

# Histological study of galls induced by aphids on leaves of *Ulmus minor*: *Tetraneura ulmi* induces globose galls and *Eriosoma ulmi* induces pseudogalls

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**Abstract** The histological study of galls may provide information on the evolution of the organisms that induce them. The walls of two aphid-induced galls on leaves of *Ulmus minor* were therefore studied histologically: a globose gall induced by *Tetraneura ulmi* and a pseudogall induced by *Eriosoma ulmi*. Galls are regarded as extended phenotypes of aphids, and therefore, they can be used as tools for phylogenetic studies. The walls of the galls induced by *T. ulmi* are not reminiscent of the ungalled leaf structure of *U. minor* in any area, showing both cellular hypertrophy and hyperplasia. Galls induced by *E. ulmi* resemble the leaf structure of *U. minor* in certain aspects, but in most aspects they do not, showing only cellular hypertrophy. Processes of growth and differentiation are observed in both galls. Based on the findings of this study and other recent publications, we propose to categorize the galls induced by aphids into four types: (1) pseudogalls; (2) closed galls with a “door”; (3) closed galls determined by active processes of growth and differentiation of the lamina of the leaf; and (4) closed galls determined by active processes of growth and differentiation of the midvein.

**Keywords** Gall · Pseudogall · *Tetraneura ulmi* · *Eriosoma ulmi* · *Ulmus minor* · Histological study

## Introduction

More than 15,000 species of organisms capable of inducing the formation of galls are known, among which there are viruses, bacteria, algae, fungi, protozoa, rotifers, nematodes, mites and insects (Felt 1940).

Among the gall-forming organisms are several insect families, including various aphid families. Approximately 10–20 % of the 4,700 known aphid species worldwide are gallicolous (Chakrabarti 2007; Chen and Qiao 2012).

Galls can form on leaves (lamina, veins or petiole), twigs, branches and roots (Price et al. 1987; Hartley and Lawton 1992; Stone and Schönrogge 2003; Allison and Schultz 2005; Suzuki et al. 2009; Aoyama et al. 2012; Chen and Qiao 2012).

Galls that are induced by a single plant louse usually harbor several of its offspring. Individual lice inside the gall feed by sucking the phloem sap that circulates through the phloem of the usually hypertrophied vascular bundles (Álvarez et al. 2009; Álvarez 2012). Galls provide plant lice with abundant nutrition, a favorable microenvironment and protection against natural enemies (Price et al. 1986, 1987; Martinez 2010).

The shape of the gall is specific to each aphid species (Wool 2004). In fact, the shape of the galls is determined by the inducing aphids (Stern 1995; Crespi and Worobey 1998; Inbar et al. 2004), which allows considering galls as extended phenotypes of aphids (Stern 1995). For this reason, in phylogenetic studies of gallicolous aphids, galls are also analyzed from several points of view (Sano and Akimoto 2011).

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Until now, two types of galls are recognized. One type consists of more or less closed galls with one or more chambers, in which the aphids are born, grow and develop. At a given moment, these galls open or literally break partially, which allows the aphids that have reached a certain stage of maturity to leave. The other type of galls is permanently open and does not have chambers. This type has the appearance of rolled-up leaves, and these galls are called pseudogalls (Chen and Qiao 2012).

Several types of galls induced by aphids belonging to the tribe Eriosomatini (family Aphididae, subfamily Eriosomatinae) have been described on elm leaves. In the Iberian Peninsula, these are species belonging to the genera *Eriosoma*, *Colopha*, *Kaltenbachiella* and *Tetraneura* (Nieto-Nafría et al. 2002). Species belonging to the last three genera induce the formation of globose galls, whereas species of the first genus induce pseudogalls.

In this paper, the wall structure of two types of galls is studied microscopically: a globose gall induced by *Tetraneura ulmi* and a pseudogall induced by *Eriosoma ulmi*. The classification of galls induced by aphids is discussed. The study may provide data on the evolution of galls.

## Materials and methods

Galls induced by *T. ulmi* and *E. ulmi* on leaves of *Ulmus minor* (Fig. 1) were collected in the west of the province of León (Spain) in late April (young galls), early June (mature galls) and mid-May (intermediate galls).

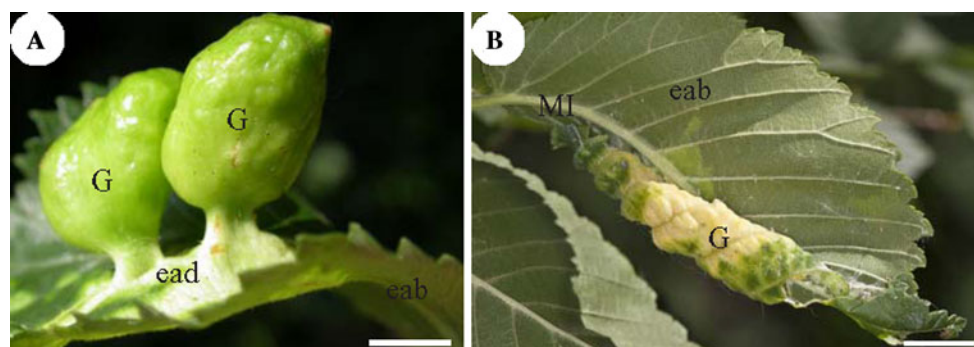
In each case, five samples were taken and fixed immediately in FAA (formaldehyde, acetic acid and ethyl alcohol). To facilitate the penetration of fixative, galls of *T. ulmi* were partially cut with a scalpel. Samples for light microscopic studies were embedded in paraffin after dehydration in an ethanol series. Once the block was obtained, 12- $\mu$ m-thick sections were made using a rotary microtome. The sections were placed on six slides

**Fig. 2** Gall induced by *T. ulmi*. **a** Globose gall forming toward the foliar adaxial face. Closed gall with inner chamber and a closure zone with trichomes. **b-d** Leaf of *U. minor*. Note the presence of chlorophyll palisade parenchyma and glandular trichomes (**b**). Detail of glandular trichome (**c**) and non-glandular trichome (**d**). **e** Wall of a young gall. Parenchymal cells have thickened walls, and the epidermis-lumen stays intact. **f** Wall of an intermediate gall. The parenchymal cells exhibit conspicuous inclusions, and the epidermis-lumen presents discontinuities. **g** The epidermis-lumen shows recesses. **h** Wall of a mature gall. A cuticle is observed in the epidermis-air. The vascular bundle is very close to the lumen of the gall. **a, b, e, f** Safranin-fast green. Bright field optical microscope. **c, d, g** SEM. **h** Fluorescence microscope. *AB* abaxial surface; *AD* adaxial surface; *c* cuticle; *CZ* closure zone; *ea* epidermis-air; *eab* abaxial epidermis; *ead* adaxial epidermis; *el* epidermis-lumen; *gt* glandular trichome; *L* lumen of the gall; *MI* midvein; *ph* phloem; *pp* chlorophyll palisade parenchyma; *sp* storage parenchyma; *t* non-glandular trichome; *vb* vascular bundle; *W* wall of the gall; *x* xylem. Scale bars: **a** = 1,500  $\mu$ m; **b, d** = 50  $\mu$ m; **c** = 10  $\mu$ m; **e-h** = 100  $\mu$ m

previously impregnated with Mayer's albumin. Odd slides (numbers 1, 3 and 5) were deparaffinized and stained with safranin and fast green. Even slides were used as follows: Numbers 2 were deparaffinized and stained with Lugol's iodine for the detection of starch (Johansen 1940); numbers 4 were deparaffinized and used for observation under the fluorescence microscope without staining; and numbers 6 were stored in our histology repository. All preparations were permanently mounted using Entellan mounting medium. Observations were made with a bright field microscope, a polarizing microscope and a fluorescence microscope. The thickness of the walls of the galls was measured using a bright field microscope with an ocular grid.

For observation under the scanning electron microscope (SEM), the fixed samples were dehydrated in an ethanol series and coated with gold; an FEI Quanta 600 environmental scanning microscope (ESEM) was used.

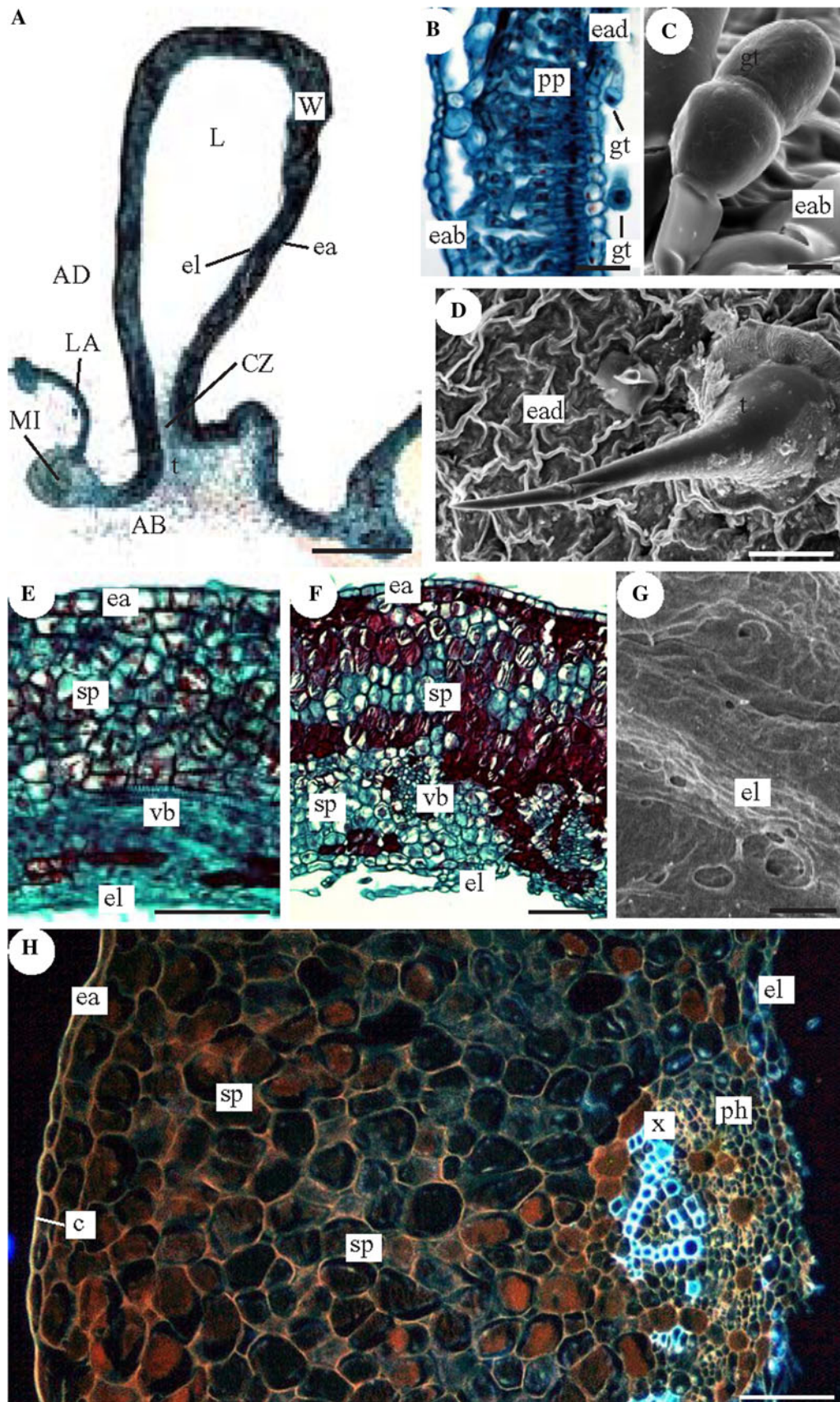
Statistical analysis of the data on the thickness of the walls of the galls (young, intermediate and mature) was done using linear mixed-effects models using the statistical



**Fig. 1** Galls induced by *T. ulmi* **a** and *E. ulmi* **b**. **a** Globose gall forming toward the foliar adaxial face. **b** Pseudogall that forms by curling—toward the abaxial surface—of half a leaf of *U. minor* upon

itself. *eab* abaxial epidermis; *ead* adaxial epidermis; *G* gall; *MI* midvein. Scale bars: **(a-b)** = 5 mm





package R; gall species and group were considered as fixed factors, and galls and measures within galls as random factors.

## Results

Gall induced by *T. ulmi* (Fig. 2).

Results are summarized in Table 1.

Globose gall forming toward the adaxial face of the leaves (Fig. 2a). Microscopically, the wall of the gall is not reminiscent of the lamina of the leaf (Fig. 2b). As they mature, galls gain in thickness. Mature gall walls reach a thickness of about 0.6 mm (all observed differences were highly significant ( $P < 0.001$ )). About 20 cell layers make up the wall in areas without vascular bundles.

Histological features include the following:

- Uniseriate epidermis-air. Large squamous cells. No inclusions in young galls. Squamous cells of mature galls are particularly flat and are filled with inclusions and covered by a cuticle (Fig. 2h). Stomata are absent.
- Uniseriate epidermis-lumen. Squamous, small cells in young galls (Fig. 2e). In the rest of the galls, the epidermal lumen is not defined (Fig. 2f, g). No stomata are observed.
- Live unicellular trichomes were observed in the area where the galls close (Fig. 2a). In general, the trichomes that characterize leaves of *U. minor* were not observed (Fig. 2b–d). Mucilaginous cells characteristic of the leaves were not observed either (Fig. 3d).
- Amyloplasts were generally not observed. Neither were calcium oxalate crystals observed.
- Approximately the upper two-thirds of the gall's wall (the part farthest removed from the lumen) are formed by large cells. The remaining third (closest to the chamber) has smaller cells. All of them are storage parenchymal cells with thickened cell walls (Fig. 2e, f, h).
- Young galls have few inclusions. In general, these have the shape of large granules and are associated with the

**Table 1** Histological characteristics of galls induced by *T. ulmi*

<i>T. ulmi</i>	Young	Intermediate	Mature
Wall thickness (mm)	0.29	0.49	0.68
Cell layers in wall	Around 20	Around 20	Around 20
Epidermis-air	Uniseriate	Uniseriate	Uniseriate
Cells	Large squamous	Large squamous	Very squamous and low
Inclusions	No	Fine granular	Homogeneous and dense
Cuticle	No	Yes	Yes
Stomata	No	No	No
Epidermis-lumen	Uniseriate	Not defined	Not defined
Cells	Small squamous	–	–
Stomata	No	No	No
Alive unicellular trichomes	In closure zone	In closure zone	In closure zone
Other trichomes	No	No	No
Mucilaginous cells	No	No	No
Amyloplasts	No	No	Yes
Crystals	No	No	No
Parenchyma cells			
Size	Upper 2/3-large Lower 1/3-small	Upper 2/3-large Lower 1/3-medium-sized	Upper 2/3-large Lower 1/3-medium-sized
Walls	Slightly thickened	Thickened	Thickened
Inclusions	Few Large granules	Many Homogeneous and dense and in strands	Quite a lot In strands and homogeneous and dense
Vascular bundles			
A single bundle	Yes	Yes	Yes
Phloem oriented	Toward lumen	Toward lumen	Toward lumen
Position in the wall	Middle/lower area	Middle/lower area	Lower area

Wall, epidermis-air, epidermis-lumen, trichomes, mucilage cells, amyloplasts, crystals, storage parenchyma cells and vascular bundles of young, intermediate and mature galls. Differences between the values of wall thickness are statistically significant ( $P < 0.001$ )

cell wall (Fig. 2e). In the later stages of the remaining galls, the inclusions are thread-shaped (predominantly in mature galls), homogeneous and dense (Fig. 2f).

- There is only one collateral vascular bundle in the gall's wall, with the phloem facing the lumen of the chamber (Fig. 2h). In mature galls, the vascular bundles are arranged in the lower part of the wall, very close to the lumen.

Gall induced by *E. ulmi* (Fig. 3).

Results are summarized in Table 2.

Pseudogall that forms by curling—toward the abaxial surface—of half a leaf of *U. minor* upon itself (Fig. 3a, b). Curling does not result in the formation of a chamber isolated from the external environment. The wall of the gall shows an increase in thickness, and the walls of mature galls reach an average thickness of about 0.40 mm (all observed differences were highly significant ( $P < 0.001$ )). Histological features are as follows:

- Only in young galls, a thin cuticle is observed on the epidermis of the adaxial face. In the other galls, no cuticle is observed. The epidermal cells are large and cuboidal. Slightly elevated anomocytic stomata are observed (but not in young galls) (Fig. 3c, d). Two characteristics of the leaves of *U. minor* are observed in the modified leaf as a whole: (1) two types of trichomes, glandular and non-glandular (Fig. 3c, i), and (2) mucilaginous cells (Fig. 3d).
- The parenchyma located between the epidermis of the adaxial surface and the epidermis of the abaxial surface has a non-uniform morphology, showing three conformations (Fig. 3e–h)—(1) areas structurally similar to the mesophyll of *U. minor*: Chlorophyll palisade parenchyma oriented toward the adaxial face of the leaves, and aeriferous parenchyma. Cells are small in both cases (Fig. 3f). (2) Lacunar chlorophyll parenchyma with large cells (Fig. 3g). (3) Storage parenchyma consisting of large cells without chloroplasts (Fig. 3h). These three conformations coexist even in mature galls, although the third one is the most abundant. The number of cell layers in areas without vascular bundles (between 5 and 7) remains more or less constant over time.
- There is a single collateral vascular bundle in the wall. The vascular bundles in young galls have a morphology similar to that observed in elm leaves: The bundles are surrounded by cells with inclusions, such as a bundle sheath. The inclusions are predominantly in the form of threads (sometimes as granules). In intermediate and mature galls, the vascular bundles barely have such a bundle-sheath-like appearance (Fig. 3d).
- In young galls, a cuticle is also observed on the abaxial epidermis. Anomocytic stomata are slightly elevated

(Fig. 3f). As in the epidermis of the adaxial face, there are two types of trichomes (Fig. 3d, i) (glandular trichomes are not seen in mature galls) and mucilaginous cells (Fig. 3d). The epidermal cells are similar in size to those of the adaxial face, and like these, they are cuboidal.

- Calcium oxalate crystals were not found, except for in young galls where microcrystals are abundant. Starch was not detected.

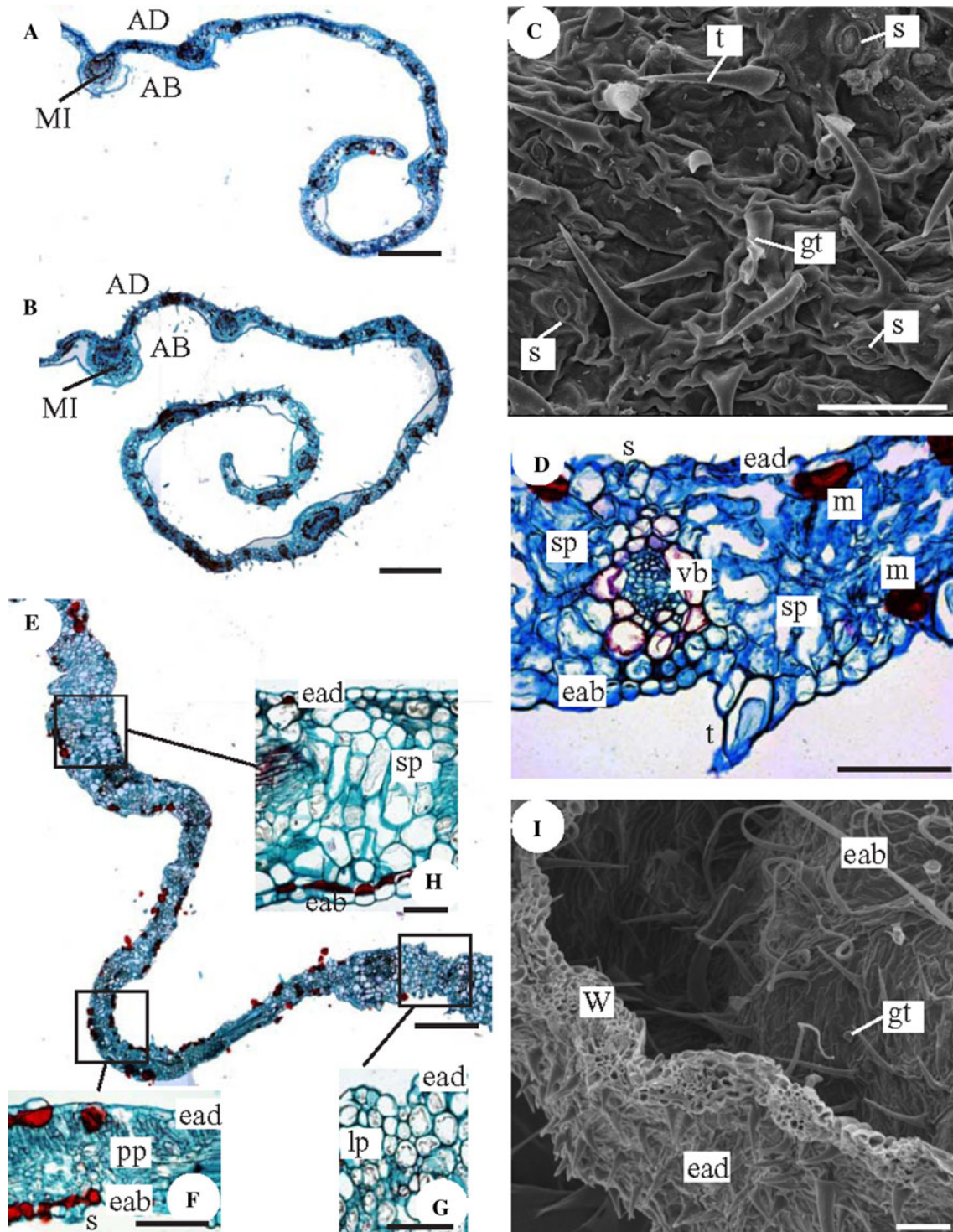
## Discussion

Aphids of the tribe Eriosomatini (Aphididae: Eriosomatinae) are typically associated with *Ulmus* and *Zelkova* (Urticales: Ulmaceae), in which they induce two types of galls: (1) leaf rolls and (2) galls resembling completely or incompletely closed pouches (Sano and Akimoto 2011). Evidently, in the present study, *T. ulmi* is of the “closed pouch” type while *E. ulmi* is of the “leaf roll” type.

The wall of *T. ulmi* is not reminiscent of the lamina of the leaf of *U. minor*. In this entire wall, both hyperplasia (about 20 cell layers) and hypertrophy (very large parenchymal cells) were observed. On the other hand, galls induced by *E. ulmi* show hypertrophy, albeit in a non-homogeneous fashion: Areas are observed that are still reminiscent of the lamina of the elm leaf (palisade parenchyma and small cells) and other areas—more abundant in mature galls—that do not resemble elm leaves (storage parenchyma consisting of large cells). In these areas of *E. ulmi* as well as in the whole of *T. ulmi*, the inquilines determine a disruption in the pattern of the development of leaf blade. As an example, in *E. ulmi* stomata are observed both on the adaxial face and on the abaxial surface, whereas in the intact elm leaf, they are observed only on the abaxial surface. Perhaps, the settling of an aphid in a specific area of the gall determines that in that particular area a malformation occurs, while other areas that are not visited by the plant lice appear less modified. Future investigations may provide data on whether the galls are induced only by the first host, thus making it an irreversible process. Alternatively, the contribution of each individual within the gall may be essential for its later normal development.

It should be assessed in more detail if the two malformations studied in this paper are really galls. According to Chen and Qiao (2012), galls can be described in terms of type, location, size, shape and structure. Regarding the type of gall, they suggest that aphids can induce both “pseudogalls” and “true galls.” Pseudogalls are commonly found on leaves and appear as leaf folds or leaf rolls. True galls come in various shapes (spherical, banana-shaped, pouch-shaped, etc.). These authors suggest that galls can also be





**Fig. 3** Gall induced by *E. ulmi*. **a, b** Various stages of development of young galls. **c** Adaxial face of mature gall, which shows the presence of glandular and non-glandular trichomes, and slightly elevated stomata. **d** Wall of an intermediate gall. Note the presence of mucilaginous cells in the epidermis of the adaxial and abaxial surfaces and a vascular bundle without bundle-sheath-like. **e–h** Wall of mature gall in which areas can be observed with chlorophyll palisade parenchyma (**f**), others with lacunar chlorophyll parenchyma (**g**) and still others with particularly large reserve parenchyma cells.

**i** Epidermis of the adaxial and abaxial surfaces of a mature gall. **a, b, d, e–h** Safranin–fast green. Bright field optical microscope. **c, i** SEM. *AB* abaxial surface; *AD* adaxial surface; *eab* abaxial epidermis; *ead* adaxial epidermis; *gt* glandular trichome; *lp* lacunar chlorophyll parenchyma; *m* mucilaginous cell; *MI* midvein; *pp* chlorophyll palisade parenchyma; *s* stoma; *sp* storage parenchyma; *t* non-glandular trichome; *vb* vascular bundle; *W* wall of the gall. Scale bars: (**a, b, e**) = 500  $\mu$ m; (**c, d, f–i**) = 100  $\mu$ m

**Table 2** Histological characteristics of galls induced by *E. ulmi*

<i>E. ulmi</i>	Young	Intermediate	Mature
Wall thickness (mm)	0.12	0.19	0.39
Adaxial epidermis			
Cuticle	Yes	No	No
Stomata	No	Yes	Yes
Trichomes (two types)	Yes	Yes	Yes
Mucilaginous cells	Yes	Yes	Yes
Epidermal cell size	Large	Large	Large
Shape	Cuboidal (squamous)	Cuboidal (squamous)	Cuboidal (squamous)
Parenchyma			
Cell layers	5	5/6	6/7
Chlorophyll palisade	Yes	Yes	Yes
Cell size	Small	Small	Small
Chlorophyll lacunar	Yes	Yes	Yes
Cell size	Large	Large	Large
Storage	No/-	Yes	Yes
Cell size	–	Large	Large
Crystals	Microcrystals	No	No
Starch	No	No	No
Vascular bundles			
A single bundle	Yes	Yes	Yes
Bundle-sheath-like	Yes (inclusions)	No	No
Abaxial epidermis			
Cuticle	Yes	No	No
Stomata	Yes	Yes	Yes
Non-glandular trichomes	Yes	Yes	Yes
Glandular trichomes	Yes	Yes	No
Mucilaginous cells	Yes	Yes	Yes
Epidermal cell size	Medium	Large	Large
Shape	Cuboidal (squamous)	Cuboidal (squamous)	Cuboidal (squamous)

Wall thickness, adaxial epidermis, parenchyma, crystals, starch, vascular bundles and abaxial epidermis of young, intermediate and mature galls. Differences between the values of wall thickness are statistically significant ( $P < 0.001$ )

classified into “open galls” and “closed galls.” Some galls close in the early stages of development and remain closed until maturity. Other galls, however, remain open throughout their existence (Chen and Qiao 2012).

On the other hand, Stone and Schönrogge (2003) state that galls are structures that are imposed on the host and in which active processes of growth and differentiation take place. In view of the results obtained in the present study, *T. ulmi* evidently fits this concept of galls, and so does *E. ulmi*.

Histological studies of galls induced by *Paracletus cimiciformis*, *Forda formicaria*, *Forda marginata*, *Geoica utricularia* and *Baizongia pistaciae* on *Pistacia terebinthus* (Álvarez et al. 2009; Álvarez 2012) show that in all cases galls are induced structures in which these processes of active growth and differentiation occur, again in agreement with Stone and Schönrogge (2003). Galls induced by *P. cimiciformis*, *F. marginata* and *F. formicaria* are open galls from which the winged individuals eventually leave after the galls open “like a door.” On the other hand, galls

induced by *G. utricularia* and *B. pistaciae* are closed galls, which when the time comes literally explode on some part of their surface area, and the winged individuals leave the inside.

Therefore, maybe the existence of three types of gall should be considered: (1) closed galls that explode when mature (e.g., *G. utricularia*, *T. ulmi* and *Pemphigus populi*) on black poplar leaves (Álvarez, unpublished personal observation); (2) closed galls that open when it is time (e.g., *F. marginata*); and (3) galls that are permanently open (e.g., *E. ulmi* and the definitive gall of *Thecabius affinis* on black poplar leaves (Álvarez, unpublished personal observation). The first gall type involves severe alterations in the original structure of the leaf on which they settle. The second type involves less severe alterations, and the third type still milder alterations. All three types should then be considered galls, although those that are permanently open and appear as leaf rolls (or similar) are called pseudogalls. The fact that the gall-wall structure

of *E. ulmi* is not homogeneous is an additional reason for classifying them as pseudogalls. Phylogenetically speaking, pseudogalls and “leaf roll” type galls evolutionarily predate the fully closed gall type and the pouch-with-incomplete-closure type (Sano and Akimoto 2011).

Histological studies of the different types of galls will have to be done to see whether developmental arguments can be added to the ones already mentioned. For example, both in not-closed galls (e.g., *F. marginata*) (Álvarez et al. 2009) and in pseudogalls (e.g., *E. ulmi*, studied in the present paper), only a single, generally hypertrophied vascular bundle is seen in the wall. In that sense, there is homology between the two types of galls. However, microscopic study of the walls of two globose galls as the ones induced by *G. utricularia* and *T. ulmi* does not establish a common pattern in the formation of globose galls: The wall of *G. utricularia* has two vascular bundles, while in the wall of *T. ulmi* only one single vascular bundle is seen. The difference is perhaps due to the fact that the first one originates in the midvein of *P. terebinthus* (Álvarez 2011), whereas the second one originates in the lamina of the leaf of *U. minor*. This fact invites to propose the existence of four types of galls induced by aphids on leaves: (1) pseudogalls; (2) closed galls with a “door”; (3) closed galls determined by active processes of growth and differentiation of the lamina of the leaf; and (4) closed galls determined by active processes of growth and differentiation of the midvein.

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## References

- Allison SD, Schultz JC (2005) Biochemical responses of chestnut oak to a galling Cynipid. *J Chem Ecol* 31:151–166. doi:10.1007/s10886-005-0981-5
- Álvarez R (2011) Initial stages in the formation of galls induced by *Geoica Utricularia* in *Pistacia Terebinthus* leaflets: origin of the two vascular bundles which characterize the wall of the galls. *A J Plant Sci* 2:175–179. doi:10.4236/ajps.2011.22019
- Álvarez R (2012) Microscopic study of the walls of galls induced by *Geoica utricularia* and *Baizongia pistaciae* in *Pistacia terebinthus*: a contribution to the phylogeny of Fordini. *Arthropod-Plant Interact* 6(1):137–145
- Álvarez R, Encina A, Pérez Hidalgo N (2009) Histological aspects of three *Pistacia terebinthus* galls induced by three different aphids: *Paraclotus cimiciformis*, *Forda marginata* and *Forda formicaria*. *Plant Sci* 176:303–314
- Aoyama T, Akimoto S-I, Hasegawa E (2012) Gall distribution as a compromise between the optimal gall-site selection and the synchrony to host-plant phenology in the aphid *Kaltenbachella japonica*. *Arthropod-Plant Interact* 6:461–469. doi:10.1007/s11829-012-9196-1
- Chakrabarti S (2007) Diversity and biosystematics of gall-inducing aphids (Hemiptera: Aphididae) and their galls in the Himalaya. *Orient Insect* 41:35–54
- Chen J, Qiao G-X (2012) Gallling aphids (Hemiptera: Aphidoidea) in China: diversity and host specificity. *Psyche* 2012: 11. doi:10.1155/2012/621934 (ID 621934)
- Crespi B, Worobey M (1998) Comparative analysis of gall morphology in Australian gall thrips: the evolution of extended phenotypes. *Evolution* 52:1686–1696
- Felt EP (1940) *Plant galls and gall makers*. Comstock Publishing Company, Ithaca, NY
- Hartley SE, Lawton JH (1992) Host-plant manipulation by gall insects: a test of the nutrition hypothesis. *J Anim Ecol* 61: 113–119
- Inbar M, Wink M, Wool D (2004) The evolution of host plant manipulation by insects: molecular and ecological evidence from gall-forming aphids on *Pistacia*. *Mol Phylogen Evol* 32:504–511
- Johansen DA (1940) *Plant microtechnique*. McGraw-Hill Book Company, New York, London
- Martinez J-JI (2010) Anti-insect effects of the gall wall of *Baizongia pistaciae* [L.], a gall-inducing aphid on *Pistacia palaestina* Boiss. *Arthropod-Plant Interact* 4:29–34
- Nieto-Nafria JM, Mier-Durante MP, Binazzi A, Pérez-Hidalgo N (2002) Hemiptera. Aphididae II. In: Ramos MA et al (ed) *Fauna Ibérica*. Museo Nacional de Ciencias Naturales, C.S.I.C, Madrid, vol 19, pp 1–351
- Price PW, Waring GL, Fernandes GW (1986) Hypotheses on the adaptive nature of galls. *Proc Entomol Soc Wash* 88:361–363
- Price PW, Fernandes GW, Waring WG (1987) Adaptive nature of insect galls. *Environ Entomol* 16:15–24
- Sano M, Akimoto S-Y (2011) Morphological phylogeny of gall-forming aphids of the tribe Eriosomatini (Aphididae: Eriosomatinae). *Syst Entomol* 36:607–627
- Stern DL (1995) Phylogenetic evidence that aphids, rather than plants, determine gall morphology. *Proc R Soc Lond B Biol Sci* 260:85–89
- Stone GN, Schönrogge K (2003) The adaptive significance of insect gall morphology. *Trends Ecol Evol* 18:512–522
- Suzuki DK, Fukushi Y, Akimoto S (2009) Do aphid galls provide good nutrients for the aphids?: comparisons of amino acid concentrations in galls among *Tetraneura* species (Aphididae: Eriosomatinae). *Arthropod Plant Interact* 4:241–247. doi:10.1007/s11829-009-9064-9
- Wool D (2004) Gallling aphids: specialization, biological complexity, and variation. *An Rev Entomol* 49:175–192