Feeding and Other Gall Facets: Patterns and Determinants in Gall Structure

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Abstract

Galls are neoformed structures induced by specific animals, fungi, bacteria, virus or some parasitic plants on their host plant organs. Developmental processes are well known in *Agrobacterium tumefasciens* galls, but the animal-induced galls have a striking anatomical diversity, concerning several patterns, which were reunited herein. Anatomical traits observed in animal-induced galls involve manipulation of plant morphogenesis in convergent ways. Nematode, mite and insect galls usually contain homogeneous storage parenchyma and develop due to hyperplasia and cell hypertrophy. The development of typical nutritive tissues, giant cells, or hypertrophied vascular bundles may occur. Some other anatomical features may be usually restricted to galls induced by specific taxa, but they may eventually be related to the developmental potentialities of the host plants. The combination of distinct morphogenetic peculiarities in each gall system culminates in extant gall structural diversity. Convergent anatomical traits are observed according to the feeding mode of the gall inducers, representing potentiation or inhibition of similar events of host plant morphogenesis and cell redifferentiation, independent of gall-inducing taxa.

Keywords Cell redifferentiation · Eriophyidae galls · Insect galls · Nematode galls · Nutritive tissue · Plant anatomy

Introduction

The galls or cecidia are neoformed structures on plants, induced by very specific inducers, such as some species of animals, fungi, bacteria, virus and some parasitic plants (Mani, 1964; Meyer & Maresquelle, 1983; Meyer, 1987). The galls are usually species-specific structures, and their anatomy and metabolism are strongly related to the

gall inducer species and to the host plants (Stone & Schonrögge, 2003; Moura et al., 2008; Carneiro et al., 2015; Ferreira et al., 2017b, 2018). The structural rearrangements in galls make them interesting models for the study of plant developmental processes, their causes and variations. The galls induced by the bacteria *Agrobacterium tumefasciens* on several plants, including crops, were studied in all plant development levels, since gall histogenesis to gene expression. These galls are induced by plasmidial DNA transference, from the bacterial genome to the host plant cells, which will induce several changes in the developmental features of the infested organ (Tooker & Helms, 2014; Taiz et al., 2015). However, in the case of galls induced by animals, no gene transference was observed. Until now, only some signaling molecules, but not all the reactions, are known to cause the initial modifications in plant cell development (see details in "Gall induction mechanisms" subsection, in this review).

Animal-induced galls, the zoocecidia, may develop on all plant organs, under the stimuli of gall-inducing organisms (the cecidozoa) (Mani, 1964; Meyer & Maresquelle, 1983; Roskam, 1992; Stone & Schonrögge, 2003; Oliveira et al., 2016). Gall anatomical structure may protect the gall inducers against natural enemies and unfavorable environmental conditions (Price et al., 1987; Fernandes & Price, 1992; Stone & Schonrögge, 2003). Moreover, gall tissue organization has been usually related to the taxa of insects and their feeding habit (Larew, 1981; Meyer & Maresquelle, 1983; Bronner, 1992; Rohfritsch, 1992; Ferreira et al., 2017a). Even though nematode and mite galls also have their own patterns and histological peculiarities (Mani, 1964; Larew, 1981), a thorough comparison among galls induced by Nematoda, Acarina and Insecta has been rarely performed (Larew, 1981; Meyer & Maresquelle, 1983; Ferreira et al., 2017a), and few of their systems has been well-studied (Table 1).

The histological profiles of the zoocecidia may be simple, i.e., similar to those of their host organs, or complex, with several neoformed tissues or structures, which provide a better microenvironment for the development of the gall inducers (Wells, 1920; Mani, 1964; Larew, 1981; Meyer & Maresquelle 1983; Ferreira et al., 2017a). Regarding the histological profiles, galls may be classified as organoids or histioids. The organoid galls do not histologically differ from their host organs, but macroscopic alterations may be observed (Sinnott, 1960). They are generally induced by fungi, viruses or bacteria, and may be simply shortened branched shoots, or sometimes with leaves with reduced surface area (Meyer, 1987). Witches' brooms and fasciations are typical organoid galls. Fasciations modify host plant meristems, and originate ribbon-like, elongated, or crisped structures instead of polygonal or rounded axis (White, 1948). The histioid galls comprise alterations in histological structure and are usually induced by animals (Mani, 1964). They are divided into kataplasmatic galls (without a constant external shape and size), and prosoplasmatic galls (with a typical, constant and definitive shape and size) (Küster, 1911; Wells, 1920; Mani, 1964). Herein, we considered the number of events of structural modification (Ferreira et al., 2017a) to evaluate the level of gall complexity. Tissue reorganizing events, such as: (a) parenchyma homogenization; (b) occurrence of hyperplasia; (c) occurrence of cell hypertrophy or hypotrophy; (d) increment in the density of trichomes/emergences; (e) redifferentiation of a nutritive tissue and/or a storage tissue; (f) redifferentiation of a mechanical layer; (g) hypertrophy of vascular bundles; and (h) neoformation (or redifferentiation) of specialized structures are discussed in the following sections. Simple and complex zoocecidia induced by Nematoda, Acarina and Insecta will be comparatively categorized.

Table 1 Representative cecidozoa (gall-inducing animals) clades and general features

Phylum	Order (n. of galling families)	Main groups	Feeding habit	Feeding tissue	Aggregation habit	Main host organs
Nematoda	Tylenchida (4)	Heteroderidea	Piercing-sucking	Giant NC	Colonial	Root
		Meloidogynidae	Piercing-sucking	Giant NC	Colonial	Root
		Anguinidae	Piercing-sucking	NT	Colonial	Leaf, Seed, Stem, Root
Arthropoda	Trombidiformes (4)	Tarsonemidae	Piercing-sucking	NT	Colonial	Leaf
		Eriophyidae	Piercing-sucking	NT	Colonial	Leaf, Bud
	Thysanoptera (2)	Phlaeothripidae	Piercing-sucking	NT	Colonial	Leaf, Bud
		Thripidae	Piercing-sucking	NT	Colonial	Leaf, Bud
	Hemiptera (11)	Psylloidea [a]	Piercing-sucking	Phloem	Solitary	Leaf, Bud
		Aphididae	Piercing-sucking	Phloem	Colonial	Leaf
		Phylloxeridae	Piercing-sucking	NT	Colonial	Leaf / Root
		Adelgidae	Piercing-sucking	NT	Colonial	Bud, Leaf
		Coccoidea [a]	Piercing-sucking	Phloem or Parenchyma	Solitary	Leaf
	Coleoptera (8)	Curculionoidea [a]	Chewing	NT	Solitary	Stem, Bud, Leaf, Root
	Hymenoptera (5)	Cynipidae	Chewing	NT	Solitary / Coalescent	Leaf, Bud, Stem, Root
		Chalcidoidea [a]	Chewing	NT	Solitary / Coalescent	Leaf, Stem, Flower
		Tenthredinidae	Chewing	NT	Solitary	Leaf
	Lepidoptera (20)	Tortricoidea [a]	Chewing	NT	Solitary	Stem, Bud, Leaf
	Diptera (6)	Cecidomyiidae	Sucking disrupted-cell fluids (extracorporeal digestion)	NT	Solitary	Leaf, Bud, Stem, Flower, Fruit, Root

[a] Superfamilies with more than one important galling family. Abbreviations: NC = Nutritive cells; NT = nutritive tissue. Less representative families were suppressed. Note that there are exceptions for each case

Mani (1964), Meyer (1987), Roskam (1992), Mound (1994), Williams (1994), Wool (2004), Raman et al. (2005), Sano and Akimoto (2011), Burckhardt and Queiroz (2012), Fernandes et al. (2012)

In gall structural studies, plant developmental machinery is supposed to be similarly stimulated by the feeding habit of distinct gall-inducing taxa. In this case, the colonial habit is responsible only for potentiating the cecidogenetic factors, and therefore gall histological pattern do not alter according to the colonial or solitary habits of the cecidozoa. Recently discovered novelties on Neotropical galls, which have shown more diverse histological and cytological patterns from those studied in the Temperate regions, guided current discussion. Reuniting a vast literature data from 20th and 21th centuries, we expect to demonstrate that galls are results of a combination of distinct morphogenetical potentialities of the host plants, which results in the extant gall structural diversity. Therefore, the host plants should also be "protagonists" in the determination of gall structure, as the gall-inducing organisms are.

Glossary

The main terms used in this review are defined herein in order to make the reading easier:

- **Cecidium (*plural:* cecidia):** gall (*plural:* galls).
- **Cecidozoa:** animals capable of inducing galls.
- **Chamber:** the locule or internal space inside the gall, where the inducer and/or its offspring lives and feeds. In some articles, it may be referred as crypt or "cell".
- **Coalescent galls:** polythalamous or multilocular galls. A group of galls fused during the morphogenetic process, containing several gall chambers, usually with one gall inducer per chamber.
- **Colonial galls:** galls with several gall inducers per chamber.
- **Common storage tissue (CST):** an outer storage parenchyma or sclerenchyma with intense accumulation of starch and other metabolites, which are not directly involved in the inducer's feeding, but are important energy source for growth and maintenance of gall tissues.
- **Emergence:** an appendicular structure of an organ, formed by epidermal and subepidermal tissues (ground system tissues and sometimes vascular tissues).
- **Filzgall:** a mite-induced gall formed exclusively by increased density of trichomes and emergences, and sometimes parenchyma homogenization.
- **Gall:** a structure originated by the stimuli of specific species of animals, fungi, bacteria, virus, or parasitic plants, causing simple or complex alterations in plant histogenesis and/or morphogenesis.
- **Inquilines**: insects that cohabit galls induced by other insects, feeding on the gall tissues, but uncapable of inducing their own galls. Some inquilines may induce tissue alterations (a new gall) in the gall they cohabit.
- **Monothalamous galls:** galls with one single gall chamber.
- **Nutritive-like tissue (NLT)**: tissue surrounding gall chambers, usually of hemipteran (phloem-sucking insect) galls, which is not a feeding source for the inducers. Its cells have prominent nucleus, dense cytoplasm, rich in proteins, lipids, reducing sugars, and/or starch.
- **Polythalamous galls:** galls with two or more gall chambers.
- **Solitary galls:** galls containing one chamber with one gall inducer.

- **Typical nutritive tissue (TNT):** tissue surrounding gall chambers, directly used for the inducer's feeding. Nutritive cells have dense cytoplasm, prominent nucleus, commonly rich in proteins, lipids and/or reducing sugars.
- **Zoocecidia:** galls induced by animals (mites, insects or nematodes).

Gall Types

Some Simple Galls May Be Called Pseudogalls

Phylogenetic studies suggested that the galling habit, at least in some groups, evolved from leaf rolling and leaf folding galls (Inbar et al., 1995; Crespi & Worobey, 1998; Nyman et al., 2000). Therefore, the simplest galls should be the leaf rolling/folding galls, which may be induced by mites, thrips, aphids, psylloids, lepidopterans, hymenopterans, and cecidomyiids (Raman & Ananthakrishnan, 1983; Inbar et al., 1995; Nyman et al., 2000; Souza et al., 2000; Arduin et al., 2005; Rancic et al., 2006; Álvarez et al., 2009, 2016; Magalhães et al., 2014; Portugal-Santana & Isaias, 2014; Bedetti et al., 2013). These galls may be slight modifications of host tissues, as the eriophyid galls on *Cirsium arvense* (Rancic et al., 2006), or may also be formed by hyperplasia, cell hypertrophy and/or parenchyma homogenization, as demonstrated for thrips-induced galls on several host plants (Raman & Ananthakrishnan, 1983; Gopinathan & Ananthakrishnan, 1985; Jorge et al., 2016), aphid galls induced by *Eriosoma ulmi* on *Ulmus minor* (Sano & Akimoto, 2011; Álvarez et al., 2013; Ferreira et al., 2017a), psyllid galls on *Baccharis reticularia* (Formiga et al., 2015), cecidomyiid galls induced by *Dasineura affinis* on *Viola odorata* (Meyer, 1987), and sawfly (hymenopteran) galls on *Salix* spp. (Nyman et al., 2000).

Some authors consider leaf rolling galls as pseudogalls (Wool, 2004), since their development depends on the feeding activity and death of epidermal cells, which causes host leaf deformation. However, several leaf rolling galls are considered true galls, for they result from hypertrophy of vascular bundles, parenchyma and epidermal cells, overdifferentiation of trichomes, hyperplasia and parenchyma homogenization (Mani, 1964; Álvarez et al., 2013; Formiga et al., 2015; Jorge et al., 2016; Ferreira et al., 2017a). More complex leaf folding galls may have mechanical tissues (sclerenchyma layer surrounding gall chamber), multiseriate epidermis, and nutritive-like tissues or common storage tissues, as observed for some aphid galls (Álvarez et al., 2009, 2016; Kurzfeld-Zexer et al., 2015).

The concept of galls as new organs may be applied to galls containing redifferentiated tissues with new specialized functions (Oliveira & Isaias, 2010a, 2010b; Ferreira & Isaias, 2013, 2014; Ferreira et al., 2015; Richardson et al., 2017). Due to the variety of tissue reorganization, it is controversial to consider the leaf rolling/ folding galls as new organs. Generally, the concept of galls as new organs will depend on the occurrence of tissue neo-formation and cell redifferentiation, and also on altered physiological parameters. Independent of the galls being new organs or not, Mani (1992, p. 3–4) amplified the concept of galls to "*a bewildering variety of plant structures and growth forms, ranging from the nearly normal plant organs to extreme bizarre and highly complex growth abnormalities*", recognizing all types of tissue manipulation as galls.

Colonial, Solitary and Coalescent Galls

Herein, we consider colonial galls as those sheltering several individuals of the gall-inducing species in a single gall chamber. They are commonly induced by nematodes and mites, and sometimes by insects (such as Thysanoptera, Hemiptera: Aphididae and Hemiptera: Adelgidae) (Table 1). Solitary galls are those galls, which have one gall-inducing individual per gall chamber, and are mostly induced by insects. Several Hymenoptera may induce galls by ovipositing in very close sites of the host organs (Table 2). In such cases, the coalescent galls share common tissues, but each larva is solitary and occupies an exclusive chamber (Mani, 1964; Meyer, 1987) (Table 1). Coalescent galls are usually product of the morphogenetic fusion among solitary galls. Each coalescent gall has two or more gall chambers, and they can also be called polythalamous, multichambered or multilocular galls. The advantages of coalescent galls should be the relative protection of some individuals from predation or parasitism, considering that the individuals occupying superficial chambers are more susceptible to the attack of parasitoids (Stone & Schonrögge, 2003), while those inside the inner chambers are more difficult to access. It is important to stress that monothalamous galls are those galls with one single chamber, independent of the number of inducers inside the chamber.

Influence of Induction Modes on Solitary, Coalescent and Colonial Habits

The induction habit of the gall-inducing species is determinant for the colonial or solitary habit (Table 2). When a female induces galls by its feeding activity, and oviposits or generates its offspring parthenogenetically, these galls are usually colonial, containing the mother and its offspring. When the feeding activity (chewing or sucking plant tissues) of the larva or the nympha is the stimuli for gall induction, galls are usually solitary. In a few groups, the oviposition is responsible for the first steps of gall induction, and galls may be solitary or coalescent. Independent on the solitary or colonial feature, gall induction usually occurs in meristematic tissues (Mani, 1964; Álvarez, 2011; Dias et al., 2013a; Ferreira & Isaias, 2014; Fleury et al., 2015), but there are some cases in which parenchymatic or epidermal tissues are the oviposition sites (Oliveira & Isaias, 2010b; Ferreira & Isaias, 2013). These cases demonstrate that most living plant cells are truly totipotent cells, being capable of redifferentiating into any other plant cell type (see Lev-Yadun, 2003).

Both colonial and solitary galling habits are strategies that have arisen independently among Arthropoda. Colonial insect galls are induced by Thysanoptera, and Hemiptera such as Aphididae, Phylloxeridae and Adelgidae. The Thysanoptera females induce galls by feeding stimuli prior to oviposition, and the nymphs may intensify plant tissue responses. Similarly, aphid and phylloxerid galls are induced by a female, the fundatrix, and its offspring maintain the galling stimuli (see below). The solitary galls arose independently in distinct taxa of insects, and usually have one gall-inducing individual per chamber (Table 1, Table 2). The galls with chewing and rasping-sucking larvae are predominantly solitary (Table 2). It is important to notice that colonial galls are usually induced by hemimetabolous species (such as Thysanoptera and Hemiptera) (Kjer et al., 2006), cases in which the adults and their offspring have the same feeding habits. The solitary galling habit is of higher occurrence in taxa of Endopterygota (the

Table 2 Comparison among feeding habit, type of gall induction and aggregation habit

Feeding habit	Gall induction	Aggregation habit	
		Colonial gall groups	Solitary gall groups
Piercing-sucking (NT)	Feeding of matrix female and offspring (by penetration in meristems, or on meristematic surfaces)	• Nematoda: Anguinidae	–
Piercing-sucking (NT)	Feeding of matrix female and offspring	• Acarina: Eriophyidae • Insecta: Hemiptera: Adelgidae	–
Piercing-sucking (NT/epidermal cells)	Oviposition inside plant tissues and/or feeding of matrix female and offspring	• Insecta: Thysanoptera	–
Piercing-sucking (phloem)	Mainly feeding of fundatrix	• Insecta: Hemiptera: Aphididae	–
Piercing-sucking (phloem)	Feeding of the nymph	–	• Insecta: Hemiptera: Psylloidea
Piercing-sucking (NT)	Feeding of fundatrix	• Insecta: Hemiptera: Phylloxeridae	–
Piercing-sucking (phloem or NT)	Feeding of the nymph	–	• Insecta: Hemiptera: Coccoidea
Chewing (NT)	Oviposition and/or feeding of the larva	–	• Insecta: Coleoptera • Insecta: Hymenoptera
Chewing (NT)	Feeding of the larva	–	• Insecta: Lepidoptera
Rasping-sucking (NT)	Feeding of the larva	–	• Insecta: Diptera: Cecidomyiidae

Felt (1936), Mani (1964), Meyer (1987), Mound (1994), Wool (2004), Raman et al. (2005), Sano and Akimoto (2011), Burckhardt and Queiroz (2012)

holometabolous, such as Hymenoptera, Coleoptera, Lepidoptera and Diptera), with chewing or rasping larvae as inducing individuals.

Among the hemimetabolous, some Hemiptera (Psylloidea and Coccoidea) may induce solitary galls, where the nymphs, and not the adult females, are responsible for gall induction. The distinct stages of an individual, i.e., larva, pupa and adult of the holometabolous organisms usually inhabit solitary galls, while for the hemimetabolous, distinct generations may cohabit a colonial gall. Among the holometabolous, the Diptera: Cecidomyiidae and Hymenoptera: Cynipidae induce the most diverse galls (Espírito-Santo & Fernandes, 2007), which are histologically and histochemically peculiar (Wells, 1920; Rohfritsch, 1992; Harris, 1994; Stone & Schonrögge, 2003; Ferreira & Isaias, 2014). Such diversity may be consequence of the capability of these solitary gall-inducing organisms to both manipulate plant tissues and tolerate chemical constraints imposed by the host plants (Amorim et al., 2017).

A very interesting type of gall induction is performed by inquilines over the tissues of other growing galls. Inquilines are herbivores, which feed in the gall tissues. Some species of inquilines evolved from an ancestral gall-inducing species, and some of them may induce tissue alterations in the galls they cohabit (Roskam, 1992; Yang et al., 2001). The occurrence of morphological alterations induced by inquilines of the superfamily Psylloidea was firstly described by Yang et al. (2001). In this case, the inquiline *Pachypsylla cohabitans* (Psylloidea) induces alterations in the galls induced by several other species of *Pachypsylla* on *Celtis* spp. (Ulmaceae). The galls induced by the "true" *Pachypsylla* gall-inducers may be solitary or colonial. However, the inquilines (*P. cohabitans*) can only induce galls over a gall, producing a new lateral gall chamber in the original *Pachypsylla* galls. These galls, therefore, may be considered coalescent galls, specially induced by distinct species. Similar cases commonly occur in several Cecidomyiidae (Roskam, 1992) and Cynipidae galls (Yang et al., 2001; Brooks & Shorthouse, 1998). Brooks and Shorthouse (1998) described the histological alterations caused by the inquiline *Periclistus pirata* (Cynipidae) on the galls induced by *Diplolepis nodulosa* (Cynipidae) on stems of *Rosa blanda* (Rosaceae). One or more *P. pirata* females oviposit several eggs into the chamber of the young solitary galls of *D. nodulosa*. Several histological modifications were described, resulting in the formation of a bigger coalescent gall, with several chambers, over the original solitary gall. This multilocular gall is result of the redifferentiation of storage parenchyma cells surrounding nutritive tissues (Brooks & Shorthouse, 1998). Therefore, in both cases cited above, the galls modified by the inquilines are products of a rearrangement of the previous morphogenetic development. Considering the concepts used here, we must consider these inquilines as gall inducers, although they can only induce galls over the tissues of specific galls.

Influence of the Number of Individuals in Gall Growth and Development

The solitary and colonial habit may influence the size of the gall and the rates of hypertrophy and hyperplasia, but the tissue arrangement tends to be similar. In mite galls, the number of inducers and gall size are positively correlated, even though additional tissue layers and larger cells are not observed (Moura et al., 2009b). In galls induced by several species of thrips on *Acacia* spp., the higher the number of generations inside a gall, the greater is the gall inner surface area related to gall volume (Crespi & Worobey, 1998). The histological patterns of galls induced by colonial (aphids) (Fig. 2a, Fig. 3b) and solitary phloem-sucking insects (psylloids) are similar (Fig. 1). The size of aphid-induced galls is also directly related to the number of individuals inside the gall chamber (Zha et al., 2016). In such case, the lateral growth seems to be potentiated by the action of a plate meristem-like tissue (see Evert, 2006), with predominant anticlinal cell divisions in gall walls. Coalescent galls may also have potentiation of cell growth directly related to number of individuals inside their structure, as observed by Arduin et al. (1989) for hymenopteran galls induced on *Struthanthus vulgaris* leaves, and by Brooks and Shorthouse (1998) for galls induced by *Diplolepis nodulosa* (Cynipidae) on *Rosa blanda* stems. These data suggest that the number of inducers does not affect gall histological patterns, but only gall size, which seems to be merely a local response to increased concentrations of growth signals. Therefore, colonial and coalescent galls should be structurally similar to the solitary galls induced by closely-related gall-inducing species with the same feeding habit, reaching greater dimensions than those of solitary galls.
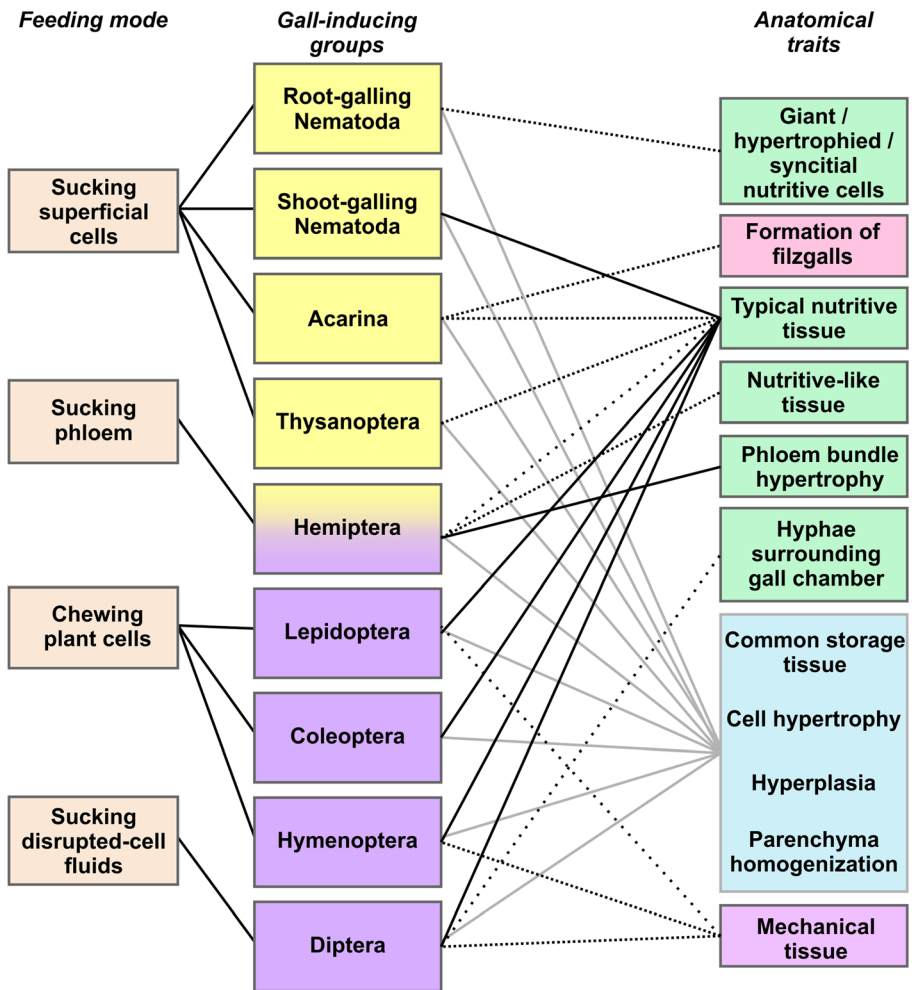
Fig. 1 Network of feeding modes, gall-inducing groups, and gall anatomical traits. In the *gall-inducing groups*, clear boxes (yellow) indicate groups with colonial galls and darker boxes (purple) indicate groups with solitary galls. Uninterrupted lines indicate more frequent anatomical traits, and dashed lines indicate less frequent traits. The more spaced are the dashed lines, less frequent is the indicated feature. In *anatomical traits*, clear boxes (green) are related to feeding tissues, the box surrounded by a light grey board indicate the anatomical traits common to galls induced by all groups of animals, and the other boxes are features occurring in galls of a restricted gall-inducing taxon

Multiple Evolution of Galling Taxa

Taxonomical Distribution of Gall Inducers

Insecta is the richest group of independently-evolved families with gall-inducing species (Mani, 1964; Meyer, 1987; Roskam, 1992) (Table 1). Considering that only the most representative clades of gall-inducing species have been listed in Table 1, the galling habit appeared several independent times in metazoan evolution – representing more than 52 insect families (133,000 estimated species) (Fernandes et al., 2012), 4 mite

families (3600 described species) (Raman et al., 2005), and at least 4 nematode families (without estimations on the number of galling species) (Meyer, 1987). The galling habit evolved in parallel in several distinct families of insects, from ancestral guilds with distinct life habits (Roskam, 1992). The gall-inducing Cecidomyiidae seems to have evolved directly from detritivorous/mycetophagous ancestors, while other insect groups have evolved from: spores/pollen feeders (such as Thysanoptera: Phloeothripidae); plant sap feeders (as Hemiptera: Adelgidae, Eriosomatidae, Psyllidae, and Coccidae); foliage feeders (as Coleoptera: Curculionidae and Hymenoptera: Tenthredinidae); stem borers (as Hymenoptera: Cephidae); leaf miners (as Lepidoptera: Gelechiidae, and Diptera: Tephritidae and Agromyzidae); and from zoophage parasitoids (as Hymenoptera: Cynipidae) (Roskam, 1992).

Gall Induction Mechanisms

Nematoda Galls

The most common nematode galls are induced in roots, where the adult females (*Nacobbus, Rotylenchulus, Tylenchulus*) or second-stage juveniles (*Globodera*, *Heterodera*, *Meloidogyne*) usually penetrate into plant tissues (Krusberg, 1963; Dropkin, 1969; Meyer, 1987; Wyss, 1997). The nematodes perforate cell walls and introduce salivary secretions, which immediately induce cytoplasm aggregation around the stylets (Krusberg, 1963; Dropkin, 1969; Wyss, 1997). Some proteins trigger cytoplasm changings, and influence the genetic expression of plant cells (Favery et al., 2016), activating the differentiation of meristematic cells into nutritive cells, or the redifferentiation of parenchymatic cells into new cell types (Goodey, 1948; Bird, 1961; Ferreira et al., 2017b).

Usually, the first feeding sites are meristematic cells, which respond to the galling stimuli of nematodes. The feeding of the nematodes causes the surrounding cells and nuclei to become larger, and the cytoplasm to be denser (Krusberg, 1963; Dropkin, 1969). There is an increase in ribosomes, polyribosomes and cell organelles in cortical parenchyma (as in *Xiphinema* galls) (Weischer & Wyss, 1976; Wyss, 1997, 2002) or in xylem parenchyma cells (as in *Meloidogyne* galls) (Bird, 1961; Yousif, 1979; Finley, 1981; Wyss, 1997, 2002; Di Vito et al., 2004) due to the nematodes feeding activity (Wyss, 1997). In general, the feeding activity of the nematodes induces the redifferentiation of meristematic or parenchymatic cells, and specialized nutritive tissues develop. The nutritive cells in root nematode galls may be multinucleate giant cells, non-hypertrophied uninucleate nutritive cells, or syncytia, depending on the gall-inducing species (Dropkin, 1969; Meyer, 1987; Wyss, 1997). The multinucleate cells are usually formed by nuclear divisions without cytokinesis, while syncytia are formed by the fusion of cell protoplasts after partial wall dissolution (Wyss, 1997). In fact, considering the distinct types of induced nutritive cells, each nematode species should be responsible for activating specific cell cycle genes of the host plant (Favery et al., 2016). Besides the formation of nutritive cells or tissues, the root parenchymatic tissues undergo hyperplasia, forming cysts or root-knots (Wyss, 1997).

In aerial parts, galling Nematoda usually penetrate young leaves or stems, inducing the redifferentiation of meristematic cells, and necrotic regions are rarely observed (Goodey, 1939, 1948; Dropkin, 1969; Watson & Shorthouse, 1979; Skinner et al.,

1980). In 2 or few days, a typical nutritive tissue may be observed surrounding the colonies (Goodey, 1939, 1948; Skinner et al., 1980). The nutritive cells may be hypertrophied or not, and may have one or more nuclei and nucleoli (Watson & Shorthouse, 1979; Skinner et al., 1980). Even though most galling nematodes penetrate plant meristems, there are some exceptions. *Ditylenchus gallaeformans* remains external to plant tissues, and induces galls by feeding on the meristematic cell surfaces of *Miconia* spp. aerial parts (Ferreira et al., 2017a, 2017b).

Acarina Galls

Eriophyidae galls are also induced by adult females (Table 2) (Meyer, 1987), which feed on young leaf surfaces. After 15-20 min, it is possible to observe a cone-shaped callose thickening surrounding the perforation region of the outer periclinal wall of the epidermal cell. In one-hour time, the first nutritive cells differentiate next to the perforation, with dispersion of chromatin, nucleoli enlargement, vacuome formation, and cytoplasm enrichment (Westphal et al., 1981). Plant tissue invagination may occur after some hours to two days of motionless position of the female (Oldfield, 2005). The mites may feed only on epidermis, inducing the differentiation of superficial nutritive cells. Meyer and Maresquelle (1983) considered the direct differentiation of epidermal cells into nutritive cells in these galls as metaplasia, since these cells proliferate before redifferentiation, and do not dedifferentiate. In other cases, the feeding activity may cause cell degradation in feeding sites, and the mites may gradually penetrate plant tissues forming a gall chamber. Nutritive cells redifferentiate from common parenchyma cells, around the feeding route of the mites, which seems to be the main stimuli for cell redifferentiation (Kendall, 1930; Westphal et al., 1981; Ferreira et al., 2017a). After a variable time of feeding, the females oviposit (the eggs are often produced by parthenogenesis), and quit the gall (Oldfield, 2005).

Insecta Galls

The real causes of the insect galls were firstly unveiled by Marcello Malpighi in the seventeenth century, with his book "De Gallis" published in 1679 (Fagan, 1918). The mechanisms of gall induction were actually experimented and discussed along the late 19th and 20th centuries, by studies applying mechanical stimuli, insects' salivary mixtures, and insects' entire extracts to plant tissues (Felt, 1936; Hough, 1953). However, the physiological mechanisms involved in the induction of insect galls remain obscure (Wool, 2004; Oliveira et al., 2016). Some experiments may stimulate hyperplasia in host plant tissues, but the growth and development is not complete as they are in galls naturally induced by the insects (Hough, 1953; McCalla et al., 1962; Mapes & Davies, 2001). Accordingly, the role of the mechanical wounding (by perforation or chewing), and mainly the insect's saliva or egg's secretions are essential for gall induction (Felt, 1936; Hough, 1953; Raman et al., 2005). Additionally, plant growth regulators may be found in the gall-inducing insect extracts, reinforcing the hypothesis of gall induction by chemical manipulation (Byers et al., 1976; Meyer & Maresquelle, 1983; Hori, 1992; Mapes & Davies, 2001). It is also assumed that the constant feeding of the inducing animal on gall tissues is essential for gall development, maturation, and dehiscence (Felt, 1936;

Hough, 1953; Oldfield, 2005). Moreover, the initial stimuli are not necessarily related to the feeding activity, as some insect galls may be induced by oviposition injury and associated secretions (Felt, 1936; Hough, 1953; Raman et al., 2005).

Feeding Activity. The inseminated female and offspring of the thrips (Thysanoptera) induce galls only by sucking on individual leaf epidermal cells (Mound & Morris, 2005; Raman, 2012), which end up dying, causing leaf distortion. The surrounding mesophyll cells are responsible for repairing this damage, originating outgrowths into the tissues often causing leaf folding (Mound, 1994; Mound & Morris, 2005; Raman, 2012). The process of leaf folding in thrips-induced galls may also be consequence of changes in the elongation axis of epidermal cells in *Myrcia retorta* (Jorge et al., 2018a) or by the development of hypersensitive areas in epidermis and mesophyll as in *Myrcia splendens* (Jorge et al., 2018b).

Some gall-inducing species of Hemiptera induce either solitary or colonial galls. Aphididae and Phylloxeridae induce colonial galls, by the feeding activity of a single female, usually the fundatrix, which reproduces parthenogenetically (Wool, 2004). Some genera of Aphididae: Fordini (*Forda*, *Smynthurodes*) may induce two distinct galls on a single plant species: the fundatrix (F1) induces a temporary solitary gall; in a few weeks, the fundatrix offspring, the fundatrigeniae (F2) induce a definitive gall. The parthenogenetic fundatrigenia oviposits inside the chamber, and therefore the definitive galls are colonial (Wool, 2004; Álvarez et al., 2014; Kurzfeld-Zexer et al., 2015). Solitary galls of Psylloidea (Hemiptera) are induced by the feeding activity of first-instar nymphs (1–3 individuals), and covering or pouch galls develop (Burckhardt, 2005), as is true for *Nothotrioza* spp. (Triozidae) on leaves of *Psidium* spp. (Myrtaceae) (Carneiro et al., 2014b; Carneiro & Isaias, 2015). Nevertheless, some species such as *Baccharopelma dracunculifoliae* (Psyllidae) nymphs may induce galls with one to 21 individuals inside the chamber. The sucking activity of *B. dracunculifoliae* nymphs is the stimulus responsible for the hyperplasia and cell hypertrophy, which culminate in the entire folding of *Baccharis dracunculifolia* (Asteraceae) leaves (Arduin et al., 2005). Bud galls may be induced by Psylloidea members, and, more rarely, stem, flower, rosette and root galls, as exemplified by Hodkinson (1984). Even though the similar feeding activity represents an important induction stimulus, the growth of these galls follows patterns other than those involved in pouch and leaf covering galls.

In Coccoidea (Hemiptera), the first nymphs (crawlers) were known to induce solitary galls by sucking on phloem or on parenchymatic tissues (Meyer, 1987). In the Neotropics, second-instar Eriococcidae nymphae are responsible for gall induction in three systems: *Pseudotectococcus rolliniae* – *Rollinia laurifolia* (Annonaceae), *Eriogalococcus isaias* – *Pseudobombax grandiflorum* (Malvaceae), and *Bystracoccus mataybae* – *Matayba guianensis* (Sapindaceae). The first-instar nymphs of *P. rolliniae* induce dormancy stem galls on *R. laurifolia*, and sexually dimorphic leaf galls are induced by the second-instar nymphs (Gonçalves et al., 2005, 2009). In the other two studied systems, the fist-instar nymphae use the bark of *M. guianensis* and *P. grandiflorum* as the sites for dormancy (diapause), but no tissue alteration is observed. After molting, they move to leaves and induce dimorphic galls, i.e., the female-induced galls are distinct from the male-induced galls (Hodgson et al., 2013; Magalhães et al., 2015).

In the case of Cecidomyiidae (Diptera), the main gall-inducing factor is cell disruption caused by the larva, in most cases using the prothoracic spatula for puncturing superficial cells (Rohfritsch, 1992; Harris, 1994). The released cellular fluids are extracorporeally digested and then sucked by the larvae. Probably the cell disruption and salivary fluids triggers the development of a pouch, covering growth, or distinct growth of buds (Rohfritsch, 1992; Harris, 1994; Ferreira & Isaias, 2014; Fleury et al., 2015). The larva may induce galls on the epidermal surface (and metaplasia may occur) or may penetrate into plant tissues, depending on the oviposition site and its behavior (Meyer, 1987).

The Lepidoptera induce galls through the voracious feeding of their larva, leading to the redifferentiation of typical nutritive cells. The oviposition occurs on superficial tissues, and when the eggs hatch (Meyer, 1987; Miller, 2005), the larvae chew plant cells, and enter the host plant organ. The nutritive cells accumulate lipids and are capable of self-regeneration (Meyer, 1987; Ferreira & Isaias, 2013; Vecchi et al., 2013; Ferreira et al., 2015). Even though Hymenoptera and Coleoptera also have chewing mouthparts, and their feeding activity is important to maintenance of gall development, their galls are initially induced by oviposition, and therefore they will be discussed below.

Oviposition. The oviposition is an important induction factor in Hymenoptera and Coleoptera galls (Table 2). Cynipidae (Hymenoptera) oviposition into plant tissues stimulates cell lysis and the formation of a gall chamber (Meyer, 1987; Brooks & Shorthouse, 1998; Csóka et al., 2005). The cells surrounding the oviposition site go through metaplasic reaction, and the cytoplasm becomes granulose. Gall development proceeds by cell hypertrophy and hyperplasia of surrounding tissues. Several Cynipidae galls, however, are induced only after the eclosion of the larvae (McCalla et al., 1962), which feeds, and induces the redifferentiation of additional nutritive cells in the outer layers (Meyer, 1987; Bronner, 1992; Ferreira et al., 2017a).

The oviposition is also the determinant factor for tissue modification in Coleoptera galls (Korotyaev et al., 2005). The adult females of Curculionidae excavate the host stems, oviposit and immediately leave plant tissues. Controlled experiments have shown that the females digging without oviposition is followed by fast reintegration of stem tissues. Accordingly, the oviposition fluids and the egg secretions were essential for the formation of hyperplasic and nutritive tissues in these galls (McCalla et al., 1962; Barnewall & De Clerck-Floate, 2012). However, the complete development of Coleoptera- and Hymenoptera-induced galls requires larval feeding by chewing the typical nutritive cells (Meyer, 1987; Rohfritsch, 1992; Barnewall & De Clerck-Floate, 2012).

Histological and Histochemical Convergences in Galls

During gall development, the more morphogenetic changes there are, the more complex galls are (Formiga et al., 2015; Ferreira et al., 2017a). Therefore, histochemical, histological, and histometric evaluations must be considered in order to determine the comparative complexity levels of galls (Ferreira et al., 2017a), considering distinct types of developmental alterations (Table 3).

Comparing galls induced by mites, nematodes and insects, not only the feeding habit, but also the gall-inducing taxa, determine patterns in gall development.

For example, nematodes and mites have similar feeding habits, and induce galls with several cytohistological distinctions, mainly their nutritive tissue types (Fig. 1). Mite-induced galls are usually simple, and a typical nutritive tissue is not always essential, while nematode-induced galls may have different levels of complexity. Nematode galls may have diverse nutritive tissues, whose patterns are related to the inducing species. Sucking animals, as eriophyids, nematodes, hemipterans, and thrips induce distinct galls, according to their feeding sites on plant organs (Fig. 2a-e, Fig. 3a-b). Phloem-sucking insects, with long stylets, induce phloem hypertrophy (Figs. 2a and 3b), while superficial sucking animals, as thrips, mites, nematodes, and rasping-sucking and chewing insects may induce galls with typical nutritive tissues around the larval chamber (Figs. 2c–e and 3a). Usually, the gall-inducing individuals induce the growth and enrichment of the cells,which are sources of their feeding. Simple galls of distinct groups result at least from one of these three basic processes: parenchyma homogenization, cell hypertrophy or hyperplasia (Fig. 1). Complex galls result from these processes and additional ontogenetic alterations (Table 3).

Hyperplasia

The increasing cell divisions, hyperplasia, is observed in almost all galls (Fig. 1), and must be diagnosed by the increment of cell layers or number of cells per tissue area (Goodey, 1948; Mani, 1964; Meyer, 1987; Moura et al., 2008; Ferreira & Isaias, 2013; Ferreira et al., 2017a). In some cases, the intumescence of host organs results only from parenchyma hyperplasia (Goodey, 1948; Ferreira et al., 2017a).

Hyperplasia occurs mainly in the beginning of gall development, being persistent in most galls until the end of gall growth and development phase (Rohfritsch, 1992; Arduin & Kraus, 1995). The increment of cell layers occurs mainly before cell hypertrophy and differentiation, and contributes to the final shape of the galls, depending on its topographical concentration. The intumescence of a stem gall is due to the hyperplasia in the cortical cells, where periclinal divisions occur during growth and development phase (Goodey, 1948; Ferreira & Isaias, 2013). Similarly, the formation of pouch galls (Moura et al., 2009b; Oliveira & Isaias, 2010a; Álvarez, 2011; Dias et al., 2013a; Carneiro & Isaias, 2015), leaf rolling and folding galls (Souza et al., 2000; Arduin et al., 2005; Álvarez et al., 2009; Ferreira et al., 2017b) occur by unequal hyperplasia and hypertrophy rates between the adaxial and abaxial ground meristems. In the formation of a covering gall (Arduin & Kraus, 1995), periclinal and oblique divisions give rise to emergences, which cover the gall-inducing egg, larva or nymph. In some galls, the hyperplasia rates are high until the end of the maturation phase, due to the constant feeding activity of the larva (Ferreira & Isaias, 2013).

Cell Hypertrophy

Cell hypertrophy may occur either in outer or inner gall tissue compartments (sensu Bragança et al., 2017). In the most complex galls induced by nematodes, cell hypertrophy is limited to the inner compartment, with redifferentiation of giant nutritive cells (Bird, 1961; Watson & Shorthouse, 1979). Such cells are polynucleated, which may explain

Table 3 Indicators of complexity in a gall

Complexity level	Morphogenetic steps	Examples
Simple	Parenchyma homogenization / changes in patterns of cell elongation	• Changes from dorsiventral mesophyll to homogeneous mesophyll
		• Changes in patterns of cell elongation
	Tissue hyperplasia	• Intense cell divisions during growth and development
		• Increase in number of parenchyma layers
	Overdifferentiation of trichomes or emergences	• Changes of indumentum density
	Parenchyma hypertrophy	• Parenchyma cell hypertrophy
		• Hypertrophy of inner secretory cells and cavities
Intermediary	Redifferentiation of a common storage tissue	• Presence of an outer parenchyma with vacuolated cells and storing starch
	Redifferentiation of a 'typical nutritive tissue'	• Cell layers surrounding gall chamber, with dense cytoplasm and feeding reserves (proteins, lipids or soluble sugars)
		• Giant polynucleated nutritive cells, polynucleated nurse cells, syncytial nutritive tissue (usually in nematode galls)
	Hypertrophy of vascular bundles	• Hypertrophy of phloem and xylem bundles (usually in phloem-sucking insect galls)
Complex	Redifferentiation of a 'nutritive-like tissue'	• Cell layers with dense cytoplasm, accumulation of starch and other metabolites, not directly eaten by the inducers (usually in phloem-sucking insect galls)
	Presence of mechanical layers	• Presence of sclerenchyma layers surrounding nutritive tissues
		• Presence of outer sclerenchyma layers
	Redifferentiation of other ground system cell types	• Differentiation of cells or tissues absent in the host organ (aerenchyma, collenchyma, hypodermis, spongy parenchyma, isolated sclereids, idioblasts, secretory tissues, etc.)
	Changes in epidermis	• Suppression of stomata differentiation / changes in stomatal pattern
		• Suppression of a trichome type / changes of trichome types
		• Stratification of epidermis
		• Epidermal holes/channels for re-absorption of the honeydew (some aphid galls)
	Promeristematic activity	• Axillary meristems capable of originate new leaf primordia
		• Nutritive cells capable of redifferentiating cells of ground, dermal and vascular systems, providing indeterminate growth

their great hypertrophy rates, when compared to other galls (Jones & Northcote, 1972; Rodiuc et al., 2014). In mite-induced galls, the hypertrophy may occur in the outer
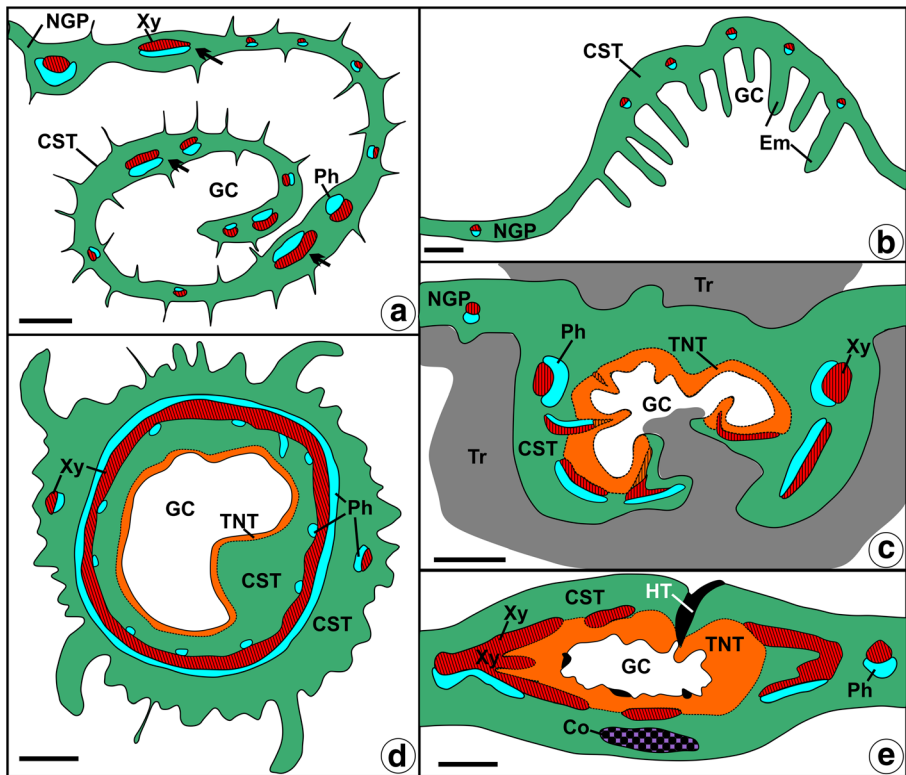
Fig. 2 Schematic drawings of cross-sectioned galls induced by insects, mites and nematodes. a Leaf-rolling gall induced by *Eriosoma ulmi* (Hemiptera: Aphididae) on *Ulmus minor* (Ulmaceae). Hypertrophied vascular bundles (arrows) in hypertrophic regions of this gall. **b** *Filzgall* induced by an unidentified Eriophyidae on leaves of *Miconia ibaguensis* (Melastomataceae). The overdifferentiated indumentum is formed by emergences. **c** Leaf gall induced by *Ditylenchus gallaeformans* (Nematoda) on *Miconia albicans* (Melastomataceae). The trichomes are longer and denser when covering galls, and occur also in adaxial surface of epidermis, which does not occur in non-galled portions of leaves. **d** Fusiform stem gall induced by unidentified Lepidoptera on *Marcetia taxifolia* (Melastomataceae). **e** Lenticular leaf gall induced by *Anguina balsamophila* (Nematoda) on *Wyethia amplexicaulis* (Asteraceae). Abbreviations: CST, common storage tissue; Em: emergence; GC: gall chamber; HT: healing tissue; NGP, non-galled portion of leaf; Ph, phloem; TNT, typical nutritive tissue; Tr: trichomes; Xy, xylem. Scale bars: (a), (c), (d) 500 μm; (b) 200 μm; (e) 3 mm

parenchyma cells, even though it is not a strict pattern (Moura et al., 2009b; Ferreira et al., 2017a). Nevertheless, insect-induced galls usually have outer tissue compartments with a large rate of cell hypertrophy (Kostoff & Kendall, 1929; Mani, 1964; Kraus et al., 2002; Álvarez et al., 2009; Isaias et al., 2011; Ferreira & Isaias, 2013, 2014; Suzuki et al., 2015), which develop from the end of growth and development toward the maturation phase. Outer parenchyma cells are usually vacuolated and store starch, being named the 'common storage tissue' (see next subsection), for they are not directly involved in the nutrition of the galling insect (Oliveira et al., 2011; Bragança et al., 2017; Ferreira et al., 2017a). Outer parenchyma cells may also accumulate secondary metabolites, being related to UV protection, defense against natural enemies, or to conferring distinct colors to the galls (Dias et al., 2013b; Bragança et al., 2017; Ferreira et al., 2017c). Phenolics and auxins have been co-localized in these tissue compartments, which have been associated with cell hypertrophy (Hori, 1992; Bedetti et al., 2014; Suzuki et al., 2015).
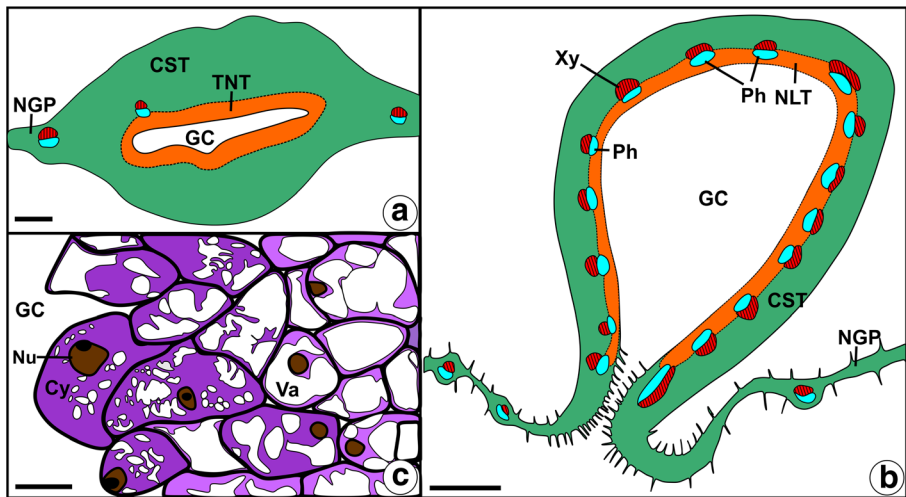
Fig. 3 Schematic drawings of galls showing histological patterns of galls and of a typical nutritive tissue. **a** Cross-sectioned lenticular gall induced by *Aceria tristriata* (Eriophyidae) on *Juglans regia* (Juglandaceae). **b** Globoid gall induced by *Tetraneura ulmi* (Aphididae) on *Ulmus minor* (Ulmaceae), longitudinal section. **c** Detail of nutritive cells of fusiform galls induced on the midribs of *Eucalyptus camaldulensis* (Myrtaceae) leaves by *Leptocybe invasa* (Hymenoptera: Eulophidae). The typical nutritive tissue shows a gradient of density of the cytoplasm (shown by darker shades of purple) towards the gall chamber; and smaller vacuoles (white) near gall chamber. Typical nutritive cells in contact with the inducer have more prominent nuclei and nucleoli. More information about anatomy and cytology of these galls may be encountered in the article of Isaias et al. (2018). Abbreviations: CST, common storage tissue; Cy: cytoplasm; GC, gall chamber; NGP, non-

Hypertrophy of Internal Glands

Internal glands are common on some host plant families and the activity of the gall inducing agents causes their hypertrophy. Hypertrophied internal glands immersed on phloem commonly occur in galls induced by phloem-sucking hemipterans on Anacardiaceae (Álvarez, 2011; Dias et al., 2013a; Álvarez et al., 2014, 2016; Muñoz-Viveros et al., 2014). In this case, the hypertrophy of the internal glands accompanies the hypertrophy of the phloem, the primary feeding source of the inducing aphids, and therefore the responsive tissue in their associated galls. Other phloem-sucking insects induce the hypertrophy of secretory cavities not associated to vascular bundles in host leaves (Arduin et al., 2005). The hypertrophy of secretory structures seems to accompany the common processes of hypertrophy and hyperplasia of the outer parenchyma cells (Arduin et al., 2005; Magalhães et al., 2014), which is not necessarily associated to the direct stimuli of the feeding activity. Instead, it may be an indirect response to hormonal (e.g., auxins and cytokinins) translocation and synergism, and consequent alteration of cell expansion and proliferation.

Parenchyma Homogenization

Independent on gall ontogenesis, the occurrence of parenchyma homogenization in galls induced by nematodes, mites, and insects is common (Fig. 1). It is observed in simple leaf rolling galls (Álvarez et al., 2013; Ferreira et al., 2017a), *filzgalls* (Ferreira

et al., 2017a), leaf folding galls (Souza et al., 2000; Álvarez et al., 2009; Bedetti et al., 2013; Magalhães et al., 2014; Formiga et al., 2015), pouch galls (Moura et al., 2009b; Carneiro et al., 2014b; Carneiro & Isaias, 2015), covering galls (Ferreira et al., 2017a), and stem/root swelling galls (Kraus & Tanoe, 1999; Ferreira & Isaias, 2013). Parenchyma homogenization may be related to some developmental factors: (1) the overwhelming of gall-inducing stimuli upon the environmental and endogenous signals for cell elongation in the host plant organ; (2) the maintenance of some meristematic sites in gall tissues; and (3) the combination of high hypertrophic and hyperplasic rates all over gall structure. These developmental factors isolated or grouped are commonly diagnosed in gall developmental sites.

Regarding gall development, some histological features reflect cytological aspects, such as the rearrangement of cellulose microfibrils, which favors the homogenization of gall tissues, at least in the beginning of gall development (Magalhães et al., 2014; Suzuki et al., 2015). Homogeneous parenchyma may persist until gall maturity and senescence (Moura et al., 2008, 2009b; Isaias et al., 2011; Ferreira & Isaias, 2014; Ferreira et al., 2017a), or change during the final phases of growth and development depending on the final gall morphotype (Ferreira & Isaias, 2013; Magalhães et al., 2014; Suzuki et al., 2015).

Changes in Indumentum Density

A dense indumentum is usually related to the increment of a boundary layer in plants, which ends up decreasing the transpiration rates and reflecting the excessive light, as well as increasing the defenses against herbivores (Schreuder et al., 2001; Carmona et al., 2011). The increment of indumentum may occur in several gall systems (Ferreira et al., 2017a), and is usually related to the protection of the gall-inducing agent against abiotic stresses and natural enemies, even though these effects must be tested (Stone & Schonrögge, 2003).

The overdifferentiation of trichomes or emergences (Fig. 2b) may be the unique process involved in the formation of *filzgalls* (Fig. 1), which are considered the simplest mite galls for they are characterized by the formation of dense indumentum and no or few other modifications (Mani, 1964). These galls are open, and the trichomes or emergences are usually the feeding sites of eriophyids (Mani, 1964; Ferreira et al., 2017a). The cells of these emergences or hypertrophied trichomes usually have scanty protoplasm (Mani, 1964), and no other cytological features of typical nutritive cells, such as granulose cytoplasm and hypertrophied nucleus, occur. In *filzgalls* induced on *Miconia ibaguensis*, the cells of the emergences accumulate reducing sugars (Ferreira et al., 2017a).

Feeding and Storage Tissues

There are three types of storage tissues in galls: common storage tissues, typical nutritive tissues, and nutritive-like tissues (sensu Ferreira et al., 2017a), which are herein grouped as storage tissues *lato sensu*.

Important developmental alterations in histological profiles of complex galls usually involve the increment and enrichment of the gall-inducer feeding tissues (Ferreira et al., 2017a). Most complex zoocecidia present differentiation of specialized nutritive or reserve cells (Fig. 1). Typical nutritive tissues of complex nematode, mite and insect galls have cells with conspicuous nucleus, dense or granulose cytoplasm, which store

proteins, reducing sugars and/or lipids, and are sources for the nutrition of the inducers (Kendall, 1930; Bird, 1961; Dropkin, 1969; Westphal et al., 1981; Brooks & Shorthouse, 1998; Ferreira et al., 2015, 2017a, 2017b; Bragança et al., 2017). These cells are in direct contact with the inducers (Fig. 2c-e, Fig. 3a), and their redifferentiation may involve the process of metaplasia (Meyer & Maresquelle, 1983; Meyer, 1987), when the cells redifferentiate into cells with higher metabolic and cytological activities, without previous dedifferentiation and proliferation. The cytoplasm granulation (Fig. 3c), observed in these nutritive cells, may be consequence of an accumulation of ribosomes and enzymes, increment of Golgi apparatus and endoplasmic reticulum, and in the number of mitochondria, as observed in some Neotropical galls (Oliveira et al., 2011; Vecchi et al., 2013; Ferreira et al., 2015). A nutritive cell may have one or several nuclei, depending on the gall-inducing or host plant species (Mani, 1964). In nematode galls, independent on the host plant or organ, the nutritive tissues may have promeristematic and totipotent cells or giant polynucleated cells (Fig. 1). Polynucleated nutritive cells are usually very hypertrophied, as those giant cells of root-knot nematode galls (Bird, 1961; Jones & Northcote, 1972; Rodiuc et al., 2014). Cyst nematode galls have syncytial nutritive tissues, formed by the induced digestion of parenchyma cell walls (Rodiuc et al., 2014). Promeristematic nutritive tissues, i.e., with totipotent cells, are observed in galls induced by the nematode *Ditylenchus gallaeformans* on *Miconia* spp. (Fig. 2c) (Ferreira et al., 2017a, 2017b). Distinctly from most cases, the nucleus may be absent in nutritive cells of some galls, a feature reported for the lepidopteran galls on *Tibouchina pulchra* (Vecchi et al., 2013), and for the cecidomyiid horn-shaped galls on *Copaifera langsdorfii* (Fabaceae) (Oliveira et al., 2011). These cells are supposedly controlled by adjacent cells, similarly to the role of companion cells over phloem sieve elements.

But how have the nutritive cells been stimulated to granulate? Nutritive cells with their conspicuous nuclei, accumulation of high-quality reserves (Fig. 3c), and few unpalatable secondary metabolites, are similar to meristematic cells, such as the cambium initials (Vecchi et al., 2013), or the cells in axillary buds (Ferreira et al., 2017b). Vascular cambium cells may store starch and lipids, and respond to several plant signals to begin or to cease cell divisions for a while (Evert, 2006; Begum et al., 2010). Maybe the gall inducers' stimuli are responsible for the maintenance of the meristematic features of these cells, representing a convergence among galls induced by phylogenetically distant organisms. Distinct taxa of galling organisms may induce the differentiation of granulose cells, even though their galls may be histologically very distinct. Contrary to the groups cited above, the phloem-sucking insects (as Psylloidea, Coccoidea and Aphididae) induce galls with hypertrophied phloem bundles (Fig. 3b). These galls do not have typical nutritive tissues (Larew, 1981; Bronner, 1992; Ferreira et al., 2017a), reflecting the direct influence of the feeding habit on the differentiation of nutritive cells. The increment in area of phloem in phloem-sucking galls should reflect the increment of sieve elements, companion cells, and/or transfer cells, which are nutrient-rich cells, and therefore are comparable to nutritive tissues in the galls induced by other zoocecidia.

As the inner tissue compartments of galls are usually related to the nutrition of the gall-inducing agents (Bragança et al., 2017), secondary metabolites may be suppressed or at least less accumulated in such gall tissues. For instance, an impairment of accumulation of terpenes and of phenolics occurs in the nutritive tissues of the Cecidomyiidae galls on *Piper arboreum* (Bragança et al., 2017), and of Lepidopteran

galls on *Marcetia taxifolia* (Ferreira & Isaias, 2013), as well as in the inner storage tissues of Psylloidea galls on *Psidium* spp. (Carneiro et al., 2014a).

In general, "common storage tissues" (Fig. 1, Fig. 2c-e, Fig. 3a), with vacuolated starch-rich cells, and peripheral cytoplasm (Ferreira et al., 2017a) largely occur in galls induced by distinct taxa (Brooks & Shorthouse, 1998; Álvarez et al., 2009, 2013; Oliveira & Isaias, 2010a; Isaias et al., 2011; Carneiro & Isaias, 2014, 2015; Ferreira et al., 2017a; Richardson et al., 2017). When the storage cells are cytologically similar to the typical nutritive cells of galls, but are not directly involved in the inducer's feeding, they are called "nutritive-like tissues" (Ferreira et al., 2017a; Richardson et al., 2017). The reserves accumulated in these cells are probably used for the energetic maintenance of gall structure (Oliveira & Isaias, 2010a). Some exceptions of this general pattern may occur, for example in galls induced by *Pachypsylla* spp., a piercing-sucking Psyllidae, on *Celtis occidentalis*. This insect feeds directly on nutritive polynucleated cells developed by the dissolution of cell walls, and not in phloem cells, as usually occur in hemipteran galls (Meyer, 1987).

Ambrosia Galls

Some Cecidomyiidae galls do not have a typical nutritive tissue (Arduin & Kraus, 2001; Dorchin et al., 2002; Rohfritsch, 2008; Sá et al., 2009), instead, their larva feed on a mycelium inoculated in plant tissues by oviposition time (Arduin & Kraus, 2001; Stone & Schonrögge, 2003; Rohfritsch, 2008; Sá et al., 2009; Chao & Liao, 2013). The nutritive resources are provided by the hyphae, which are intimately associated with the surrounding plant cells (Fig. 1), forming a nutritive 'pseudoparenchyma' (Rohfritsch, 2008). Similar to the ectomycorrhizae associated to some plant roots, the hyphae do not penetrate the cells at gall developmental site, but surround cell walls, increasing the absorption surface (Nylund & Unestam, 1982; Münzenberger et al., 2012). In ambrosia galls, pseudoparenchyma plant cells with dense cytoplasm may be observed adjacent to the inoculated mycelium (Meyer, 1987; Arduin & Kraus, 2001; Chao & Liao, 2013). Similar to the ectomycorrhizae, these enriched plant cells may provide water and nutrients to the fungi, which are consumed by the gall-inducing cecidomyiid. Similarities between the ectomycorrhizae and the fungi of ambrosia galls need further studies toward elucidating the physiological and ecological functions of the fungi in the associated gall systems.

The habit of inducing ambrosia galls is considered plesiomorphic in gall-inducing Cecidomyiidae, and the derived clades of gall inducers specialize in herbivory (Roskam, 1992; Arduin & Kraus, 2001; Rohfritsch, 2008). The complexity of ambrosia galls may vary according to their associated inducing species, and they may be histologically simple and parenchymatic, or may be complex structures consisting of a mechanical layer and outer neoformed tissues (Chao & Liao, 2013).

Outer Tissue Compartments

In general, the galls may be divided into outer and inner tissue compartments (Bragança et al., 2017). The inner compartments of several galls comprise the typical nutritive tissues, while the outer compartment is of general occurrence, and may constitute or not a common storage tissue (Figs. 1, 2 and 3).

The outer compartment usually accumulates secondary metabolites, such as phenolic derivatives (hydrolysable tannins, flavonoids, anthocyanins), alkaloids, and terpenoids (Ferreira & Isaias, 2013; Carneiro et al., 2014a; Bragança et al., 2017). These secondary metabolites are supposed to function as protective barriers against excessive sun radiation and UV light (Dias et al., 2013a, 2013b; Bragança et al., 2017), as well as against the natural enemies of the galling organism (Stone & Schonrögge, 2003; Bragança et al., 2017). Another possibility is the attractiveness of the gall inducer. The type of monoterpenes and sesquiterpenes accumulated in galls, such as those induced on *Lantana camara* (Verbenaceae), for instance, determines the choice of the galling *Aceria lantanae* (Eriophyidae) for plants with red flowers instead of plants with white or rose flowers (Moura et al., 2008, 2009a, 2009b). The volatile compounds are important for the recognition of host plants and for gall induction. Once in contact with host plant tissues, the differential content of terpenes of the host plants requires an adaptive development of the inducers, which must be able to detoxify for their successful gall induction and establishment.

The cells of the gall outer compartments may have more rigid walls than those of the inner compartments due to their distinct lignin and pectin composition (Formiga et al., 2013; Oliveira et al., 2014; Carneiro et al., 2015). As the cells of the gall outer tissues are usually hypertrophied, it is also possible that the pectin composition influences water uptake to these cells. The rigidity of gall walls may also be guaranteed by cell wall lignification of sclereids redifferentiated from parenchyma cells (Álvarez et al., 2009, 2016; Carneiro et al., 2014a, 2014b, 2015; Kurzfeld-Zexer et al., 2015). The sclerenchymatic cells may also provide mechanical protection for the gall inducers against natural enemies in maturation phase (Stone & Schonrögge, 2003; Carneiro et al., 2014b).

A sclerenchyma layer with sclereids or fibers may occur between the typical nutritive tissue and the outer tissue compartments in insect galls (Fig. 1), mainly Diptera and Hymenoptera galls (Arduin et al., 2005; Oliveira et al., 2011, 2016; Castro et al., 2012; Fleury et al., 2015; Amorim et al., 2017). The differentiation of sclerenchymatic cells may rely on the morphogenetic pattern of the host plant (Ferreira & Isaias, 2014). Mechanical layers may differentiate from the vascular cambium or pericyclic cells, similarly to the non-galled host organs (Fig. 2d) (Bedetti et al., 2013; Ferreira & Isaias, 2013). The differentiation of sclerenchyma layers surrounding the gall nutritive or nutritive-like tissues seems to be consequence of the accumulation of reactive oxygen species (ROS) due to the feeding activity of the gall inducers (Isaias et al., 2015; Oliveira et al., 2016). The ROS are captured by cinnamyl alcohols (precursors of lignins) and immobilized when deposited in cell walls (Barceló, 1997; Apel & Hirt, 2004). Outside the sclerenchymatic cells, specialized types of parenchyma, as an aerenchyma, for instance, may differentiate in the gall outer tissue compartment, and favor gas exchanges among the cells in galls deprived of stomata (Amorim et al., 2017). Collenchyma cell layers may also differentiate as a conservative feature of the host organs (Amorim et al., 2017), or as a neoformed feature (Goodey, 1948).

Changes in Dermal System

Some galls outer epidermal pavement cells may be suberized (Kraus et al., 2002) or metacutinized (Oliveira & Isaias, 2010b; Formiga et al., 2011), protecting the gall from

desiccation (Isaias et al., 2013). Moreover, distinct epidermal appendages, such as trichomes, may be related to mechanical protection against natural enemies and stabilization of the microclimate inside the gall (Moura et al., 2008; Dias et al., 2013a). Stomata can also be deformed or suppressed in galls induced by nematodes, mites and insects (Goodey, 1939; Moura et al., 2008; Álvarez et al., 2009, 2016; Dias et al., 2013a; Amorim et al., 2017), which affect gas exchanges in gall outer tissue compartments. Inner epidermal cells, limiting the chamber, in phloem-sucking insect galls may have reduced cell surface area and thin cuticle (Dias et al., 2013a; Carneiro & Isaias, 2014), facilitating the feeding of the galling organism (Carneiro & Isaias, 2014).

As commented in other sections, metaplasia may occur during induction and development of the galls under the feeding stimuli of gall inducers. The epidermal cells of Eriophyidae and Cecidomyiidae galls may directly redifferentiate into nutritive cells, or nutritive hairs (Westphal et al., 1981; Oliveira & Isaias, 2010b), without previous cell dedifferentiation and proliferation (Meyer & Maresquelle, 1983).

Promeristems

The cell layers lining the larval chamber may keep their meristematic feature. Moreover, some galls maintain promeristems or totipotent regions capable of redifferentiating the three plant tissue systems (Ferreira et al., 2017b). The maintenance of a unique promeristematic nutritive tissue impacts the longevity of *D. gallaeformans* galls on *Miconia* spp. (Fig. 2c), once it allows the replication of several generations of nematodes in the same gall (Ferreira et al., 2017a, 2017b). Accordingly, lateral buds differentiated in rosette galls of *Pisphondylia brasiliensis* (Cecidomyiidae) on *Guapira opposita* (Nyctaginaceae) produce true chlorophyllous leaf primordia (Fleury et al., 2015). The activity of these lateral buds is distinct from that of the non-galled buds, for instead of ordinary leaves, they produce modified leaves responsible for the rosette shape of the galls.

Conclusions

Plant development follows the morphogenetic patterns determined in plant meristems, which however can be manipulated by galling organisms, leading to the overdifferentiation or inhibition of some plant features, as well as the differentiation of distinct cell types. Gall development obeys the inducer's feeding chemical and mechanical stimuli toward convergent anatomical traits observed in galls induced by at least 50 independently evolved animal groups. Even though galls may be considered extended phenotypes of their inducers (Carneiro et al., 2015), their host plant genome and cell machinery may be stimulated in similar ways related both to the mode of feeding and feeding sites (Fig. 1). This concept is aligned with galls as new plant organs, as stated by Shorthouse et al. (2005, p. 407): "*they* [the insect galls] *are in a sense new plant organs because it is the plant that produces the gall in response to a specific stimulus provided by the invading insect. Each species of inducer produces galls that are anatomically and physiologically different from those induced by other related species*". The combination of anatomical convergent traits in each gall system culminates in the extant gall structural diversity.

We propose galls as elegant models for developmental studies due to their constant and repetitive cycles in nature, and hope such studies may help elucidate the roles of signaling molecules in plant developmental processes. The studies focusing on the developmental patterns of galls induced by unrelated animal taxa on related host plant species should help elucidating the pathways on plant cell redifferentiation. We also propose that structurally simple galls, i.e., with few anatomical alterations, should be the starting point to studying gall development using transcriptomes.

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