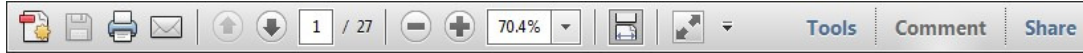
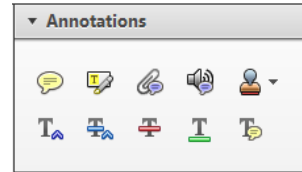


Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



### 1. [Replace \(Ins\)](#) Tool – for replacing text.

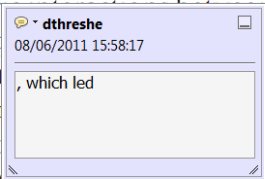


Strikes a line through text and opens up a text box where replacement text can be entered.

#### How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

standard framework for the analysis of microeconomic activity. Nevertheless, it also led to the development of a number of strategic approaches. The number of competitors in an industry is that the structure of the industry is a main component. At the industry level, are externalities important? (Mankiw henceforth) we open the 'black b



### 2. [Strikethrough \(Del\)](#) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

#### How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by market clearing. Blanchard and ~~Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply shocks in the classical framework assuming monopolistic competition. An exogenous number of firms

### 3. [Add note to text](#) Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

#### How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups consistent with the VAR evidence

sation by Markov processes. The number of competitors and the impact on the structure of the sector is that the structure of the sector



### 4. [Add sticky note](#) Tool – for making notes at specific points in the text.



Marks a point in the proof where a comment needs to be highlighted.

#### How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

and supply shocks. Most of the time, the number of competitors and the impact on the structure of the sector is that the structure of the sector



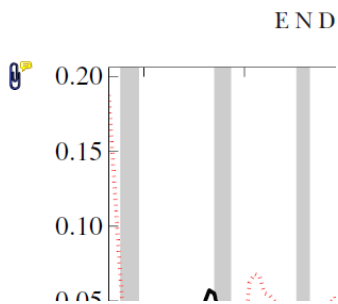
5. **Attach File** Tool – for inserting large amounts of text or replacement figures.



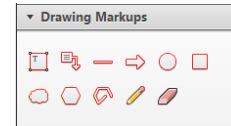
Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it

- Click on the **Attach File** icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

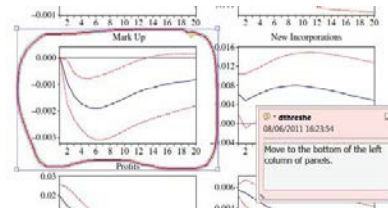


6. **Drawing Markups** Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks. Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



How to use it

- Click on one of the shapes in the Drawing Markups section.
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- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



## RESEARCH PAPER

# Contribution of gall microscopic structure to taxonomy of gallicolous aphids on *Pistacia*

R. Álvarez<sup>1</sup>, J.-J. I. Martínez<sup>2,3</sup>, A. L. Muñoz-Viveros<sup>4</sup>, P. Molist<sup>5</sup>, J. Abad-González<sup>6</sup> & J. M. Nieto Nafria<sup>7</sup>

<sup>1</sup> Departamento de Biología Molecular-Área de Biología Celular, Universidad de León, León, Spain

<sup>2</sup> Department of Animal Sciences, Faculty of Sciences and Technology, Tel Hai College, Tel Hai, Israel

<sup>3</sup> Laboratory of Animal Ecology & Biodiversity, MIGAL - Galilee Research Center, South Industry Zone, Kiryat Shmona, Israel

<sup>4</sup> Laboratorio de Control de Plagas, Facultad de Estudios, Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Mexico

<sup>5</sup> Department of Functional Biology and Health Sciences, University of Vigo, Vigo, Spain

<sup>6</sup> Departamento de Economía y Estadística, Universidad de León, León, Spain

<sup>7</sup> Departamento de Biodiversidad y Gestión Ambiental, Universidad de León, León, Spain

## Keywords

Dendrogram; Fordini; galls; microscopy study; *Pistacia*.

## Correspondence

R. Álvarez, Departamento de Biología Molecular-Área de Biología Celular, Universidad de León, León, Spain.

E-mail: ralvn@unileon.es

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## ABSTRACT

Aphids inducing galls on *Pistacia* plants belong to the tribe Fordini. According to the classification of Heie & Wegierek (2009), the genera are grouped into three subtribes. Previous microscopic studies showed that this taxonomy is not consistent with the histological characteristics of the galls. In this paper, galls induced by *Aploneura lentisci*, *Asiphonella cynodonti*, *Forda riccobonii*, *Slavum wertheimae* and *Smynthuroides betae* were analysed for the first time, together with nine other galls previously described, and new groupings were determined based on histological features. The main results indicated three groups of galls: the first group comprised closed galls induced by *Baizongia pistaciae*, *Geoica utricularia*, *Rectinasus buxtoni* and *Slavum wertheimae*; the second group included two species of *Geopemphigus* (*G. blackmani* and *G. torsus*); and the third group was divided into two subgroups, the first comprised *Aploneura lentisci*, *Asiphonella cynodonti* and *Geopemphigus morral*, and the other included all the remaining species (*Forda formicaria*, *F. marginata*, *F. riccobonii*, *Paracletus cimiciformis* and *Smynthuroides betae*). The taxonomic value of these results is discussed.

## INTRODUCTION

Species of aphids that typically induce galls in plants of the genus *Pistacia* (Anacardiaceae) belong to 13 genera. These are included in the extended classification of Remaudière, Stroyan & Quednau (Nieto Nafria & Favret 2011) – together with the five genera that induce galls in the genus *Rhus* (Anacardiaceae) – in the tribe Fordini (Aphididae, Eriosomatinae). In their classification, the *Pistacia*-galling genera are placed in the subtribe Fordina and the *Rhus*-galling genera in the subtribe Melaphidina. However, in the alternative classification proposed by Heie & Wegierek (2009), these two groups are raised to the level of tribes, the former becoming tribe Fordini and the latter becoming tribe Melaphidini. In the Heie & Wiegorek classification, the *Pistacia*-galling genera are distributed among three subtribes (Heie & Wegierek 2009): Fordina Acloque 1897, Baizongiina Börner 1944 (1914) and Geoicina Mordvilko 1921. *Forda* von Heyden 1837, *Paracletus* von Heyden 1837, *Rectinasus* Theobald 1914, *Smynthuroides* Westwood 1849 and *Tramaforda* Manheim 2007 are allocated to Fordina. *Aloephagus* Essig 1950, *Aploneura* Passerini 1863, *Asiphonella* Theobald 1923, *Baizongia* Rondani 1848, *Geopemphigus* Hille Ris Lambers 1933 and *Slavum* Mordvilko 1927 are allocated to Baizongiina, and *Geoica* Hart 1894 and *Chaetogeioica* Remaudière and Tao 1957 to Geoicina (see Table 3).

A number of studies have suggested that the identified groups of genera should be revised. Some authors base their argument on the increasingly frequent molecular analyses (e.g. Inbar 2006; Zhang & Qiao 2007; Ortiz-Rivas *et al.* 2009; Ortiz-Rivas & Martínez-Torres 2010; Yang *et al.* 2010), while others stress the importance of morphological studies of the stage of the life cycle that occurs on the roots of herbaceous plants (Blackman & Eastop 2007; Williams & Dixon 2007). Moreover, two recent studies examined aphid-induced galls microscopically: one described three species of the genus *Geopemphigus* (Muñoz-Viveros *et al.* 2014), while the other examined galls induced by *Rectinasus buxtoni* (Álvarez *et al.* 2014). In both studies, it was proposed that these species should be placed in subtribes other than those indicated in the aforementioned classification of Heie & Wegierek (2009). Specifically, it was proposed that the genus *Rectinasus* should not be grouped together with the genera *Forda* and *Paracletus* in the subtribe Fordina. It was also proposed that the genus *Geopemphigus* should not accompany the genus *Baizongia* in the subtribe Baizongiina. In these studies it is assumed that the galls are extended phenotypes of the aphid species that induce them (Stern 1995; Stone & Schönrogge 2003); the morphological characteristics, including the microscopic characteristics, of the galls can be used as tools in the various classifications or groupings of the gallicolous aphids and even in phylogenetic

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studies (Inbar 2006; Sano & Akimoto 2011; Chen & Qiao 2012; Álvarez *et al.* 2013).

The main aim of this study was to describe the microscopic features of galls induced by five species of aphid that have not been analysed to date, and to present a new classification for the gallicolous aphids based on histological features, using the results from this study together with known, published anatomical data on nine other final galls (Inbar 2006) induced by aphids (Álvarez *et al.* 2009, 2014; Álvarez 2011, 2012; Muñoz-Viveros *et al.* 2014).

## MATERIAL AND METHODS

Mature galls induced by the following five aphid species were studied microscopically (Table 1): *Aploneura lentisci* (AL) on *Pistacia lentiscus*, *Asiphonella cynodonti* (AC) on *P. palaestina* and *Forda riccobonii* (FR), *Smynthuroides betae* (SB) and *Slavum wertheimae* (SW) on *P. atlantica* (Fig. 1). For the joint study of the 14 galls, the abovementioned gallicolous aphids were considered together with other gallicolous aphids from previously published studies (Table 1): *Paracletus cimiciformis* (PC), *Forda marginata* (FM) and *F. formicaria* (FF) (Álvarez *et al.* 2009)

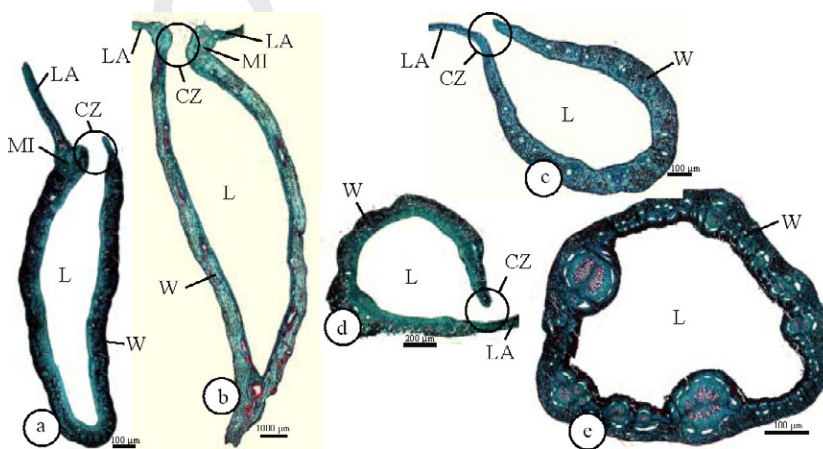
and *Geoica utricularia* (GU) and *Baizongia pistaciae* (BP) (Álvarez 2011; Álvarez *et al.* 2012), all on *P. terebinthus*; *R. buxtoni* (RB) (Álvarez *et al.* 2014) on *P. palaestina*; and *Geopemphigus blackmani* (GB), *G. morral* (GM) and *G. torsus* (GT) (Muñoz-Viveros *et al.* 2014) on *P. mexicana*.

All galls were fixed in FAA (formaldehyde, acetic acid and ethyl alcohol) and subsequently stored in 70% ethyl alcohol. They were studied with both optical and electron microscopy. For bright-field microscopy, polarised light microscopy and epifluorescence microscopy, galls were embedded in paraffin and sectioned with a microtome, to produce 12- $\mu\text{m}$  thick transverse sections of the leaflet midrib region containing the gall. The following features of the sections were studied (see Fig. 1): the closure zone of the galls and the wall interior, the epidermis-air (outer epidermis), the wall itself ('gall body (excluding the vascular bundles)' in the Results) and the vascular bundles, and the epidermis-lumen (inner epidermis). For galls induced by GU, BP, RB and SW, only histological sections of the wall of the gall were made. Some sections were stained with Safranin-Fast Green and were mounted permanently on microscope slides. Other sections were deparaffinised and mounted directly without staining for epifluorescence studies. Scanning

**Table 1.** Species analysed in the present study

Species	<i>Pistacia</i>	Location	Month	Subtribe	Published
<i>Aploneura lentisci</i>	<i>P. lentiscus</i>	Barcelona, Spain	June	Baizongiina	Present study
<i>Asiphonella cynodonti</i>	<i>P. palaestina</i>	Malkya, Israel	June	Baizongiina	Present study
<i>Forda riccobonii</i>	<i>P. atlantica</i>	Malkya, Israel	June	Fordina	Present study
<i>Smynthuroides betae</i>	<i>P. atlantica</i>	Malkya, Israel	June	Fordina	Present study
<i>Slavum wertheimae</i>	<i>P. atlantica</i>	Malkya, Israel	June	Baizongiina	Present study
<i>Paracletus cimiciformis</i>	<i>P. terebinthus</i>	León, Spain	July	Fordina	Álvarez <i>et al.</i> (2009)
<i>Forda marginata</i>	<i>P. terebinthus</i>	León, Spain	July	Fordina	Álvarez <i>et al.</i> (2009)
<i>Forda formicaria</i>	<i>P. terebinthus</i>	León, Spain	July	Fordina	Álvarez <i>et al.</i> (2009)
<i>Geoica utricularia</i>	<i>P. terebinthus</i>	León, Spain	August	Geoicina	Álvarez (2012)
<i>Baizongia pistaciae</i>	<i>P. terebinthus</i>	León, Spain	August	Baizongiina	Álvarez (2012)
<i>Rectinasus buxtoni</i>	<i>P. palaestina</i>	Baram, Israel	August	Fordina	Álvarez <i>et al.</i> (2014)
<i>Geopemphigus morral</i>	<i>P. mexicana</i>	Hidalgo, Mexico	July	Baizongiina	Muñoz-Viveros <i>et al.</i> (2014)
<i>Geopemphigus torsus</i>	<i>P. mexicana</i>	Hidalgo, Mexico	July	Baizongiina	Muñoz-Viveros <i>et al.</i> (2014)
<i>Geopemphigus blackmani</i>	<i>P. mexicana</i>	Hidalgo, Mexico	July	Baizongiina	Muñoz-Viveros <i>et al.</i> (2014)

The names of the gall species studied, the tree on which the gall is induced, the sampling location, the sampling month, the subtribe to which the species belong according to the classification of Heie & Wegierek (2009) and the origin of the analysed data are presented.



**Fig. 1.** General appearance of the galls examined in the present study. (a): *A. lentisci*. (b): *A. cynodonti*. (c): *F. riccobonii*. (d): *S. betae*. (e): *S. wertheimae*. (a–e): Safranin-Fast Green. (a–e): Bright-field microscope. CZ = closure zone, L = lumen of the gall, LA = lamina of unmodified leaflet, MI = midvein of the leaflet, W = wall of the gall.

electron microscopy was performed on both the inner and outer surfaces of the galls. Gall fragments were dehydrated in an ascending ethanol series and directly coated with gold.

All data obtained after microscopic examination were subjected to a hierarchical cluster analysis using Ward's agglomerative clustering algorithm and squared Euclidean distances (Hair *et al.* 1999). IBM SPSS Statistics 21 software (Chicago, IL, USA) was used. First, the 14 species were analysed using the 27 variables they hold in common. Subsequently, the 39 variables common to eight of the 14 species were analysed. To conduct these analyses, data regarding presence/intermediate/absence in eight of the 14 species (see Table 2) were transformed into the numerical values 1/0.5/0, respectively. A second study was conducted combining the 'intermediate' values with 'presence', and a third study combined the 'intermediate' values with 'absence'. All results were essentially similar, and data from the second study ('presence/absence') are presented.

## RESULTS

The microscopic characteristics of *AL*, *AC*, *FR*, *SB* and *SW* are shown in Figs 1–3. A summary of the results for all 14 galls is shown in Table 2.

### General characteristics

Regarding the presence of an unmodified leaflet accompanying the gall (Fig. 1), two states are observed: (1) the gall originates from the modification of part of a leaflet, thus it is observed as being accompanied by part of an unmodified leaflet (Fig. 1a–d); (2) no unmodified parts of a leaflet are observed to be associated with the gall. In this case it is assumed that galls are caused by modification of a bud (of a leaflet, leaf or branch; Fig. 1e). Galls without presence of an unmodified leaflet were found in *SW*, *BP*, *GT* and *GB*; the other species all presented galls with presence of part of an unmodified leaflet. Most of the galls studied can be considered as folds of the leaflet lamina. This is not the case for galls induced by *SW*, *GU*, *BP*, *RB*, *GT* or *GB*, where the gall is voluminous and has an approximately spherical shape. When making transverse sections at the midvein of the leaflet containing the gall, the following types of galls are observed: (1) galls with the chamber at about the same level as the midvein of the leaflet: (1a) *SB* and *FM* induce more or less circular galls (Fig. 1d); and (1b) *PC* induces flattened galls; (2) *FR* and *FF* induce neither circular nor flat galls (they can be considered ovoid) and the gall chamber is below the midvein of the leaflet (Fig. 1c); (3) *AL*, *AC* and *GM* induce longitudinal galls parallel to the midvein of the leaflet (Fig. 1a,b). In all cases, the outer epidermis of the galls (called epidermis-air in this paper) derives from the abaxial epidermis of the leaflet and the epidermis that lines the gall chamber (called epidermis-lumen) derives from the adaxial epidermis of the leaflet. The midvein of the leaflet is involved in the galls in most cases. It is not involved in the galls of *FR*, *PC*, *FM* and *FF*. Galls induced in *SB* often 'lean' on the midvein in the area near the petiole, and the midvein is not involved when the gall extends towards the apex of the leaflet. Tannins are widespread and are usually located throughout the entire wall. In most galls crystals are observed. They are for the most part druses preferentially located in the upper part of the wall (Fig. 3k). Prisms are observed in *AC* and microcrystals are observed in *AL* (Fig. 2b).

### Epidermis-air

In all cases, the epidermis-air is uniseriate, comprising a cuticle and stomata (Figs 2a,e,f and 3a,d,g,h). It presents microcrystals in *PC*. Trichomes are observed in *AC*, *SB*, *GM*, *GT* and *GB* (Fig. 2e). They may be multicellular and glandular, or unicellular and elongated with a circular cross-section. In addition, characteristic trichomes are observed in *SB*: they are unicellular, flat and their surface is covered with papillae (Fig. 3i,j).

### Gall body (excluding the vascular bundles)

In all cases, the walls of the galls consist of storage parenchyma cells (Figs 2a,f,g and 3a,b,g,i,l). In some cases the parenchyma of the upper part of the wall is distinct from the parenchyma of the lower part of the wall (Fig. 2a). The difference between the upper and lower parts is, among others, determined by the arrangement and size of the cells, and by the presence of tannins. Sclereids are observed in the upper parts of the wall in *SB* and *FM* (Fig. 3f,g). Fibres are observed in *AC* (Fig. 2f).

### Vascular bundles

In all cases the vascular bundles are collateral vascular bundles with conspicuous schizogenous ducts in the phloem (Figs 2a,c,f and 3a,b,c,g,k,l). In *GT* and *GB* the phloem is hypertrophied to such an extent that the vascular bundles may appear to be amphicribal. With the exception of *PC*, many vascular bundles are present. These vascular bundles are sometimes particularly hypertrophied (Fig. 3a). The size is markedly heterogeneous in *SW* and *GB* (Fig. 3k,l). In most galls a single vascular bundle is observed in the wall. Its xylem is oriented towards the lumen of the galls, *i.e.* (lumen)-xylem-phloem (Figs 2a,f and 3a,b,c,g). In *SW*, *GU*, *BP* and *RB*, two vascular bundles are observed facing the wall. With respect to the lumen of the gall, the bundles are oriented as follows: (lumen)-phloem-xylem/xylem-phloem (Fig. 3l). The vascular bundles of *AC* present a periphloematic sheath of fibres (Fig. 2f). In *FR* this sheath is observed only in the vascular bundles close to the closure zone of the gall (Fig. 3c).

### Epidermis-lumen

In all cases, the epidermis-lumen is multiseriate (three to five cell layers; Figs 2a,f and 3a,b,g). This epidermis does not present trichomes or stomata. In most galls a cuticle is observed (Figs 2f and 3a,b,g) and there are no dimples in the epidermal surface (Figs 2h and 3e). Nevertheless, there is no cuticle in *SW*, *GU*, *BP* and *RB*, and these species also present a dimpled epidermal surface (Fig. 3m).

### Closure zone

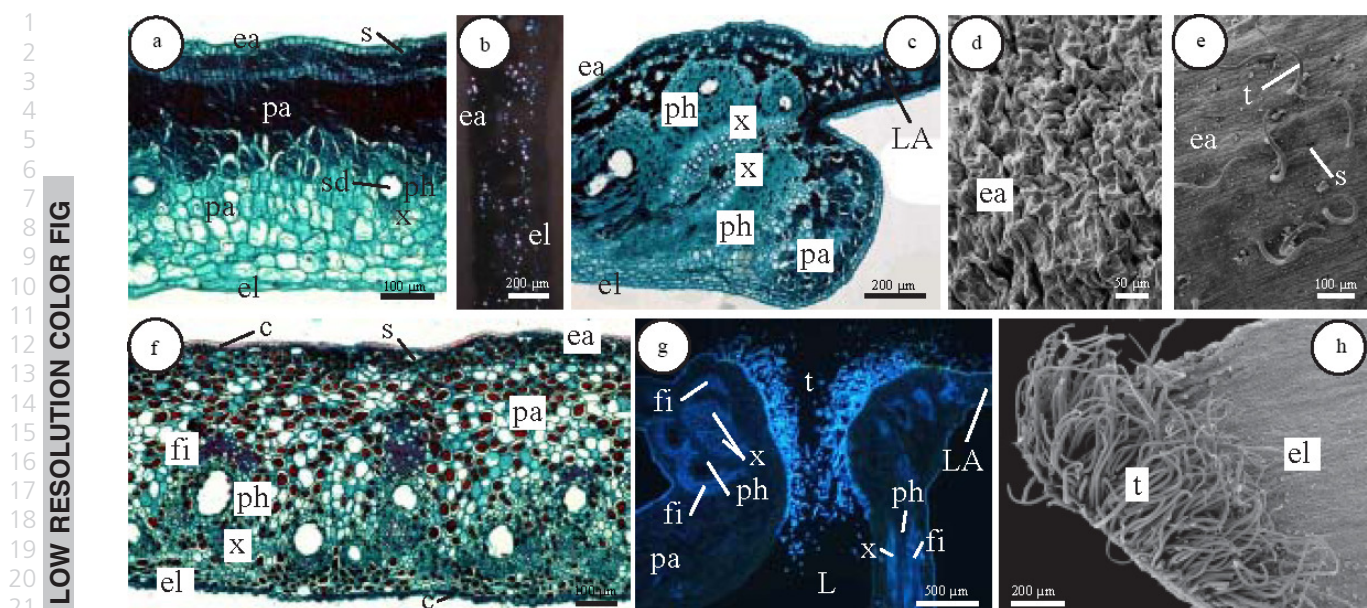
In all cases the closure zone involves morphological adaptation (usually flattening) of parts of the leaflet that form the 'door' (Fig. 1a–d). In *AC*, *FF*, *GM*, *GT* and *GB* unicellular trichomes are observed in the two areas that approach each other to form the closure zone (Fig. 2g,h). In *AC*, *FR*, *FF* and *GM* there is an accumulation of crystals (Fig. 3c), and in *PC* there is an accumulation of tannins. In *FR*, *SB* and *FM* an accumulation of sclereids is observed (Fig. 3c,f,g).

**Table 2.** Microscopic characteristics considered in the comparative study of the galls

	AL	AC	FR	SB	SW	PC	FM	FF	GU	BP	RB	GM	GT	GB
General characteristics														
On <i>Pistacia lentiscus</i> a	+	–	–	–	–	–	–	–	–	–	–	–	–	–
On <i>Pistacia palaestina</i> a	–	+	–	–	–	–	–	–	–	–	+	–	–	–
On <i>Pistacia atlantica</i> a	–	–	+	+	+	–	–	–	–	–	–	–	–	–
On <i>Pistacia terebinthusa</i>	–	–	–	–	–	+	+	+	+	+	–	–	–	–
On <i>Pistacia mexicana</i> a	–	–	–	–	–	–	–	–	–	–	–	+	+	+
With unmodified leaflet	+	+	+	+	–	+	+	+	+	–	+	+	–	–
Fold of the leaflet lamina	+	+	+	+	–	+	+	+	–	–	–	+	–	–
Longitudinal shape	+	+	–	–	n/a	–	–	–	n/a	n/a	n/a	+	n/a	n/a
Ovoid shape	–	–	+	–	n/a	–	–	+	n/a	n/a	n/a	–	n/a	n/a
Circular shape	–	–	–	+	n/a	–	+	–	n/a	n/a	n/a	–	n/a	n/a
Flattened shape	–	–	–	–	n/a	+	–	–	n/a	n/a	n/a	–	n/a	n/a
Involvement of midvein	+	+	–	(+)	+	–	–	–	+	+	+	+	+	+
Tannin inclusions	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tannins throughout the wall	–	+	+	–	+	–	+	+	+	+	+	(+)	–	–
Only in upper part of the wall	+	–	–	+	–	+	–	–	–	–	–	–	(+)	+
Crystals	+	(+)	+	(+)	+	+	(+)	+	–	+	–	+	(+)	(+)
In upper part of the wall	+	–	+	+	+	+	+	+	n/a	+	n/a	+	+	–
Microcrystals	+	–	–	–	–	–	–	–	n/a	–	n/a	–	–	–
Prisms	–	+	–	–	–	–	–	–	n/a	–	n/a	–	–	–
Druses	+	–	+	+	+	+	+	+	n/a	+	n/a	+	+	+
Epidermis–air														
Uniseriate epidermis	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cuticle	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Stomata	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Microcrystals	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Trichomes	–	+	–	+	–	–	–	–	–	–	–	(+)	+	+
Gall body														
Parenchyma cells	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Upper part and lower part	+	–	–	+	+	–	+	+	–	(+)	–	+	+	+
Sclereids	–	–	–	+	–	–	+	–	–	–	–	–	–	–
Fibers	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Vascular bundles														
Collateral	+	+	+	+	+	+	+	+	+	+	+	+	(+)	(+)
Schizogenous ducts	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Many	(+)	+	+	(+)	+	–	(+)	+	+	+	+	+	+	(+)
Hypertrophied	–	–	+	–	+	–	–	+	+	+	+	–	+	+
Heterogeneous size	–	–	–	–	+	–	–	–	–	–	–	–	–	+
One vascular bundle	+	+	+	+	–	+	+	+	–	–	–	+	+	+
Xylem oriented towards lumen	+	+	+	+	–	+	+	+	–	–	–	+	+	+
Two vascular bundles	–	–	–	–	+	–	–	–	+	+	+	–	–	–
Sheath of fibers	–	+	(+)	–	–	–	–	–	–	–	–	–	–	–
Epidermis–lumen														
Multiseriate epidermis	(+)	+	+	(+)	+	+	+	+	+	+	+	+	+	+
Trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cuticles	(+)	+	+	+	–	+	+	+	–	–	–	+	+	+
Dimples	–	–	–	–	+	–	–	–	+	+	+	–	–	–
Closure zone														
With adaptation	+	+	+	+	n/a	+	+	+	n/a	n/a	n/a	+	+	+
Trichomes	–	+	–	–	n/a	–	–	+	n/a	n/a	n/a	+	+	+
Accumulation of crystals	–	+	+	–	n/a	–	–	+	n/a	n/a	n/a	+	–	–
Accumulation of tannins	–	–	–	–	n/a	+	–	–	n/a	n/a	n/a	–	–	–
Accumulation of sclereids	–	–	+	+	n/a	–	+	–	n/a	n/a	n/a	–	–	–

Microscopic characteristics studied in galls of 14 species of gallicolous aphids (AC: *A. cynodonti*; AL: *A. lentiscii*; BP: *B. pistaciae*; FF: *F. formicaria*; FM: *F. marginata*; FR: *F. riccobonii*; GB: *G. blackmani*; GM: *G. morrali*; GT: *G. torsi*; GU: *G. utricularia*; PC: *P. cimiciformis*; RB: *R. buxtoni*; SB: *S. betae*; SW: *S. wertheimae*): general characteristics, epidermis–air, gall body, vascular bundles, epidermis–lumen and closure zone. + indicates presence, – absence, (+) intermediate situation. n/a: not applicable.

<sup>a</sup>Variables submitted to analysis.



**Fig. 2.** Galls induced by *A. lentisci* (a–d) and *A. cynodonti* (e–h). (a): Wall of *A. lentisci*. The xylem of the vascular bundles (x) is oriented towards the lumen of the gall. (b): Presence of abundant microcrystals (bright points) in the wall of *A. lentisci*. (c): Hypertrophied midvein of *A. lentisci* in which the double vascular bundle (ph-x/x-ph) is observed. Note the absence of trichomes on the epidermis of the midvein participating in the closure zone (see Fig. 1a). (d): External surface of *A. lentisci*. (e): External surface of *A. cynodonti* on which some trichomes (t) are observed. (f): Wall of *A. cynodonti*. The xylem of the vascular bundles (x) is oriented towards the lumen of the gall. Note the sheath of fibres (fi) accompanying the phloem. (g–h): Closure zone of *A. cynodonti* with abundant trichomes (t). (a, b, c, f): Safranin-Fast Green. (a, c, f): Bright-field microscope; (b): Polarized light microscope; (d, e, h): SEM; (g): Epifluorescence microscope. c = cuticle, ea = epidermis-air, el = epidermis-lumen, fi = fibres, L = lumen of the gall, LA = lamina, pa = parenchyma, ph = phloem, s = stoma, sd = schizogenous duct, t = trichome, x = xylem.

The hierarchical nature of the cluster analysis used enables us to establish groupings of galls that are graphically represented by means of a dendrogram. The dendrogram resulting from the analysis of 27 variables common to all 14 galls (Fig. 4) establishes the existence of two very distant groups. One group comprises *RB*, *GU*, *SW* and *BP*, while the other group includes all the other ten studied galls, but with *GT* and *GB* clustering separately from the rest. The dendrogram made with the eight remaining galls (Fig. 5), using the 39 variables that they have in common, reveals the existence of two groups. One group comprises *AL*, *GM* and *AC*, while the other group includes *FR*, *FF*, *SB*, *FM* and *PC*.

## DISCUSSION

Microscopic study of the 14 galls allows us to determine the characteristics that are common to all of them, as well as those that distinguish between them. All the galls studied present tannin inclusions. In addition, the vascular bundles are collateral with clear schizogenous ducts in the phloem. The presence of these ducts and tannin inclusions are attributes of the Anacardiaceae, and of the genus *Pistacia* (Watson & Dallwitz 1992; Álvarez *et al.* 2008). Moreover, in all galls the epidermis-air is uniseriate, covered with cuticle, and contains stomata. The walls of the galls comprise storage parenchyma cells interspersed with vascular bundles. The epidermis-lumen is multiseriate, and lacks stomata and trichomes. Some galls have unicellular trichomes in the epidermis-lumen in the closure zone, an adaptation of the two walls of the gall to form the ‘door’.

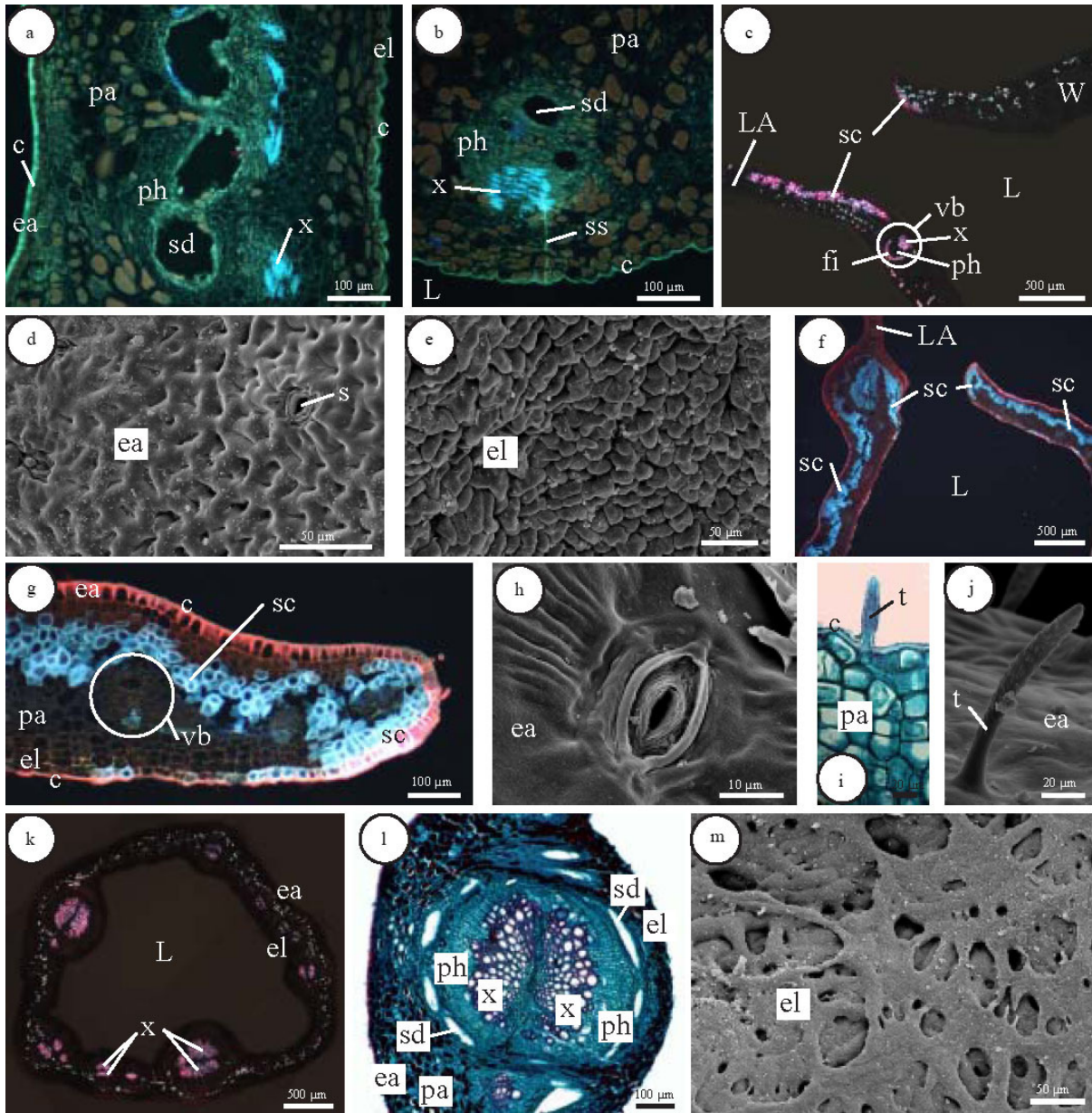
The group consisting of *RB*, *GU*, *SW* and *BP* is differentiated from the others by the two opposed vascular bundles in the

wall, and phloem as the conductive tissue closest to the chamber of the gall. The vascular bundles are hypertrophied. In addition, the galls of this group have an epidermis-lumen with dimples, but without cuticle. These galls are closed, lacking the ‘door’ present in the other galls; this may be related to evolutionary issues (Inbar 2006; Álvarez *et al.* 2013).

Two subgroups emerged in relation to the presence or absence of an unmodified leaflet accompanying the gall: the gall was associated with an unmodified portion of the leaflet in *GU* and *RB*, while this association was absent in *BP* and *SW*. Whereas *BP* and *SW* induce bud galls (established on a branch, leaf or leaflet), *GU* and *RB* induce hyperplasia and cell hypertrophy in the midvein region, and the gall is associated with a portion of the unmodified leaflet. *BP* is banana-shaped and is induced on *P. terebinthus*, while *SW* resembles a cauliflower (Inbar 2006) and is induced on *P. atlantica*. *GU* is globoid, and occurs on *P. terebinthus*, while *RB*, with its spherical and elongated shape, occurs on *P. palaestina*.

The remaining galls (*GT*, *GB*, *SB*, *AL*, *PC*, *AC*, *GM*, *FM*, *FF* and *FR*) constitute the second group, distinguished from the first group by the single vascular bundle in the wall, with xylem as the conductive tissue closest to the gall chamber. Furthermore, the galls of this group have an epidermis-lumen with a cuticle and without dimples. Some are not accompanied with an unmodified leaflet (*GT* and *GB*), whereas the rest have an unmodified part of a leaflet (*SB*, *AL*, *PC*, *AC*, *GM*, *FM*, *FF* and *FR*).

The group formed by *GB* and *GT* is characterised by a few crystalline inclusions, and by trichomes on the epidermis-air and in the closure zone. Both are induced on *P. mexicana*, but *GB* has a globoid gall whereas *GT* has a fusiform gall. Perhaps

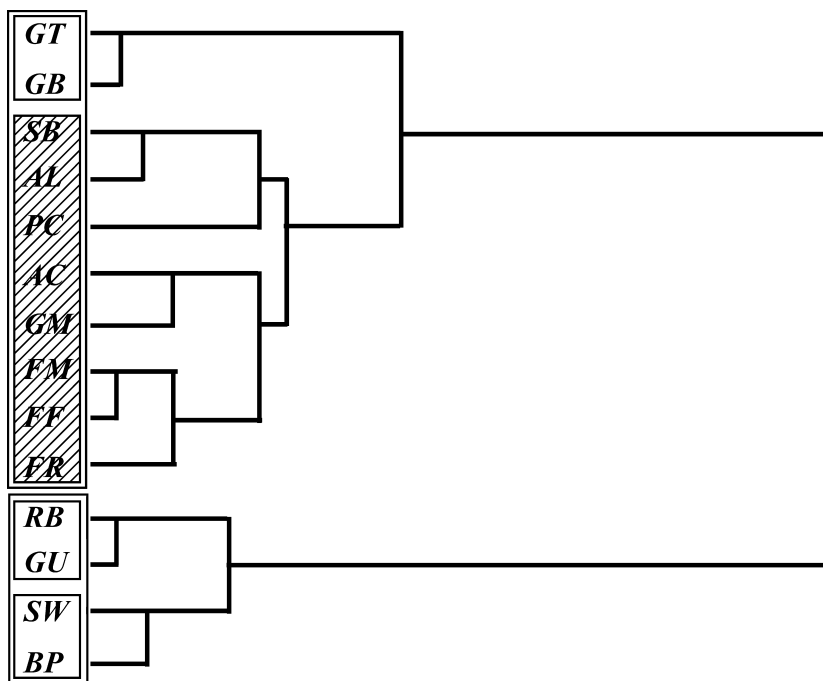


**Fig. 3.** Galls induced by *F. riccobonii* (a–e), *S. betae* (f–j) and *S. wertheimae* (k–m). (a): Wall of *F. riccobonii*. Large vascular bundles with the xylem (x) facing the lumen. (b): Detail of a vascular bundle of *F. riccobonii*. Note the xylem (x) facing the lumen (L) and the presence of a stylet sheath (ss). (c): Closure zone of *F. riccobonii* containing cells with birefringent secondary walls (sc) on both sides of the ‘door’. Note the abundance of bright spots (druses) and the presence of periphloematic fibres (fi) in the vascular bundle (vb). (d): External surface of *F. riccobonii* on which stomata (s) are observed. (e): Surface lining the chamber of *F. riccobonii*. It has a padded appearance without dimples. (f): Closure zone of *S. betae*. Sclereids (sc) are also observed in the wall of the gall. (g): Distal portion of the modified leaflet participating in the closure zone of *S. betae*. The wall has parenchyma (pa), vascular bundles (vb) with the xylem oriented towards the lumen and sclereids (sc). On both epidermises the cuticle (c) is conspicuous. (h): Stoma present on the external surface of *S. betae*. (i, j): Characteristic trichome (t) of the gall induced by *S. betae*. (k): The section shown in Fig. 1e observed under a polarised light microscope reveals pairs of packages of xylem (x) and abundant druses (the remaining bright spots) in the wall of the gall. (l): The vascular bundles of *S. betae* are double, face each other, and have the phloem oriented towards the lumen of the gall (phloem – xylem / xylem – phloem). Compare with the vascular bundles in Figs 2a, 2f, 3a, g. (m): Inner surface of the gall induced by *S. betae* in which dimples are observed. Compare with Fig. 3e. (c, i, k, l): Safranin-Fast Green. (a, b, f, g): Epifluorescence microscope; (b, i, l): Bright-field microscope; (c, k): Polarised light microscope; (d, e, h, j, m): SEM. c = cuticle, ea = epidermis-air, el = epidermis-lumen, fi = fibres, L = lumen of the gall, LA = lamina, pa = parenchyma, ph = phloem, s = stoma, sc = sclereids, sd = schizogenous duct, ss = stylet sheath, t = trichome, vb = vascular bundle, W = wall of the gall, x = xylem.

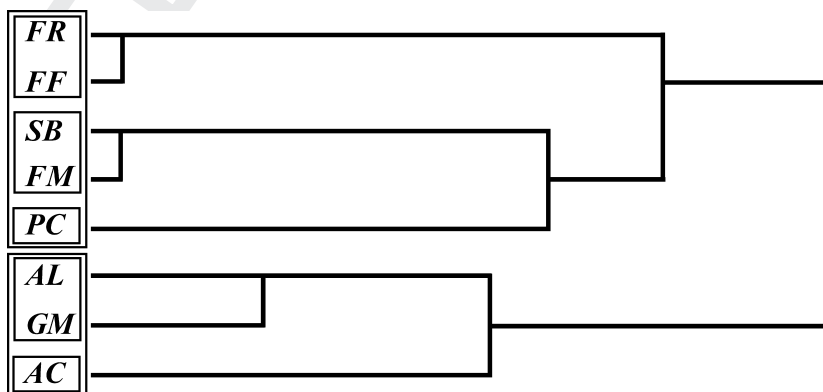
these galls originate, like *BP* and *SW*, from the complete modification of a bud. However, the latter are induced on *P. terebinthus* (*BP*) and *P. atlantica* (*SW*), which are known to have a

supernumerary vascular bundle next to the vascular bundle of the midvein (Álvarez *et al.* 2008; see Fig. 2c). The hypertrophy and hyperplasia of the vascular bundle of the midvein and also





**Fig. 4.** Dendrogram obtained by considering the 27 variables common to the 14 galls (AC: *A. cynodonti*; AL: *A. lentisci*; BP: *B. pistaciae*; FF: *F. formicaria*; FM: *F. marginata*; FR: *F. riccobonii*; GB: *G. blackmani*; GM: *G. morral*; GT: *G. torsus*; GU: *G. utricularia*; PC: *P. cimiciformis*; RB: *R. buxtoni*; SB: *S. betae*; SW: *Slavum wertheimae*). The groupings obtained are boxed: RB, GU, SW and BP comprise one group and the remaining species form a second group. Within this latter group a subgroup formed by GT and GB is apparent; the other species (cross-hatched) form a second subgroup that is further analysed in Fig. 5.



**Fig. 5.** Dendrogram obtained by considering the 39 variables common to the group of galls highlighted in Fig. 4 (AC: *A. cynodonti*; AL: *A. lentisci*; FF: *F. formicaria*; FM: *F. marginata*; FR: *F. riccobonii*; GM: *G. morral*; PC: *P. cimiciformis*; SB: *S. betae*). The groupings obtained are boxed: FR, FF, SB, FM and PC form one group and AL, GM and AC form another group.

of the supernumerary vascular bundle, determines the existence of two vascular bundles in the walls of the galls under discussion (Álvarez 2012). Perhaps the leaflets of *P. mexicana* do not have a supernumerary vascular bundle, so that the single vascular bundle constitutes the wall of the gall, although the phloem is developed to such an extraordinary extent that the vascular bundles in those galls sometimes appear to be amphicribal (Muñoz-Viveros *et al.* 2014).

The group comprising AL, GM and AC consists of galls induced on the middle portion of the leaflet. Both GM (induced on *P. mexicana*) and AL (induced on *P. lentiscus*) are pocket-shaped: in GM, the two leaflet margins (to the right and the left of the midvein) fold over the midvein towards each other, forming the ‘door’ of the gall with trichomes on both sides. In AL, one of the hypertrophied leaflet margins approaches the midvein. The presence of abundant microcrystals is remarkable. The gall induced by AC on *P. palaestina*, which is also pocket-shaped, has a unique feature among all the studied galls – a periphloematic sheath of fibres. Groups of (non-vascular) fibres are also seen in the wall of the gall. The

presence of fibres in the wall is probably related to the primary function of the sclerenchyma – to provide support (Evert 2006) – given that the galls are relatively large and do not have particularly hypertrophied vascular bundles. Note that the xylem, apart from being conductive tissue, consists of lignified cells that support the structures in which they are found (Evert 2006).

The similarities between the five remaining galls (FR, FF, SB, FM and PC) are remarkable. They are all folding galls, with a closure zone, and the midvein of the leaflet does not participate in the formation of the gall. Nevertheless, there are specific features that can be used to differentiate them into pairs: the group comprising SB and FM is characterised by rounded galls with few crystal inclusions and, above all, by abundant sclereids in both the upper part of the wall and the closure zone. Both FM, which is induced on *P. terebinthus*, and SB, which is induced on *P. atlantica*, have peculiar trichomes on the epidermis-air. These trichomes have not been previously described in the genus *Pistacia* or in any gall induced on this genus by aphids. Future studies will clarify whether these trichomes

(apparently non-glandular, flattened and with papillae) can be considered to be common trichomes with atypical growth caused by the aphid. This also applies to other morphologically similar trichomes observed in mutants of *Arabidopsis thaliana* (Johnson *et al.* 2002).

Galls induced by *FR* and *FF* are ovoid, *i.e.* they are neither circular nor flattened. They have many especially hypertrophied vascular bundles. *FF* is induced on *P. terebinthus* and presents trichomes in the closure zone. *FR*, which is induced on *P. atlantica*, does not present any trichomes although it does have sclereids in the closure zone.

*Paracletus cimiciformis* (*PC*) induces flattened galls on *P. terebinthus*. It presents microcrystals in the epidermis-air, a feature shared with the leaflets of *P. terebinthus* (Álvarez *et al.* 2008). It also presents tannin accumulation in the closure zone. Of all the galls studied that form on the leaflet margin, the microscopic characteristics of this species' galls are most

similar to those of the leaflets on which they develop. In other words: *PC* is the species that induces the fewest morphological changes in the leaflet margins. It is striking that the pairs of galls considered, *SB-FM* and *FR-FF*, share common features, but that some are induced on *P. terebinthus* while others are induced on *P. atlantica*. In this context of convergent patterns, perhaps the galls induced by *Tramafora wooli* (*TW*) on *P. atlantica* (Manhein 2007) should be considered similar to *PC*. They are both flattened galls. Future studies will indicate whether *PC* and *TW* may be considered similar galls.

Heie & Wegierek (2009) divide the genera analysed in this study into three groups (regardless of taxonomic category): (1) *Forda* – *Paracletus* – *Rectinasus* – *Smynthuroides* – *Tramafora*; (2) *Aploneura* – *Asiphonella* – *Baizongia* – *Geopemphigus* – *Slavum*; and (3) *Geoica*. It is clear that these groupings are not related to the phenotypes of the galls established in the present study. The groupings of gallicolous aphids based on microscopic features determined in the present study (Table 3) should be taken into consideration when conducting the necessary taxonomic review of the tribe Fordini.

All observations made in this study can be summarised as a taxonomic key.

**Table 3.** Different groupings of the analysed species

Remaudière, Stroyan & Quednau extended classification Fordina (Aphididae, Eriosomatinae, Fordini)	Heie & Wegierek revised classification Fordini (Eriosomatidae, Fordinae)	Present study Three groups with two subgroups on the third one
Just one group	Three groups	
	Subtribe Fordina	
Aloephagus	<sup>a</sup> Forda	Baizongia pistaciae
<sup>a</sup> Aploneura	<sup>a</sup> Paracletus	Geoica utricularia
<sup>a</sup> Asiphonella	<sup>a</sup> Rectinasus	Rectinasus buxtoni
<sup>a</sup> Baizongia	<sup>a</sup> Smynthuroides	Slavum wertheimae
Chaetogeioica	Tramafora	
<sup>a</sup> Forda	Subtribe Baizongiina	Geopemphigus blackmani
<sup>a</sup> Geoica	Aloephagus	Geopemphigus torsus
<sup>a</sup> Geopemphigus	<sup>a</sup> Aploneura	
<sup>a</sup> Paracletus	<sup>a</sup> Asiphonella	Aplonerura lentisci Forda formicaria
<sup>a</sup> Rectinasus	<sup>a</sup> Baizongia	Asiphonella cynodonti Forda marginata
<sup>a</sup> Slavum	<sup>a</sup> Geopemphigus	Geopemphigus morral Forda riccobonii
<sup>a</sup> Smynthuroides	<sup>a</sup> Slavum	Paracletus cimiciformis
Tramafora	Subtribe Geoicina	Smynthuroides betae
	Chaetogeioica	
	<sup>a</sup> Geoica	

In the extended classification of Remaudière, Stroyan & Quednau (Nieto Nafría & Favret 2011), one group is established; three groups (subtribes) are defined in the revised classification of Heie & Wegierek (Nieto Nafría & Favret 2011); and three groups (the third one with two subgroups) are presented in this study based on histological features. Genera alphabetically arranged.

<sup>a</sup>Genera analysed in the present study.

1.	Galls with two vascular bundles in the wall and epidermis-lumen with dimples	2
	Galls with a vascular bundle in the wall and epidermis-lumen without dimples	5
2.	Without remains of a healthy leaflet	3
	With remains of a healthy leaflet	4
3.	Induced on <i>P. terebinthus</i> and banana-shaped	<i>Baizongia pistaciae</i>
	Induced on <i>P. atlantica</i> and cauliflower-shaped	<i>Slavum wertheimae</i>
4.	Globose, induced on <i>P. terebinthus</i>	<i>Geoica utricularia</i>
	Globose and elongated, induced on <i>P. palaestina</i>	<i>Rectinasus buxtoni</i>
5.	Without remains of a healthy leaflet	6
	With remains of a healthy leaflet	7
6.	Induced on <i>P. mexicana</i> , elongated	<i>Geopemphigus torsus</i>
	Induced on <i>P. mexicana</i> , globose	<i>Geopemphigus blackmani</i>
7.	Located on the margin of the leaflet	8
	Located on the middle part of the leaflet	12
8.	Ovoid cross-section, contains abundant, large vascular bundles	9
	Circular cross-section, contains sclereids	10
	Flattened cross-section	11
9.	Induced on <i>P. terebinthus</i> , has trichomes in the closure zone	<i>Forda formicaria</i>
	Induced on <i>P. atlantica</i>	<i>Forda riccobonii</i>
10.	Induced on <i>P. terebinthus</i>	<i>Forda marginata</i>
	Induced on <i>P. atlantica</i>	<i>Smynthuroides betae</i>
11.	Induced on <i>P. terebinthus</i>	<i>Paracletus cimiciformis</i>
	Induced on <i>P. atlantica</i>	<i>Tramafora wooli</i>
12.	Formed by one leaflet lamina	<i>Aploneura lentisci</i>
	Formed by two leaflet laminae	<i>Geopemphigus morral</i>
	Fibres in the vascular bundles and the wall	<i>Asiphonella cynodonti</i>

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