### Chapter 4 Gall Morphotypes in the Neotropics and the Need to Standardize Them

Rosy Mary dos Santos Isaias, Renê Gonçalves da Silva Carneiro, Jean Carlos Santos, and Denis Coelho de Oliveira

Abstract A morphotype can be defined as a specimen that illustrates a morphological variation within a species or, in the case of galls, a characteristic neo-formed plant organ generated by the interaction between a gall-inducing organism and a host plant. Once each gall morphotype is unique and derived from a species-specific interaction, there is a great confidence in using them to identify the different galling systems. In the Neotropics, where the biodiversity is high but somewhat unknown from the taxonomical point of view, the use of morphotypes helps assessing the abundance and richness of galling herbivores. This kind of knowledge would remain inaccessible if its report depended strictly on the taxonomic identification of the involved taxa. An effort on the standardization of the nomenclature used for inventories in the Neotropics revealed that some tridimensional shapes such as the globoid, ellipsoid, and lenticular are quite common, and may be the result of a series of similar events of cell division and expansion. When these morphotypes concomitantly occur on super-hosts of galling herbivores, special attention should be given to the possibility of overestimations, because variables such as the developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to the sex of the inducer may be difficult to be visualized. In specific cases, the phenological and anatomical analyses are crucial to avoid misinterpretations.

Keywords Gall shapes • Inventories • Richness • Super-hosts • Terminology

e-mail: rosy@icb.ufmg.br

J.C. Santos

#### D.C. Oliveira Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Brazil

R.M.S. Isaias (🖂) • R.G.S. Carneiro

Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

Instituto de Biologia, Universidade Federal de Uberlândia, Campus Umuarama, Bloco 2D, Rua Ceará s/n Umuarama, Caixa-Postal: 593, 38400-902 Uberlândia, MG, Brazil e-mail: jcsantosbio@gmail.com

#### 4.1 Why Standardizing the Gall Morphotypes

A morphotype can be defined as a specimen that illustrates a morphological variation within a species (Allaby 1999) or, in the case of galls, a characteristic neo-formed plant organ generated by the species-specific interaction between an inducing organism and a host plant (Isaias et al. 2013). Given that each gall-inducing insect is able to alter the morphogenesis of an organ of definite growth in very conservative patterns (Rohfritsch 1992), the morphotypes may be a confident mode of referring to several types of plant galls. The specificity between the involved taxa is strongly linked to the choice of the site of oviposition, which requires an efficient mode of attachment to plant surfaces (Eigenbrode and Jetter 2002). In fact, this event may be preceded by a series of contacts between the gall inducing organism and the plant surface leading to the recognition of the adequate host plant, beginning with host cell, host tissue and consequently host organ. In the temperate region, due to its relatively low biodiversity in comparison to the tropics (Fernandes and Price 1988; Price et al. 1998; Espírito-Santo and Fernandes 2007), the gall inducer – host plant systems are already well explored on the taxonomical basis (cf. Quercus spp. - Hymenoptera, Salix spp. - Diptera, Fagus spp. - Diptera systems). Therefore, studies in this region have advanced to the evaluation of global contexts (Kamata et al. 2002, 2006; Irwin and Lee 2003), trophic relationships among the gall inducer and the associated guild (Abrahamson and Weis 1997; Craig et al. 2007), and the search for experimental evidence of various gall traits (Inbar et al. 1998; Gish and Inbar 2006). On the other hand, the Neotropical region still presents a great unexplored biodiversity (see Espírito-Santo and Fernandes 2007), where new gall systems are frequently discovered and studied, generally bringing up a series of undescribed species of gallinducing insects (cf. Arduin et al. 1991; Kraus et al. 1996, 2002; Motta et al. 2005). The lack of knowledge on the taxonomy of galling herbivores in Neotropical fauna could constitute a barrier for the correct identification and reference of the systems in further publication. This barrier can be somewhat surpassed by the use of morphotypes in the inventories of abundance and richness of galls and galling herbivores, as proposed by many authors (cf. Carneiro et al. 2009). Nevertheless, a brief view on the inventories reveals a large and sometimes confusing terminology, which is used to refer to similar shapes or morphotypes (Table 4.1).

An effort to standardize this terminology seems to be useful and is here presented based on the list of the most common morphotypes reported in the Neotropical literature (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012) (Table 4.1).

The patterns extracted from this list are generated considering the most common and recurrent forms found in literature concerning Neotropical galls. Also, some possible causes of overestimations when super-hosts are included in the inventories are discussed. As it can be seen, nomenclature standardization of the approximate forms of the galls, i.e. their morphotypes, is necessary in order to avoid confusing and redundant terminology. Also, special attention is called to practical and methodological ways of avoiding overestimations by using phenological and developmental approaches.

Table 4.1 Morphotypes of neotropical gall systems as reported by Maia and Fernandes (2004), Oliveira and Maia (2005), Maia et al. (2008), Carneiro et al. (2009), and Santos et al. (2011, 2012)	Morphotypes	$\frac{\text{Galls per}}{(n)}$	(%)
	(n=613  galls)		
	Amorphous	16	2.61
	Bivalve-shaped	1	0.16
	Blister-shaped	1	0.16
	Circular	19	3.10
	Clavate	3	0.49
	Conical	40	6.53
	Cylindrical	8	1.31
	Discoid	59	9.62
	Elliptical	156	25.45
	Fusiform	9	1.47
	Globoid	169	27.57
	Horn-shaped	1	0.16
	Leaf fold	2	0.33
	Legume	7	1.14
	Lenticular	16	2.61
	Mamiliform	1	0.16
	Marginal roll	7	1.14
	Ovoid	5	0.82
	Pine-shaped	1	0.16
	Pocket-shaped	1	0.16
	Rosette	2	0.33
	Spheroid	35	5.71
	Spot	1	0.16
	Star	1	0.16
	Succulent	1	0.16
	Swelling	42	6.85
	Triangular	3	0.49
	Tubular	3	0.49
	Not described	3	0.49
	Total	613	100

#### 4.2 Patterns for Gall Morphotypes in the Neotropics

The description of gall morphotypes usually follows some common and naturally established procedures. In order to standardize the description of gall morphotypes, some procedures and terminologies are recommended: (1) identification of the host plant, (2) identification of the galling herbivore to the lowest possible taxonomical level, (3) description of the host organ, which should precise which organ is attacked and where in this organ the galls are located (sensu Bell 2008), (4) description of the neo-formed organ (i.e., the gall), classifying it into sessile (when it is inserted in the host organ) or pedunculated (with a narrow stalk which connects it to the host organ, making the gall easily detachable), (5) precise color description using a standardized color chart (http://www.immigration-usa.com/html\_colors.html), (6) geometrical form approximation made by comparison to standard spatial forms (sensu Radford et al.



**Fig. 4.1** Mature galls on *Psidium myrtoides* O. Berg (Myrtaceae) (**a**–**b**) and *Rollinia laurifolia* Schltdl. (Annonaceae) (**c**–**d**). (**a**) Extralaminar leaf gall. The peduncle is formed by a small contact area between the gall base and the leaf lamina. (**b**) Schematic diagram of the extralaminar leaf gall on *P. myrtoides* in cross section evidencing the *continuum* between the gall and the non-galled leaf tissues. This gall protrudes from the abaxial leaf surface. (**c**) Intralaminar leaf gall. There is a relatively large contact area between the leaf lamina and the base of the gall. (**d**) Schematic diagram of the intralaminar leaf gall on *R. laurifolia* in cross section evidencing the *continuum* between the gall and the non-galled leaf tissues. *GC* gall cortex, *L* non-galled leaf tissues, *La* larva, *LC* larval chamber. Bars=0.5 cm

1974). For instance, conical galls have the format of a true cone, ellipsoid galls with axes in the proportion of 2:1 and 3:2, globoid galls with the axes in the proportion of 5:6, lenticular galls with the axes in the proportion of 1:3 - 1:6, and amorphous galls as those with no standard morphological pattern or approximated geometrical format.

For host leaves, the galls may occur just on one surface or protrude to both sides of the lamina, being considered extralaminar or intralaminar (Fig. 4.1). Even the precise topographical position may be adequately referred as apical (distal end), medium or basal (proximal end), in veins or in the regions between the veins (out of the veins) (Fig. 4.2).

The most common morphotypes listed in Neotropical inventories are the conical, ellipsoid, globoid and lenticular galls (Table 4.1). Some of the morphotypes are not



**Fig. 4.2** (a-c) Leaves evidencing the possible sites for gall induction. (a) Division of leaf lamina in apical (Ap), medium (Me) and basal (Ba) region. (b) The leaf veins are indicated by *reddish lines*. (c) The leaf region between the veins are indicated by *reddish areas* 

strictly geometrical, because they are constituted by grouped galls, or present an object-like shape. In these cases, the terminology may indicate the similarity to a resembling object as exemplified by the horn-shaped, cup-shaped or crown-shaped galls (Fig. 4.3).

Gall size, ornamentation and color generally confer conspicuousness to arthropod galls (Inbar et al. 2010). In the Neotropical region, galls tend to be as not as large as in some systems of the temperate region (cf. galls associated to Pistacia species that reach 25 cm) (Inbar et al. 2010). Nevertheless, insects with long life cycles should tend to induce larger galls when compared to those with short life cycles. It occurs because of the longer interaction with host cell genotype which imposes a long lasting chemical battle between the associated species (Price et al. 1987). The variation in size may be also a response to the number of developing larvae (Arduin et al. 1989), i.e., the maximum gall size attained reflects the interaction of insect and plant genome and the environment (Weis and Abrahamson 1985, 1986; Weis and Gorman 1990; Egan et al. 2011). As proposed by Rohfritsch (1971), Stone et al. (2002) and Egan et al. (2011), in many species of gall inducers, gall growth is maintained by active larval feeding. Thus, gall maximum size is attained at the completion of the larvae active feeding prior to pupation or it may be interrupted in case the larvae succumbs to the effects of natural enemies, host plant defenses, or pathogens (Mani 1964).



Fig. 4.3 Object-like gall morphotypes induced on *Copaifera langsdorffii*. These shapes do not fit any common geometrical shape. (a) Horn-shaped galls. (b) Crown-shaped gall. (c) Cup-shaped gall. Bars = 1 cm

Even though it is an easy trait to be recorded, the color of 37.7 % of the gall morphotypes is unreported in the inventories. The great majority are referred as greenish (37.7 %), 15.8 % are brownish, 5.3 % are yellowish, 2.3 % are reddish, 0.8 % whitish and just 0.4 % are black (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012). This variation in color is due to changes in the accumulation of plant pigments (Fig. 4.4). According to Inbar et al. (2010), the color of galls may change during development, especially from green to red. Dias et al. (2013) measured the levels of pigments of the leaf galls on Schinus polygamus (Cay.) Cabrera. (Anacardiaceae), and demonstrated that the color change occurred due to gall senescence when the carotenoids and anthocianins are not masked by chlorophyll content anymore. This phenomenon is also common in other gall morphotypes (Fig. 4.4a, b). Chlorophyll concentration may also increase with gall age, which turns from red to green (Fig. 4.4c, d). Sometimes, the color of the same gall morphotype may vary from dark to yellowish green, reaching the red and even the brown tones, depending on the stimuli of the gall inducing insect and environmental conditions (Fig. 4.4e, f), such as the exposure to sun light (Carneiro et al. 2013; Dias et al. 2013).

Gall covering may vary considerably. In fact, it can be constituted of an unaltered *continuum* with the host organ epidermis or may be transformed in several ways. In Neotropical galls, 72.8 % of the galls do not cause macroscopic alterations in their host plant epidermis, and consequently has no differentiation of a singular indumentum. For 16 % of the morphotypes, no report on gall covering is presented, and just 11.2 % has conspicuous alterations. A cork (phellem) covering may develop either in stem or leaf galls, which may confer brown color, as is common in some *Copaifera langsdorffii* Desf. (Leguminosae Caesalpinioideae) galls (Oliveira et al. 2008) and was also observed in leaf galls on *Struthanthus vulgaris* Mart. (Loranthaceae) (Kraus et al. 2002). Also, gall surface may be either completely glabrous or densely hairy. Other common traits are a great variety of projections, such as emergences and even small leaves. All these structures may confer some protection against natural enemies and alter the final color of the gall morphotypes (Stone et al. 2002). To avoid some kind of overestimation or misleading with gall morphological variation during field evaluations of gall morphotypes, only mature galls with larvae next to pupation



**Fig. 4.4** Color variation in gall morphotypes. (**a**–**b**) Gall induced by a Lepidoptera on an unidentified host plant evidencing color change from *light greenish* to *dark reddish* due to gall senescence. (**c**–**d**) Galls induced by a Cecidomyiidae on *Andira humilis* evidencing color change from *deep red* to *greenish brown* due to tissue maturation. (**e**–**f**) Gall induced by a Triozid on *Psidium myrtoides* evidencing color variation as an evidence of the presence (*green gall*) or absence (*red gall*) of parasitoids. Bars = 1 cm

or in its last instar should be taken into account. The documentation of such morphological aspects should help identifying and accounting precisely the number of gall morphotypes of a given area.

### 4.3 The Most Common Morphotypes in Neotropical Inventories

In the Neotropical inventories of galling herbivores and their related galls, only a few reports identify the systems at the species level. The classification of the morphotypes is generally based on their geometric shapes, color, indumentum, and

	Host organs						
	Leaf	Stem	Buds	Reproductive organs	Roots		
Morphotypes	$\overline{\mathrm{N}^{\circ}\left(\% ight)}$	$\overline{\mathrm{N}^{\circ}\left(\% ight)}$	$\overline{\mathrm{N}^{\circ}\left(\% ight)}$	$\overline{\mathrm{N}^{\circ}\left(\% ight)}$	$\overline{\mathrm{N}^{\circ}(\%)}$		
Amorphous	10 (3.1)	_	5 (7.69)	1 (10)	_		
Bivalve-shaped	_	_	1 (1.54)	-	-		
Blister-shaped	1 (0.31)	_	_	-	-		
Circular	19 (5.90)	_	_	-	-		
Clavate	_	3 (1.40)	_	-	_		
Conical	34 (10.56)	2 (0.93)	4 (6.15)	-	-		
Cylindrical	7 (2.17)	_	1 (1.54)	-	_		
Discoid	57 (17.70)	_	2 (3.08)	-	-		
					-		
Elliptical	38 (11.80)	104 (48.37)	13 (20)	-	1 (100)		
Fusiform	3 (0.93)	4 (1.86)	1 (1.54)	1 (10)	-		
Globoid	70 (21.74)	73 (33.95)	23 (35.38)	3 (30)	_		
Horn-shaped	1 (0.31)	_	_	-	-		
Leaf fold	2 (0.62)	_	_	-	-		
Legume	7 (2.17)	_	_	-	-		
Lenticular	16 (4.97)	_	_	-	-		
Mamiliform	1 (0.31)	_	_	-	-		
Marginal roll	7 (2.17)	_	_	-	-		
Ovoid	1 (0.31)	_	2 (3.08)	2 (20)	-		
Pine-shaped	_	_	1 (1.54)	-	-		
Pocket-shaped	1 (0.31)	_	_	-	-		
Rosette	_	_	2 (3.08)	-	-		
Spheroid	30 (9.32)	2 (0.93)	3 (4.62)	-	-		
Spot	1 (0.31)	_	_	-	-		
Star	1 (0.31)	_	_	-	-		
Succulent	_	1 (0.47)	_	-	-		
Swelling	10 (3.11)	25 (11.63)	6 (9.23)	1 (10)	_		
Triangular	2 (0.62)	_	_	1 (10)	_		
Tubular	2(0.62)	_	1 (1.54)	_	_		

 Table 4.2 Distribution of gall morphotypes on neotropical plant host organs

position on the host plant (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012). In these inventories, 52.6 % of the galls occurred on leaves, 35.2 % on stems, 5.2 % on apical meristems, 4.9 % on buds, 2 % on reproductive organs, and just 0.1 % on roots (Table 4.2). This may be partly due to the greater availability of some plant organs all over the year, which allow more interactions to be established or even the lack of field observations on some sites of oviposition which are difficult to check.

65 (100)

1 (10)

10 (100)

1 (100)

Considering the available inventories on the diversity and richness of galling herbivores, it can be noticed that some tridimensional shapes are recurrent while others are rare. Also, some shapes may be grouped to avoid inconsistencies and

Not described

Total

1 (0.31)

322 (100)

1 (0.47)

215 (100)



**Fig. 4.5** Common shapes of Neotropical gall morphotypes. (a) Cylindrical galls induced by a Cecidomyiidae on *Eschweilera ovata* (Cambess.) Miers (Lecythidaceae). (b) Globoid galls induced by a Cecidomyiidae on *Apeiba tibourbou* Aubl. (Tiliaceae). (c) Cylindrical galls on *Matayba guianensis* Aubl. (Sapindaceae). (d) Lenticular galls on an unidentified host plant. Bars = 1 cm

facilitate the standardization of terminologies to be used in future inventories. The most common morphotypes referred in the literature for the Neotropics are the cylindrical, the globoid, and the lenticular galls (Fig. 4.5). In fact, globoid morphotypes are similar to the globose and spheroid, while ellipsoid, elliptical and ovoid means the same tridimensional shapes, and the lenticular morphotypes have been commonly referred as circular or discoid.

A closer look at the descriptions of gall morphotypes reveals that the lack of standardization may provide confusing data, although it reveals some peculiar aspects of the relationship between the occurrence of galls and their form in specific host organs. As it is seen in Table 4.2, leaves are the most affected host organs referred in the Neotropical inventories, accounting 321 gall systems with several shapes, hence being the most plastic organ. On the other hand, stems host a considerable number of galls (215 galls), but with few variations in shape. This is believed to be due to the constraints imposed by the host organ over the morphogenesis of the gall, since stems are considered to be less plastic organs when compared to leaves (Valladares et al. 2006). Galls in buds and reproductive organs are more difficult to be accounted since these organs are not always present or active in the plant body. Even though they are poorly reported as host organs, they still present a considerable amount of morphotypes, which is probably due to the great morphogenetical potentialities conferred by the meristematic tissues. Roots seem to be the most difficult host organs to be reported, probably due to their common underground position, which constitutes a barrier to the majority of galling insects, or even difficult the observation.

Despite the great variability in structures, no relationship could be established between the most common gall shapes and groups of host plants or insect *taxa*. What they are and why these repetitive processes lead to these convergent patterns is still unknown.

## 4.4 Super-hosts for Galling Herbivores: The Same House for Several Inducers

The development of gall structures requires a continued physical contact and tuned relationship between the host plant and the galling insect. Some of the important parameters that may define the possibility of gall formation are the co-occurrence of both taxa, the feeding habit of the galling herbivore, plant local abundance (Crawley 1989; Fernandes and Price 1991; Fernandes 1992; Gonçalves-Alvim and Fernandes 2001), and the systems of recognition established by plant surface traits (Eigenbrode and Spellie 1995; Eigenbrode and Jetter 2002). The diversity of shapes, sizes and colors makes the gall-inducing insects some of the most bizarre and interesting living organisms (Espírito-Santo and Fernandes 2007).

Even though the majority of the host plants, 64.5 % in the Neotropical inventories (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012), are associated to just one taxon, some may support two or more galling herbivores and will be herein referred as super-hosts. This diversity of associated insects is intriguing for host plant-galling herbivore systems are, largely, species-specific (Dreger-Jauffret and Shorthouse 1992; Carneiro et al. 2009). According to Hardy and Cook (2010), gall-inducing insects are more host-specific than their non-galling relatives, even though there is no general significant increase in the diversification rate in galling herbivores. Gall induction on plants has evolved multiple times among insects, with over 13,000 species currently described (Hardy and Cook 2010). However, the perspective is of over 132,000 species in a global perspective including the undescribed taxa (Espírito-Santo and Fernandes 2007). More than taxa specific, gall-inducing herbivores seem to be exceptionally tissue specific, which make the super-hosts excellent models for the study of plant morphogenetical potentialities (Oliveira et al. 2008). The same specific host organ tissues respond distinctly to the stimuli of several and different biotic signalers. The galling herbivores are certainly very successful because the gall represents new tissues, at least initially, enemy-free (Price et al. 1987; Stone and Schönrogge 2003; Hardy and Cook 2010).

The alterations observed among four gall morphotypes co-occurring on *Copaifera langsdorffii* (Fabaceae) revealed that the distinct responses are consequence of the wide morphogenetical potentialities of the host plant (Oliveira et al. 2008). Each of the galling associated herbivores manipulated its host tissues in a peculiar mode, and generated particular qualitative responses in divergent patterns, resulting in the

variety of morphotypes. More than denoting the specificity of the relationship, this peculiarity makes the insect galls important taxonomical tools (Floate et al. 1996), either in the botanical or entomological level (Fernandes et al. 1997). Curiously, the insects associated to *C. langsdorffii* are Cecidomyiidae, which represent such a diverse group of very specialized galling insects (Gagnè 1994). The number of Cecidomyiidae associated to this host plant species may range from 5 to 23 (Oliveira et al. 2008; Costa et al. 2010), and the generated morphotypes may occur either on leaves or stems.

The analyses of some inventories in Brazil (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012) have accounted for 128 systems on super-hosts but it seems like there are no relationships between these plant *taxa* and their higher susceptibility to the attack by galling arthropods. A common host plant in the Neotropics, *Lantana camara* L. (Verbenaceae), hosts three *taxa* of galling arthropods (Moura et al. 2009). All these taxa explore the leaves and flowers of *L. camara* and induce very distinct galls. The diversification of the morphotypes does not permit misidentification of each system. *Asphondylia camarae* (Diptera: Cecidomyiidae) explores a very special niche, the flowers and consequently must have a peculiar life cycle adjusted to that of its host plant. *Schismatodiplosis lantanae* (Diptera: Cecidomyiidae) and *Aceria lantanae* (Acarina: Eriophyiidae) explore the leaves and may occur concomitantly on the same lamina, but are easily distinguishable (Moura et al. 2008).

When the super-host plants are found in nature, special attention should be given to the possibility of overestimations, because variables such as developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to the sex and alternation of generations of the gall inducers may be difficult to be visualized. In specific cases, the phenological and anatomical analyses are crucial to avoid misinterpretations.

# 4.5 Phenological and Anatomical Analysis: Special Care to Avoid Overestimations

The relationships between host plants and gall inducing insects are subjected, most times, to a highly complex net of ecological relationships. Besides the parasitic relationship established upon gall induction, the host plant – gall inducer systems can be the base for many other associated trophic levels, such as predators and parasitoids (*cf.* Sanver and Hawkins 2000; Espírito-Santo et al. 2004; Santos et al. 2010). Parasitoids are known to disturb and/or stop the feeding activity of the gall inducers, since they can cause their premature death. Since gall development and structure directly depend on the action of the gall inducer, interferences such as those imposed by parasitoids should significantly affect the structure of the gall (Fernandes et al. 1987; Wiebes-Rijks and Shorthouse 1992). Yet, it should be taken into account that gall development can be either fast or slow, depending on the rate of cell division, growth and differentiation in each



Fig. 4.6 Variation in shapes in two gall morphotypes induced by Cecidomyiidae on *Copaifera langsdorffii*. (**a–b**) Horn-shaped gall, passing through four distinct developmental stages. (**a**) Young dome-shaped gall. (**b**) Protrusion of two horns at the early growth and developmental stage. (**c**) Developed horns at the late growth and developmental stage. (**d**) Mature horn-shaped galls. (**e–f**) Development of the cup-shaped gall, passing through two distinct stages. (**e**) Ellipsoid galls at the growth and developmental stage. (**f**) Mature cup-shaped gall. Bars = 1 cm

specific gall system. During this process, gall shape may present great variance, which without phenological and developmental analyses, could be understood as different gall morphotypes, unrelated whatsoever. For instance, the cup-shaped gall on C. langsdorffii is red when mature, and may occur either on the abaxial or adaxial leaflet surface, with a membranous texture. The larval chamber is located at the basal portion of the gall which is monotalamous (Oliveira et al. 2008). This gall is structurally very simple and its development lasts 2-3 days, when it changes from light green to red. At the beginning of its development, the gall is globoid and closed, but it elongates axially and opens in its apical portion along linear preexisting scars. The alteration in shape is so drastic that these morphotypes could be easily misinterpreted as two distinct ones if the temporal variable is not evaluated. Another C. langsdorffii gall morphotype that may lead to this kind of overestimation in field studies is the horn-shaped gall, which can be either green or red when mature. It may occur in the abaxial or adaxial leaflet surface, and is pedunculated. The development of this gall morphotype lasts about 1 year. At the very beginning of its development, the gall assumes a volcano shape, from whose inner portion firstly emerges a large amount of trichomes. Secondarily, two hairy projections develop and form the gall body. Towards maturity, the basal portion develops originating the peduncle (Fig. 4.6). These two morphotypes indicate the importance of periodic field observation to follow the phenotypical changes along gall development.



**Fig. 4.7** Gall morphotypes induced by *Pseudotectococcus rolliniae* on *Rollinia laurifolia*. (a) Host leaf with female induced (*white arrows*) and male induced galls (*black arrows*). (b) Detail of a male induced gall. (c) Detail of a female induced gall. (d) Stem galls for dormancy induced by first instar nymphs resembling enlarged lenticels (*white arrows*) compared to the true regular sized lenticels (*black arrows*). Bars = 1 cm in a, d; 0.25 cm in b, c

Another peculiar case concerns the relationship between Rollinia laurifolia (Annonaceae) and the gall inducer Pseudotectococcus rolliniae (Erioccocidae) (Goncalves et al. 2005, 2009). In this system, a reckless observer is subjected to committing several mistakes on the description of the galls. At the first sight, two different gall morphotypes can be accounted, being one of them larger and round and the other, smaller and conical. These two morphotypes could also be understood as two different developmental stages of the same gall, due to their relative size. However, anatomical, phenological and entomological analyses helped elucidating the occurrence of sexual dimorphism on these galls. In this specific case, females are sessile and spend their whole lives inside the gall chamber, while males are ephemeral and spend little time inside their galls, before leaving them to fertilize the females. The time spent by each gender of P. rolliniae inside their galls is believed to be the main determining factor of the distinct gall phenotypes (Gonçalves et al. 2005). Still, the phenological studies performed for this system indicated a lag-time between the adult forms and the nymphs that induce the galls of the following year. The nymphs could not host themselves on the leaves of their host plant, which is deciduous, shedding all its leaves during the winter. A third gall morphotype, resembling a lenticel, was found on the shoots of the host plant, in which the first instar nymphs induce a gall for dormancy (Gonçalves et al. 2009) (Fig. 4.7). This case illustrates an especially complex insect life cycle and evidences the importance of phenological and anatomical analyses for the reliability of gall morphotyping.

#### 4.6 Conclusions and Remarks

The standardization of the nomenclature used in the inventories of the diversity of galls in the Neotropics should facilitate future comparative analyses of galling herbivores distribution, and patterns of gall development in Brazilian biomes. By properly accounting the gall morphotypes from the Neotropics, ecological parameters such as richness and abundance of galling herbivores should be accessed, and increase the knowledge on the biodiversity in such areas. The most common tridimensional morphotypes reported, the globoid, ellipsoid, and lenticular ones, are repetitive on several distinct systems which reinforces the necessity of taxonomical identification of the organisms to the lowest possible level, whenever it is possible. As well, the repetitiveness of these shapes elects such host plants-gall inducers systems for developmental studies in cytological level so as to explain how plant cell morphogenesis is manipulated in such convergent patterns.

It is particularly evident that the alterations in host plant organs, and the development of the morphotypes should be studied taking into consideration the developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to sex and alternation of generations of the inducers. These characteristics may be difficult to be visualized in field conditions but may be key elements which allied to phenological and anatomical analyses would help avoiding misinterpretations or overestimations of gall diversity in nature.

#### References

- Abrahamson WG, Weis AE (1997) Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies. Chicago University Press, Chicago, p 456
- Allaby M (1999) "Morphotype". A dictionary of zoology. Encyclopedia.com. http://www. encyclopedia.com. Accessed 2 Apr 2013
- Arduin M, Kraus JE, Otto P, Venturelli M (1989) Caracterização morfológica e biométrica de galhas foliares em *Struthanthus vulgaris* Mart. (Loranthaceae). Rev Bras Biol 49:817–823
- Arduin M, Kraus JE, Venturelli M (1991) Estudo morfológico da galha achatada em folha de *Struthanthus vulgaris* Mart. (Loranthaceae). Rev Bras Bot 14:147–156
- Bell AD (2008) Plant form: an illustrated guide to flowering plant morphology. Timber Press, Portland, p 431
- Carneiro MAA, Borges RAX, Araújo APA, Fernandes GW (2009) Insetos indutores de galhas da porção sul da Cadeia do Espinhaço, MG, Brasil. Rev Bras Entomol 53:570–592
- Carneiro RGS, Burckhardt D, Isaias RMS (2013) Biology and systematics of gall-inducing triozids (Hemiptera: Psylloidea) associated with *Psidium* spp. (Myrtaceae). Zootaxa 3620:129–146
- Costa FV, Fagundes M, Neves FS (2010) Arquitetura da planta e diversidade de galhas associadas à *Copaifera langsdorffii* (Fabaceae). Ecol Aust 20:9–17

- Craig TP, Itami JK, Horner JD (2007) Geographic variation in the evolution and coevolution of a tritrophic interaction. Evolution 61:1137–1152
- Crawley MJ (1989) Insect herbivores and plant population dynamics. Annu Rev Entomol 34:531–556
- Dias GG, Moreira GRP, Ferreira BG, Isaias RMS (2013) Why do the galls induced by *Calophya duvauae* Scott on *Schinus polygamus* (Cav.) Cabrera (Anacardiaceae) change colors? Biochem Syst Ecol 48:111–122
- Dreger-Jauffret F, Shorthouse JD (1992) Diversity of gall-inducing insects and their galls. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 8–33
- Egan SP, Hood GR, Ott JR (2011) Natural selection on gall size: variable contributions of individual host plants to population-wide patterns. Evolution 65:3543–3557
- Eigenbrode SD, Jetter R (2002) Attachment to plant surface waxes by an insect predator. Integr Comp Biol 42:1091–1099
- Eigenbrode SD, Spellie KE (1995) Effects of plant epicuticular lipids on insect herbivores. Annu Rev Entomol 40:171–194
- Espírito-Santo MM, Fernandes GW (2007) How many species of gall-inducing insects are there on earth, and where are they? Ann Entomol Soc Am 100:95–99
- Espírito-Santo MM, Faria ML, Fernandes GW (2004) Parasitoid attack and its consequences to the development of the galling psyllid *Baccharopelma dracunculifoliae* (Hemiptera). Basic Appl Ecol 5:475–484
- Fernandes GW (1992) Plant family size and age effects on insular gall-forming species richness. Glob Ecol Biogeogr 2:71–74
- Fernandes GW, Price PW (1988) Biogeographical gradients in galling species richness: test of hypotheses. Oecologia 76:161–167
- Fernandes GW, Price PW (1991) Comparisons of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds) Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York, pp 91–115
- Fernandes GW, Martins RP, Tameirão Neto E (1987) Food web relationship involving Anadiplosis sp (Diptera: Cecidomyiidae) leaf galls on Machaerium aculeatum (Leguminosae). Rev Bras Bot 10:117–132
- Fernandes GW, Araújo RC, Araújo SC, Lombardi JA, Paula AS, Loyola JRR, Cornelissen TG (1997) Insect galls from savanna and rocky fields of the Jequitinhonha Valley, Minas Gerais, Brazil. Naturalia 22:221–244
- Floate KD, Fernandes GW, Nilsson JA (1996) Distinguishing intrapopulational categories of plants by their insect faunas: galls on rabbitbrush. Oecologia 105:221–229
- Gagnè RJ (1994) The gall midges of the region neotropical. Comstock, Ithaca, 352 p
- Gish M, Inbar M (2006) Host location by apterous aphids after escape dropping from the plant. J Insect Behav 19:143–153
- Gonçalves SJMR, Isaias RMS, Vale FHA, Fernandes GW (2005) Sexual dimorphism of *Pseudotectococcus rolliniae* Hodgson & Gonçalves 2004 (Hemiptera Cocooidea Eriococcidade) influences gall morphology on *Rollinia laurifolia* Schltdl. (Annonaceae). Trop Zool 18:161–169
- Gonçalves SJMR, Moreira GRP, Isaias RMS (2009) A unique seasonal cycle in a leaf gall-inducing insect: the formation of stem galls for dormancy. J Nat Hist 43:843–854
- Gonçalves-Alvim SJ, Fernandes GW (2001) Biodiversity of galling insects: historical, community and habitat effects in four neotropical savannas. Biodivers Conserv 10:79–98
- Hardy NB, Cook LG (2010) Gall-induction in insects: evolutionary dead-end or speciation driver? BMC Evol Biol 10:257. http://www.biomedcentral.com/1471-2148/10/257/. Accessed 7 Jun 2013
- Inbar M, Doostdar H, Sonora RM, Leibee GL, Mayer RT (1998) Elicitors of plant defensive systems reduce insect density and disease incidents. J Chem Ecol 24:135–149

- Inbar M, Izhaki I, Koplovich A, Lupo I, Silanikove N, Glasser T, Gerchman Y, Perevolotsky A, Lev-Yadun S (2010) Why do many galls have conspicuous colors? A new hypothesis. Arthropod Plant Interact 4:1–6
- Irwin JT, Lee RE Jr (2003) Cold winter microenvironments conserve energy and improve overwintering survival and potential fecundity of the goldenrod gall fly, *Eurosta solidaginis*. Oikos 100:71–78
- Isaias RMS, Carneiro RGS, Oliveira DC, Santos JC (2013) Illustrated and annotated checklist of Brazilian gall morphotypes. Neotrop Entomol. doi:10.1007/s13744-013-0115-7
- Kamata N, Esaki K, Kato K, Igeta Y, Wada K (2002) Potential impact of global warming on deciduous oak dieback caused by ambrosia fungus *Rafaellea* sp. carried by ambrosia beetle *Platypus quercivorus* (Coleoptera: Platypodidae) in Japan. B Entomol Res 92:119–126
- Kamata N, Sato S, Kodani J (2006) Guild structure of gall midges on *Fagus crenata* in relation to snow gradient: present status and prediction of future status as a result of global warming. In: Osaki K, Yukawa J, Ohgushi T, Price PW (eds) Galling arthropods and their associates: ecology and evolution. Springer, Tokyo, 304 p
- Kraus JE, Sugiura HC, Cutrupi S (1996) Morfologia e ontogenia em galhas entomógenas de Guarea macrophylla subsp. tuberculata (Meliaceae). Fitopatol Bras 21:349–356
- Kraus JE, Arduin M, Venturelli M (2002) Anatomy and ontogenesis of hymenopteran leaf galls of Struthanthus vulgaris Mart. (Loranthaceae). Rev Bras Bot 25:449–458
- Maia VC, Fernandes GW (2004) Insect galls from Serra de São José (Tiradentes, MG, Brazil). Rev Bras Biol 6:423–445
- Maia VC, Magenta MAG, Martins SE (2008) Ocorrência de galhas de insetos em áreas de restinga em Bertioga (São Paulo, Brasil). Biota Neotrop 8:167–197
- Mani MS (1964) The ecology of plant galls. Dr Junk Pub, The Hague, 434 p
- Motta LB, Kraus JE, Salatino A, Salatino MLF (2005) Distribution of metabolites in galled and non-galled foliar tissues of *Tibouchina pulchra*. Biochem Syst Ecol 33:971–981
- Moura MZD, Soares GLG, Isaias RMS (2008) Species-specific changes in tissue morphogenesis induced by two arthropod leaf gallers in *Lantana camara* L. (Verbenaceae). Aust J Bot 56:153–160
- Moura MZD, Soares GLG, Isaias RMS (2009) Ontogênese da folha e das galhas induzidas por *Aceria lantanae* Cook (Acarina: Eriophyidae) em *Lantana camara* L. (Verbenaceae). Rev Bras Bot 32:271–282
- Oliveira JC, Maia VC (2005) Ocorrência e caracterização de galhas de insetos na restinga de Grumari (Rio de Janeiro, RH, Brasil). Arch Mus Nac 63:669–675
- Oliveira DC, Drummond MM, Moreira ASFP, Soares GLG, Isaias RMS (2008) Potencialidades morfogênicas de *Copaifera langsdorffii* Desf. (Fabaceae): super-hospedeira de herbívoros galhadores. Rev Biol Neotrop 5:31–39
- Price PW, Roininnen H, Tahvanainem J (1987) Plant age and the attack by the bud galler, *Euura mucronata*. Oecologia 73:334–337
- Price PW, Fernandes GW, Lara ACF, Brawn J, Gerling D, Barrios H, Wright MG, Ribeiro SP, Rothcliff N (1998) Global patterns in local number of insect galling species. J Biogeogr 25:581–591
- Radford AE, Dickison WC, Massey JR, Bell CR (1974) Vascular plant systematics. Harper & Row, New York, 891 p
- Rohfritsch O (1971) Développment cécidien et role due parasite dans quelques in galles d'Arthropodes. Marcellia 37:233–339
- Rohfritsch O (1992) Patterns in gall development. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 60–86
- Santos JC, Silveira FAO, Pereira EC, Fernandes GW (2010) Pattern of attack of a galling insect reveals an unexpected preference-performance linkage on medium-sized resources. Rev Bras Entomol 54:96–103
- Santos JC, Almeida-Cortez JS, Fernandes GW (2011) Richness of gall-inducing insects in the tropical dry forest (Caatinga) of Pernambuco. Rev Bras Entomol 55:45–54

- Santos JC, Almeida-Cortez JS, Fernandes GW (2012) Richness of gall inducing insects in the Atlantic forests of Pernambuco, Northeastern Brazil. Biota Neotrop 12:196–212
- Sanver D, Hawkins BA (2000) Galls as habitats: the inquiline communities of insect galls. Basic Appl Ecol 1:3–11
- Stone GN, Schönrogge K (2003) The adaptive significance of insect gall morphology. Trends Ecol Evol 8:512–522
- Stone GN, Schönrogge RJ, Atkinson RJ, Bellido D, Pujade-Villar J (2002) The population biology of oak gall wasps (Hymenoptera: Cynipidae). Annu Rev Entomol 47:633–668
- Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. J Ecol 94:1103–1116
- Weis AR, Abrahamson WG (1985) Potential selective pressures by parasitoids on the evolution of a plant-herbivore interaction. Ecology 66:1261–1269
- Weis AR, Abrahamson WG (1986) Evolution of host-plant manipulation by gallmakers: ecological and genetic factors in the Solidago-Eurosta system. Am Nat 127:681–695
- Weis AE, Gorman WL (1990) Measuring selection on reaction norms: an exploration of the Eurosta-Solidago system. Evolution 44:820–831
- Wiebes-Rijks AA, Shorthouse JD (1992) Ecological relationships of insects inhabiting cynipid galls. In: Shorthouse JD, Rohfristsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, 285 p