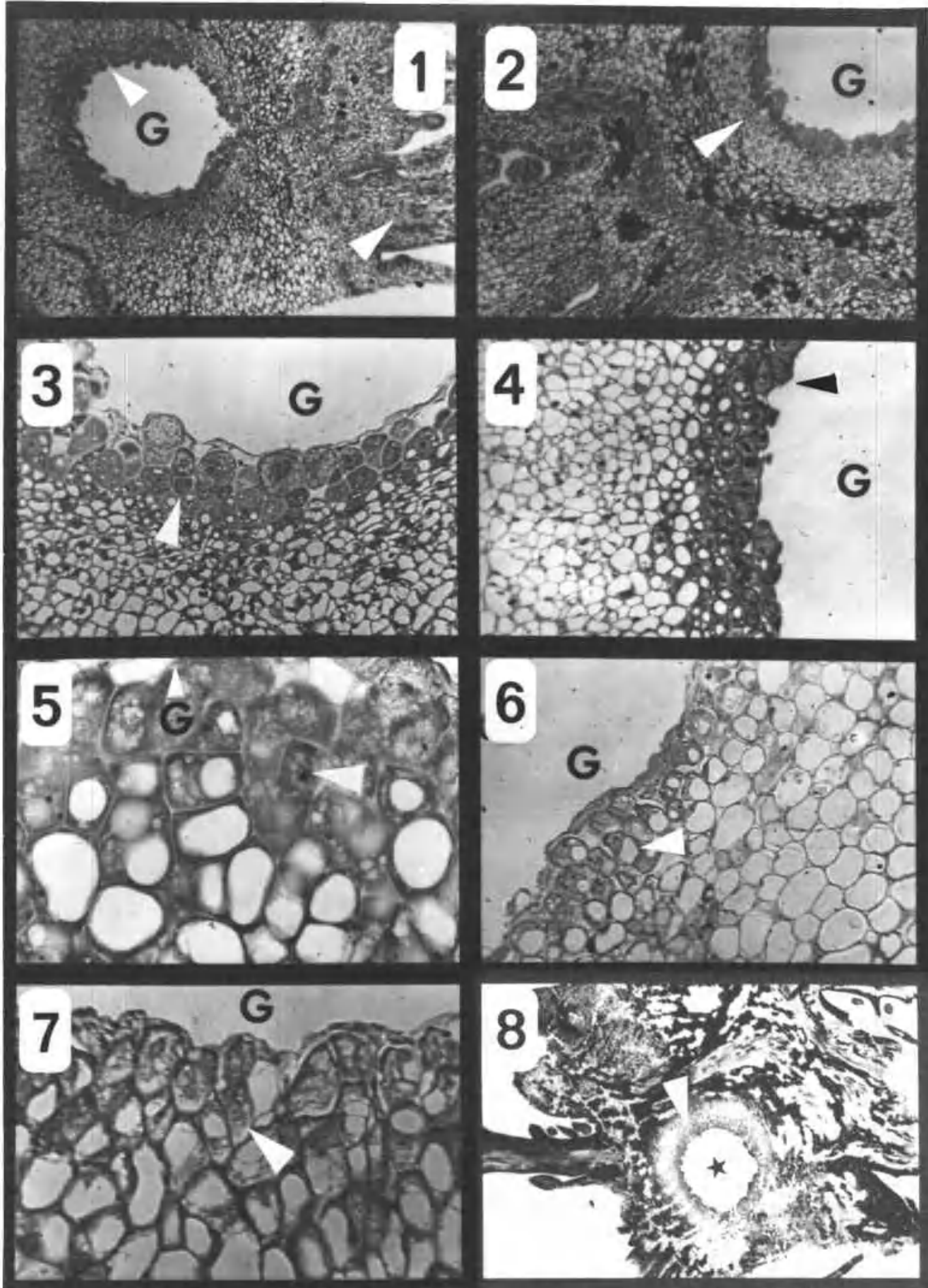


PLATE 32

Figure 1. Section through larval cavity (G) of mossy rose gall stained for tannins showing nutritive region (right arrow) and underlying, darkly stained region (left arrow). (VIII/12/80). 60X.

Figure 2. Section through larval cavity (G) of mossy rose gall stained for tannins, showing nutritive region (right arrow) and "moss" fibers (left arrow). (IX/21/80). 180X.

Figure 3. Young speckled oak apple (arrow) on _Quercus garryana_ Dougl. caused by _Besbicus mirabilis_ (Kinsey). Note that gall is emerging from split midvein. (V/31/80). Scale in mm rulings.

Figure 4. Speckled oak apple on Garry oak. (IX/21/80). Scale in mm.

Figure 5. Cut-away view of speckled oak apple on Garry oak, showing outer gall wall (lower arrow), point of attachment (upper arrow), and fibers suspending central larval capsule (star is just above capsule). (IX/23/80). Cm scale.

Figure 6. Cut-away view of larval capsule (arrow) of speckled oak apple on Garry oak. (VIII/18/80). 12X.

Figure 7. Adult _Besbicus mirabilis_. (OSU Insect Collection). 9X.

Figure 8. Mandibles of larva pulled from speckled oak apple on Garry oak. (VIII/19/80). 300X.

PLATE 32

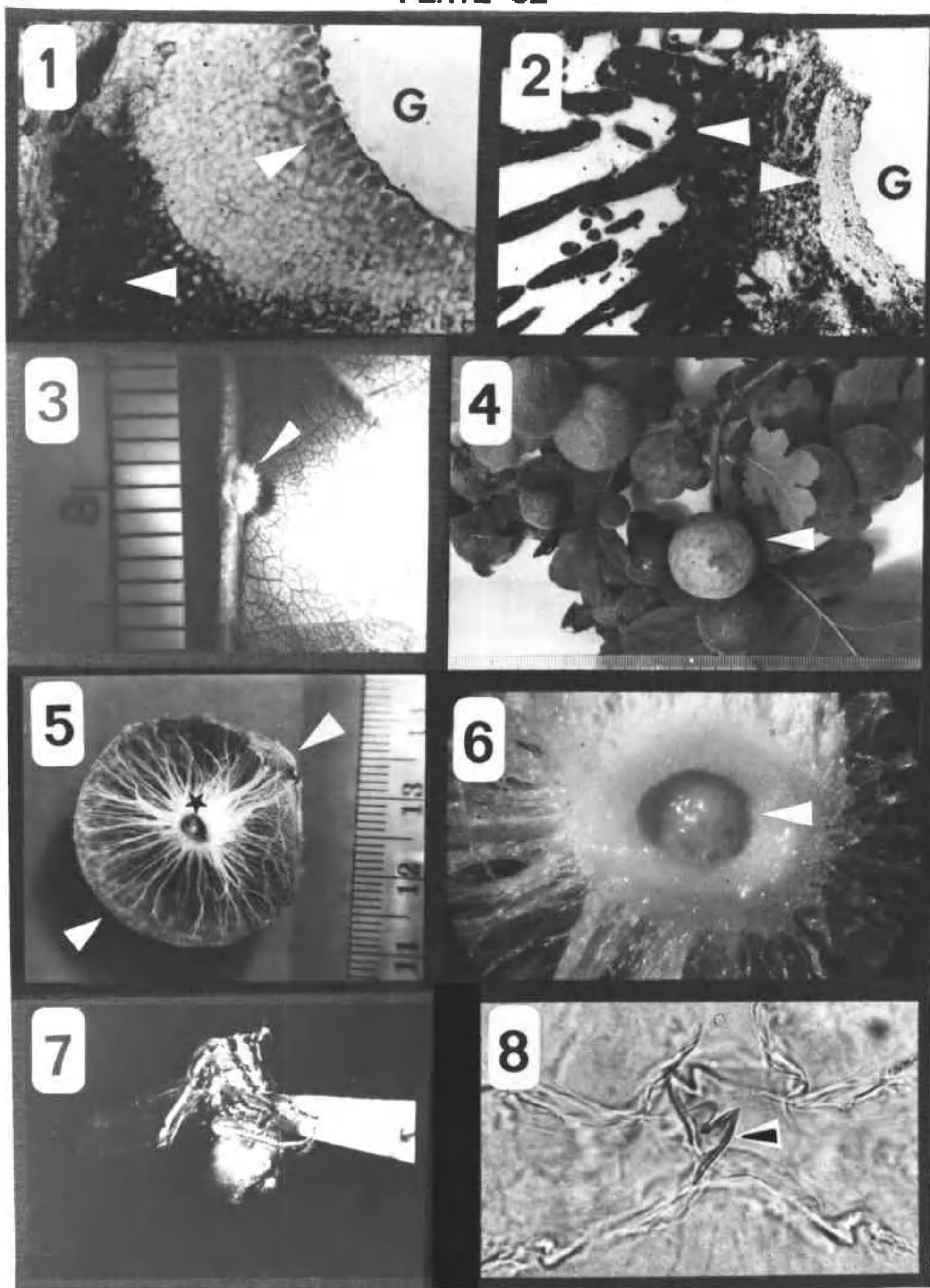


PLATE 33

Figure 1. Section through midvein (V) and young speckled oak apple on Garry oak, showing the larval cavity (G at arrow). (V/31/80). 15X.

Figure 2. Small galls (arrow) on underside of Garry oak leaf. (IX/22/80). Scale in mm.

Figure 3. Junction of midvein (right arrow) and speckled oak apple on Garry oak showing gall cavity (G) and stalk of gall (left arrow). (V/31/80). 30X.

Figure 4. Section through speckled oak apple on Garry oak showing base of fibers (white arrow) at capsule wall (black arrow). Larval cavity is out of photograph above upper edge. (VI/17/80). 120X.

Figure 5. Section through speckled oak apple on Garry oak showing nutritive region (white arrow), larval cavity (star), and capsule wall (black arrow). (VI/17/80). 290X.

Figure 6. Section through speckled oak apple on Garry oak showing fibers (arrow). Larval cavity (G) is in direction of arrow, out of photograph. (VIII/12/80). 50X.

Figure 7. Section through speckled oak apple on Garry oak showing nutritive cells with prominent nuclei (Nc) and nucleoli (Nu) and remnants of early capsule wall (below star). Larval cavity (G) is out of photograph at upper left hand corner. (VIII/12/80). 300X.

Figure 8. Section through speckled oak apple on Garry oak showing larval cavity (G) and bordering nutritive tissue (arrow). (IX/22/80). 30X.

PLATE 33

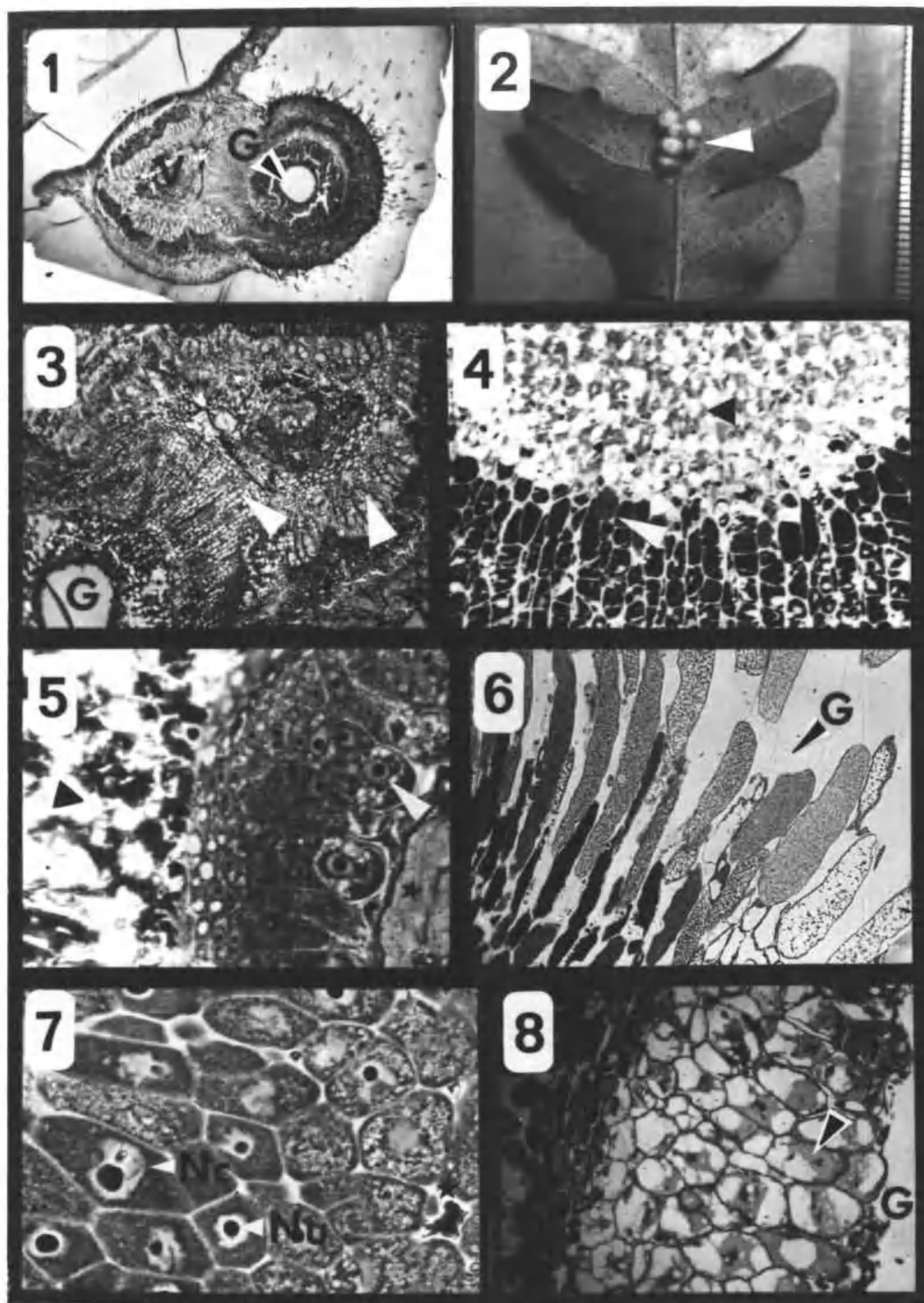


PLATE 34

Figure 1. Cecidomyiid gall (arrow) on _Artemisia tridentata_ Nutt. (ART) (IX/11/80). Scale in mm.

Figure 2. ART, showing midge larva (arrow) in cavity. (IX/11/80). 12X.

Figure 3. Trans. section through ART showing 4 adjacent larval cavities (G) each with larva (arrow). (X/18/80). 17X.

Figure 4. Trans. section through ART showing spongy gall wall. Vascular bundles (left arrow) and larval cavity (right arrow) are seen. (IX/11/80). 40X.

Figure 5. Trans. section through ART showing nutritive tissue (arrow) bordering larval cavity (G). (IX/19/80). 75X.

Figure 6. Head capsule of midge found in ART. (IX/11/80). 250X.

Figure 7. Cecidomyiid galls (arrow) on _Artemisia tridentata_. (ARC) (IX/11/80). Scale in mm.

Figure 8. Cut-away view of ARC showing larval cavities (upper arrow) that rest on dome-like platform (lower arrow). (IX/11/80). 9X.

PLATE 34

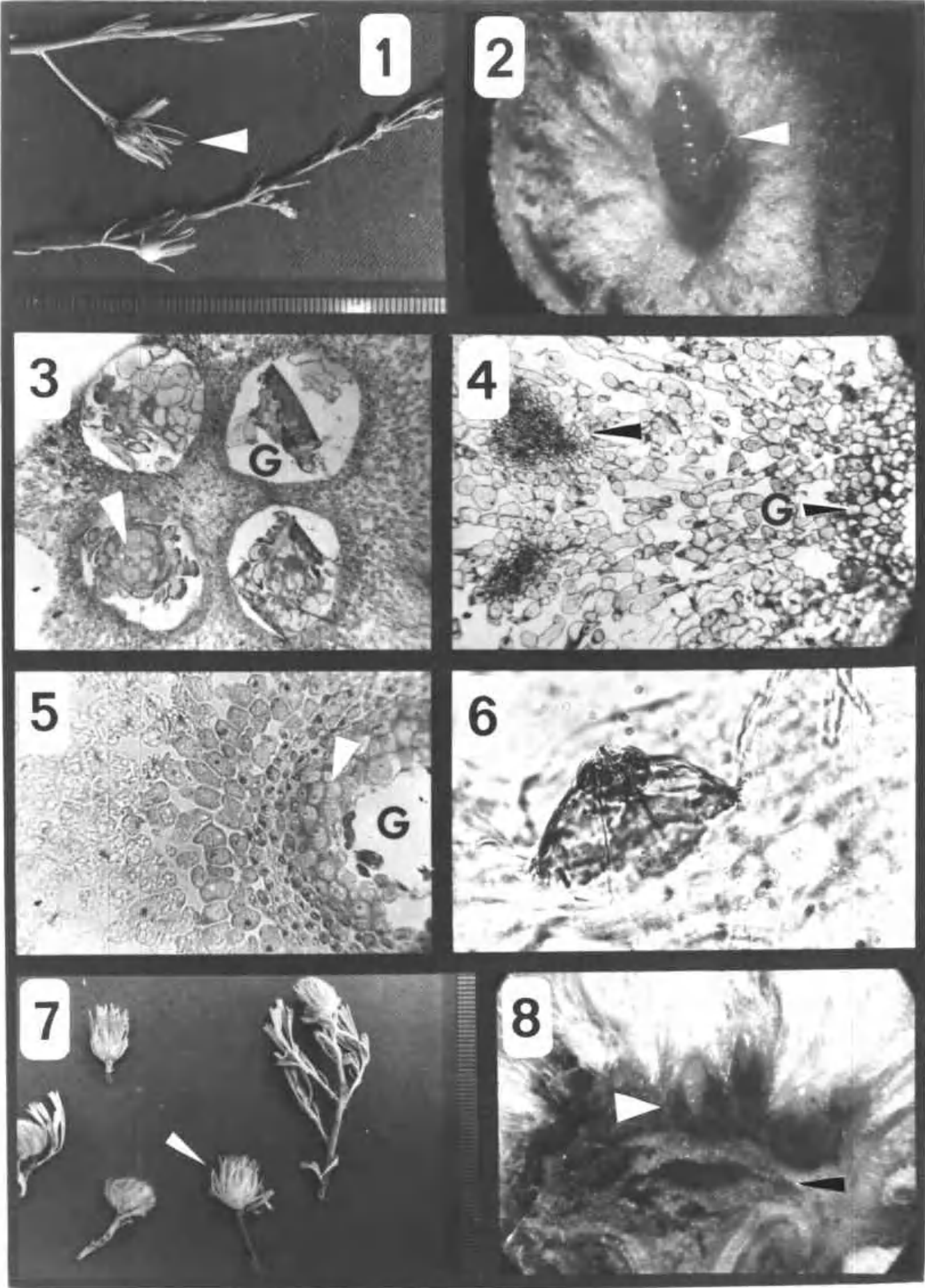


PLATE 35

Figure 1. Trans. section through ARC at base of 3 larval cavities (G at arrow). Nutritive tissue at base of cavities seen as circles of tissue in micrograph. (IX/19/80). 25X.

Figure 2. Trans. section through ARC at larval cavity (G) showing nutritive tissue bordering cavity (arrow). (IX/19/80). 70X.

Figure 3. Head capsule of larva found in ARC. (IX/19/80). 260X.

Figure 4. Section through eriophyoid gall on *Artemisia tridentata*, ANP, showing leaf (arrow) and gall cavity (star). (IX/19/80). 20X.

Figure 5. Section through ANP showing gall cavity (G) with mites (m) and leaf (star). (IX/19/80). 85X.

Figure 6. Section through ANP showing nutritive cells (arrow) lining gall cavity, and mites (m). (IX/19/80). 190X.

Figure 7. Nutritive cells of speckled oak apple on Garry oak showing dispersed nuclear area (star at arrow). (IX/22/80). 130X.

Figure 8. Section through speckled oak apple on Garry oak stained for tannins with larval cavity (G) and lightly stained nutritive tissue (arrow). (VI/25/80). 100X.

PLATE 35

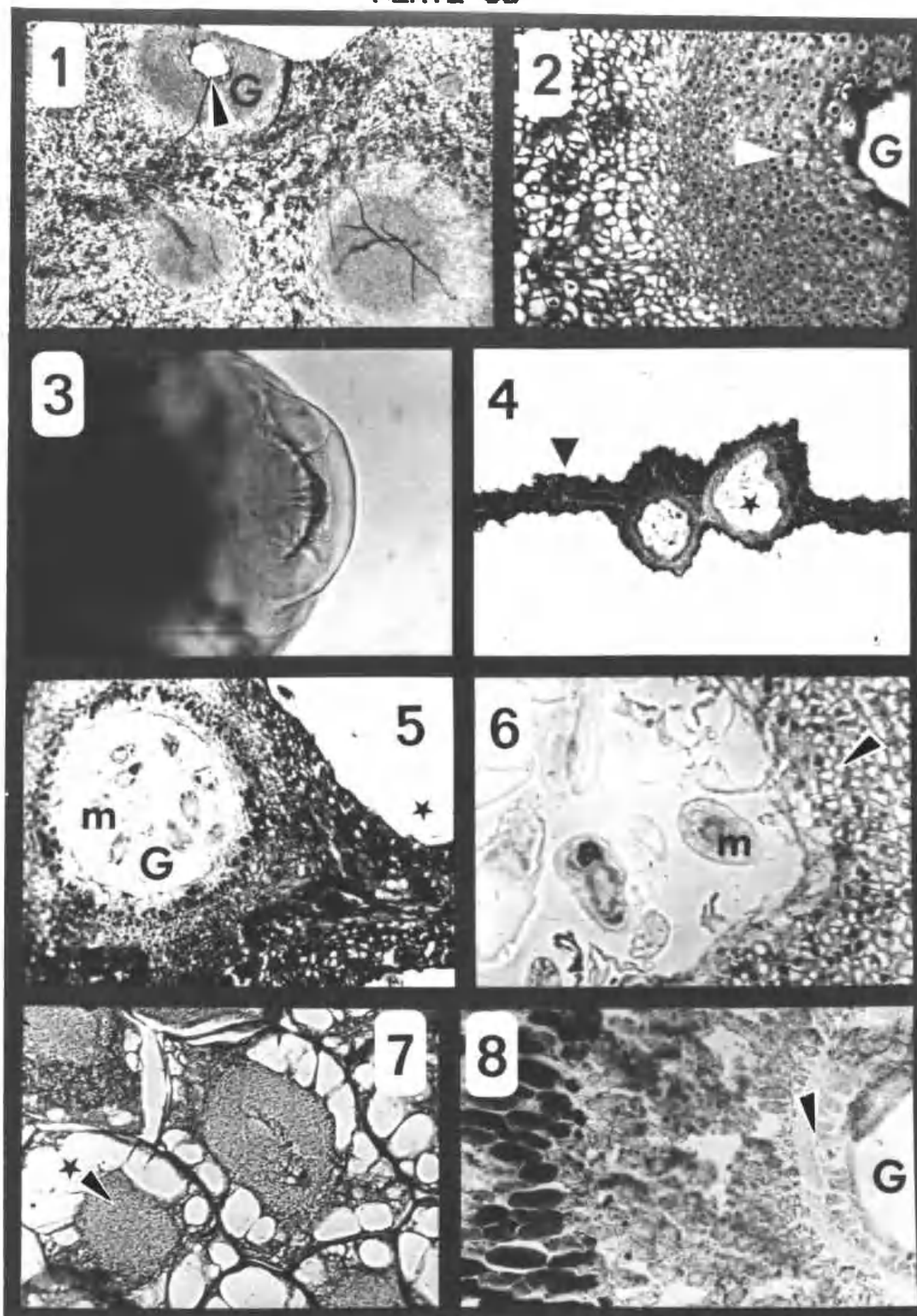


PLATE 36

Figure 1. Cecidomyiid gall (arrow) on *Chrysothamnus nauseosus* (Pall.) Britt.. (CRC) (IX/10/80). Cm. scale.

Figure 2. Long. cut-away through CRC showing larval capsules (upper arrow) resting on top of dome-like structure (lower arrow). (IX/10/80). 6X.

Figure 3. View looking down into CRC from above with some hairs removed. Tops of larval capsules are seen (arrow). (IX/10/80). 8X.

Figure 4. Long. section of CRC through larval cavity (G) containing a larva, and bordered by nutritive tissue (arrow). (IX/10/80). 50X.

Figure 5. Wall of larval capsule of CRC with cavity (G) and larva (arrow). (IX/10/80). 180X.

Figure 6. Tephritid galls on *C. nauseosus*. (COT) (VI/14/80). Scale in mm.

Figure 7. Trans. section of COT showing larval cavity (arrow). (IX/12/80). 7.5X.

Figure 8. Section of COT showing larval cavity (G). (IX/12/80). 20X.

PLATE 36

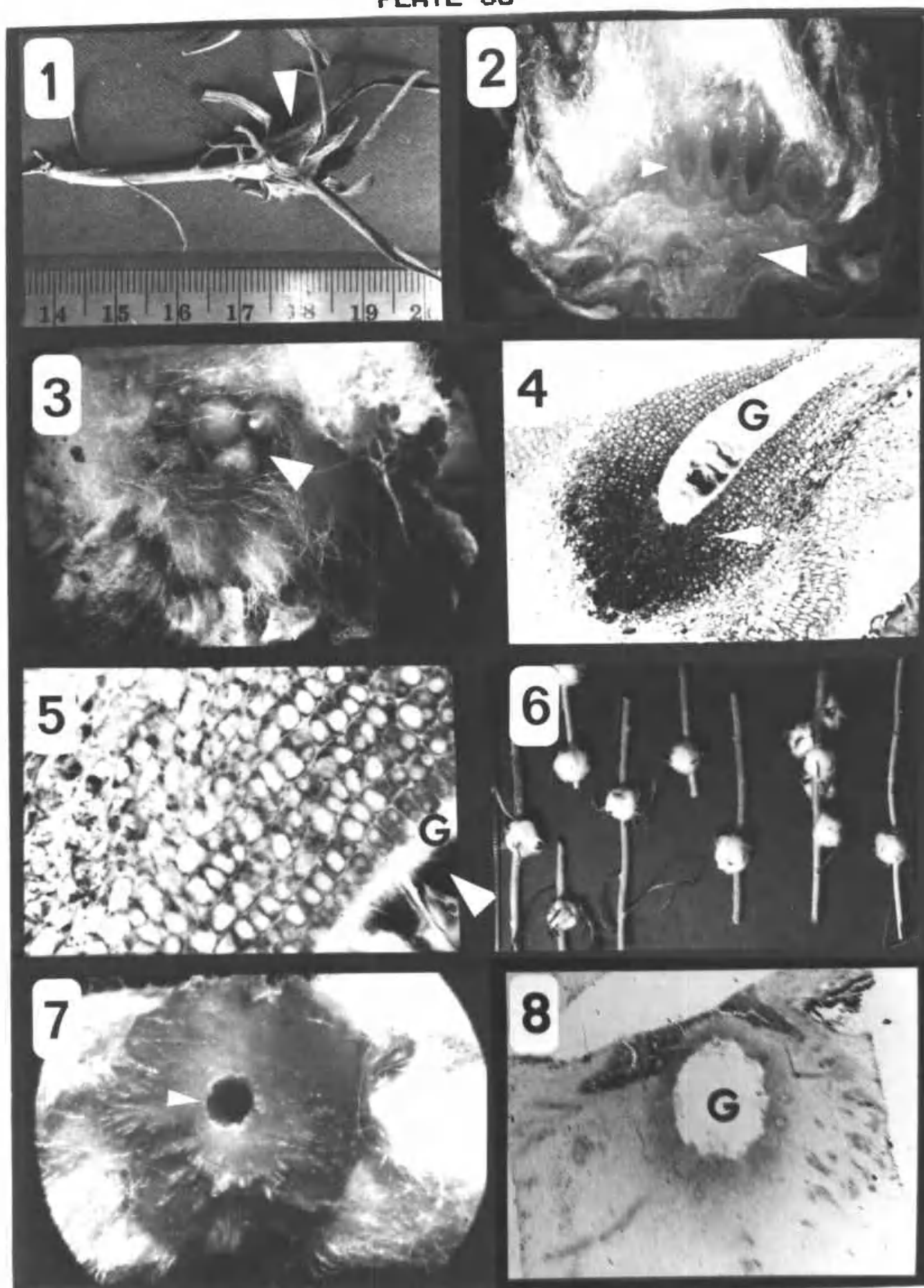


PLATE 37

Figure 1. Section through larval cavity (G) of COT showing nutritive tissue bordering cavity. (IX/12/80). 95X.

Figure 2. Pharyngeal skeleton of tephritid larva taken from COT showing anterior tooth (arrow). (VIII/29/80). 150X.

Figure 3. Cecidomyiid gall (arrow) on C. nauseosus. (CPG). (VI/14/80). Cm scale.

Figure 4. Cut-away view through CPG showing pith (right arrow), larval capsule (middle arrow), and portal (left arrow). (VI/14/80). 75X.

Figure 5. Section through CPG larval cavity (G) with larva, showing nutritive region (arrow). (VI/14/80). 100X.

Figure 6. Section through CPG nutritive region that borders larval cavity (G, on top of larva). (VI/14/80). 315X.

Figure 7. Section through larval cavity (star) of CPG stained for tannins. (VI/14/80). 70X.

Figure 8. Head capsule of larva pulled from CPG. (VI/14/80). 260X.

PLATE 37

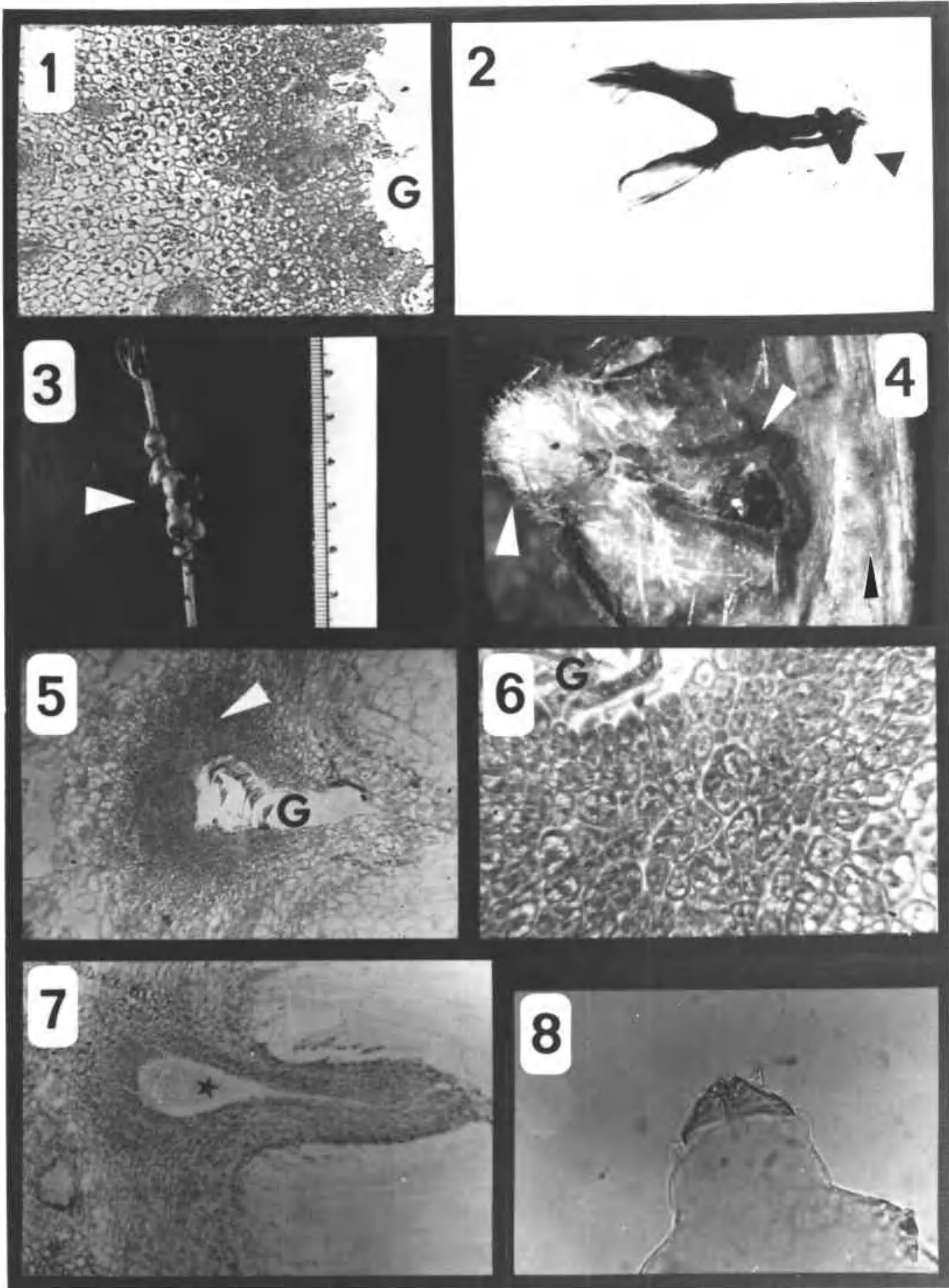


PLATE 38

Figure 1. Stem gall (arrow) on _Tetradymia_ _spinosa_ H. and A. caused by _Gnorimoschema_ _tetradymiella_ Busck. (TES) (VI/14/80). Cm scale.

Figure 2. Trans. section through ungalled stem of _T. spinosa_, showing pith (P), vascular tissue (V), and cortex (C). (VI/14/80). 120X.

Figure 3. Trans. section showing outer portion of TES wall. Arrow points towards gall cavity, and rests near a vascular bundle. (VI/14/80). 75X.

Figure 4. Section through gall cavity (G) of TES showing nutritive region (arrow). (VI/14/80). 120X.

Figure 5. Gall on _T._ _glabrata_ caused by _G._ _tetradymiella_ (?). (TET) (VI/14/80). Cm scale.

Figure 6. Head capsule of larva pulled from TET. Note mandibles (arrow). (VI/14/80). 160X.

Figure 7. Trans. section through TET showing larval cavity (right arrow) and gall wall (left arrow). (VI/14/80). 30X.

Figure 8. Nutritive cells bordering larval cavity (in direction of arrow) of TET. (VI/14/80). 75X.

PLATE 38

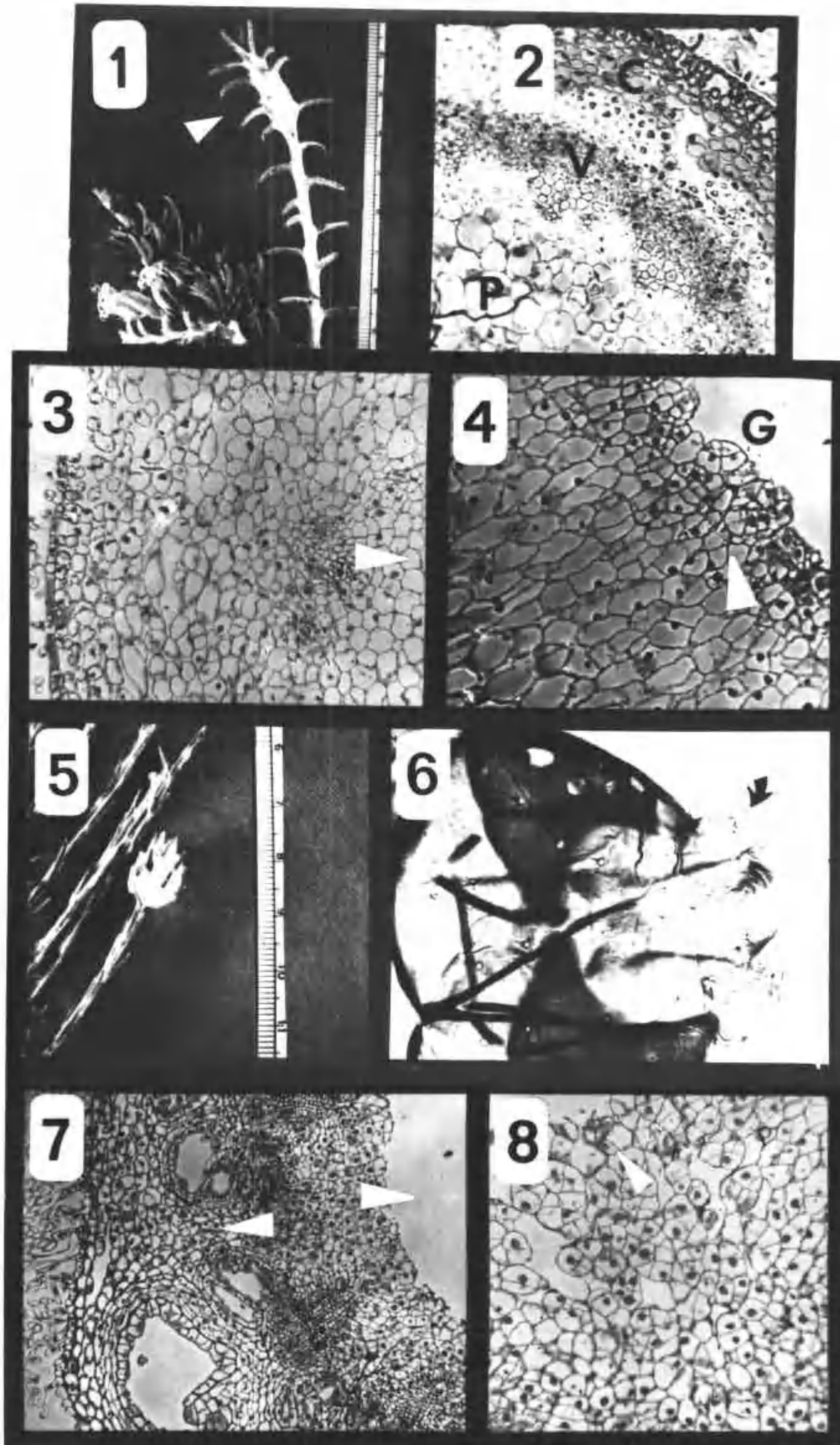


PLATE 39

Figure 1. Very early stage of petiole gall (arrow) caused by Pemphigus populi-caulis Fitch on Populus trichocarpa T. and G.. Viewed from underside. (IV/15/80). 2X.

Figure 2. Early stage of poplar petiole gall (arrow). Upper surface view (IV/30/80). 2X.

Figure 3. Petiole and major veins of Populus plio-tremuloides Axel. from Alvord Creek, Oregon Lower Pliocene). Note twisted petiole (arrow). (Axelrod, 1944; U. C. Berkeley, Paleon. Coll.). Scale in mm.

Figure 4. Close up of Pl. 39, Fig. 3, showing twisted petiole (arrow). 10X.

Figure 5. Swollen petiole (arrow) of Populus eotrem-uloides kn. from Miocene Trapper creek flora of southern Idaho (Axelrod, 1964; U. C. Berkeley Paleon. Coll.). Scale in mm.

Figure 6. Close up of Pl. 39. Fig. 5, showing swollen petiole (arrow). 12X.

Figure 7. Twisted petiole (arrow) of Populus payettensis (Kn.) Axel. from the Mio-Pliocene floras of west-central Nevada (Axelrod, 1956; U.C. Berkeley Paleon. Coll.). Scale in mm.

Figure 8. Possible mine (arrow) in leaf of Quercus nevadensis (Lesq.) from the La Porte flora of California (Potbury, 1935; U.C. Berkeley Paleon. Coll.). 4X.

PLATE 39

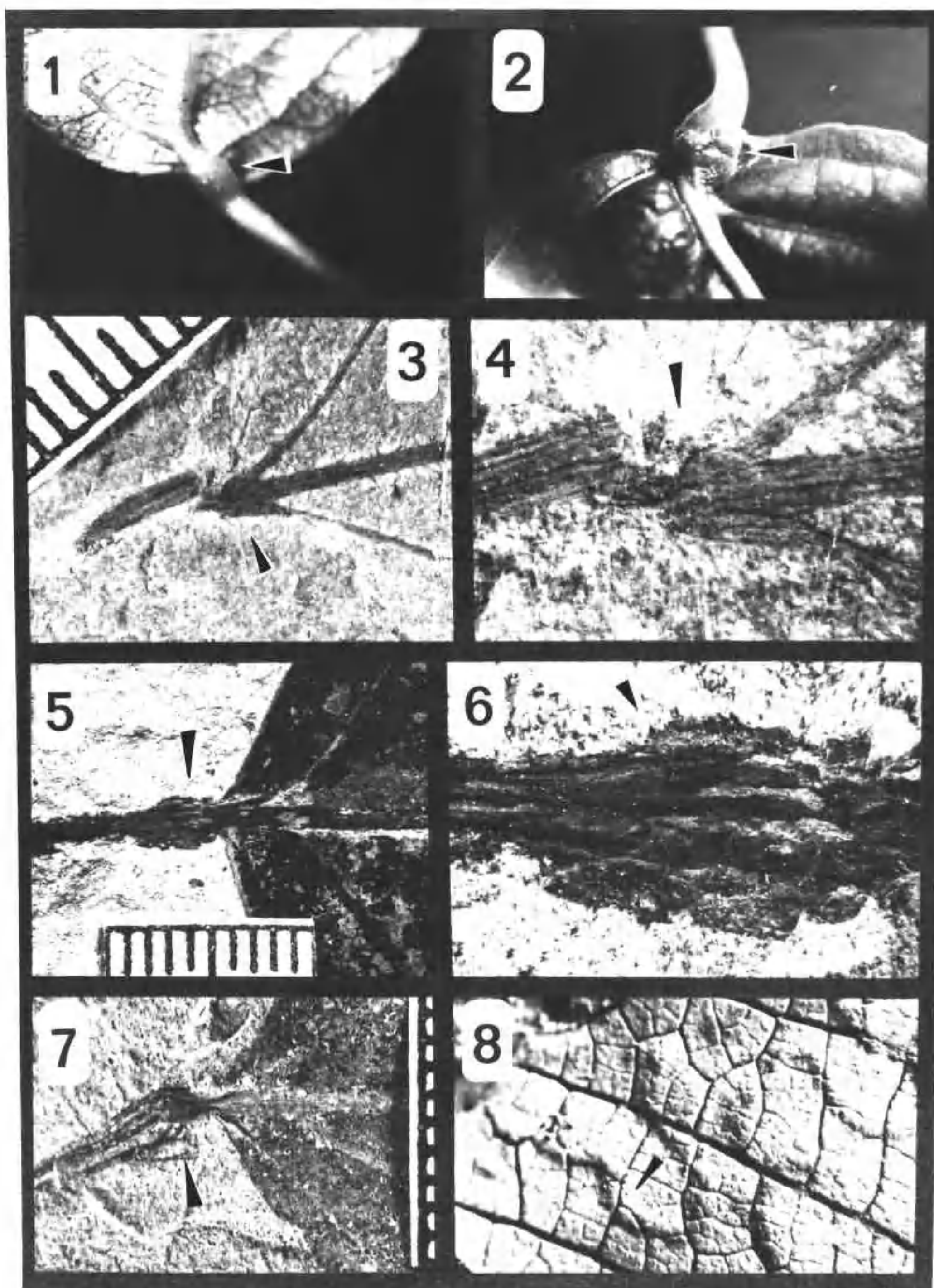


PLATE 40

Figure 1. Galled acorn of Quercus agrifolia Nee from the La Brea Tar Pits. Plesiotype No. PB 1481, Page Museum, Los Angeles. Note two opened larval chambers (arrows). Scale in mm.

Figure 2. Galled acorn of undetermined species from the La Brea Tar Pits. Specimen No. 1418B, Pit 3 (2001/495), Page Museum, Los Angeles. Note prominent, opened larval chamber (arrow). Scale in mm.

Figure 3. Acorn of Q. wislizenii A. de Cand. galled by Callirhytis milleri Weld. Cut-away view of chambers (arrow). (Cal. Acad. Sci. specimen). Scale in mm.

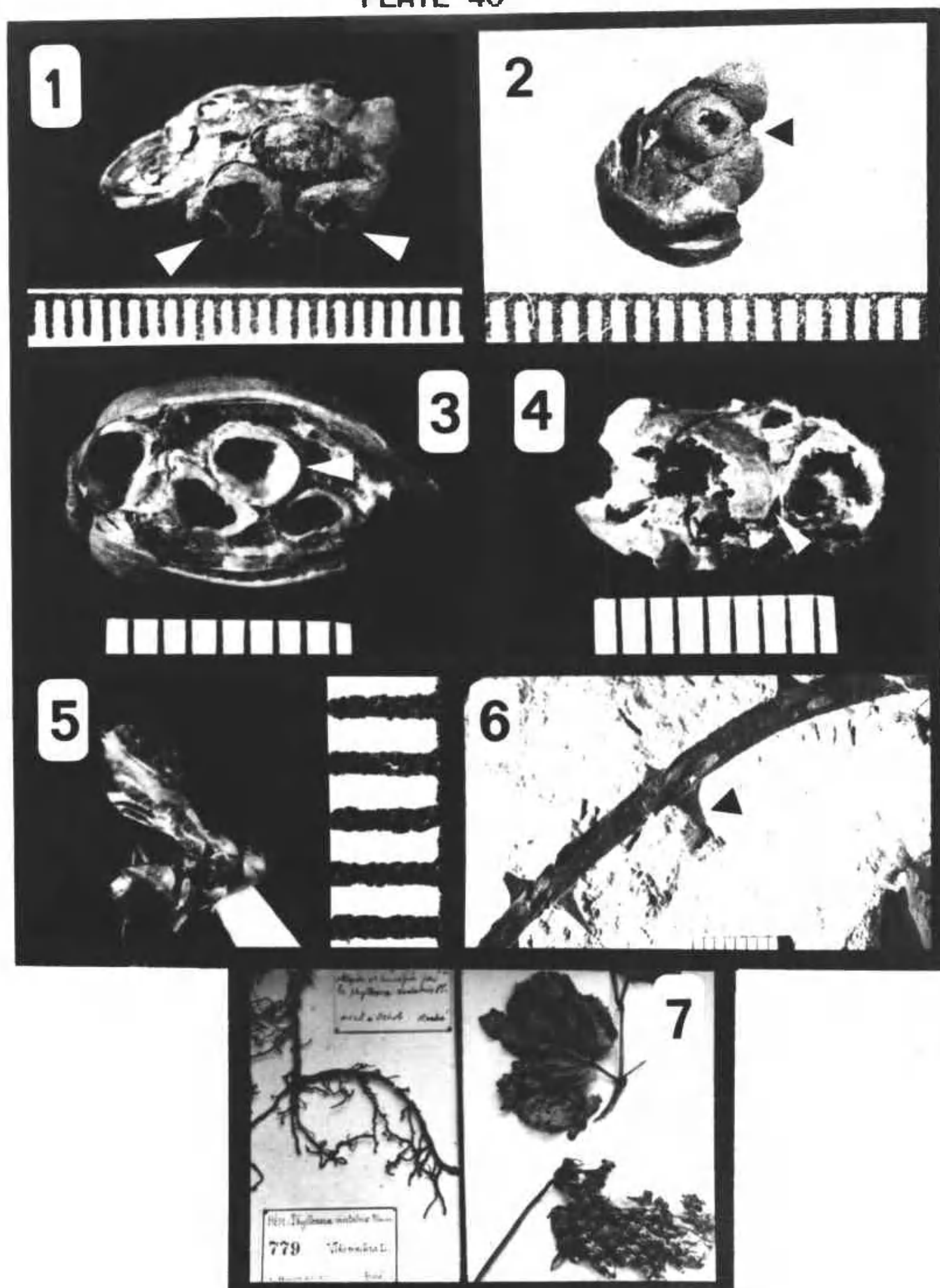
Figure 4. Woody mass of cotyledons from acorn of Q. wislizenii galled by C. milleri. Remnant of chamber wall (arrow) is similar to chamber wall in La Brea material. (Cal. Acad. Sci. specimen). Scale in mm.

Figure 5. Adult C. milleri (Hymenoptera: Cynipidae). Antennae are missing. USNM specimen. Scale in mm.

Figure 6. Stem with thorns (arrow) of Rosa hilliae Lesq. from Crooked River Basin, Or. (Eocene-Oligocene) (Chaney, 1927; U.C. Berkeley Paleon. Coll.). Scale in mm.

Figure 7. Leaves and roots of Vitis vinifera L. galled (arrow) by Phylloxera vastatrix Planchon. (Houard Coll, Musee Entomol., Paris). 0.25X.

PLATE 40



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APPENDICES

APPENDIX 1: EASTERN OREGON GALLS

The diversity of galls that occur on dryland shrubs has been noted in the literature. Jones (1971), for example, detected 35 species of gall midges on sagebrush (mostly on *Artemisia tridentata*), all with morphologically distinct galls. He states that "it is doubtful that all midge species associated with Artemisia spp. in Idaho have been found." Wangberg (1976) described 12 tephritid gall-formers on four species of rabbitbrush (*Chrysothamnus*) in Idaho. In a non-systematic scanning of galls in eastern Oregon (primarily from Malheur National Wildlife Refuge, and the shores of Lake Abert) I have collected at least 25 types of galls from the following host plants:

Family: Cupressaceae

Juniperus occidentalis Hook.

Family: Salicaceae

Salix spp. L.

Family: Chenopodiaceae

Atriplex confertifolia (Torr. and Frem.) Wats.

Sarcobatus vermiculatus (Hook.) Torr.

Family: Compositae

Artemisia tridentata Nutt.

Chrysothamnus nauseosus (Pall.) Britt.

C. viscidiflorus (Hook.) Nutt.

Tetradymia spinosa H. and A.

T. glabrata Gray.

Of these host plants, *A. tridentata*, *C. nauseosus*, and *C. viscidiflorus* bear the majority of gall types observed, with the remaining species hosting one to three types of galls.

Not only is the diversity high, but the incidence of galls per plant is also remarkable. Observations indicate that the majority of plants are galled, and frequently each branch bears more than one gall. In this regard, a careful sampling of the vegetation to determine the density of galls would be instructive.

The purpose of this appendix is to review the published accounts of dryland shrub galls, to provide the results of a first attempt to describe features of the internal structure of certain of these galls, and finally, to offer speculative explanations for the diversity of gall insects on these shrubs.

Published Accounts of Galls on Dryland Shrubs. The earliest published notice of galls on dryland shrubs was by Townsend (1893). This report included a description of a tephritid that galled *Chrysothamnus* in New Mexico.

Townsend observed numerous hymenopterous parasites in the galls.

Until recently the most detailed list of dryland shrub gall-formers was provided by Felt (1911, 1916, 1965). In his book (1965) he listed seven different types of galls on _Artemisia tridentata_ (six cecidomyiids, one tephritid), 14 types on _Bigelovia graveolens_ (=_Chrysothamnus nauseosus_; Hitchcock et al, 1955) (12 cecidomyiids, one tephritid, one cynipid), two types on _Tetradymia spinosa_ (one moth, one cecidomyiid) seven types on southwestern _Atriplex_ spp. (five cecidomyiid, 2 scales), and nine types on _Juniperus_ spp. (six cecidomyiids, one cynipid, one mite, one fungus).

Although his descriptions are helpful, they by no means are a definitive treatment. Felt never collected dryland shrub galls himself so that biological information and thorough mapping of the geographical occurrence of the gall was not included in his descriptions.

Fronk et al (1964) in a short article listed the insects, both gall-formers and others, that they reared from tephritid and cecidomyiid galls on _Artemisia tridentata_ in Wyoming. The authors did not discuss the biology of the insects or galls, but did say that "sagebrush, _Artemisia tridentata_ Nutt., is one of the

most conspicuous plants in western North Ameriaca. Galls are often found on it, but they seem to have been little studied."

The next account of gall insects on dryland shrubs was given by Jones (1971). In his dissertation he described 34 species of cecidomyiids (all but one are in the genus _Rhopalomyia_) that form galls on the persistent leaves, ephemeral leaves, branch tips or nodes of _A. tridentata_ (four subspecies), _A. nova_, _A. arbuscula_, _A. longiloba_, _A. cana_, and _A. tripartita_. Most of his collections were made in Idaho, but a few were made in Montana, Nevada, Utah, and Washington.

For each midge species, he described the seasonal occurrence of all life stages, host plant preference, geographical distribution, and external gall appearance. He also began a checklist of parasites and inquilines that were reared from the galls.

The life histories of all the midge species that he studied were similar. Adult mating flight activity was usually at sunrise in late summer for a few days only. Eggs were laid immediately after mating and young galls were first observed in early autumn through late winter. Eggs were laid on the plant surface near the plant part that had been galled. (He did not observe eclosion or entry into the plant.) Larval and pupal development was

completed within the gall. Early larval instars were thought to overwinter.

A particularly interesting observation was that Rhopalomyia ampullaria had two generations per year, and, unlike any other cecidomyiid, the two generations formed different types of galls.

In describing the impact of the galls on the host plant, Jones stated that most of the galls had no apparent detrimental effect on the plant. In one case (Rhopalomyia sp. 13) he suspected that tip galls were responsible for branch death. In another case (Diarthronomyia artemisiae) he counted 1185 leaf galls on a plant, yet "no plant or branch mortality was...the direct result of this gall formation."

Wangberg (1976) studied 12 species of tephritids on four species of Chrysothamnus (seven species on C. nauseosus and five species on C. viscidiflorus). In six of the species, the eggs overwintered, and the galls were generally leafy. The egg overwinterers hatched in spring and their galls became visible in late spring. Adults emerged in the summer and the eggs were laid in axillary buds at this time. The egg stage lasted for eight to ten months.

The other six species had larvae that overwintered as third instars in the stem galls that they incited as

first instars in the fall. Interestingly, as first and second instars the larvae (at least of *Aciurina bigeloviae*) fed only occasionally in the young gall. Instead, most feeding occurred in a tunnel through the vascular tissue that the larva carved in the stem just beneath the gall. As winter approached, more feeding occurred in the gall. The gall continued to grow at least into late fall if not through winter, and third instars continued to feed in spring. Wangberg made the point that in those cases in which the larvae overwintered, the galls were actively growing after the host plant had finished its active seasonal growth.

The adult tephritids lived for two to three weeks and were active from mid-morning to late afternoon. Host plant specificity was strong. Both field observations and caging experiments indicated "that those species associated with *C. nauseosus* never form galls on *C. viscidiflorus*," and vice versa. Additionally, he showed that morphological differences between galls on four subspecies of *C. nauseosus* caused by *Aciurina bigeloviae* were due not to differences in the flies but to differences between subspecies of the host plant. Wangberg also noticed that the general appearance of a type of gall varied with geographical location.

Two of the galls (those caused by *Aciurina*

bigeloviae and Procecidochares sp. A) were studied by Wangberg for the effect thay had on the host plant. In both cases the galled stems were significantly shorter than ungalled stems, and the number of new stems or leaves that developed from galled stems was significantly less than the number from unattacked stems. The observed effects were "due to the incorporation of (leaf and stem) tissues into gall tissue." The number of galls per plant was not recorded, but infestation frequently appeared heavy. The plants, however, apparently survived heavy attacks. "It seems probable that the vitality of such heavily infested plants would be less than non-affected plants but what effect this has on mortality rate is unknown" (Wangberg, 1976). No mention was made of the effect of infestation on host plant fitness.

In his conclusion, Wangberg listed those parameters which serve to separate the niches occupied by the tephritids. He speculated that host plant specificity, area on the plant attacked, organ attacked, the seasonal occurrence of the gall-formers, and adult gall fly behavior act in combination to minimize interspecific competition for host space.

The most recent publication on the galls of dryland shrubs was by McArthur et al (1979). Their findings showed that tephritid galls were host specific on four

sub-species of _Chrysothamnus nauseosus_ in Utah. A "callus" gall was found only on ssp. _albicaulis_, while a "cotton" gall occurred on ssp. _consimilis_ and _graveolens_. "Mace" galls occurred on all four ssp, but were the only type of gall found on ssp. _salicifolius_. Host plant specificity was not as tight in Idaho (Wangberg, 1976), and McArthur et al (1979) suggested that specificity broke down at the margins of the host plant's range -- fewer host plants at the edge of the range necessitated a broader host selection by the fly.

Anatomical Studies. The studies of dryland shrub galls have provided valuable information particularly with respect to the pattern of specificity and the biology of the gall-formers. No report, however, is available on the anatomy of these galls. I know of only two descriptions of the internal structure of the galls. One is provided by Wangberg (1976) in his discussion of the galls of _Aciurina bigeloviae_ on _Chrysothamnus nauseosus_:

> Regardless of the outer appearance of the galls, all are similar in general anatomy. They are comprised entirely of thickened tissue....The galls are monothalamous and are made up of three distinct tissue layers. The tissue layer immediately surrounding the central cavity is firm and quite hard at maturity. The next layer is of similar thickness but soft. The third layer is an outer, thin epidermis, making the galls sticky to the touch.

The second description is mentioned by Kuster (1903) where he cites Kustenmacher's findings that the cecidomyiid galls on Artemisia campestris contain oil pores that "act completely passively."

A study of the internal anatomy of the dryland galls should provide a first indication of how gall insects flourish on host plants such as Artemisia tridentata, a species that contains foliar terpenes that are alleopathic (Weaver and Klauch, 1977) and antibacterial (Nagy and Tengerdy, 1967). Leaves and green twigs of A. tridentata contain one to five percent volatile terpenes (a mixture of alpha-pinene, cineole, eucalyptole, 1-camphere methacrolein, camphene, beta-pinene, arthole, 1,8-cineole, and p-cymene) (Kinney et al, 1941; Nagy and Tenegerdy, 1968).

The secondary chemistry of Chrysothamnus is poorly studied. Like most composites, however, members of the genus probably contain sesquiterpene lactones (Hall and Goodspeed, 1919). Sarcobatus vermiculatus, a chenopod that is heavily galled in eastern Oregon, is known for its foliar soluble oxalates (10-22%) (Kingsbury, 1964)

Whether these compounds occur in gladular trichomes (as they do in some composites) is not known. If terpene synthesis and storage is found only in trichomes, then any insect feeding within a leaf or stem (e.g. miners or

gall-formers) would avoid these compounds. If, however, the compounds are found in the leaf mesophyll, then internal leaf feeders would have to avoid or contend with these compounds.

Some gall-forming insects avoid host plant tannins by directing the development of a nutritive layer that contains low amounts of these compounds. The primary purpose of this anatomical survey was to determine the extent of nutritive layer development in the galls of dryland shrubs.

I studied the internal structure of eight galls on four species of dryland shrubs. During the late spring and summer of 1980 I either collected or received galls from eastern Oregon. All material was processed for microtomy, and sections were stained for light microscopy (see Material and Methods). Because most of the galls were collected only once, a study of changes through time in the structure and in feeding tissue characteristics was not possible.

Identification of the cecidozoan was taken at least to family and further if possible. Attempts to rear adults usually failed so that determination to genus was possible only if the gall had been previously described. The type of feeding damage caused by the gall insects should be suggested by the type of mouthparts they

possess. For this reason I have included photographs of the head capsules. The galls will be treated by host plant. For convenience, each gall is given an acronym.

GALLS ON ARTEMISIA TRIDENTATA

1) This gall (Pl. 34, Fig.1) was abbreviated ART. It was caused by cecidomyiid larvae. The galls were collected by Dick Halse on September 11, 1980 in Bend Oregon (Deschutes Co.). I presumed from the collected specimens that larvae overwintered in galls.

The gall did not resemble any of the midge galls described by Jones (1971). It was found at the tips of short side branches and appeared as a sub-spherical swollen and stunted branch tip. Leaves arose particularly from the distal surface of the gall (the proximal end of the gall was not obscured by leaves or leaf bases). Rather than pointing in all directions, the leaves on the gall pointed up over the (distal) top of the gall. The gall resembled a minature kohlrabi. Its surface bore a felt-like tomentum. The gall was easily crushable, and after handling it, one suspected a spongy internal matrix. When collected, the galls were 0.5-1.0 cm long and were 0.3-0.5 cm in diameter at the widest point.

Internally the bulk of the gall was composed of very

light green spongy tissue (Pl. 34, Fig. 2). At the center of the gall, one found one to six bright orange cecidomyiid larvae each within a cell of succulent, dark green tissue (nutritive tissue). The occurrence of chlorophyllic tissues in galls is apparently unusual (Kuster, 1903), but its significance is unknown. Larval cells abutted (Pl. 34, Fig. 3).

When sectioned, the spongy tissue resembled an aerenchymatous tissue (Pl. 34, Figs. 3 and 4); cells were separated by large air spaces so that contact between adjacent cells was minimal. The contents of these cells stained lightly and were coarsely granular. Nuclei were not prominent. Vascular bundles ran the length of the gall but it was not clear how the nutritive tissue was serviced by the vascular system.

As one moved from the spongy tissue toward the larval cell, the most noticeable change was the increase in cell wall contact. The cells of the nutritive tissue (Pl. 34, Fig. 5) showed no intercellular spaces. Along with this change one observed a general increase in the cytoplasmic density of the cells. The cells closest to the larva showed no prominent vacuoles, had a granular cytoplasm and a fairly prominent nucleus and nucleolus.

The larval head capsule (Pl. 34, Fig. 6) was small and was recessed in body folds. Mouth parts were very

small and were concentrated in the most heavily sclerotized anterior region of the head. For these reasons, the type of mandibulation possessed by this midge was not clear.

2) The second gall was abbreviated ARC. It was another cecidomyiid gall. It was collected by Dick Halse on September 11, 1980 in Bend, Oregon (Deschutes Co.). Apparently, the larvae overwintered.

ARC (Pl. 34, Fig. 7) resembled the gall caused by Jones's *Rhopalomyia* sp. 19 which he collected in Idaho on *A. tridentata tridentata* and *A. t. vasevana*. His observations indicated that the galls began to form in the field in mid-July and that adults emerged in late April. He described the gall as a bud gall. The gall, like ART, was located at the tips of short side brances. Unlike ART, however, this gall had no solid subspherical structure in which larval cells were embedded. Instead, the tip of the branch flared out to form a dome-like platform upon which the larval cells were borne (Pl. 34, Fig. 8). The arrangement of gall parts was analogous to that seen in composite flower heads. The platform in the gall resembled the compound receptacle and the larval cells were arranged on it much like composite flowers or seeds on the receptacle. Short leaves and many long

white hairs were also borne on the platform. The hairs arose from both the platform and from the outer surface of the larval cells. The larval cells occurred between and at the base of these leaves so that, externally, one could not see the cells. Ten to twenty larval cells occurred per gall with one larva per cell.

The external appearance of the gall resembled a very small artichoke, or a mature composite seed head with the dense whorls of stunted leaves looking like floral bracts and the intermingled hairs looking like achene pappi. The galls were 0.7-1.5 cm long and 0.7-1.0 cm in diameter at their widest point.

In all of the collected specimens much of the tissues that supported the platform were dead or beginning to die (Pl. 34, Fig. 8) so that cavities at the base of the platform were apparent. The tissue upon which the larval cells rested, however, was succulent as were the larval cells walls.

When the platform was sectioned transversely at the level at which larval cells arose (Pl. 35, Fig. 1), it was seen that the cells making up the bulk of the platform possessed large vacuoles that either did or did not contain darkly staining material. The nature of this material was not known, but it may have been phenolic or terpenic.

As one moved through the platform tissue to the base of a larval cell, a zone or halo approximately ten cells thick that encircled the nutritive tissue was recognized by its lightly stained cells. The nutritive tissue, on the other hand, was composed of evenly stained cells that show no large vacuoles. Instead these cells were endowed with a rich cytoplasm and prominent nuclei. As one moved from the outer cells layers of the nutritive tissue toward the larva, the cells' nuclei and nucleoli became larger (Pl. 35, Fig. 2).

The nutritive tissue at the bottom of the larval cell was approximately 20-25 cell layers thick. The inner surface of the larval cell was coated with contents of ruptured (fed upon) cells or, more likely, of a ruptured larva.

The larval head capsule was very lightly sclerotized, and the mouthparts were very small (Pl. 35, Fig. 3).

3) This gall was abbreviated ANP. It is the first mite-caused gall to be described on any of the dryland shrubs of western North America. Houard (1922) recorded six different eriophyid galls on various species of _Artemisia_ in the Old World. ANP was collected by Dick Halse on September 19, 1980 in Bend, Oregon (Deschutes

Co.).

The ANP gall was accidentally studied. Originally I preserved and sectioned the gall thinking that it was the very early stage of a nipple-like cecidomyiid gall caused by Rhopalomyia ampullaria. It was only after observing sections of the galls and seeing that the gall cavity was filled with eriophyids that I realized the nature of the true cecidozoan. No mites were mounted for identification.

The galls occurred singly or in fused groups of two to five on the leaves. They were sub-spherical, and were 0.1 to 0.2 cm in diameter. Because of their small size, they could easily be overlooked. The galls were visible from both surfaces of the leaf (Pl. 35, Fig. 4).

As one moved from the mesophyll toward the gall cavity there was a marked change in staining properties of the cell contents. Most of the cells that made up the wall of the gall cavity possessed large vacuoles, the contents of which stained poorly (Pl. 35, Fig. 5). Prominent nucleoli were found in these cells. The cells in closest proximity to the mites were empty, and in many cases were ruptured (Pl. 35, Fig. 6). The large number of mites in the cavity along with the disruption of the cells that lined the cavity (most likely due to feeding) suggested that the galls were relatively old. If this

was so, then it would be instructive to study younger galls to characterize young nutritive cells.

It appeared likely, however, from the available material, that the cells upon which the mites fed contained low amounts of the deeply stained compounds that were found in abundance in mesophyll cells (see below). The diet of the gall mites was different (probably more nutritious) from what it would be if they fed on unaltered mesophyll cells. The same could be said of the diet of the cecidomyiids that formed the two previously described galls.

The means by which mites formed and eventually left the gall was not clear. Mature galls showed no sign of an aperture, and most likely the mites escaped as the gall wall dried and ruptured.

In studying this gall I also examined cross sections of sagebrush leaves. According to Metcalf and Chalk (1950) the mesophyll of composite leaves was very variable. In the case of _A_. _tridentata_, I found that a clearly discernable palisade and spongy mesophyll were not present. Instead, the mesophyll was composed of densely packed, isodiametric cells that possessed cellular contents which stained very deeply (and thus, to a degree, obscured internal leaf structure). The nature of the deeply stained material within the mesophyll cells

was not known, but I suspected that it was either terpenic or phenolic. If such suspicions were correct, then any phytophage feeding on unaltered sagebrush leaves would have to contend with these defensive compounds.

GALLS ON CHRYSOTHAMNUS NAUSEOSUS

1) This gall was abbreviated CRC. The material that was examined for this discussion came from specimens that were collected September 10, 1980 in Bend, Oregon (Deschutes Co.) by Dick Halse. I had previously collected the gall at the edge of Lake Abert (Lake Co.) on April 21, 1979.

CRC was an undescribed cecidomyiid-caused gall. It was borne on the tips of young stems and resembled a composite seed head (much like ARC). The gall was 1.0 to 1.3 cm in length and about 1.0 cm in diameter (Pl. 36, Fig. 1). A whorl of two to five brown bract-like leaves with broad bases formed the perimeter wall of the gall -- they formed a cup-like structure. All that could be seen when looking down into the gall from above was a very dense accumulation of white hairs (not visible in Pl. 36, Fig. 1, but seen in Pl. 36, Fig. 2).

When the gall was cut longitudinally (Pl. 36, Fig. 2) the resemblance to a composite seed head became sharper. The stem tip, for example, was flared into a

circular, thickened platform that formed the base of the gall, much like a compound receptacle formed the base of a composite flower head. The enlarged leaves encircled the platform and arose from its side. The platform, in its center, bore five to ten cylindrical larval cells (much like the seeds on a receptacle). Each cell contained a single larva. The base of each cell was embedded in the platform's tissues. White hairs that arose from the upper surface of the platform, as well as from the surface of the larval cells, surrounded and covered the cells, so that only when the hairs were removed did the cells become visible (Pl. 36, Fig. 3).

Thin sections through a larval cell indicated that the cell cavity was lined by cells with dense cytoplasms (Pl. 36, Fig. 4). The larva was found at the lower (proximal) end of the cavity where the plant cells (10-12 cell layers deep) showed a very dense cytoplasm (Pl. 36, Fig. 5). Thus the larva was surrounded by an enriched nutritive tissue.

2) This gall was abbreviated COT. Specimens of this gall were collected on August 29, 1980, and on September 12, 1980 in Bend, Oregon (Deschutes Co.) by Dick Halse. It was also collected on June 14 at Malheur Field Station (Harney, Co.). Each gall was caused by a single

tephritid larva. A single gall was collected on December 28, 1980 in eastern Oregon by Jim McIver. An adult emerged from the gall that showed a wing coloration pattern similar to that of *Aciurina bigeloviae* (see Fig. 102, Wangberg, 1976). According to Wangberg (1976) there was variation in the wing coloration pattern in this species. The gall, however, did not fit the description of any of the five types caused by *A. bigeloviae* (Wangberg, 1976). I concluded that COT was caused by an undescribed tephritid species. The September 12 material was used for the following description.

The galls were located on the stem at nodes (Pl. 36, Fig. 6). The galls probably arose from axillary buds, but developmental work would be required to establish this. The galls were spherical and measured 0.9–1.3 cm in diameter. They were covered by a thick, nonsticky white tomentum. Four to ten stunted leaves emerged singly from the tomentum. The short pedicel that connected the gall to the stem was roughly circular and was 0.3 cm in diameter. The attachment point covered only a portion of the circumference of the stem, so that the side of the stem opposite the gall was visible, and other than being slightly flared, appeared normal.

Internally the gall was a spherical mass of succulent green tissue. The single larval cell was in

the center of the gall and was completely embedded within the gall wall tissue (Pl. 36, Fig. 7) (i.e. it was not free standing as in CRC). The cells of the gall wall stained lightly for the presence of cytoplasm (Pl. 36, Fig. 8). They contained large vacuoles (Pl. 37, Fig. 1). As one approached the larval cell, however, the cytoplasm of the nutritive cells became denser so that the cells that lined the larval cavity were rich with cytoplasm (Pl. 37, Fig. 1).

The tephritid larva possessed a heavily sclerotized cephalopharyngeal skeleton (Pl. 37, Fig. 2), the front scythe-like edge of which was used to slice through cells. Ruptured cells that lined the larval cavity were visible in Plate 37, Figure 1.

3) This gall was abbreviated CPG. It was one of the most common galls on <u>Chrysothamnus</u> <u>nauseosus</u> in eastern Oregon. It was a stem gall caused by cecidomyiids. Felt (1965) described a gall caused by the midge, <u>Rhopalomyia chrysothamni</u> Felt on <u>Chrysothamnus</u> that resembled CPG: "Conical stem or oval bud gall, with a variable amount of cottony fibers protruding, dimension, 1/4 to 1/2 inch, midge, summer." I collected the gall from the shore of Abert Lake (Lake Co.) and from the Malheur National Wildlife Refuge (Harney Co., OR). I also received

specimens of CPG from Bend, Oregon (Deschutes Co.). Material from the Refuge was collected June 14, 1980, and was the material from which this discussion was drawn.

The gall was green and was covered with a very light tomentum (like that seen on the normal stem). The gall was a stem swelling that was associated with an axillary bud (Pl. 37, Fig. 3). The stem swelling involved only 1/2 to 3/4 of the circumference of the stem, and the side of the stem opposite the swelling remained nearly to completely unaffected by the gall. When viewed from the side or straight on, the gall looked very much like a drop of wax that had run down and cooled on the side of the stem. Its shape was roughly that of a tear drop. Frequently the galls were found bunched along the stem, and in such cases, some coalescing of peripheral gall tissues occurred. Even if the galls were bunched along the stem, however, each gall could have been visually separated from its neighbor by the most prominent feature of the gall; I called this gall the portal gall because of the circular aperture located at the center or slightly lower than the center of the gall's outer surface. Numerous white hairs plugged the aperture.

The bulk of the gall involved space normally occupied by the stem cortex (Pl. 37, Fig. 4). The pith was unaffected. A single cone-shaped larval cell

(occasionally more than one per gall) had its long axis perpendicular to the stem's axis directly under the portal. The broad base of the cell's cone was embedded in the stem in or near the cambial zone. The side walls and tip of the larval cell, on the other hand, were not embedded in gall tissue but were surrounded by long hairs. The hairs arose from the surface of the tissue at the base of the larval cell, and they passed along the cell wall to emerge from, and plug the portal.

If the hairs were removed from the gall the arrangement of tissues became clear. The outer gall wall rose dome-like over the larval cell, and was only incomplete at the circular portal directly over the distal tip (or point) of the cell. The base of the outer wall, around its entire circumference, was thickened (cells resembling those in the stem cortex were responsible for the thickening). The wall tapered such that at the portal, this outer gall wall was thin. The space between the outer gall wall and the larval cavity wall was occupied by the long, prominent hairs.

A longitudinal thin section of the larval cavity showed a nutritive zone at the base and lower sides of the cavity wall (Pl. 37, Fig. 5). The larva was located in this proximal end of the cavity. Cytoplasmic density of the plant cells surrounding the larva was marked, as

was the prominence of nuclear and nucleolar regions in these cells (Pl. 37, Fig. 6). Thus the nutritive layer resembled that seen in other types of galls.

When stained for tannins the tissue forming the larval cavity stained slightly positively (Pl. 37, Fig. 7), a result that suggested that the gall larva contended with low levels of tannins in the diet. How this compared with amounts of tannins found in other plant parts was not known.

The mouthparts of the midge larva were very small and sclerotized (Pl. 37, Fig. 8). Because of their size and compact arrangement they did not easily lend themselves to interpretation.

GALLS ON TETRADYMIA SPP.

Stems galls were collected on two species of *Tetradymia*. 1) The first, abbreviated TES, was collected from *T. spinosa* on June 14, 1980 on the north shore of Harney Lake (Harney Co., OR) (Pl. 38, Fig. 1). Each gall contained a single lepidopteran larva. The gall was probably caused by *Gnorimoschema tetradymiella* Busck. (Family: Gelechiidae). Felt (1965) described the gall as follows: "fusiform, wooly, stem enlargement, length 1 1/2 inches, on *T. spinosa*, caterpillar, summer."

Most of the galls occurred at stem tips and were

covered by a white tomentum that was of a similar density to that which occurred on ungalled stems. The recurved spines that occurred over the surface of the ungalled stems were also seen on the surface of the gall. The diameter of the gall at its widest point was 0.6-0.9 cm while the diameter of an ungalled stem was 0.3 cm.

When cut longitudinally the gall was seen to contain a long narrow larval cavity that ran the length of the gall. One white larva (with brown, sclerotized head capsule) lived in the cavity. The cavity was in the stem space normally occupied by the pith.

Transverse sections of the gall showed that, unlike the ungalled stem (Pl. 38, Fig. 2) which had clearly distinguishable pith and cortex, the gall wall was fairly homogenous (Pl. 38, Fig. 3). Cellular hypertrophy occurred throughout the gall wall, and vascular bundles, instead of being arranged side by side like in the ungalled stem, were widely separated. Vascular bundle cap cells were also not as common in the galled stem as in the ungalled stem.

A large central vacuole in most of the cells that formed the gall wall pushed the thin strip of cytoplasm with nucleus to the periphery of the cell. As one moved inward through the gall wall just past the vascular bundles toward the larval cavity, the plant cells became

oval in transverse section, and arranged in irregular radial rows.

The plant cells that bordered the larval cavity, on the other hand, were irregular in shape and orientation. They were generally small and a few stained deeply for the presence of a cytoplasm. A band of these cells that was five to eight layers thick lined the larval cavity (Pl. 38, Fig. 4).

The general impression that one was left with was that the cells of the gall wall were all fairly similar. Distinctive tissue layers were not clearly apparent as they were in the cecidomyiid galls. All cells in the gall stained poorly for the presence of tannins, all had prominent vacuoles, and most all showed very little cytoplasm. The plant cells that lined the larval cavity were sometimes richer in cytoplasm than were cells elsewhere in the gall, and were completely free of tannins.

2) The second gall on <u>Tetradymia</u> was found on <u>T. glabrata</u> (Pl. 38, Fig. 5). It was abbreviated TET. It was collected on June 15, 1980 at the Malheur National Wildlife Refuge Field Station (South Coyote Butte). TET was usually found at the tip of a young stem. A thick white tomentum covered the gall's surface, and leaves

emerged through the tomentum. The gall was ovoid or broadly fusiform with a broad proximal end and a tapered distal end. It was usually 1.0-1.3 cm long, and 0.8-1.0 cm wide at its widest point.

This gall, as TES, was caused by a lepidopteran. The insect was unidentified, but may have been a species closely related to, or identical to Gnorimoschema tetradymiella.

The gall wall (Pl. 38, Fig. 7) maintained many of the feature of a healthy stem. The most noticeable features of the gall wall were the presence of prominent ducts that occurred throughout the cortex, as well as the unremarkable nature of the cells that formed the nutritive band 10-12 layers deep around the larval cavity (Pl. 38, Fig. 8). These food cells showed a prominent nucleus, but otherwise, appeared completely vacuolated and resembled the nutritive cells in TES.

Many of the cells that bordered the cavity were ruptured (most likely from being fed upon). The food cells were apparently scraped by the sclerotized, toothed mandibles of the larva (Pl. 38, Fig. 6).

The galls on Tetradymia were similar to other moth galls. For example, Beck (1953) studied the stem gall on Solidago caused by Gnorimoschema gallaesolidaginis Riley. Initially the larva invaded the plant by boring down

through the stem tip and fed on young pith, rays, and vascular tissue. Once gall growth began the larva fed on "small proliferating cells" derived from the ray and xylem parenchyma. Beck believed that stimuli for tissue proliferation included mechanical wounding of the tissue (caused by the sclerotized manidibles of the larvae) as well as active compounds in the silk secreted by the larva. I observed no mass of silk in the *Tetradymia* galls. Entry into the *Tetradymia* stems was most likely as described by Beck.

Summary of Eastern Oregon Galls

The observations made on the galls of eastern Oregon dryland shrubs indicated that in most cases a well defined nutritive layer was present in the galls. The two galls caused by moth larvae, like most moth-caused galls (Kuster, 1903) showed a simple structure with a feeding region that was composed of cells that were reminiscent of undifferentiated callus. This was in contrast to cytoplasm-charged nutritive cells seen in many cecidomyiid and cynipid galls.

I suspect that the gall-forming insects that occurred on dryland shrubs were able to avoid many host plant secondary compounds such as terpenes by feeding on plant cells that contained relatively low amounts of

these compounds. Additionally, the nutritive tissue most likely provided a diet relatively rich in proteins, oils, and carbohydrates.

A convergence in gall structure was observed. A cecidomyiid gall on _A. tridentata_ (ARC) closely resembled the midge gall on _C. nauseosus_ (CRC). It was possible that the two galls were formed by the same species of midge, but this was unlikely given the strict monophagy exhibited by most dryland cecidomyiids. It was also intriguing that both of the galls resembled composite flower heads. Perhaps the gall insect in some way called up the floral developmental pattern of the host plant (see also, Wangberg, 1976).

The significance of this trend was not clear. Apparently certain gall forms (particularly the artichoke type) had distinct advantages. A convergence in the structure of oak galls was noted (Meyer, 1969a). Whether a similar phenomenon has been seen in other plant genera that host a rich gall flora (e.g. _Eucalyptus_, _Ficus_, _Salix_, _Populus_) is not known.

DRYLAND SHRUB GALLS - A DISCUSSION

Three patterns emerged when the dryland gall flora was considered. Each pattern was worthy of brief discussion.

Pattern 1. The gall-forming fauna on the dryland shrubs was noteworthy for its preponderance of fly-caused galls (either cecidomyiid or tephritid) and for the almost complete lack of wasp-caused galls. This pattern seemed to hold on a worldwide basis. Of the 49 galls Houard (1922) described on _Artemisia_ from the Old World, 30 were caused by cecidomyiids, six by eriophyids, five by muscoid flies, and three by lepidopterans. No hymenopterous gall-formers were reported. In fact, in the Old World relatively few wasps attacked any composites. Of the 180 galls he reported on composites, 16 were caused by wasps. Of the 164 galls on 22 genera of composites that he reported from South America (Houard, 1933) there were no wasp-caused galls. Instead in both areas of the world the cecidomyiids, muscoids (tephritids) and eriophyoids were the dominant cecidozoans on composites. Why this pattern exists is not clear.

Pattern 2. The impression one was left with when returning from a visit to the drylands of eastern Oregon was that the gall-formers constituted a large portion of those insects that fed on the shrubs. One would even be led to believe that the gall-formers were favored in such

a setting. Some of the literature, scanty though it is, supported this impression. Furniss and Barr (1975) listed nine species of insects that attacked but did not gall Artemisia spp in the Pacific Northwest. Similarly they listed five species of non-gall-forming phytophagous insects on Chrysothamnus. These figures were in contrast to reports that in Idaho alone, 35 species of cecidomyiids galled Artemisia (Jones, 1971), and that 12 tephritid gall flys on Chrysothamnus (Wangberg, 1976) occurred in the same region. Cobb et al (1981) provided a checklist of insects that occurred in the Alvord Basin sand dunes of southeastern Oregon. Several orders (e.g. Orthoptera, Homoptera, Coleoptera, and Lepidoptera) were well represented by plant-feeding species. The gall-forming Diptera, however, were not intensively collected and thus, comparisons between guilds were not possible.

Undoubtedly additional species in all guilds of phytophagous insects remain to be detected and described from the dryland shrubs. The literature and my observations suggested, however, that regardless of the length of future checklists, gall-formers will constitute a large percentage of the total number of insect species (and perhaps of the total number of insects) that feed on dryland shrubs.

An explanation for the success of this type of feeding in the drylands of course is speculative. Perhaps features of gall living were particulary suited for existence under semi-arid conditions. For example, the temperature within a gall may have fluctuated less, or may have fluctuated more slowly than the temperature outside a gall. In this regard, it was interesting that many of the galls on dryland shrubs were covered with a dense white tomentum or were packed with hairs, and that many had walls that were thick and spongy. These features perhaps increased the insulatory properties of the gall.

The relative humidity within the gall was perhaps also maintained at a more constant and higher level than externally. Buffering of temperature and humidity would be advantageous to a developing insect in an environment such as the Great Basin's in which ambient conditions flucuate greatly on both a diurnal and seasonal basis. The fact that many of the gall insects on dryland shrubs overwintered in the gall (Jones, 1971; Wangberg, 1976) suggested that the gall provided some insulatory protection.

The gall perhaps also protected the insect from precipitation, from UV light, and from ants (general predators) that patrolled the stems. Also, a

gall-former, unlike an external feeder, did not contend with the heavy tomentum or stout thorns that frequently covered many healthy parts of a dryland shrub. Instead, it fed on succulent tissue.

Interestingly, most all of the above advantages could be shared by any endophytic insect. No mention, however, was made in the literature of leaf mining or stem boring insects on the dryland shrubs. Neil Cobb (personal communication), however, observed a leaf miner on sage.

Furthermore, many of the benefits of gall-living outlined above could be enjoyed by any insect that invaded the gall. To what extent parasitism affected the success of gall-formers in the drylands was not known, but we know that parasitism occurred. The studies by Jones (1971) and Wangberg (1976, 1977), and my own casual observations indicated that galls caused by dipterans on these shrubs were frequently parasitized by chalcidoids. Inquilines and predators were detected as well (Wangberg, 1976).

I did not observe parasites in the galls caused by Gnorimoschema but predict that parasites and other gall inhabitants will be found when these galls are studied further. Eriophyid galls usually do not host parasites, but predators and inquilines do occur in mite galls.

Whether the eriophyid galls on *Artemisia* were attacked was not known.

Pattern 3. Like the gall-forming insects on oaks (and, I suspect, on eucalypts) the gall-forming insects on the dryland shrubs (particularly those on sagebrush) probably avoided host plant defensive compounds by directing the development of a nutritive tissue. The important point, however, is that in these three groups of host plants, there is an abundance of foliar defensive compounds (phenols and/or terpenes) as well as a rich gall flora. Relative to other phytophagous guilds, gall-formers may succeed on these types of host plants because of their unique ability to control or lower the amounts of these detrimental compounds in their diet.

In addition, oaks, eucalypts, figs, willows, poplars, and some of the dryland shrubs (e.g. *Artemisia*, *Chrysothamnus*) are taxonomically difficult groups (Hutchinson, 1967; Blakely, 1955; Brayshaw, 1976; Hall and Goodspeed, 1919), a fact that is symptomatic of the apparent frequency and ease with which species within these genera hybridize. Perhaps there is something in the abundance of species and hybrid intermediates, in the diversity of host-plant substrates within these genera, that facilitates radiative speciation of the

gall-formers.

Not only are the oaks, eucalypts and dryland shrubs rich in species and sub-species, but they also are long-lived dominants in their respective communities, and they occur over relatively wide geographic areas. In other words, they are predictable both in time and space, and thus may allow close host-plant tracking by the gall insect. Such tracking could lead to specialization on a host plant (Edmunds and Alstad, 1978), which in turn could lead to development of races, sub-species, or species of gall insects.

In addition, Patrice Morrow (personal communication) has pointed out that in Australia, gall insects have few host plant options other than eucalypts. The same can be said of the gall insects on dryland shrubs. The abundance of long-lived dominants in habitats where few other host plant species are found may encourage and force gall-insects to radiate on those host plants.

Rich gall faunas such as found on the dryland shrubs occur unevenly throughout the plant kingdom. On a worldwide basis, certain plant genera are more prone to attack by gall insects than others. Attempts to explain the host plant preferences of insect guilds have not been made before. Any first attempt with its dependence on data sets not tailored to its questions, must be

tentative. I nonetheless suggest that when acting in combination, all of the host plant characteristics described above lead to and maintain the preferences of gall insects for dryland shrubs.

APPENDIX 2: EVIDENCE FOR PLANT-INSECT INTERACTIONS IN THE FOSSIL RECORD

Recently there has been increasing speculation about the pace of evolution. Boucot (in preparation) has provided numerous examples which suggest that evolutionary and co-evolutionary behavorial radiations occur rapidly and are followed by long periods of minimal change in characteristics. He draws some of his support for this view from published examples that describe paleo-interactions between insects and plants. It is the primary objective of this appendix to compile those and additional examples, and to indicate the potential for finding others.

The attempts to integrate what is known about the evolution of plants with that of insects have used two basic approaches. The first has focused on the evolution of secondary plant compounds -- compounds thought to defend the plant against herbivores. Swain (1976) studied both evidence from the fossil record and analysis of relictual plants to sketch the origins of secondary plant chemicals, and to suggest reasons for their subsequent proliferation. He estimated the points in time that insects and other herbivores influenced the secondary chemistry of plants. Perhaps his most

important point, and one that needs to be kept in mind for both chemical and structural plant defenses, is that what is now viewed as a defense may have developed under environments in which herbivores did not occur or had little impact. He suggested that defense systems arose as offshoots of more basic physiological systems, and perhaps initially served in capacities other than that of defense. This suggestion leads one to suspect that antecendents of defense systems (i.e. those systems seen in the fossil record) might appear more generalized than do present day systems.

The second approach has lifted morphological information from the fossil record that suggests interactions. The angiosperm flower has attracted the most attention. Its structure is thought to fairly precisely reflect a particular mode of pollination. Leppik (1960), Crepet (1979), and Dilcher (1979) have described finely preserved angiosperm flowers, the structures of which suggest insect pollination. For example, based on fossil floral morphology, Crepet believes that beetle, fly, bee, and butterfly pollination systems were established by the Middle Eocene (Claiborne formation).

Features of flowers that suggest interaction, and that might be found in well preserved specimens, include

the arrangement, color, and amount of fusion of sepals and/or petals (for visual cues, landing platforms, and development of nectar tubes), the presence of floral nectaries, the placement of pistils and stamens (the well-studied pin and thrum arrangement in some extant species presumably requires entomophyily), and the presence of food tissue in the flower (such as in Calycanthus - a beetle-pollinated primitive flower). Because of their short visits pollinators would not be expected to be preserved in the flower (except in those unusual cases, such as in some figs and in Yucca where the pollinator lives in the flower), but other insects (such as thrips) that live in flowers might be detected in excellently and quickly preserved material such as in amber. S. Chitaley recently presented information on well preserved (petrified) flowers from India (American Institute of Biological Sciences meeting, Bloomington, Indiana, 1981). I hope to contact her about checking material for thrips.

As Crepet and Dilcher have suggested, the study of the evolution of specialized pollinator mouthparts that are matched to flower morphology should yield some of the best evidence for reciprocal changes that occur in co-evolutionary partners. This appendix is also concerned with structures of plant fossils that suggest

insect- or herbivore-plant interactions. Unlike Dilcher and Crepet, however, I focus not on flowers, but on the seeds and vegetative structures. This is a first attempt at scanning the paleo-botanical literature for mention of those normal vegetative plant structures that are suspected of imparting some protection to the plant against herbivory (e.g. thorns). Additionally, I summarize the incidence of fossilized abnormal plant structures that arose when the plant was attacked (e.g. galls, mines), or of structures that indicate a symbiotic relationship with arthropods (e.g. domatia).

Fossil Plant Parts

The scanning of an angiosperm for structures other than the flower that may indicate interactions, and which might be found in fossil material, would best be approached by dividing the plant into its parts.

1) Pollen. The science of palynology has as a primary purpose the description of the floral composition (and thus climate) of prehistoric regions. I suggest, however, that it might also be used to study the integration between pollen structure and pollen carrier. For example, the size, shape, and surface sculpturing of pollen grains indicate the general mode of dispersal

(wind vs. insect pollination).

I am unaware of studies that correlate present day pollen grain morphology (exine sculpturing), or packaging (such as in pollinia) to type of insect pollination. If such correlations exist today, they should also be checked for in fossil pollens. Possible fossil pollinators should also be scanned. Pollen baskets in Hymenoptera, or pollen scattered over the surface of amber-trapped insects, for example, would indicate that pollen gathering had occurred.

2) Fruits and Seeds. The nut beds of Eastern Oregon may provide evidence, if they already have not, of fruit structures that indicate animal dispersal of seed. Such structures include fleshy coverings around the seeds, or barbs on the fruits. Thick husks, or hard seed coats, such as seen in walnuts of John Day (Bones, 1979), may in part develop to protect the embryo from damage by seed predators or dispersers.

Damaged fruits, hollowed out fruits, tunnelled, chewed or punctured fruits would indicate the presence of seed predators. Tiffney (1980) has described middle to late Oligocene seeds of *Zanthoxylum* (Rutaceae) with "bug holes."

I thank Dr. Harry Phinney for calling my attention

to B. C. Templeton's doctoral thesis (1964) entitled "The fruits and seeds of the Rancho La Brea Pleistocene deposits." The tar pits at La Brea are widely known for their vertebrate bone material, but as her thesis points out, they also include very finely preserved examples of seeds estimated to be of very late Pleistocene or early Holocene age (10-15,000 years old).

Templeton extracted several acorns from the tar matrix in excavated sabre-tooth cat skulls. Of the acorns figured in her dissertation, one is described as a "fossil acorn of Quercus agrifolia showing insect infestation" (legend from Templeton's Fig. 34). This acorn (No. PB 1481, Templeton collection, G. C. Page Museum) was borrowed for examination (Pl. 40, Fig. 1). It had been excavated from Pit A at Rancho La Brea. I recently found still another similarly damaged acorn in the Templeton collection (Pl. 40, Fig. 2). It had been removed from a sabre-tooth cat skull in Pit 3, and was of an undetermined species of oak (No. 1418B, Templeton collection, G. C. Page Museum). This acorn was also borrowed for examination. Both specimens had been cleaned with kerosene so that external features were evident. Comparisons with modern day acorns attacked by gall wasps were made using material from the L. H. Weld cynipid collections (California Academy of Sciences, and

Smithsonian Institution).

The La Brea specimen PB 1481 (Pl. 40, Fig. 1) consists of disrupted cotyledon tissue and remnants of the testa. The seed coat and cup are not present. The outer surface of the specimen bears 10 blister-like swellings that have deformed the cotyledons. The swellings are actually hollow chambers; in most cases the outer surface of the swellings has been worn away (or chewed through) so that an internal cavity is exposed. The swellings are ovoid, and measure 5 mm long, 4 mm wide, and 1.5 mm deep on the average.

The second acorn (1418B) shows remnants of the shell and hilum-like structure at the cup end of the seed. Damaged cotyledon tissue makes up the bulk of the specimen. This acorn bears 2 swellings on the cotyledons, and the swellings are hollow, sub-spherical, and measure 3 mm in diameter.

When the damaged fossil acorns are compared to modern day acorns that have been attacked by gall wasps (Pl. 40, Figs. 3 and 4), it is clear that the La Brea acorns have been galled, and that each galled acorn is a mass of several confluent sub-spherical chambers. A single cynipid larva lived within each chamber.

More specifically, the La Brea acorns are similar in structure to those galled by the extant _Callirhytis_

milleri Weld (Pl. 40, Fig. 5). This cynipid attacks acorns of Quercus agrifolia Nee, Q. wislizenii A. de Candolle, and Q. californica Cooper (= Q. kelloggii Newberry). Weld (1922) described the damage caused by this wasp as a

> compact stony-hard mass containing four to a score or more confluent cells (chambers)...more or less filling the interior of the acorn, which is frequently reduced in size. The woody mass thus occupies the center of the acorn..., extends its whole length, and when the acorn is cut open can be lifted out intact.

It is this woody mass that has been preserved in the La Brea specimens.

The development of acorn galls is poorly studied, but is presumed to be as follows. A female wasp oviposits eggs into young acorns. The developing larvae not only feed on the seed tissue, but stimulate young cotyledon tissue to proliferate so that soon, each larva is enclosed within a gall chamber. Pupation occurs in the chamber. The adults bore out through the chamber wall, and then through the seed coat (Weld, 1922). The holes in the chamber walls of the La Brea specimens may be exit holes through which cynipid adults escaped.

It appears that a species of cynipid wasp with gall-forming habits very similar to those of C. milleri galled the two Rancho La Brea acorns. A study of the internal structure and anatomy of the well preserved, tar

impregnated galls may be possible, but must await discovery of additional paratypic specimens.

Additional points about Rancho La Brea should be mentioned. First, all types of plant material have been excavated from the pits. For example, Templeton provides photographs of three tree trunks with portions of intact root systems that have been pulled from the pits. At least one trunk was identified as Cupressus arizonica var. Hancockii n. var.. Templeton frequently mentions "masses of plant material" or "quantites of plant material" or considerable brush and roots" that are mixed with bones. Leaves ("mostly parts"), twigs, wood and seeds (flowers?) have been observed. This abundance of plant material has, for the most part, been ignored.

Secondly, Templeton mentions that in processing material, she sorted out insect parts. Dr. William Akersten, Curator of the La Brea fossil collection, has indicated that most of the insect material is unstudied (but see Miller, 1978). Thus, there is a very good chance that much "interaction" material occurs in the pits and is awaiting study.

Thirdly, the plant material from the tar pits may provide plant tissue with a preserved internal structure. Scott (1972) describes sections of leaves taken from the pits that show cell protoplasm. As will be discussed,

the chance to section through fossil leaf tissue that has a preserved internal structure is one that should not be ignored.

Well preserved specimens of galled *Sequoia* seeds in cones from Miocene? deposits in Germany have also been reported (Mohn, 1960). The galls contained cecidomyiid larvae and pupae. The damage resembles that caused by members of the genus *Contarinia* to the seeds of Douglas fir in the Pacific Northwest (Furniss and Carolin, 1977).

3) *Bark and Stems*. Present day bark and/or phloem is frequently tunnelled by a variety of beetles. With this in mind, the tree trunks taken at La Brea should be scanned for beetle damage. Suss (1979) described pith flecks in Miocene conifers (e.g. *Pruninium*, *Callitris*) caused by cambium tunnelling agromyzids (*Phytobia*). The tunnels are filled with altered tracheids that preserve well. These filled mines (pith flecks) strongly resemble those caused by *Phytobia* in modern day hosts. Interestingly, however, the fossil specimens are gymnosperms, while extant *Phytobia* mine only angiosperm woods.

Stems are also frequently galled, but no example of a fossil galled stem is available. Stems may display extra-floral nectarys or spines. One clear example of

fossil stem spines on Crataegus is shown in an article by Berry (1925) on the Pleistocene plants of North Carolina. Axelrod (1956) describes a thorn from Crataegus middlegatei Axelrod. Berry (1925) refers to Pleistocene prickly twigs that resemble Rubus stems. Kellogg (1927) describes an imprint of a lower Eocene to lower Oligocene stem of Rosa hilliae that shows thorns (Pl. 40, Fig. 6). Spines from the Pliocene have also been described by Szafer (1946). All of these thorn specimens indicate that as early as the Eocene-Oligocene, plants had developed recognizable structural defenses.

The presence of intercalary meristems in grasses, if possible to detect in fossil grass stems, would suggest the presence of grazers. Knowlton provides plates of what he believes are grass stems and rhizomes in his 1925 paper. Templeton (1964) mentions that "grass or grass roots similar to Bermuda grass" have been found at La Brea. Additionally, Heer (1855) figures several Tertiary grass stems from Europe, many of which have attached crowns and roots. Thus, the material is available -- it merely needs to be studied.

(K. B. Leslie and C. H. Driver, from the University of Washington, have recently described a paleopathogen on grass stems taken from pack rat middens in Nevada (1981, paper presentation at Northwest Scientific Association,

Corvallis, OR). The material is estimated at 3500 years. Pironzynski (1976) reviewed the literature on fossil fungi. Fossil evidence for the association between fungi and plants dates from the Devonian. See Heer (1855) and Meschinelli (1898) for several figures of fossil plant parasitic fungi.)

4) Roots. Although many must exist, I have only Templeton's (1964) reference to preserved roots. She states that roots are very frequently encountered in the tar pits of La Brea. It would be interesting to know if these roots are galled (many extant oak bear cynipid root galls), or are damaged from chewing or tunnelling.

5) Leaves. With the exception of pollen and possibly wood, more fossil leaves have been collected, described and photographed than any plant part. Both internal and external features of leaves may suggest interactions with herbivores. One might wish for fossil material in which the internal cellular structure of the leaf had been preserved. Such material would be very valuable for at least two reasons. The presence of silica crystals (in grasses), calcium oxalate deposits (many plant families) or calcium carbonate crystals (Ficus) within the leaves might be observed (Esau, 1977).

The function of leaf crystals is unclear, but they may in part serve to deter herbivores. Silica crystals, for example, are thought to have influenced the dentition of grazing herbivores. In the same vein, the foliar anatomy of C4 plants (a type of photosynthetic pathway) has been suggested recently to intefere with herbivory (Caswell and Reed, 1975). Presumably, the foliar proteins in C4 leaves are bound in thick walled (easily preserved?) bundle sheath cells that may not be easily digested by an herbivore. This feature would be one that could only be detected in fossil material with intact internal leaf structure. Plant physiologists should have an interest in the search for such paleo-anatomical features.

Giannasi and Niklas (1981) have reported using biochemical techniques to identify several secondary plant compounds from Miocene leaf material. Niklas (1981) has also exhibited electron micrographs that show the ultrastructure of 20 million year old angiosperm leaves. This work should add a new dimension to paleobotanical and paleoecological studies.

External leaf features that suggest interactions include marginal spines, examples of which have been observed in fossil material from the Pleistocene (figured in Berry, 1925; Axelrod, 1964). Foliar spines undoubtedly occur on leaves of some of the 28 species of

Ilex that have been described from fossil material (Knowlton, 1898). Additionally, foliar investiture and/or glandular trichomes may deter herbivores. Their presence on the surface of fossil leaves (Scott, 1972) would be suggestive of deterrence, but as of yet, pertinent observations have not been checklisted.

Other external leaf features that point to interactions with insects include galls, mines, and domatia.

FOSSIL GALLS

Kinsey (1919) comments that it is almost pointless to attempt identification of the cecidozoan from preserved galls. He relys more on the promise of preserved gall insects. After scanning a leaf imprint collection, I would agree that difficulty exists in first, determining if a leaf blemish is a gall, and then, suggesting a causative agent. The more galls that are available to study, however, the easier it may be to identify the causal agent. Kinsey's remark begins to pale when specimens such as Mohn's (1960) are discovered.

Reports of galls in the North America and Europe follow. In most cases, fossil galls are compared to similar extant types. The reports are treated chronologically by publishing date, and are checklisted

in Table Fo-1. Trotter (1903) and Kuster (1911a) compiled lists of accounts of Tertiary galls. As of yet, I have been unable to track all of their references, but those that I have found are included.

1) Scudder (1886) states that "two or three" cynipid galls have been obtained from the Florissant. Kinsey states, however, that these galls are not caused by cynipids (1919).

2) Marty (1894) figured a cecidomyiid gall on Fagus from the Pliocene deposits of Pas-de-la-Mougudo.

3) Cockerell (1908) described a cecidomyiid gall (Cecidomyia (?) pontaniiformis sp. nov.) on the leaf of Myrica drymeja (Lx) from the Florissant Formation that "very closely resembles those formed by the species of Pontania (a genus of sawflies) on Salix. The gall is about 8 mm long, 5 mm broad, being contiguous to the midrib. Several examples were found." In the same paper he described galls on what is possibly a Salix leaf taken from the Florissant that he believed were caused by the eriophyid mite, Eriophyes (?) beutenmulleri sp. nov.. These were described as being "small subtriangular galls, about 2 mm in diameter, at the angles formed by the junction of the principal lateral veins of the leaf with the midrib; four galls on the leaf found, 2 to 5 mm apart." Extant genera of Salix are heavily galled by

eriophyoids and, it is possible that Cockerell's leaves were galled by mites. Both of these specimens should be confirmed, in as much as the published photographs are somewhat unclear.

4) Brues (1910) described a galled leaf on _Myrica obscura_ Lx. or _M. drymeja_ (Lx.) from the Florissant that he suggested was caused by a cynipid (_Andricus myricae_ sp. nov.). He mentioned that Lesquereux also figured galls that resembled this gall in early papers. Once again, the specimen should be reconfirmed and photographed. Houard (1922) describes an eriophyid leaf gall on _Myrica fava_ that does not fit Brues' description. This is the only described gall on extant _Myrica_. If both Cockerell's and Brues specimens of _Myrica_ are indeed galled, then one might suspect that the incidence of galling of this genus has changed through time.

5) Berry (1916) figures a gall on the petiole of _Cedrela puryearensis_ (Family: Meliaceae), and galls on _Rhamnus_ leaves from the Wilcox formation of Tennessee. He suggested that the _Cedrela_ gall was caused by a cynipid or hemipterans. The _Cedrela_ specimen resembles none of the described galls on extant species of _Cedrela_ (Houard, 1922). Berry suggested that the _Rhamnus_ galls were either cecidomyiid or aphid caused. Houard (1922) describes a cecidomyiid gall on 2 extant species of

Rhamnus, one of which resembles the fossil gall: "Small projecting growths on the upper surface of the leaf, very numerous, measuring from 0.5 to 3.0 mm in height; tinged green." Both fossil specimens should be studied further.

6) Cockerell (1927) mentioned the galls of Cecidomyia chaneyi on the leaves of Acer osmonti, and eriophyoid galls on alder leaves from the Bridge Creek Flora.

7) Hoffman (1932) published photographs of a preserved leaf of Quercus cognatus from the late Miocene shales of Douglas County, Washington. The leaf shows "25 gall-like impressions, circular in outline, ranged in diameter from 0.3 cm to 0.4 cm, and were characterized by a dotlike protuberance at their centers." He likened the galls to cynipid or cecidomyiid galls on extant oaks. Many species of cynipids are known to form spherical galls (frequently in large numbers) on the underside of oak leaves. The "dotlike protuberance" may be the imprint of the hard wall larval capsule.

8) Madler (1936) provided a photograph of a Tertiary petiole gall on Populus latior. The gall was probably caused by Pemphigus aphids.

9) Berger (1949) described a cynipid gall on Pliocene oak leaf material. He suggested that the gall was caused by Neuroterus.

10) Brooks (1955) described the preserved leaf galls on _Cupanites formosus_ from Puryear, Tennessee (Wilcox Formation: Eocene) that resemble "recent simple pouch galls like those produced...by gall mites (Eriophyidae), aphids (Aphidae), jumping plant lice (Chermidae=Psyllidae) and several other types of lowly arthropods." Cupanities is an extinct genus that resembles the extant genus _Cupania_ or _Cupaniopsis_ (Sapindaceae), both of which have leaf pocket galls recorded from New Calcedonia that are caused by eriophyoids and insects (Houard, 1922).

Brooks also provided plates of a gall on a leaf of _Nectandra pseudocoriacea_ (Lauraceae) from the same formation that "bears eleven well preserved cone galls. The structures are mammilliform and seem to be separated from the leaf by a constriction at the point of attachment." He goes on to say that "immediately surrounding the galls, the leaves are darkened which probably reflect sclerotized leaf tissue in the vicinity of the galls as the coloration is due to a greater amount of lignified leaf residue." He compares these galls to mite, psyllid, gall midge and gall wasp galls. Houard (1933) lists galls on _Nectandra_ from Central and South America, many of which are on the leaves, are stalked, and are caused by cecidomyiids.

11) Straus (1977) provided photographs of 34 leaf galls (the richest gall flora yet described) from the Miocene clay pits of Willerhausen, Germany. Included are many presumed mite, aphid, midge, and wasp galls.

12) Ambrus and Hably (1979) provided a photograph of a presumed eriophyoid gall on a Daphogene leaf from a Hungarian upper Oligocene deposit.

In summary, to my mind the clearest example of a fossil gall is that provided by Mohn (1960) from the Miocene. There are older specimens (Eocene), but many of these are equivocal. One can certainly say, however, that recognizable galls occurred in the mid-Tertiary.

GALL INSECTS

Brooks (1955) provides a list of those gall-forming arthropods that have been found in fossil material. Larsson (1978) briefly discusses the cynipid and cecidomyiid material that has been collected in baltic amber.

Southcott and Lange (1971) discovered an eriophyoid mite (a rust mite, I believe) in Australia (Eocene).

Preserved remains of insects that belong to a taxon that today contains gall-formers is suggestive, but does not definitely indicate that the fossil insects formed galls; all of the extant taxa containing gall-formers

also contain insects of non-gall-forming habits. Malyshev (1968), for example, suggested that the early members of the gall-forming lineage of hymenopterans were free-living.

"HIDDEN" FOSSIL GALLS

There is reason to believe that more fossil galls will be described. Collections continue to be made in deposits containing beautifully preserved leaves (such as those in Eastern Oregon). What is even more assuring is that undescribed examples of galled leaves are to be found in museum collections of fossils. For example, R. W. Chaney in 1920 reported that "leaf galls are present on a number of specimens" of *Quercus psuedo-lyrata* taken from the Eagle Creek Formation (Oligocene) of Northeast Oregon (collection housed at the Field Museum, Chicago). When one considers that Chaney reports collecting 1600 leaves of this species his "a number of" becomes significant, and yet, this statement has not been pursued. Chaney published no photographs of these galled leaves, and did not speculate as to the causative agent(s).

Another example suggestive of unnoticed gall material is provided by plates in Knowlton (1925). The petioles of three of these leaves of *Populus heteromorpha*

leaves from the Miocene of Spokane and Coeur D'Alene appear to have either been bent or thickened -- much like the early stages of petiole galls on poplars that are caused by *Pemphigus* aphids (Plate 39, Figs. 1 and 2) or *Ectoedemia* moths today.

In quickly scanning the collection of leaf imprints at the University of California at Berkeley Paleobotanical collection, I found six leaf imprints of various species of *Populus* that showed unusual petiole features (bent, curved, or thickened). Representatives are shown in Plate 39, Figures 3-7. All resemble early stages of aphid or moth petiole galls. Pertinent fossil specimens are available -- and await appreciation.

With the exception of Madler's work, larger petiole galls have not been observed, but work by Smith (1932) is suggestive. In her Master's thesis (University of Oregon) she studied the fossil flora of Rockville, Oregon (Malheur County). When describing the leaves of *Populus Lindgreni* Kn. she says,

> The base is either rounded or cordate, petiole not preserved. The specimens give the unique impression of having the upper part of the petiole lost in the substance of the leaf as in no instance is the midrib distinguishable in the lowest portion of the blade although it is very prominent above.

Such a comment should be pursued, for any abnormality observed in poplar petioles suggests the presence of

galls. Unfortunately her photographs are not clear enough to see this character of the leaves.

A SEARCH METHOD FOR DISCOVERING FOSSI GALLS IN COLLECTIONS

If one compares a list of fossil plant genera with a list of extant plant genera that are known to have galls, one should derive a list of fossil plant genera that could be expected to show plant galls (or mines, or domatia). I have compiled such a list. I used Knowlton's (1898) "A catalogue of the Cretaceous and Tertiary plants of North America," and various volumes by C. Houard and E. P. Felt that describe galls of the world.

Limitations of such a survey need to be mentioned. First, I assume that the floral distribution of galls was similar in the Cretaceous and Tertiary to that seen today. Also, Knowlton's list is old. More recent catalogues of this type are available but, at the generic level, Knowlton's is fairly up to date. His list does not distinguish between plants known only from pollen and those known from vegetative material. Also, his list includes only North American material. I do not know how such a list would change if world wide paleo-floras were included. In some cases I have been unable to determine

if a plant genus in Knowlton is extinct or extant. In terms of gall floras, Houard's volumes are as thorough as we have. Undoubtedly more galls exist than he described, but his list is a representative one.

Of the 384 fossil genera listed by Knowlton, 280 have no recorded galls on extant members, while 104 do. I do not know how many of the 280 genera that have no galls are extinct.

There are 26 genera that have both many fossil species (most likely, many fossil specimens) and a rich gall flora (Table Fo-2). Based on the number of fossil species and the richness of the gall flora, five of those genera are particularly apt to provide examples of galls. Both in the field and in museum collections, fossilized vegetative material of _Salix_, _Eucalyptus_, _Ficus_, _Populus_, and _Quercus_ should be thoroughly studied for galls. If I had one day in an extensive fossil leaf collection I would scan the oaks.

Knowing the type of cecidozoan responsible for galls on extant genera, one might more easily predict the type of gall that should be found in preserved material. Similarly, given the size, shape, and location of a fossil gall, one should have some idea of the gall-former. For this reason, I briefly list the cecidozoans, and the features of their galls.

- Nematode galls are predominantly found on roots - a plant part that is infrequently preserved.

- Eriophyid galls may be difficult to detect in fossil material because the galls are usually only a swollen bud, or a dense patch of hairs on the leaves, particularly at vein axes or along veins. If the mites form pocket or spherical galls on the leaves, the galls are frequently small and numerous.

- Aphids frequently cause leaf rolls or leaf crinkling. The spiral petiole galls caused by aphids on poplars should be fairly distinct.

- Thrips galls are primarily leaf rolls or small pimples on the surface of leaves, usually found many per leaf. These might be confused with mite galls.

- Psyllid galls are usually pit or pouch galls on leaves. They might be confused with midge galls.

- Scale galls are usually tubular swellings (the galls of males) on the leaves of Eucalyptus. The La Brea woody stem material should be checked for the presence of the common pit scale gall that occurs on many oaks.

- Beetles and moths generally form stem galls that should preserve nicely.

- Sawfly leaf galls are usually sub-spherical, contain frass, and are frequently found on Salix. Stem swelling on willows are often caused by a sawfly.

- Cynipid galls are morphologically diverse. Any gall on oak should first be suspected of being a cynipid gall (but see Kinsey, 1919).

- Cecidomyiid galls are variable in shape. They are usually foliar, and can involve everything from a leaf roll to a blister to a fairly large chamber. They occur on many host species.

FOSSIL LEAF MINES

Evidence is strong that by Upper Miocene the leaf mining habit was well established. New evidence from Poland pushes the habit back to the Cretaceous (Skalski, personal communication). Table Fo-3 compiles the published accounts of fossil leaf mines. Table Fo-4 indicates those extant plant families that host 3 or 4 orders of insect miners (from Hering, 1951). If miners' preferences for certain host plant families were similar in the past to those exhibited today, then those plant families listed in Table Fo-4 should contain examples of fossil mines. Thus, one would predict that at the generic level, *Populus*, *Quercus*, and *Salix* would likely contain mined paleo-specimens. (Fossil *Eucalyptus* leaves will also perhaps be found to contain mines -- see CSIRO, 1970.)

Using such predictions, I scanned the Berkeley

collection for mines and found the specimen shown in Plate 39, Figure 8. In Paul Opler's opinion (personal communication) this is a leaf mine (perhaps two) of Ectoedemia (Lepidoptera: Nepticulidae). It occurs on a leaf of Quercus nevadensis (Lesq.) from the La Porte flora of California (Potbury, 1935). The tunnel is linear and meanders near the edge of the leaf. The tunnel is raised above the level of the leaf imprint -- an unusual feature, in that all other fossil leaf mines that I have seen photographs of show little relief. The tunnel shows no frass (suggesting a microlepidopteran mine), and it crosses numerous leaf veins.

According to Hering (1951):

> We are familiar with mines in a fossilized condition only from the Tertiary. Pre-Tertiary specimens described as mines cannot be considered as such; they are in many cases other types of feeding patterns, mostly furrows in the leaves caused by worms lying at the bottom of lakes.

Unfortunately, he does not detail how worm damage can be distinguished from that of miners. In this regard, Crane and Jarzembowski (1980) provide useful criteria for recognizing fossil mines.

DOMATIA

These are structures on leaves that are used by mites as domiciles. They are not caused by the mites,

but once formed by the plant, are used by the mites. There is considerable interest in why plants should form domatia, and undoubtedly with additional work the association between the domatia and their inhabitants should become clearer. Here, however, I ignore the controversy and simply assume that domatia are leaf structures which are indicative of a plant-arthropod association.

Although many forms have been described, there are two basic types of domatia. One is a pocket that is formed by the leaf lamina at vein axils. A dense patch of hairs (erineum) at the vein axils constitutes the second type. Both types are found on the underside of the leaf. I have compiled a list of plant families (taken from Penzig, 1903) that have 10 or more species with domatia (Table Fo-5).

After scanning this table one would be tempted to look at rubiaceous fossil material (particularly, Coffea) for the presence of domatia. Knowlton (1898), however, lists none of the rubiaceous genera that Penzig tallies. In other words, rubiaceous material from North America, up to 1898, was unavailable, and is most likely still very scarce. Comments by paleobotantists at the 1981 AIBS meetings in Bloomington, Indiana, however, indicate that a few specimens of Rubiaceous fossil leaves exist.

Imprints of Aesculus (Family: Aesculaceae) or Tilia (Family: Tiliaceae) might provide first examples of erineal domatia. Straus (1977) describes what he suspects is a fossil erineal domatium on Tilia-like leaves (Pliocene). This is the only reference to fossil domatia.

SUMMARY AND CONCLUSIONS

I have attempted here to point out plant structures that suggest an interaction and that might fossilize. The task now is one of thorough examination of the fossils for these features.

In terms of host plant genera, Quercus seems to be a genus in which more work with fossil material will prove productive. "Few plants are so variously and so characteristically deformed by gall insects as are the oaks..." (Trelease, 1924). One could also add mines and domatia to the unusual features found on oaks. The abundance of Quercus leaves in North American fossil collections has been mentioned frequently (see Trelease, 1924, for a list of fossil species with collection site data).

Published evidence of paleo-herbivory is neither abundant nor compiled. Such evidence should, on the one hand, come from morphological features (e.g. mouthparts)

of the paleo-herbivores (only rarely mentioned in this review), and on the other hand, come from features of paleo-plants that suggest or demonstrate that herbivory occurred.

The relatively small number of published accounts of fossil specimens, and the uncertainty surrounding many of these specimens make detection of reciprocal changes through time in plant and herbivore difficult. Nonetherless, the recent increase in paleo-examples of mines and galls in the U.S. and in Europe indicates that these habits were well established in the Tertiary.

It is the degree of subsequent changes that is difficult to discern. Two examples suggest that shifts in host plant preference have occurred through time. Suss's stem-mining agromyzid that has presumably moved from gymnosperms to angiosperms is one such example. Likewise, no extant seed gall midges are recorded from _Sequoia_ in the western U.S., while several occur in cone of _Pinus_ and _Psuedotsugae_. Thus, Mohn's fossil _Sequoia_ cone midge suggests a host shift.

TABLE Fo-1

PUBLISHED ACCOUNTS OF FOSSIL GALLS*

Source	Plant	Cecidozoan	Age
Scudder, 1886	?	Cynipid	Oligocene-Miocene
Marty, 1894	Fagus	Cecidomyia fagi	Pliocene
Cockerell, 1908	Myrica drymeja	Cecidomyiid	Oligocene-Miocene
"	Salix	Eriophyoid	"
Brues, 1910	Myrica obscura	Cynipid	Oligocene-Miocene
Berry, 1916	Cedrela	Cynipid or hemipteran	Eocene
"	Rhamnus	Cecid or aphid	Eocene
Chaney, 1920	Quercus pseudo-lyrata	?	Oligocene
Cockerell, 1927	Acer osmonti	Cecidomyia chaneyi	Upper Miocene
"	Alnus carpinoides	Eriophyes laevis	"
Hoffman, 1932	Quercus cognatus	Cynipid or cecid	Miocene
Madler, 1936	Populus latior	Pemphigus	Upper Miocene
Berger, 1949	Quercus	Neuroterus	Pliocene
Brooks, 1955	Cupanites formosus	Stylet-bearer	Eocene
"	Nectandra	?	Eocene
Mohn, 1960	Sequoia langsdorfii	Sequoiomyia krauseli	Miocene
Straus, 1977	Several	Several	Pliocene
Ambrus and Hably, 1979	Daphnogene bilinica	Eriophyes daphonogene	Upper Oligocene

* See Trotter (1903) and Kuster (1977a) for additional examples.

TABLE Fo-2

GENERA OF FOSSIL PLANTS ON WHICH

GALLS ARE LIKELY TO BE FOUND

Acacia	Celtis	*Ficus	Pistachia	*Salix
Acer	Cinnamomum	Grewia	*Populus	Spirea
Amelanchier	Crataegus	Juniperus	Prunus	Tilia
Betula	*Eucalyptus	Pinus	*Quercus	Ulmus
Carex	Eugenia	Piper	Rhus	Viburnum
				Vitis

*Richest fossil remains, and extant members most commonly galled.

TABLE Fo-3

PUBLISHED ACCOUNTS OF FOSSIL MINES

Source	Plant	Miner	Formation
Berry, 1916	Several	Lepid. : Tineidae	S. E. North America
Berger, 1949	*Cinnamomum* ?	Agromyzidae	Sarajevo
Brooks, 1955	*Proteoides wilcoxensis*	Lepid.: Nepticulidae	Wilcox
Freeman, 1965	?	Lepid.: *Lithocolletis* ?	White Lake, B. C.
Opler, 1973	Several (*Quercus*)	Lepidoptera	Western U.S.
Hickey and Hodges, 1975	*Quercus* ?	Nepticulidae	Latah
"	*Cedrela*	Lepid.: *Phyllocnistis*	Wind River
Straus, 1977	Several	Several orders	Willershausen
Crane and Jarzembowski, 1980	?	*Nepticula*, *Phytomyza*, *Bucculatrix*, *Stigmella*,	Woolrich and Reading

TABLE Fo-4

PLANT FAMILIES ATTACKED BY MINERS

(From Hering, 1951)

Those plant families mined by four orders of insects:

Juncaceae	Ranunculaceae
Salicaceae	Rosaceae
Betulaceae	Geraniceae
Ulmaceae	

Those plant families mined by three orders of insects:

Graminae	Capparidaceae	Campanulaceae	Labiatae
Orchidaceae	Cruciferae	Aceraceae	Scrophulariaceae
Fagaceae	Crassulaceae	Tiliaceae	Plantaginaceae
Polygonaceae	Leguminosae	Malvaceae	Caprifoliaceae
Chenopodiaceae	Tropaeolaceae	Primulaceae	Dipsacaceae
Caryophyllaceae	Oleaceae	Gentianaceae	Compositae

TABLE Fo-5

EXTANT PLANT FAMILIES SHOWING DOMATIA

Family	No. of species with domatia
Apocynaceae	12
Bignoniaceae	21
Cornaceae	15 (mostly *Cornus*)
Fagaceae	22 (mostly *Quercus*)
Lauraceae	18
Oleaceae	23 (mostly *Fraxinus*, *Jasminum*, *Linociera*, and *Olea*)
Rubiaceae	156 (56 genera)
Solanaceae	14 (mostly *Solanum*)
Tiliaceae	32 (mostly *Elaeocarpus*)

APPENDIX 3: GALLS OF IMPORTANCE TO HUMANS

When considered in sum, gall-forming organisms are economically and scientifically important. When one realizes that such a group encompasses everything from nitrogen-fixing bacteria to fig pollinating wasps, a diversity of activities and impacts should be expected.

This appendix has a two-fold purpose. First, it contains a checklist of gall organisms that are important to humans. Although long, the list is undoubtedly not complete. Perhaps most disturbing are the omissions that result from our North American - European bias. Although briefly covered here, the Oriental and Tropical galls will undoubtedly contribute more to such a list in future years.

Secondly, during the course of reviewing the important galls, I detected patterns that suggest reasons for the destructive or non-destructive nature of plant galls. I also noticed a convergence in anatomical features of the host-parasite interface. A discussion of these patterns will be integrated with the descriptions of the galls. In the summary and conclusions I will discuss what these patterns indicate about the usefulness of galls.

Galls are significant either because of the damage they cause to crops, or because of their potential benefit to humans. I have organized the appendix with these two types of impact in mind.

DETRIMENTAL GALL-FORMING ORGANISMS

The most familiar and studied gall-forming organisms are those that cause damage to crop plants. Most crop damaging gall-formers are either pathogens or nematodes - there are few gall-forming mites or insects that are considered crop pests.

The purpose of this section is to review the detrimental gall-forming pathogens, nematodes, and insects. Possible reasons for the difference in agricultural importance between gall-forming pathogens and arthropods will be also discussed.

1) Slime Molds. The most important slime mold plant pathogen is the clubroot organism, *Plasmodiophora brassicae*. As is indicated by the common name, this pathogen causes an abnormal swelling of the roots. Crucifers are the most susceptible plants, and when a field becomes infested not only is the current year's crop lost, but the field can never be replanted with crucifers. Resistant plant varieties have only been

marginally useful (Agrios, 1973).

The slime mold invades the root system via wounds or root hairs. Moving intracellularly within the host root, the plasmodium spreads from the cortex to the cambium and then into the xylem. The invaded root cells are frequently stimulated by the pathogen to a hypertrophic and hyperplastic state such that their overall size is five times that of the normal cell. The nuclei and nucleoli of the infected cell are also greatly enlarged, and the cytoplasm of these cells is abnormally dense and fine-grained (Stevens, 1925; Williams, 1966).

Meristematic host tissue, such as the cambium, is more susceptible to invasion and alteration by the pathogen than is non-meristematic tissue. Damage to the host plant is caused by the diversion of foodstuffs to the diseased tissues (Mitchell and Rice, 1979) as well as by the disruption of the transport system through the roots. Wilting and stunting are common above-ground symptoms.

2) Bacteria. *Pseudomonas savastanoi* causes tumors on the stems of *Oleander* spp.. The bacterium produces indole acetic acid which presumably affects plant cells that neighbor the bacterial colony such that they are enlarged and multinucleate. The enlarged cells

eventually undergo cytokinesis such that many cells are formed from each enlarged cell. The new cells are meristematic, and have a denser cytoplasm, and more prominent nuclei and nucleoli than do normal cells (Strobel and Mathre, 1970).

Of all detrimental gall-forming organisms, the most thoroughly studied is crown gall. This is a disease primarily of fruit trees caused by the bacterium, *Agrobacterium tumafaciens*. Diseased plants generally grow poorly, show reduced yield, and if severely infected, may die. Galls are usually located at the stem-root junction of the plant.

Crown gall bacteria enter the host through wounds and move within the crown tissue intercellularly. Host cells near the bacteria become hyperplastic, and multinucleate. Rapid division by these cells results in a fleshy mass of undifferentiated parenchymatous tissue with an unorganized vascular system. The growth of the gall crushes adjacent normal tissue. Vascular transport from the roots to the stem and leaves is frequently reduced one half to one fifth the normal flow (Agrios,1973).

We now know that the hyperplasia, or oncogenecity of host plant cells caused by the bacteria is incited or induced by genes on a plasmid which are transferred from

a bacterium to the plant cells. The mechanism of plasmid transfer between parasite and host, and between host cells, however, is not clear (Lippincott and Lippincott, 1975).

Besides becoming hyperplastic, the multinucleate invaded host cells also produce relatively large amounts of basic amino acid analogs (e.g. nopaline, octopine). The role of these compounds is unclear, but the intriguing suggestion has been made that these compounds, produced by plant cells, are used by the bacteria as food. According to this scenario, genes carried on the bacterial plasmid that invade the host cell nucleus direct that cells to produce compounds which the bacteria can use, but which the plant cell cannot use, or can only poorly use (BCGRG, 1979).

The study of crown gall has contributed substantially to our understanding of the transformation process (normal to hyperplastic) in a gall. We do not know, however, the extent of similarities between crown gall and other types of galls. For example, plasmid tranfer is not suspected in insect galls, but at the same time, we do not understand how insect saliva induces rather specific changes in host plant cells. Additionally, we know relatively little about the products of the increased metabolism in nutritive cells,

and one wonders if these cells synthesize products tailored to the needs of the cecidozoan.

There is no reason to suspect that a single gall-forming process is shared by all gall-forming organisms. The point is, however, that for the first time the process is described well enough in one type of gall that we can begin a comparative inspection of other galls. The detrimental impact of crown gall disease pales slightly as its usefulness as a laboratory organism increases.

3) Fungi. Table Hu-1 lists those genera or species of fungi that cause a hyperplastic and/or hypertrophic response in the infected host tissues. Undoubtedly other gall-forming species exist, but the list should at least be representative.

I studied descriptions of each of these galls and noted the following shared characteristics. Sources I used include Anderson (1956), Curtis (1921), Dickson (1947), Jones and Dreschler (1920), Stevens (1925), and Stewart (1915).

A) The pathogen interferes with the plant hormone system. Usually if hormone balance has been studied, an increase in the amount of these compounds (e.g. auxins, gibberrelins, or cytokinins) at or near the infected

tissue is observed (Agrios, 1973). The increase may be caused in various ways, but in well studied examples the pathogen both produces the hormones itself, and induces the host tissue to produce the hormone (e.g. *Ustilago maydis*, *Gymnosporangium juniperi-virginianae*, and *Gibberella fujikuroi*) (Agrios, 1973).

B) Many of the more serious gall diseases are those that attack the subterranean plant parts or crown (e.g. potato wart, crown wart of alfalfa), or the reproductive structures (e.g. plum pockets, ergot, smuts). Galling of the roots or crown disrupts translocation, while galling of either the roots or fruits may destroy the harvestable portion of the plant.

C) Frequently the infection site is a meristematic tissue (e.g. *Ustilago*, *Urophlyctis*, *Taphrina*). Whether this is coincidental or an actual requirement for gall initiation in these plant pathogens is not clear.

D) The host plant cells found in close proximity to the pathogen frequently become hypertrophied and hyperplastic. The nuclei and nucleoli of the plant cells may be found more than one per cell, and/or are frequently enlarged (Strobel and Mathre, 1970; Mims and Glidewell, 1978).

In at least one example, that of the crucifer white rust (*Albugo candida*), infected plant cells have a

cytoplasm richer in ribosomes than do normal cells (Agrios, 1973). Ultrastructural studies of plant cells invaded by haustoria of rust fungi (e.g. *Puccinia*, *Melampsora*, *Gymnosporangium*) are instructive. Micrographs indicate that a rich band of cytoplasm encircles the haustorium. "Virtually every study of...haustoria shows cisternae of ER lying parallel to the extrahaustorial membrane" (Littlefield and Heath, 1979). Usually ribosomes are associated with these ER. Additionally, the haustorium is usually closely associated with the host nucleus. Future studies of the response of invaded host plant cells should consider when and where enrichment occurs.

Lastly, Dennis Gray (personal communication, North Carolina State University) observed isolated, highly enriched cortical cells in galls caused by *Gymnosporangium*. In summary, a statement made by Strobel and Mathre (1970) should be pursued:

> It is not too unusual to expect that cytological features of tumorous tissues would in many ways resemble normal meristematic tissue.... An increase in the size of the nucleus and the amount of cytoplasm per cell are additional features that may be associated with cells in tumors.

4) *Nematodes*. Two genera of plant parasitic nematodes are infamous for the root galls that they

cause. Members of the genus *Heterodera* are commonly called cyst nematodes, while those of *Meloidogyne* are known as root-knot nematodes. Damage caused by these nematodes is frequently very heavy (yield reductions of 30-75%). They both cause stunting, chlorosis, and frequent wilting of the above-ground parts as well as reduced photosynthetic rates (Loveys and Bird, 1973). The root system is also stunted and bears many individual spherical cysts (dead, egg-filled bodies) in the case of cyst nematodes, or show a general swelling due to the coalescence of numerous irregularly shaped root-knot galls.

In both cases when the larvae settle to feed in the root, the head of the nematode is usually near to, or in the pericycle (sometimes the cortex). Within a few days after the larva settles, the cells that surround its head begin to enlarge. Nuclear divisions in these cells occurs without cell wall divisions. Existing cell walls may also break down, so that by the time that the feeding site is completely established, 3-6 syncytia, or giant cells, encircle the head of the nematode (Agrios, 1973; Bird, 1974). The giant cells usually possess enlarged nuclei and nucleoli, as well as a cytoplasm that is rich in proteins, free amino acids, and nucleic acids (Owens and Novotny, 1960; Bird, 1961).

The nematode functions as a metabolic sink in the root (Bird and Loveys, 1975). Loveys and Bird (1973) showed that infested tomatoes had depressed photosynthetic rates soon after infestation when compared to uninfested plants. Additionally, the giant cells may disrupt or crush existing xylem elements. Tissues surrounding the feeding site also exhibit hypertrophy and hyperplasia, and a disrupted vascular system frequently results. Translocation of root-produced hormones may be disrupted (Bird, 1974). It would be interesting to know what portion of the damage caused by root-knot is caused by the nutrient sink and, what by the vascular disruption. The thoroughness with which root-knot has been studied increases the chance that this will be the first eucaryote-caused gall that will be thoroughly explained.

5) Mites. Jeppson et al (1975) mention many injurious eriophyoid mites, but most are rust mites, not gall mites. These authors do mention, however, that galled plants are frequently stunted. Metcalf, et al (1962) list no gall-forming eriophyoids as economically important.

6) Insects.

A) Cecidomyiids. In four volumes, Barnes (1946a,b,1948,1956) discusses the impact of about 450 species of cecidomyiid midges on various crop plants. Of those 450 species approximately 45 cause an economically important amount of damage to their host plants. Of those 45, only 17 species cause damage by actually galling the plant. Most of the midges that damage plants feed on, but do not gall, the seeds of plants (Barnes, 1956). Also, midge leaf galls rarely cause significant damage unless found, as with *Procontarinia mattiana* on mango, in very high numbers.

The most important cecidomyiids that form galls are the rice gall midges (*Pachydiplosis oryzeae*, and *Orseolia oryzae*) (Hidaka, et al, 1977) in tropical Asia. The midges attack cultivated rice, and use wild rice as a secondary host. Up to 84% destruction of tillers has been recorded. No description of the galls are given by Hidaka, but his photographs suggest that the stems are swollen by the midges.

A variety of cecidomyiids gall either the needles or twigs of conifers. According to Furniss and Carolin (1977), however, "none is a major forest pest." Some may be serious pests of ornamental conifers, and in some years *Contarinia oregonensis* Foot, by galling the coat of Douglas fir seeds, may be "the most destructive species"

of seed insects on this plant (Furniss and Carolin, 1977).

The Hessian fly is the most well known destructive cecidomyiid. Its larvae, however, do not form galls, but instead suck the saps from stem tissues, and thus cause a dwarfing of the plant.

B) Other Diptera. Stinner and Abrahamson (1979) showed that "a gall insect (either a tephritid fly or a gelechiid moth larva) represents a loss to a goldenrod plant of over 6,000 calories or approximately 6 percent of "production."" Harnett and Abrahamson (1979) found a 32-43% decrease in reproductive effort of the galled goldenrod ramet. Furthermore, parasitism of the gall-former decresed the impact of the gall by about 2000 calories. Although goldenrod is not a cultivated crop, I mention the above work because of the careful measurements of damage to the host plant.

C) Scales. Oak pit scale, a general term for galls on the twigs of deciduous and evergreen oaks, caused by members of the homopteran family, Asterolecaniidae, can cause die-back of twigs and death of a tree if infestation occurs year after year (Koehler, 1977).

D) Aphids. In the late part of the nineteenth century, the grape phylloxera (*Phylloxera vitifoliae* (Fitch) was accidentally introduced into Europe on grape

roots shipped from the U.S.. The phylloxera quickly became a pest in vineyards on the continent; the leaves and roots of European vines were heavily galled by the various life stages of the aphid-like homopteran (Pl. 40, Fig. 7). Mortality of vines became so extensive that the wine producing industry was threatened. It was only after resistant rootstocks from North America were grafted onto European scions that the industy recovered. In the U.S. the insect usually galls the foliage and causes minimal damage (Sterling, 1952; Borror and Delong, 1971).

In his study of the anatomy of *Phylloxera* leaf galls, Sterling (1952) noted that the upper surface of young leaves was attacked most frequently. The insect's stylet was usually inserted three cell layers deep into the leaf, and once inserted, it remained in the same spot for the life of the insect. (The life stage is not indicated by Sterling -- it is most likely the stem mother.)

Hyperplasia was most intense 15 cells away from the puncture site, and there was actually a depression of mitotic activity near the stylet. The cells in layers I and II, at about 15 cells away from the stylet, developed enlarged nuclei and nucleoli, and small vacuoles. Starch grains appeared in these cells. Small vascular bundles

were seen in the nutritive zone. Sterling likened this zone to that seen in other types of insect galls.

Other gall-forming aphids that cause economically important damage include species of Pemphigus (Aphididae: Eriosomatinae). The winter host of this genus is Populus. In the summer the aphids move from the leaf galls on poplars to the roots of either crucifers, chenopods, or composites. P. bursarius L., for example, attacks lettuce roots (Dunn, 1959), while summer generations of P. populi-transversus Riley move to roots of numerous crucifers (e.g. cabbage, broccoli, brussels sprouts, cauliflower, and turnips) (Jones, 1918). P. populivenae Fitch moves from poplar to roots of sugar beets (Grigarick and Lange, 1962). Members of these species do not produce galls on the summer host, but instead, remain exposed on the surface of the roots, and suck plant saps. One of the earliest symptoms of infestation is wilting of above ground parts. Damage to cultivated crops may be "considerable" (Grigarick and Lange, 1962).

A closely related genus, Eriosoma (Aphididae: Eriosomatinae), contains species that gall the leaves of elms in the spring and early summer. In the summer, aphids leave the galls and migrate to pomaceous fruit trees. Members of E. lanigerum (Hausemann) gall apple

roots and crowns. Twigs may also be attacked, but generally are not galled. Damage to the roots "sometimes causes the death of the tree, stunting, or serious retardation of growth" (Metcalf, et al, 1962). _E. pyricola_ Baker and Davidson causes a cockcomb leaf gall on elm. In the summer the aphids migrate to pear roots. Damage is caused by removal of plant sap, but no root galls are formed. The aphid can become a serious pest on European rootstocks (Swenson, 1969).

E) _Adelgids_. The adelgids attack only conifers. The sexual stage form pineapple-like galls on the twigs of various species of _Picea_. On secondary hosts (e.g. _Pinus_, _Pseudotsuga_, _Abies_) the asexuals occur on bark in large cottony masses. _Adelges piceae_ (Ratz.), a native of Europe, is a major forest pest. This insect may cause damage to, or death of Pacific silver fir, Subalpine fir, or Grand fir in the Pacific Northwest. In addition to the pineapple gall, these aphids gout twigs, and frequently cause compression-like wood at attack sites on the bole. This last form of damage can cause tree death if infestation occurs over several years (Furniss and Carolin, 1977).

Summary of Detrimental Galls

There are relatively few recorded gall-forming

insects that are pests of crop plants. I suggest that there are three reasons why this is so. First, the galls formed by seed-dwelling insects are sometimes difficult to detect. Many of the gall-midges, for example, that feed in seed heads may actually gall the ovary without this damage being noted. Such omissions in the literature would bias perceived trends.

Secondly, the majority of insect galls occur on leaves (Mani, 1964), while very few attack roots. The pattern observed with bacterial, fungal, and nematode galls shows, however, that galling of the roots or crown causes the most extensive damage. Phylloxera is a case in point. This is one of the few gall insects that attacks roots. When roots are attacked, the host plant usually dies, but if leaves are attacked, the host plant often survives. Why damage to roots should be of more detriment to the plant is not clear.

Perhaps the important factor, however, is not so much the tissue attacked, but the extent of attack. Most bacterial and fungal galls arise during the systemic infection of the host, so that large amounts of host root tissue are involved. Insect galls, on the other hand, are generally more localized. Whole leaves are rarely galled, much less whole branches. Localized galling may lead to less direct destruction of host plant tissues.

Thirdly, relatively few gall-forming insects attack crop plants. Instead, for unknown reasons, a very large percentage of them attack non-crop perennials, such as *Quercus* and *Salix*. (I do not know if the Australian timber industry considers scale galls on eucalypts as economically important pests.)

Additionally, most gall-forming insects are poor dispersers and have no spore stage that allows for extended periods of dormancy. Annual and biennial crops may escape most gall-forming insects in time. Gall-forming slime molds, bacteria, fungi and nematodes, on the other hand, saturate the soil with dormant propagules so that even annuals are attacked.

The above speculations may not be supported by patterns that emerge from future studies, say, of tropical agricultural systems. In the face of seeming convergence of traits in the gall-forming guild, however, it becomes interesting and important to perceive and understand any basic differences between groups of gall-forming organisms.

Lastly, Hering (1951) describes leaf miners that cause economically significant damage on sugar beet and crucifers. Metcalf et al (1962) mention only miners on cabbage and *Chrysanthemum* as being of economic importance. Both sources mention that mines may serve as

portals for disease entry. It would be interesting to scan this group of endo-phytophagous insects for behavioral or life-history characteristics that may be correlated with pest status.

BENEFICIAL GALL ORGANISMS

Historically galls have been used as a source of tannin in the production of hides, inks, and dyes. In a few instance galls were used as food, or in medicinal salves (Fagan, 1918). The commercial production of figs still depends upon an agaonid wasp (*Blastophaga psenes*) for pollination of the crop. The wasp lives in the fig flowers, galls some of the ovules, and with adult dispersal, pollinates the flowers (Borror and Delong, 1971).

The most beneficial of all gall-forming organisms are members of the nitrogen-fixing bacterial genus, *Rhizobium*. Estimates of amounts of nitrogen fixed by these nodule-inhabiting bacteria are given as 450 kilograms per hectare per season (Raven, Evert and Curtis, 1976).

The nitrogen fixing nodule is an unusual root gall in that unlike all other galls, the relationship between the bacterium and the host plant is mutualistic, not

parasitic. The bacterium receives reduced carbon compounds from the host plant, while the host plant receives fixed nitrogen produced by the bacterium.

The intimate association between bacteria and host plant cell has been described by Dart and Mercer (1964). The bacteria invade meristematic root cells that possess relatively large nuclei in a young nodule. Once invaded, a number of cytoplasmic changes ensue. The number of plate-like endoplasmic reticulum increases, as does the number of proplastids, miotochondria, and Golgi bodies. There is also an increase in the number of ribosomes following invasion. Starch is actively synthesized. Vacuolation stops. Cell expansion occurs. The nucleus becomes granular which suggests that activity which is usually restricted to the nucleolus (ribosome synthesis, for example) is distributed throughout the nucleus. There are numerous large gaps in the nuclear membrane suggesting that rapid exchange between cytoplasm and nucleus is occurring. The invaded cells are undoubtedly actively producing ribonucleic acids and proteins. Eventually as the transformed bacteria, the bacteroids, divide, they occupy most of the cytoplasmic space in the cell. The increased metabolism and cytoplasmic characterstics of the invaded nodule cell are similar to those seen in nutritive cells in many types of galls.

Galls as Bio-control Agents

Ever since the dramatically successful use of imported insects to control species of the cactus, *Opuntia*, in Australia, biological control has been an often used option in the war against weeds. Organisms that have been used in control programs include fungi (Wilson, 1969), nematodes (Watson and Shorthouse, 1979), and insects (Goeden, 1978).

Leaf-chewing beetles and leaf-chewing lepidoptera have been the most frequently used insects in biological control (Goeden, 1978). Apparently this mode of feeding causes considerable damage to the host weed. There is no question but what defoliation is a very visible type of damage, so that both the farmer and scientist can immediately see results of such bio-control efforts.

In a few instances, however, insects other than leaf chewers have been used in bio-control programs. Table Hu-2 lists published accounts of bio-control efforts in which a gall-forming organism has been used, or in which a gall-former has been suggested for use.

The purpose of this section is to describe the cases in which gall insects have been used in weed control efforts, and then to speculate upon how characteristics of the gall-forming syndrome influence the effectiveness

of gall-formers as control agents.

Case 1. The most successful use of a gall insect has been with a tephritid fly, *Procecidochares utilis* Stone, on the composite *Eupatorium adenophorum* Sprengel. Crofton weed, as the plant is called commonly, is a native of Mexico and was imported as an ornamental into Hawaii, Australia, and New Zealand. Soon after introduction it escaped cultivation to become a serious pasture weed. The gall fly was introduced into Hawaii in 1945, into Australia in 1952, and into New Zealand in 1958. In all three cases, substantial to moderate control of the weed by the fly has been observed. This is inspite of the fact that native parasites may cause 75% mortality in the flies in Australia.

The gall fly is highly host specific. It attacks only *E. adenophorum* in Mexico where five other species of *Eupatorium* occur. Damage to the host plant is believed to be due to disruption of the vascular system caused by the numerous galls per stem. Stem death, and a reduction in growth in both above- and below-ground plant parts result from attack.

Interestingly, the flies are also suspected of vectoring the fungus, *Cercospora eupatorii*, that attacks, and in some cases, devastates stands of Crofton weed in

Australia. This is one of the few instances in which a gall insect has been implicated in vectory of a plant pathogen.

Case 2. St. Johnswort (*Hypericum perforatum* L.) was one of the first weeds of arable fields targeted for biocontrol. The weed is not only aggressive, but also contains a compound that in small doses may cause skin irritation in livestock and in large doses, death. In those countries where the introduced weed became a problem (Australia, United States, New Zealand, Canada and Chile) the leaf chewing chrysomelid beetles, *Chrysolina hyperici* and *C. quadrigemina*, provided good control in open areas.

A less successful bio-control agent, the gall-midge *Zeuxidiplosis giardi* (Kieff.) has been imported into the affected countries from Europe. In most instances the midges failed to survive transit (the adults are fragile, and short lived) or introduction. If they survived, they performed poorly. The midges cause galls on the leaf buds, and according to some reports, if the attack is heavy, the midges can markedly reduce the vigor of the attacked host plant (Holloway and Huffaker, 1953).

Case 3. Since their introduction into North America

in the early 1950's , the knapweeds (*Centaurea* spp. and *Acroptilon* spp.) have become pests in North America. A symposium held in 1977 in Kamloops, British Columbia assessed the effectiveness of bio-control programs directed against the weeds. Two species of tephritid flies, *Urophora affinis* Frfld. and *U. quadrifaciata* (Meigen), were introduced into British Colulmbia in the early 1970's as possible control agents. Both species cause galls in the seed heads of *C. diffusa* (diffuse knapweed) and *C. maculosa* (spotted knapweed).

On the average, 3.5 *Urophora* galls occur per flower head of spotted knapweed and 1.6 occur per head of diffuse knapweed. This high incidence of attack is attributed to the lack of parasites and diseases on *Urophora* in North America (Harris, 1977a).

Harris (1977a) estimated that the gall flies were responsible for a 75% reduction in seed production in both species. The spread of the weed is thought to have been slowed by the gall fly attack.

In interesting contributions to the symposium, Harris (1977b) and Shorthouse (1977a,b) stress that galls are metabolic sinks, i.e. from inception they draw upon nutritional sources other than those of the attacked organ (Jankiewicz, et al, 1969). Thus the damage caused by gall-formers should include not only the disruption or

destruction of attacked organs, but also the drain on plant resources that lasts for as long as the gall-former feeds.

The effects of this drain are observed in figures provided by Harris (1977b). Each larva of *U. affinis* accounted for the direct destruction of 1.1 seeds (about 10 calories) in a spotted knapweed head. Each mature larva and gall in a knapweed head together represented 33.2 calories. Using typical conversion efficiency figures, Harris estimated that for each gall larva to have accumulated the calories that it did, it must have fed on 114 calories of energy provided by the plant. Thus, the energy required by the developing gall and larva was great enough that sources outside of the seed head must have been tapped. Based on this observation Harris estimated that each *U. affinis* actually causes the destruction of 4.4 diffuse knapweed seeds, and 8-9 spotted knapweed seeds. The difference in amount of destruction on the two host plant species is believed to be due to differences in flowering phenology. These figures provide the first suggestion that the damage caused by galls may be more extensive than what initially meets the eye.

Based on work done during his doctoral thesis, Watson (1975) recommended the use of the nematode,

Paranguina picridis Kirjanova and Ivanova, as a control agent against Russian knapweed (*Acroptilon repens* (L.) DC.. The nematode causes galls on the stems, leaves and root-collars of attacked plants. The host specificity of the nematode was extensively tested, and results indicated that a few host plant species closely related to Russian knapweed were attacked. Russian knapweed, however, was the only species rated as susceptible to the nematode. All other tested hosts showed some tolerance (feeding sites in gall were poorly developed) or resistance (extensive cell necrosis in gall) to the nematode. Ivanova (1966), in Russia, estimated that the nematode infected 100% of the knapweed and that 20-30% of the plants were destroyed.

Case 4. Canada thistle (*Cirsium arvense* (L.) Scopoli), a native of Eurasia, has been introduced to Africa, North and South America, Australia, and New Zealand. It has aggressively invaded extensive arable acreage. Watson and Shorthouse (1979) studied the affect of the polyphagous nematode, *Ditylenchus dipsaci* (Kuhn) Filipjev on thistle. The apical stem galls caused by the nematodes led to chlorosis near the gall, and a retardation in plant growth. Stems became twisted and frequently died, perhaps because of the disruption of

cortical and vascular systems. The internal structure of the nematode gall was also studied, and was seen to include a layer of enriched nutritive cells.

In a number of reports (Shorthouse, 1977a,b; Shorthouse and Watson, 1976; Watson and Shorthouse, 1979), the suggestion has been made that of the tissues in a gall, the nutritive tissue requires the heaviest metabolic investment by the host plant, i.e. the nutritive tissue is a strong metabolic sink. If the strength of such a sink is positively correlated with damage to the host plant, then based upon the amount of nutritive tissue seen in the gall, the amount of damage that a gall-former inflicts upon a plant should be predictable. The greater the amount of nutritive tissue, the greater the host plant damage. As support for this idea Shorthouse and Watson (1976) mention that two species of tephritids that attack Canadian thistle incite galls with no nutritive tissue (this observation should be pursued), and cause less damage to the host plant than do tephritids that form galls with nutritive tissue.

D. Berube (personal communication), on the other hand, suggests that a better predictor of host plant damage caused by a gall-former is the amount of tanniferous tissue in the galls. Such tissues are frequently found in the peripheral zones of a gall.

Tannins, he argues, are more abundant than, and more energetically expensive to produce and store than are the compounds found in nutritive cells.

Another physical indication of sink strength (damage caused) may be the amount of vascular tissue servicing the gall. To my knowledge this possibility has not been considered. The possiblilty that morphological evidence can be used to increase the efficiency with which control agents are selected is strong enough that it should be pursued.

Other Cases. Shorthouse and Watson (1976) briefly mention that the gall wasp, *Gilletea taraxaci*, has potential use as a biocontrol agent of dandelion. This is the only mention in the bio-control literature of a cynipid gall wasp.

The gelechiid moth, *Crasimorpha* sp. was introduced into Hawaii from Brazil in the mid-1950's to control Christmas berry (*Schinus terebinthifolius* Raddi). The moth causes stem galls. It was not, however, successfully established in Hawaii after repeated introductions (Goeden, 1978).

A species of gall-forming eriophyid mite (*Aceria chondrillae*) and a gall midge (*Cystiphora schmidti* G. Canestrini) have been tested as control agents against

skeleton weed (<u>Chondrilla</u> <u>juncea</u>), an important weed in Australia, and a spreading problem in the United States. The midge shows promise in trials, and further testing of the mite has been encouraged (Sobhian and Andres, 1978).

Summary of Beneficial Galls

There are three characteristics that affect the suitability of gall-forming organisms as bio-control agents.

First, it is usually true that gall-formers are host specific (strictly monophagous). A single species or a small group of related species of host plants are attacked. For example, gall insects have been used as taxonomic characteristics to separate sub-species of host plants (McArthur et al, 1979), or to detect hybridization between closely related species of host plants (Cooper-Smith, 1974). Even in the case of a presumably polyphagous species such as the gall-forming nematode, Ditylenchus dipsaci, suspicions are that the species is made up of biological races that are monophagous (Watson and Shorthouse, 1979).

The specificity exhibited by gall-formers fulfills one of the criteria required of bio-control agents, and in fact, may be the one attribute of gall-formers that makes them most attractive as possible bio-control

agents. Non-target plants are not attacked.

Specificity, however, may be correlated with features that decrease the gall-former's weed-controlling potential. Conditions that allow for successful attack by gall-formers may be so rigidly set that, when introduced into a new environment, the gall insect mis-cues, or fails to detect cues. Mating flights of adult gall midges that attack sagebrush occur, for example, at only certain temperatures and for only brief periods during the day, as does oviposition (Jones, 1971). Dispersal ability of the adults is usually poor.

Perhaps most importantly, however, successful gall induction requires that host plant tissue in the proper developmental state (meristematic) be attacked. The insects must track the plant's phenology. Because of their strict temporal, behavioral, and physiological requirments, gall insects may be prone to failure when introduced into environments that require shifts in responses.

Secondly, gall insects are frequently heavily parasitized. To what extent this is true of other gall-forming organisms is not clear. Perhaps because of the nature of the resource (a rich source of food that is sheltered from the elements), a gall and its former

attract parasitoids and inquilines. Special precautions against the introdution of parasites should be taken whenever a gall-former is used in a bio-control program. Harris's concern about the chance of introducing *Urophora* parasites into Canada if consignments from Europe are continued is well founded. He suspects that the effectiveness of *Urophora* in Canada is in part explained by the fact that when introduced, the fly escaped many of it parasites.

Thirdly, perhaps because of the seemingly tight co-evolution between gall-formers and host plants the amount of damage caused by some gall-formers may be minimal. As Shorthouse (1977a) states "it is a commonly held opinion that plant galls do little damage to their hosts." Such a view runs counter to the goals of bio-control programs where damage to the host plant is the goal. Shorthouse (1977a) was the first to challenge the view that gall formers are benign. As already discussed, the damage caused by a gall, although perhaps not a dramatic necrosis, nonetheless occurs through time as a drain on plant resources (Jankiewicz, et al, 1969; Harris, 1977b; Stinner and Abrahamson, 1979). What is unclear, however, in the vast majority of examples is the amount of damage. One can predict that for greatest damage to host plants, bio-controllers should use

gall-formers that attack roots, stems, and seeds.

Conclusion

Some gall-forming organisms are clearly either of detriment or benefit to humans. This statement rings true particularly when the non-arthropod gall-formers are considered. If a species of bacterium causes a plant gall, usually it has an impact (positive or negative) on humans.

Interestingly, however, the majority of arthropod gall-formers are neither directly beneficial nor detrimental to human welfare. Gall-forming insects are perceived as benign curiosities. We must move to the laboratory to envision how such curiosities may assume an important role in agriculture and medicine in the near future. The questions of how galls are formed, and of how the gall-former directs host plant cell metabolism become increasingly important as we attempt to manipulate genetic expression in plant and animal cells.

TABLE Hu-1

GALL-FORMING FUNGI

Fungus	Disease
Class: Phycomycetae	
Order: Chytridales	
Synchytrium endobioticum (Schilb.) Perc.	Potato wart
Synchytrium vaccinii Thomas	Cranberry wart
Urophlyctis alfalfae (Lagerh.) P. Mag.	Crown wart of alfalfa
Physoderma zeae-maydis Shaw	Brown spot of corn
Order: Peronosporales	
Albugo candida (Pers.) Roussel	White rust of crucifers
Class: Ascomycetae	
Subclass: Pyrenomycetes	
Order: Hypocreales	
Claviceps purpurea (Fr.) Tel.	Ergot
Nectria galligena Pores.	Apple stem canker
Gibberella fujikuroi	Bakanae of rice
Subclass: Discomycetae	
Order: Taphrinales	
Taphrina deformans (Fcl.) Tul.	Peach curl
Taphrina pruni (Fc.) Tul.	Plum pockets
Class Basidomycetae	
Subclass: Teliosporae	
Order: Ustilaginales	
Ustilago maydis (DC.) Cda.	Corn smut
Order: Uredinales	
Cronartium spp. Fries	Pine blister rusts
Gymnosporangium spp. Hedwig	Cedar apple rusts
Subclass: Hymenomycetae	
Order: Agaricales	
Exobasidium spp.	Azalea/Rhodedendron leaf gall

TABLE Hu-2

PUBLISHED ACCOUNTS OF GALLS
USED IN BIOLOGICAL CONTROL EFFORTS AGAINST WEEDS

INSECT	TARGET WEED	REFERENCE
Procecidochares utilis Stone	Eupatorium adenophorum	Dodd, 1961; Goeden, 1978
Zeuxdiplosis giardi (Kieff.)	Hypericum perforatum	Holloway and Huffaker, 1952
Urophora affinis Frfld.	Centaurea maculosa	Harris, 1977a
Urophora quadrifasciata (Meigen)	Centaurea diffusa	Harris, 1977a
Paraguina picridis Kir. and Ivan.	Acroptilion repens	Watson, 1975
Ditylenchus dipsaci (Kuhn) Filipjev	Cirsium arvense	Watson and Shorthouse, 1979
Crasiomorpha sp.	Schinus terebinthifolius	Goeden, 1978
Aceria chondrillae (Canes.)	Chondrilla schmidti	Sobhian and Andres, 1978