ADVANCES IN THE STUDY OF MITE GALLOGENESIS AND ITS COMPARISON WITH THE DEVELOPMENT OF INSECT-INDUCED GALLS

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ABSTRACT: The present article reviews the main parasite–host model systems that have been used in recent studies in the molecular genetic analysis and in the investigation of the morpho-functional traits of mite gallogenesis on the leaves of angiosperms. The aforementioned works focused on the development of galls with a chamber, while other types of mite galls, including the most simply organized (erinea), remain virtually unstudied. Our article discusses the possible role of endosymbiotic bacteria in the induction of mite gallogenesis, as well as changes in the adaxial-abaxial polarity of the leaf and the expression of host plant genes during gallogenesis. The need for additional testing of the hypothesis regarding the participation of bacteria of the genera *Wolbachia* and *Rhodococcus* in the induction of gallogenesis is demonstrated. We have revealed certain convergent similarities in the gallogeneses induced by the grape phylloxera and by the gall mites. In particular, in both instances, the nutritive tissue is formed, the primary gall-inducing stimulus is produced by the feeding of females on young leaves, and the gall formations are accompanied by the abaxialization of the leaf. A review of the literature suggests that the Hearn's hypothesis about the similarity of arthropod gallogenesis with the somatic embryogenesis of plants, as well as Wolpert's embryological concept of the positional information in its classical form, are not appropriate for the modeling of gallogenesis. Finally, a new impetus for the study of gallogenesis could be provided by the studies that investigate the link between the genetic heterogeneity of different zones of the leaf blade and the developmental patterns of galls formed in these zones under the influence of plant parasites.

KEY WORDS: mite–host systems, gall-forming arthropods, gene expression, leaf polarity, symbiotic bacteria, somatic embryogenesis

INTRODUCTION

Galls (cecidia) are specialized structures that develop on plants as a result of their interaction with various parasites, primarily herbivorous arthropods and nematodes (Sinnott 1960; Ferreira *et al*. 2019; Harris and Pitzschke 2020; Raman 2021). Among the known gall-formers are about 500 species of acariform mites (Eriophyoidea: Eriophyidae and Phytoptidae; Tetranychoidea: Tenuipalpidae). These tiny phytophages (their sizes range from 100 to 300 μm) stimulate the formation of acarocecidia on various organs of the angiosperms, most often on leaves (Petanović and Kielkiewicz 2010; Chetverikov *et al*. 2015; Desnitskiy and Chetverikov 2022). According to various authors, the estimated total number of gall-forming insect species (from the orders Diptera, Hemiptera, Hymenoptera and Lepidoptera) ranges 13,000–211,000 (Stone and Schönrogge 2003; Espírito-Santo and Fernandes 2007; Hardy and Cook 2010; Takeda *et al*. 2021). Both insect-induced galls and mite-induced galls—that develop out of host plant tissues—provide the parasitic arthropods living within them with nutrition, as well as with protection from predators and adverse environmental conditions. Thus, in a sense, the gall-forming arthropods act as "ecosystem engineers" (Jones *et al*. 1994). However, they would be more appropriately termed "microhabitat engineers".

More than a hundred years ago, an important assumption was made that during gallogenesis (cecidogenesis), arthropods "have gained control of the differentiation and morphogenetic mechanisms, so that animal factors come to expression in plant tissue" (Wells 1921: 375). However, at the molecular level, these processes began to be intensively studied only in recent years. There is more relevant data on insect-induced galls (Cambier *et al*. 2019; Hearn *et al*. 2019; Schutz *et al*. 2019; Takeda *et al*. 2019, 2021; Korgaonkar *et al*. 2021; Martinson *et al*. 2022; Stern and Han 2022) than on mite-induced galls (Paponova *et al*. 2018; Anand and Ramani 2021a; Klimov *et al*. 2022; Yang *et al*. 2023). In this paper, we summarize the results of the latest research on the formation of mite galls on leaves, primarily the molecular-genetic and cellular aspects of this process. We compare the developmental patterns of leaf galls induced by the members of different arthropod groups. In some cases, we use the information on insect galls and compare them with acarocecidia. Next, we consider several model parasite-host systems from modern experimental studies of mite gallogenesis

on leaves. We then move on to compare the recent data on acarocecidia with some data on the development of leaf galls induced by the grape phylloxera, *Dactulosphaira vitifoliae* Fitch, 1855 (Hemiptera: Phylloxeridae). Finally, we critically discuss the applicability of two embryological concepts to gallogenesis: the concept of positional information (Wolpert 1969, 1978) and the perspective of viewing arthropod galls as modified somatic embryos (Hearn *et al.* 2019).

RESULTS AND DISCUSSION

Variations in the development of leaf galls induced by arthropods

Galls are extremely diverse in appearance, shape, and internal structure (Mani 1964). All major gall characteristics are dictated by the species of the host plant and the parasite. Recently, several attempts have been made to classify the zoocecidia induced by the insects and mites (Isaias *et al.* 2013; Chetverikov *et al.* 2015; Corvalho-Fernandes *et al.* 2016). Nonetheless, a general theory explaining this variability is yet to be developed (Desnitskiy *et al.* 2023).

The development of leaf galls of acariform mites (Eriophyoidea: Eriophyidae and Phytoptidae), wasps (Hymenoptera: Cynipidae), flies (Diptera: Cecidomyiidae) and butterflies (Lepidoptera: Gracillariidae) is associated with the formation of nutritive tissue rich in proteins, carbohydrates and/or lipids. This tissue serves as a lining of gall chambers, in which parasitic mites or insects live and use it as their food source (Rohfritsch 2010; Raman 2011; Ferreira *et al.* 2019; Miller and Raman 2019). However, such typical nutritive tissue is absent in galls that are induced by aphids (Hemiptera: Aphididae) and jumping plant lice (Hemiptera: Psyllidae) (Arduin *et al.* 2005; Ferreira *et al.* 2017). In this case, the gall chambers are surrounded by the so-called "nutritive-like tissue". While rich in proteins and lipids, it is not thought to be a food source for the insects inside, which suck the nutrient-rich phloem sap from the conductive bundles (Ferreira *et al.* 2017, 2019). However, the structure and the functions of this tissue in the galls of aphids and jumping plant lice are not completely understood. It should be noted that the typical nutritive tissue is present in the galls induced on grape leaves by another representative of the hemipteran insects, the grape phylloxera (Álvarez *et al.* 2021).

The ability to induce cecidogenesis in different phylogenetic lineages of insects and mites has arisen independently and repeatedly (e. g., Ronquist *et al.* 2015; Giron *et al.* 2016; de Araújo *et al.* 2019; Chetverikov *et al.* 2021). The first interactions with host plants occur in different ways, depending on the arthropod group. In the case of the galling acariform mites, aphids and phylloxerans, the primary inducing stimulus for leaf gall formation is produced by the salivary glands of females when they start feeding (de Lillo and Monfreda 2004; Ferreira *et al.* 2019; Korgaonkar *et al.* 2021; Stern and Han 2022). By contrast, in the case of gall wasps of the family Cynipidae (Hymenoptera), the primary gall-inducing stimulus is egg laying in the leaf tissues (Ferreira *et al.* 2019). In the process of oviposition, the secretions released by the female's venom glands or ovaries could stimulate cecidogenesis (Cambier *et al.* 2019). In the case of gall-forming representatives of moths (Lepidoptera) and flies (Diptera), the primary signals do not come from adults, but from the saliva of feeding larvae, which damage the epidermal cells of the host leaves (Rohfritsch and Shorthouse 1982; Ferreira *et al.* 2019). It has been suggested that the excrement of these larvae could also play a role in gall initiation (Takeda *et al.* 2021).

An interesting example of an unusual pattern of insect cecidogenesis is associated with the moth *Caloptilia cecidophora* Kumata, 1966 (Lepidoptera: Gracillariidae), which damages the leaves of the subtropical tree *Glochidion obovatum* von Siebold (Phyllanthaceae). The first and second instars of *C. cecidophora* are leaf-miners. They produce galleries within the host plant leaf lamina during the process of their feeding, and they do not have any gall-inducing properties. Gall induction is initiated only by the third instar, which releases a cecidogenic substance that has not yet been analyzed (Guiguet *et al.* 2019).

Returning to the data on the diversity of leaf galls, it is interesting to compare erinea (filzgals), the most simply organized mite galls, with an example of the more complex structures discussed above—pouch galls, characterized by the presence of a gall chamber (Fig. 1; it should be noted that cases of an erineum induction by galling insects are not yet known). Erinea-inducing mites cause the intensive growth of trichomes (hairs or emergences), the structure of which depends on the plant and mite species. As a result, around the sites where the epidermis was punctured by the mites' stylets,

a leaf area densely covered with hairs, termed erineum, is formed. Mites form colonies in erinea, feed on the sap of growing trichomes and epidermal cells, reproduce and move freely from one erineum to another. The principal difference between erinea and "real (complex)" leaf galls is that during the
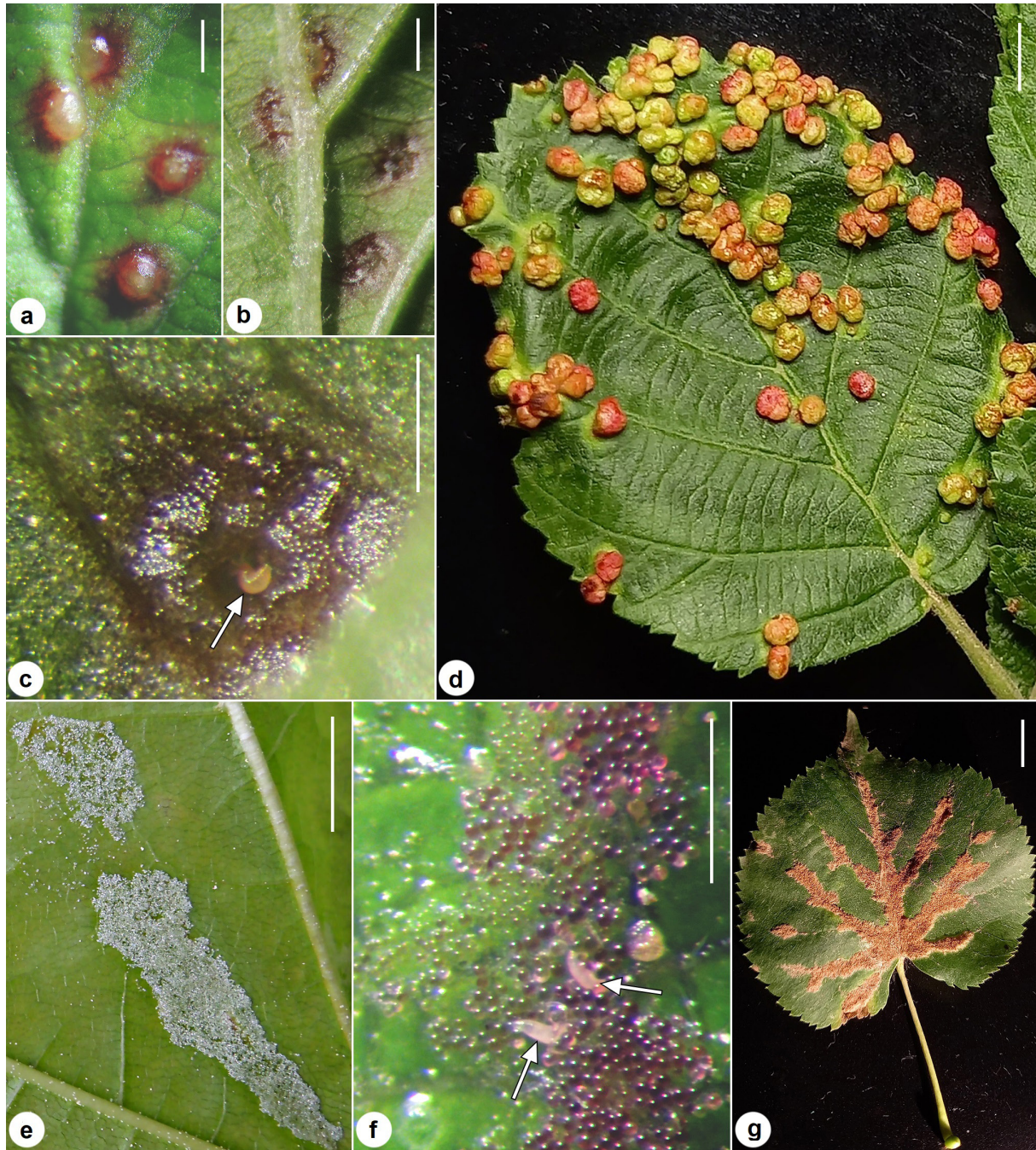

Fig. 1. Leaf galls with a chamber (a–d) and erinea (e–g) of eriophyoid mites. a, b, c, d—pouch galls of the mite *Eriophyes laevis* Nalepa, 1889 on a leaf of the alder *Alnus incana* L.: a and b—young galls at the initial stage of gall chamber formation (a—adaxial side of the leaf, b—abaxial side of the leaf); c—an overwintered female feeds on the sap of adaxial epidermal cells and induces the formation of a gall; d—galls on a mature leaf; e—erinea of the mite *Aceria platanoidea* Nalepa, 1922 between the veins on the abaxial side of the leaf of the maple *Acer platanoides* L.; f—two overwintered females of the mite *Acalitus longisetosus* Nalepa, 1892 induce the formation of an erineum of vesicular trichomes on the adaxial side of a young leaf of the birch *Betula pendula* Roth; g—erinea of the mite *Eriophyes nervalis* Nalepa, 1918 along the veins of a mature leaf of the linden *Tilia cordata* Mill. Scale bars: a, b—1 mm; c, f—0.5 mm; d, e, g—1 cm. Photographs by P.E. Chetverikov.

formation of erinea, there is no strong curving of the leaf blade and no gall chamber is formed (Mani 1964; Westphal 1992). Inside the erinea, eriophyoid mites are relatively well-protected from predators, e.g., from phytoseiid mites. This situation temporarily isolates the mite population from external influences.

The erinea, being the most simply organized, are possibly the ancestral type of mite galls (Westphal 1992). However, we cannot exclude the possibility that the simplified organization of the erinea does not represent an ancestral state, but is the result of a regressive evolution of the close relationship between parasite and host. Finally, it cannot be completely ruled out that among the various "erineum-forming mite–plant systems", there may simultaneously be not only those which are the ancestral type of mite galls, but also those in which a more complex gall has been simplified, regressing to the erineum form. In general, the problem of the evolution of the types of damage caused by gall mites remains poorly studied, and the questions of the origin and the relationships of various patterns of gall morphogenesis remain open.

Parasite–host models in the modern studies of mite gallogenesis and the problem of identifying factors contributing to gall formation

Detailed studies on the formation of galls induced by eriophyoid mites on the leaves of angiosperms have been published sporadically over many decades (e.g., Kendall 1930; Hesse 1971; Kane *et al.* 1997). However, this did not lead to the emergence of a universal model system adopted by later authors. The most detailed experimental analysis of acarocecidogenesis in the twentieth century was the work carried out by the group led by E. Westphal (e.g., Westphal *et al.* 1981; Westphal 1982, 1992;

Westphal and Manson 1996). The main model system included the eriophyoid mite *Aceria lycopersici* Wolffenstein, 1879 (=*Eriophyes cladophthirus* Nalepa, 1898) (Eriophyidae) (Lamb 1953) and the subshrub *Solanum dulcamara* L. (Solanaceae) (bittersweet nightshade). Westphal's work on this parasite–host system was reviewed in detail in one of our earlier publications (Desnitskiy and Chetverikov 2022) and is not discussed here. However, this model system was not subsequently used by other authors, possibly because only 36% of mite-infested plants formed galls, and the remaining plants were resistant to the gall-forming effects of parasites. In another parasite–host system, consisting of the eriophyoid mite *Eriophyes padi* Nalepa, 1889 (Eriophyidae) and the common bird cherry, *Prunus padus* L. (Rosaceae), it was shown that the formation of pouch galls is a multistep process (Westphal 1992, Fig. 9-3), which is characterized by an increasing complexity of morphological organization during successive stages of development (from the rudimentary state to a fully formed gall with nutritive tissue). The degree of gall development depends on the duration of exposure to the mite. Nevertheless, this parasite–host system has also not been subsequently used by other authors, perhaps because of difficulties associated with cultivating a bird cherry tree and the associated mites under laboratory conditions. The multistep pattern of the formation of pouch galls induced by mites was confirmed in later studies on other experimental systems (Paponova *et al.* 2018; Anand and Ramani 2021a, b). Table 1 provides a list of model systems used for the experimental (mainly molecular-genetic) analysis of mite gallogenesis over the past six years.

An ideal model for studying mite gallogenesis should have the following properties: (1) a plant that is small in size, easy to cultivate, viable, fast growing, and preferably herbaceous; (2) a mite that

Table 1. List of the principal gall-forming mite–host plant pairs that have been experimentally studied (mainly molecular-genetic investigations) over the past six years

Taxonomic position of parasitic species	Mite species	Host plant species	References
Acariformes, Eriophyoidea, Phytoptidae	*Fragariocoptes setiger*	*Fragaria viridis* (Rosaceae)	Paponova *et al.*, 2018; Klimov *et al.*, 2022
Acariformes, Eriophyoidea, Eriophyidae	*Aceria pongamiae*	*Pongamia pinnata* (Fabaceae)	Anand and Ramani, 2021a, b
	Aceria pallida	*Lycium barbaricum* (Solanaceae)	Yang *et al.*, 2023

is common and widespread in nature (which would simplify the process of dealing with the potential loss of culture). In addition, the availability of the host and parasite genomic and transcriptomic data through public databases is desirable. It would seem that many monocotyledonous plants—grasses or bulbous plants—could be suitable for this purpose. However, mites do not form galls on them; galls are formed mainly on dicotyledonous plants. Taking into account the above-mentioned characteristics, a model was proposed that included a *Fragariocoptes setiger* Nalepa, 1894 (Phytoptidae) mite and the green strawberry, *Fragaria viridis* Weston (Rosaceae) (Chetverikov *et al*. 2016), with which the most substantial data on mite gallogenesis have been obtained over the last decade (Paponova *et al*. 2018; Klimov *et al*. 2022). In studies using this model, the data on the changes in the expression of regulatory genes, leaf polarity and the potential involvement of mite endosymbionts in gallogenesis have been obtained.

Possible role of bacteria in mite gallogenesis

Over the past few years, the idea of a possible connection between the formation of arthropod galls and the activity of symbiotic bacteria inside them has been repeatedly suggested (Chetverikov *et al*. 2015; de Lillo *et al*. 2018; Gätjens-Boniche 2019). This assertion can be indirectly supported by the fact that some bacteria induce plant tumors, which, however, are not called galls (Raman 2011; Miller and Raman 2019).

Let us now consider the experimental system consisting of the mite *Aceria pongamiae* Keifer, 1966 (Eriophyidae) and the *Pongamia pinnata* (L.) Pierre (Fabaceae) deciduous tree, recently studied by Anand and Ramani (2021a). Bacteria, isolated from gall tissues thoroughly washed in detergents and alcohols, were inoculated and grown in Petri dishes and then identified, based on the sequencing of a fragment of the 16S rDNA gene. Based on the results of molecular barcoding, the bacteria from the galls were assigned to the species *Staphylococcus arlettae* Schleifer *et al*. (MH842166, MH842167, MH842168) and *Priestia flexa* Gupta *et al*. (MH842169). According to Anand and Ramani (2021a), the growth of galls on *P. pinnata* is initiated by mite saliva, and the subsequent development of the gall depends on the bacterial community, primarily *S.* a*rlettae* and *P. flexa*, colonizing the gall and causing gall mor-

phogenesis. The authors also report that the gall endobiome, in their opinion, is formed mainly by those bacteria that are already present on the surface or in the tissues of the plant before it is infected by mites. In our opinion, this hypothesis is dubious for two reasons. Firstly, the bacteria identified by the authors may consist of contaminants, since they are not specific symbionts of arthropods or plants and are typical for such substrates as soil, skin and the feces of vertebrates, cotton tissue, marine silt, and the rhizosphere of willow roots (Schleifer *et al*. 1984; Gupta *et al*. 2020). Secondly, the existence of a gall mite species can hardly depend on such a variable and rather random factor as the composition of the microbiome of the host plant leaves.

Recent works on the comparative transcriptomics and genomics of gallogenesis under the influence of the mite *F. setiger* on the strawberry, *F. viridis* (Klimov *et al*. 2022) and the wasp *Biorhiza pallida* L., 1758 (Insecta, Hymenoptera, Cynipidae) on oak *Quercus robur* L. (Fagaceae) (Hearn *et al*. 2019) did not provide a definitive answer to the question of the obligate participation of symbiotic bacteria in the formation of galls. However, during metagenomic analysis, in the samples of the strawberry gall mite, *F. setiger*, the gene fragments of symbiotic bacteria of the genera *Wolbachia* Hertig, *Rhodococcus* Zopf, *Pseudomonas* Migula, *Agrobacterium* Conn and *Erwinia* Winslow *et al*., known for their ability to induce new pathological morphogeneses in plant tissues, were identified (Klimov *et al*. 2022). As a result of the comparison of the transcriptomic and genomic assemblies, it was concluded that if bacteria are indeed involved in mite gallogenesis on strawberries, then the most likely gall-initiator is *Wolbachia* (Klimov *et al*. 2022).

There is published evidence on the possible participation of *Wolbachia* in the distortion of normal leaf morphogenesis. One example involves caterpillars of the moth *Phyllonorycter blancardella* Fabricius, 1781 (Insecta: Lepidoptera: Gracillariidae) (Kaiser *et al*. 2010; Zhang *et al*. 2017), which form leaf mines on the apple tree *Malus domestica* Borkh. (Rosaceae). *Wolbachia*, located in their labial glands, increase the level of cytokinins (phytohormones), which apparently modify the normal developmental process, leading to the formation of galleries inside the leaf blade.

Recently, *Wolbachia* were shown to influence the relationship of the phytopathogenic (but not

gall-forming) spider mite *Tetranychus urticae* Koch, 1836 (Acariformes: Tetranychidae) with its host plant through its effects on the secretion of the mite's salivary proteins (Bing *et al*. 2023). This suggests the potential ability of *Wolbachia* to modulate the protein composition of mite saliva, which may serve to induce gallogenesis.

Finally, in a model system consisting of the parasitic fly *Iatrophobia brasiliensis* Rübsaamen, 1907 (Insecta: Diptera: Cecidomyiidae) and the tropical shrub *Manihot esculenta* Crantz (Euphorbiaceae), the induction of galls appears to be caused by changes in the composition of plant microbiome and the genetic transformation of plant cells (Gätjens- Boniche *et al*. 2023). Based on the obtained data, the authors argue that the insect, as a result of laying eggs and feeding the larvae, introduces components of the gall-specific endophytic community into the leaf blade. The aforementioned community was isolated from the heads of the larvae and studied in culture, primarily *Rhodococcus* spp. and several other species of endosymbiotic bacteria. The symbionts transferred by the fly genetically transform the leaf cells from which the galls are formed. The developed hypothesis was confirmed by experiments involving the inoculation of an isolated line of *Rhodococcus* sp. into cultured sterile cassava leaf tissue, which resulted in the formation of gall-like structures within 1–2 weeks (Gätjens-Boniche *et al*. 2023).

The studies of the endosymbionts of moth, spider mite, and fly discussed above show the desirability of further detailed analysis aimed at elucidating the possible role of symbiotic bacteria, primarily of the genera *Wolbachia* and *Rhodococcus*, in the induction of galling.

Changes in the adaxial-abaxial leaf polarity and host plant gene expression during mite gallogenesis

Recent papers on the parasite–host systems of *A. pongamiae–P. pinnata* (Anand and Ramani 2021b) and *F. setiger–F. viridis* (Paponova *et al*. 2018) are in agreement that there is a change in the adaxial-abaxial (dorsal-ventral) polarity of the leaf during the formation of pouch mite galls. The essence of this phenomenon is that the histological analysis performed by both groups of researchers showed that the ventral structures (transformed epidermis and mesophyll) were formed on the dorsal side of the leaf blade.

Of particular interest is the gall-forming system of *F. setiger–F. viridis*, in which changes in the adaxial-abaxial polarity of the leaf were demonstrated by both histological and molecular-genetic methods (Paponova *et al*. 2018). In the above study, the authors analyzed the expression of the *FviYAB2* and *FviAS2* genes, which are homologs of the *YAB2* and *AS2* genes of the model dicotyledonous plant *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae). It is known that antagonistic interactions of a number of genes are responsible for establishing the adaxial-abaxial polarity of the leaf (Yamaguchi *et al*. 2012; Manuela and Xu 2020), and that *AS2* and *YAB2* are among the genes whose expression is specifically associated with the development of the adaxial (upper) and abaxial (lower) sides of the leaf blade, respectively. During the formation of galls induced by mites on strawberry leaves (Paponova *et al*. 2018), there is a more than tenfold increase in the expression level of the *FviYAB2* gene, which is involved in the control of the normal development of the abaxial surface of the leaf, and an approximately sevenfold decrease in the level of expression of the *FviAS2* gene, which regulates the development of the adaxial surface. The morphological and genetic changes in leaf tissues during gallogenesis that lead to the transformation of dorsal-ventral polarity have been called "abaxialization" (Paponova *et al*. 2018).

Using the same model—the *F. setiger* mite and *F. viridis* (green strawberry)—it was shown that at the stages of initiation and the early growth of leaf galls, the expression of the cell cycle genes *FviCYCD3* and *FviCYCB1* increases, which is associated with the active proliferation of leaf cells. The expression of these genes decreased sharply at the stage of gall maturation. Similar dynamics of expression changes during mite gallogenesis on strawberry leaves was also shown for the homeobox genes *FviWOX* and *FviKNOX* (Paponova *et al*. 2018). The homeobox genes, *WOX* and *KNOX*, are universal regulators of normal ontogenesis in *Arabidopsis* (Conklin *et al*. 2020). In another molecular-genetic study performed on a model system consisting of the mite *Aceria pallida* Keifer, 1964 (Eriophyidae) and the wolfberry shrub *Lycium barbarum* L. (Solanaceae)—a medicinal plant from East Asia—the expression of genes associated with both chlorophyll synthesis and photosynthesis was significantly suppressed during leaf gall formation. At the same time, the expression of

genes associated with mitochondrial energy metabolism, transmembrane transport and the synthesis of carbohydrates and amino acids was significantly enhanced (Yang *et al*. 2023).

In all the models used for the experimental study of mite gallogenesis on leaves discussed in this section of the article, we were considering the formation of galls with the chamber lined with nutritive tissue. It is necessary to note that much less attention has been paid to the development of erinea. Recent work by Freitas *et al*. (2023), using two parasite–host pairs from South America, did not identify both species of eriophyoid mite that cause the formation of erinea. The above publication does not contain data on the molecular-genetic or the cellular aspects of gallogenesis; it is concerned with purely ecological aspects of gall formation under different climatic conditions and is, therefore, not considered herein.

A comparison of galls of eriophyoid mites and of phylloxera

The galls of the grape phylloxera, *D. vitifoliae*, which lives on the leaves of the coastal grape *Vitis riparia* Michaux (Vitaceae), have a typical nutritive tissue (Álvarez *et al*. 2021). In this regard, phylloxera galls are similar to mite galls, but different from the galls of other Hemiptera from the families Aphididae and Psyllidae, which do not have this tissue (Ferreira *et al*. 2017, 2019).

Mite gallogenesis, as a result of convergent evolution, is more similar to the gallogenesis caused by phylloxerans than to that caused by insects from other families and orders. In both cases, the primary gall-inducing stimulus is produced by miniature adult females feeding on young leaves (Mani 1964). In addition, a change in the adaxial-abaxial polarity recorded during the formation of galls induced by the mite *F. setiger* on the leaves of the strawberry, *F. viridis* (Paponova *et al*. 2018), was also found during the formation of phylloxeran galls on grape leaves (Nabity *et al*. 2013). In this case, the gall-forming activity of the parasitic insect caused the formation of stomata on the adaxial side of the grape leaf, where stomata are not normally found.

A recent study of the same parasite–host pair—phylloxera and coastal grape—provided data on the partial implementation of the reproductive development program during phylloxera gallogenesis (Schultz *et al*. 2019). The activation of genes associated with the development of reproductive structures—flowers and fruits—including the *LFY*, *AG*, *SEP*, *SHP*, *CAL* and *FUL* genes, was detected. However, studies of mite gallogenesis that would target the activity of genes associated with reproductive development have not yet been conducted.

Arthropod galls and somatic embryogenesis

The formation of somatic embryos from carrot callus cells in cell culture conditions was described more than 60 years ago and was called "somatic embryogenesis" (Steward *et al*. 1958). During this process, one or more somatic cells form an embryo, which passes through the globular, heart and torpedo stages characteristic of zygotic embryogenesis, finally forming a fertile plant (Zimmerman 1993; Horstman *et al*. 2017; Méndez-Hernández *et al*. 2019; Elhiti and Stasolla 2022). Hearn *et al*. (2019) proposed a hypothesis according to which galls induced by the wasps of the family Cynipidae can be considered "modified somatic embryos", with their development being similar to somatic embryogenesis in plants. The same authors used a model involving the wasp *B. pallida* and the leaves of the *Q. robur* oak. They showed that the expression of *ENOD* genes increased in the tissues of young galls. These genes were initially discovered in the nitrogen-fixing nodules of the legume family (Fabaceae), and later in many other angiosperms, especially in developing flowers (Mashiguchi *et al*. 2009). The nodulin-like proteins encoded by these genes belong to the large family of arabinogalactan proteins, which are glycoproteins involved in plant growth and development, including somatic embryogenesis (Showalter 2001; Kishor *et al*. 2015; Ma *et al*. 2017). These proteins are similar to metazoan proteoglycans, which are important for morphogenetic processes in multicellular animals and are involved in the transmission of intercellular signals (Perrimon *et al*. 2001; Seifert and Roberts 2007). Hearn *et al*. (2019: 1) proposed that "host arabinogalactan proteins and gall wasp chitinases interact in young galls to generate a somatic embryogenesis-like process in oak tissues surrounding the gall wasp larvae".

This hypothesis has not yet received support from other researchers of arthropod-induced gallogenesis involving insects or mites. Hearn *et al*. (2019) based their hypothesis primarily on data on the *ENOD* genes encoding the arabinogalactan proteins. Meanwhile, the authors of other recent studies of somatic embryogenesis in angiosperms—without reference to gallogenesis—have assigned

a leading role in this process to other genes, primarily *LEAFY COTYLEDON* (*LEC*), *BABY BOOM* (*BBM*), *WUSCHEL* (*WUS*) and *CLAVATA* (*CLV*), as well as to the proteins that these genes encode (Méndez-Hernández *et al*. 2019; Rose 2019; Khan *et al*. 2023). Data on the participation of these genes and proteins in gallogenesis have not yet been published.

In addition, the hypothesis about the similarity of gallogenesis with somatic embryogenesis is also not strongly supported from a morphological point of view. As noted above, in the angiosperms, somatic embryos at the globular, heart, and torpedo stages are morphologically similar to the corresponding stages of zygotic embryos (Zimmerman 1993; Méndez-Hernández *et al*. 2019), whereas the developing galls of arthropods do not have such similarities with somatic or zygotic embryos and do not progress through the aforementioned stages of development. Moreover, gallogenesis and somatic embryogenesis differ physiologically. The development of somatic embryos occurs independent of the parent organism (Zimmerman 1993), whereas the development of galls requires close contact and trophic interactions with the tissues of the host plant, which partly brings gallogenesis closer to matrotrophy rather than to somatic embryogenesis.

Arthropod galls and positional information

According to the concept in animal developmental biology known as "positional information" (e. g., Wolpert 1969, 1978; Vargesson 2020), the fate of a cell or group of cells depends on their position in the developing organism. Pattern formation, both in embryogenesis and during regeneration, includes at least two steps (Wolpert 1969).

Firstly, the specification of positional information occurs, during which cells learn where exactly they are. This process precedes and is independent of molecular differentiation.

Secondly, the cells interpret this information, differentiating according to their genetic program. The aforementioned authors considered the concept of positional information to be universal and applied it to the analysis of the early embryogenesis of sea urchins, the regeneration of hydroids, as well as to the development of the chicken limb and other morphogenetic processes. This analysis used the idea of embryonic (positional) fields, indicating that "the fields can now be viewed as particular coordinate systems" (Wolpert 1978: 156). A discussion about the adequacy of such a definition of fields is beyond the scope of our review. However, it is important to emphasize that the concept of positional information assumes that "all known positional fields are less than 100 cells (or about one millimeter) in length and they are usually much smaller" (Wolpert 1978: 156).

In recent years, publications have appeared in which the development of leaf shape in angiosperms is considered using the concept of positional information (Bhatia *et al*. 2021; Strauss *et al*. 2022). In particular, this problem was studied using two related plants from the Brassicaceae family with leaves of different shapes, namely *A. thaliana* (simple leaf shape) and *Cardamine hirsuta* L. (complex shape with leaflets) (Bhatia *et al*. 2021). It has been shown that leaf shape depends on the interplay of two growth modes: a conservative mode of growth of the entire organ and a local, directed mode, which involves the formation of growth foci along the leaf edge. The diversity of leaf shapes is the result of the effects of two homeobox genes (growth regulators). The *SHOOT-MERISTEMLESS* (*STM*) gene prolongs the growth phase throughout the organ with patterning at the edges, allowing the appearance of leaflets, whereas the *REDUCED COMPLEXITY* (*RCO*) gene locally suppresses growth in areas where the leaflets would otherwise form (Kierzkowski *et al*. 2019).

The latest literature on insect gallogenesis (Diptera, Hemiptera, Hymenoptera) contains interesting examples indicating differences in the morphological structure of galls caused by the same gall-former in different zones of the leaf blade (Teixeira *et al*. 2022; Guedes *et al*. 2023; Lu *et al*. 2023). The galls of the wasp *Ophelimus migdanorum* Molina-Mercader, 2019 (Hymenoptera: Eulophidae) on the southern blue gum, *Eucalyptus globulus* Labill. (Myrtaceae) (Guedes *et al*. 2023), present a good example of this. The galls induced near the midrib of a leaf were not statistically different in size from the galls some distance away, within the leaf blade. However, there were differences in their structure; when the wasp initiated the formation of a gall near the midrib, a decrease in the area (volume) of cells of both the palisade parenchyma and the epidermis was observed at that location.

We were unable to find similar examples concerning gall mites in the literature. However, in 2018, we have encountered such different types of galls

twice on the linden *Tilia cordata* Mill. (Malvaceae) in the Leningradskaya and Pskovskaya oblasts of Russia, with the galls being caused by the same mite species, *Phytoptus tetratrichus* Nalepa, 1891 (Acariformes: Eriophyoidea: Phytoptidae). We have verified the species of the mite by using the PCR method (Chetverikov *et al.* 2021). In both cases, two types of galls were present on linden leaves: (1) marginal leaf rolling (Fig. 2a, b) and (2) bead galls (Fig. 2c, d). The first type of galls is a typical lesion caused by *P. tetratrichus*, found throughout the extensive range of linden in Europe. This typical lesion has been recorded by many authors since the mid-19th century. In this case, overwintered females crawl out onto young leaves in the spring, concentrate along the edge of the leaf, and suck out the juice of the epidermal cells, causing the thickening and curling of the leaf blade's edge.

The second type of galls is apparently much less common. Over the entire 30-year period of our work on gall mites (which started in 1994), we have encountered it only twice. In this case, the mites attack not the marginal area of the leaf, but the zones between the veins on the adaxial side. The response of the leaf tissues involves the initial formation of small depressions, followed by the appearance of multiple small bubble-like swellings, inside which the mites feed and reproduce.
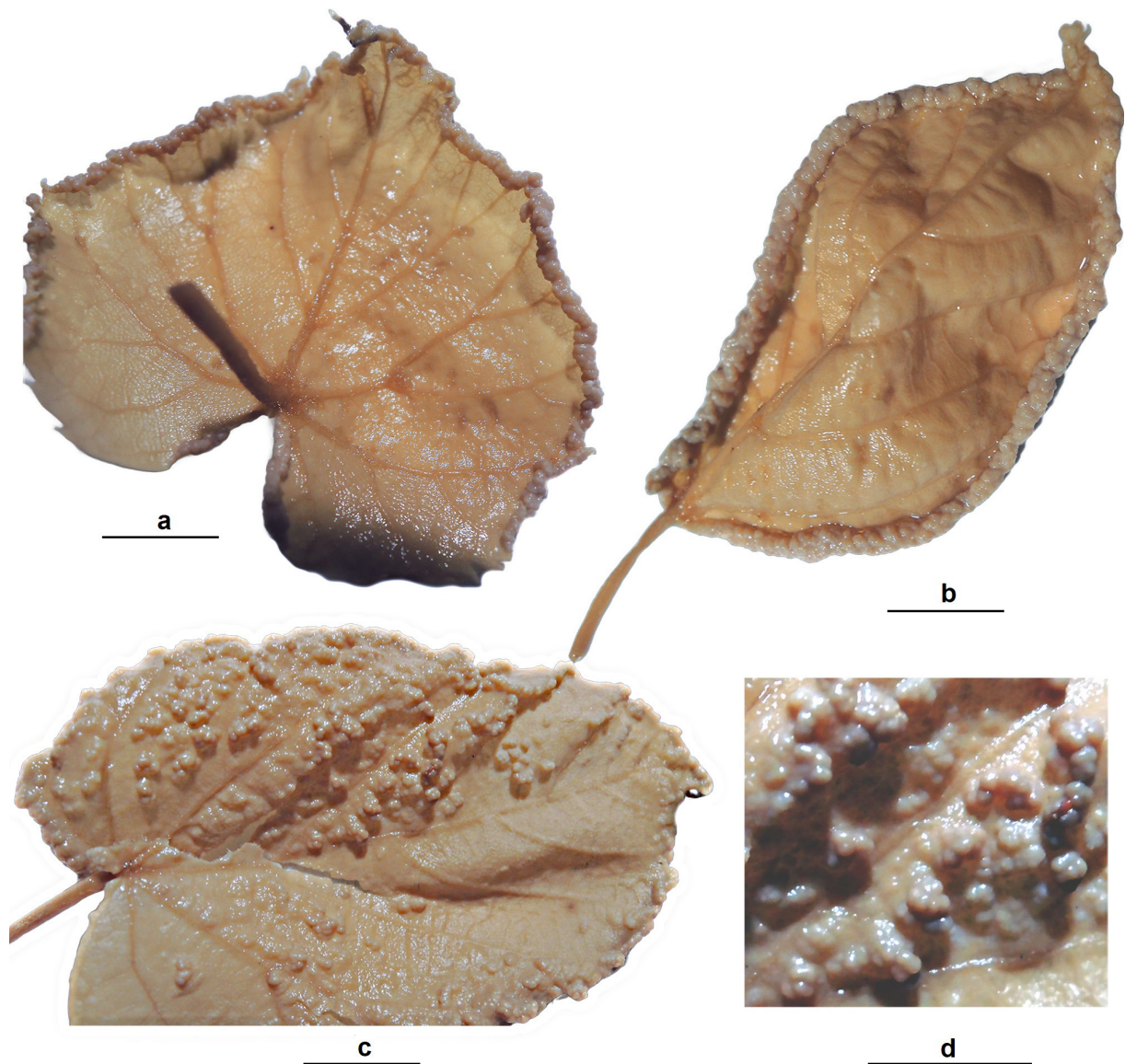

Fig. 2. Galls of the mite *Phytoptus tetratrychus* Nalepa, 1891 on the leaves of the linden *Tilia cordata* Mill. (material in alcohol from the collection of the Zoological Institute of the Russian Academy of Sciences). a, b—typical marginal galls; c, d—atypical bead galls between the veins. Scale bar—1 cm. Photographs by P.E. Chetverikov.

The presented data on the galls of the eucalyptus wasp and the linden mite show that different parts of the leaf respond differently to conspecific gall-formers. Apparently, this is due to the morphological and molecular-biochemical heterogeneity of different zones of the leaf blade along its proximal-distal and medio-lateral axes (Du *et al*. 2018; Martinez *et al*. 2021; Wu *et al*. 2021; Lv *et al*. 2023). A consequence of this is represented by various possibilities for the implementation of atypical morphogenesis as a response to gall-inducing stimuli of gall-formers. However, this case is different from the classical concept of positional information (Wolpert 1969, 1978), since the cells stimulated by gall-forming mites in different parts of the leaf no longer need to specify positional information. In addition, as noted above, this concept postulates that the linear size of the embryonic (positional) fields does not exceed 1 mm (Wolpert 1969, 1978; Vargesson 2020), whereas the leaf blades attacked by mites are much larger. Even taking into account the fact that the mite attacks a single cell, the area of the leaf adjacent to the developing gall usually has a length that significantly exceeds 1 mm.

Nevertheless, it is clear that gall-forming stimuli are "adjusted" to the specific morphological and molecular-biochemical maps of the leaf blade cells. Such adaptation entails behavioral specialization, and the gall-former is required to find exactly those zones of the leaf that can respond to the stimulus in a deterministic manner, by forming a gall. Further work on studying the influence of conspecific gall-formers on different zones of the leaf may shed light on both the nature of gallogenesis as well as on the normal leaf development process, serving as a kind of test for the presence of "positional mapping" in leaf tissues.

CONCLUSION

The reviews on arthropod-induced gallogenesis have focused on the development of insect galls, while mite galls either attract minimal attention (Ferreira *et al*. 2019; Gätjens-Boniche 2019; Miller and Raman 2019; Raman 2021) or the data on mite galls are not considered at all (Takeda *et al*. 2021). We have shown that the gallogenesis caused by the eriophyoid mites is similar to that caused by the grape phylloxera (Hemiptera: Phylloxeridae) in terms of the presence of nutritive tissue in the gall, the induction of galls

by adults, and the inversion of adaxial-abaxial polarity of the leaf.

In the recent studies of mite gallogenesis on leaves, minimal attention has been paid to the formation of erinea. Meanwhile, an example of this type of galls shows that there are cases when the inducing effects produced by mites only lead to the formation of trichomes, and not a gall chamber.

Taking into account the corresponding data on insect galls, a literature review on the possible role of endosymbiotic bacteria in the induction of mite gallogenesis shows the advisability of further research in this direction in the future, especially in terms of testing the hypothesis regarding the role of *Wolbachia* and *Rhodococcus* bacteria in the induction of galls by the eriophyoid mites.

A hypothesis emerged several years ago proposing that gallogenesis induced by the arthropods (insects or mites) is similar to somatic embryogenesis in plants. However, this hypothesis has not yet received widespread acceptance. Our review suggests that this hypothesis and the embryological concept of positional information in its classical form are not suited for gallogenesis modeling.

Very recently, evidence on the formation of some eriophyoid mite and insect gall types being associated with certain areas of the host plant leaves has begun to emerge. Further work in this direction could not only shed light on the nature of gallogenesis, but also contribute to our understanding of the mechanisms related to the normal leaf development process.

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