Diversity of galls induced by wasps (Hymenoptera: Cynipidae, Cynipini) associated with oaks (Fagaceae: *Quercus*) in Mexico

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Abstract

Background: Gall-inducing insects make up a guild of highly specialized endophagous herbivores. The cynipids (Hymenoptera: Cynipidae: Cynipini) are highly diversified gall-inducing wasps that are largely associated with oaks (Fagaceae: *Quercus*). Mexico is one of the centers of diversification for the *Quercus* genus with 161 described species, of which 109 are endemic.

Questions / hypothesis: The present study aims to identify the gall richness, gall morphological variation and degree of specificity to oaks in Mexico.

Methods: An intensive collection was conducted from March to September each year from 2008 to 2012 for a total of 80 oak species in 120 localities in Mexico.

Results: A total of 224 morphologically distinct galls associated with 73 of the 80 oak species were found. The largest number of morphotypes was found in leaves (125), followed by branches (37), buds (31), petioles (20), catkins (5), acorns (3) and roots (3). The degree of specificity between the gall-inducing wasps and their hosts was highly variable; between one to 20 distinct gall morphotypes were found in each species. Only 23 oak species had a single gall morphotype associated.

Conclusions: This study demonstrates the important interaction between oaks and gall-inducing wasps, which is a very complex co-evolutionary process. It also shows the relevance of basic taxonomic studies of little-known groups such as gall-inducing wasps, especially in a highly biodiverse country such as Mexico.

Key words: Cynipidae, herbivore guilds, insect specialization, plant – insect interaction, *Quercus*

Resumen

Antecedentes: Los insectos inductores de agallas son un gremio de organismos endófagos altamente especializados. Los cinípidos (Hymenoptera: Cynipidae: Cynipini) son avispas inductoras de agallas ampliamente diversificados que se encuentran asociados principalmente a los encinos (Fagaceae: *Quercus*). México es uno de los centros de diversificación para el género *Quercus* con 161 especies descritas de las cuales 109 son endémicas.

Preguntas / hipótesis: El presente estudio contribuyó a identificar la riqueza de agallas, su variación morfológica y el grado de especificidad a los encinos en México.

Métodos: Se realizó una colecta intensiva de marzo a septiembre de cada año de 2008 a 2012 en un total de 80 especies de encinos en 120 localidades en México.

Resultados: Un total de 224 morfotipos distintos de agallas se encontraron asociados a 73 de las 80 especies de encinos estudiadas. El mayor número de morfotipos se encontraron en hojas (125), seguidos por ramas (37), yemas (31), peciolos (20), inflorescencias (5), bellotas (3) y raíces (3). El grado de especificidad entre las avispas inductoras de agallas y sus hospederos fue muy variable; se encontraron entre uno y 20 morfotipos distintos de agallas en cada especie. Únicamente 23 especies de encinos estuvieron asociadas a un solo morfotipo de agalla.

Conclusiones: Este estudio demuestra la importancia de la interacción entre los encinos y las avispas inductoras de agallas, el cual es un proceso coevolutivo muy complejo. También muestra la relevancia de estudios taxonómicos básicos de grupos poco conocidos como las avispas inductoras de agallas, especialmente en un país con una alta biodiversidad como lo es México.

Palabras clave: Cynipidae, especialización de insectos, gremio de herbívoros, interacción planta – insecto, *Quercus*

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Galls are atypical growths of plants that offer food, shelter and protection for the gall inducer or its progeny (Cornell 1983, Schönrogge *et al*. 2000, Hernández-Soto *et al*. 2015). Close to 13,000 species of gall-inducing insects have been recorded in plants (Shorthouse *et al*. 2005), although Espírito-Santo & Fernandes (2007) estimated a larger value of gall-inducing species ranging from 21,000 to 211,000 species. The family Cynipidae (Hymenoptera) contributes with approximately 1,400 species, constituting the second-largest source of gall-inducing insects, followed by the family Cecidomyiidae: Diptera (Csóka *et al*. 2005, Liljeblad & Ronquist 1998, Nieves-Aldrey & Fontal-Cazalla 1999, Ronquist & Liljeblad 2001). Each species produces its own gall type, which is anatomically and physiologically distinct from that of other related species (Shorthouse *et al*. 2005).

Nearly a thousand species of gall-inducing wasps have been reported (Hymenoptera: Cynipidae: Cynipini) in oak species (Fagaceae: *Quercus*) (Kinsey 1936, Weld 1960, Stone *et al*. 2002), and they are among the most structurally complex and diverse galls (Liljeblad *et al*. 2008). Gall structures reflect the primary characteristics of the insect inducer, representing an extension of their phenotype (Stone & Cook 1998). The host species of the Cynipini are almost exclusively limited to the *Quercus* genus (Liljeblad *et al*. 2008), although some use other hosts within the Fagaceae family, such as *Castanea*, *Castanopsis*, *Lithocarpus* and *Chrysolepis* (Nieves-Aldrey 2001, Stone *et al*. 2002, Liu & Ronquist 2006).

Each species of wasp from the Cynipini tribe is generally associated with inducing galls in practically all the organs (*e.g*., the leaves, roots, stems, and catkins) of their host species (Weld 1960, Ronquist 1994, 1995, Liljeblad & Ronquist 1998, Nieves-Aldrey 2001, Stone *et al*. 2002, Csóka et al. 2005). This association between wasps and oaks determines the global distribution pattern of this family of insects as well as the richness of the cynipid community in a specific locality (Nieves-Aldrey 2001, Stone *et al*. 2002).

In Europe, approximately 280 cynipid species have been recorded in 25 species of European oaks, which represents all the tribes of the Cynipidae (Nieves-Aldrey 2001, Stone *et al*. 2002, Rokas *et al*. 2003). Most of these endophagous insects have a life cycle with a spring-summer sexual generation and an autumn asexual generation, *i.e*., they exhibit an alternation of generations (Stone *et al*. 2002). During each generation, cynipid species have the ability to induce specific and complex galls on oaks, and in the majority of cases, they form a different gall morphotype each generation (*e.g*., sexual and asexual). Another characteristic in some species of cynipids is host alternation (heteroecy), which occurs every generation (Askew 1984, Cook *et al*. 1998, 2002).

Due to the diversity and structural complexity of the galls induced by cynipids, they are considered to be a microcosm of intense ecological activity since they support at least three trophic levels (gall tissue, gall-inducing wasps and occupants, and parasites and predators), which makes them a complex and interesting community for ecological-evolutionary studies (Nieves-Aldrey 2001, Ronquist & Liljeblad 2001, Hayward & Stone 2005).

It is estimated that there are approximately 500 oak species in the world and that the greatest species richness occurs in Mexico (Manos *et al*. 1999). Mexico is considered one of the centers of diversification for the *Quercus* genus with 161 species, of which 76 are located in the *Lobatae* section (red oaks), and 61 species are endemic to Mexico. In addition, the genus has 81 species in the *Quercus* section (white oaks) with 47 endemic species and four species in the *Protobalanus* section (intermediate oaks), with one endemic species (Valencia-Ávalos 2004).

One issue that is unclear is the specificity of cynipids to their host plants. In some European species, the alternation of hosts from different series of oaks has been reported at each reproductive stage, which indicates that the specificity may not be exclusively limited to a particular host species (Askew 1984, Stone *et al*. 2001, 2002). The specificity of gall-forming wasps has been poorly reviewed in the literature (Stone *et al*. 2002), and in Mexico, this group of insects and their ecological interactions have been poorly studied. Although the collection effort has not been as intense as in other countries, the species richness of cynipids has been estimated to range from 250 to 700 species based on the high richness of Mexican oak species (Nieves-Aldrey 2001). It is thus important to develop a strategy for the collection, breeding and identification of this group of insects in Mexico based on the distribution of oak species.

Based on the above priorities, it is necessary to study the species richness of cynipid species

Contribuciones de los autores
Enrique Pascual-Alvarado conceived the research, collected and analyzed the data, and wrote the manuscript.
José Luis Nieves-Aldrey designed the research project, collected and analyzed the data.
Douhglas Eliseo Castillejos Lemus made the review of the specialized literature and wrote the manuscript.
Pablo Cuevas Reyes conceived and designed the research project.
Ken Oyama conceived and designed the research project, wrote and edited the manuscript.

in Mexico, the diversity of gall morphology and the degree of gall specificity to their hosts. Therefore, the specific objectives of this study were to determine 1) the variations in wasp species richness among different oak sections in Mexico; 2) the morphological variation of galls induced by wasps on different oak species; and 3) the relationship between the cynipid species richness and the amplitude in the geographic distribution of the host oak species.

Materials and methods

A literature review of cynipid species associated with oaks was conducted, leading to the construction of a database to locate the species and establish them as starting points for the collection. Sampling was performed from March to August for four years (2008-2012) in 120 localities in total. For each oak species, at least five localities were visited. Geographic coordinates were taken at each location to define the distribution pattern of the cynipids associated with the different *Quercus* species (Figure 1).

Once the different oak species were located, an exhaustive search for galls was conducted at each site by checking each structure (*i.e.*, apical buds, leaves, petioles, branches, stems, roots, catkins and acorns) of at least ten trees from each available *Quercus* species. In addition, herbarium specimens were collected to identify the oak species.

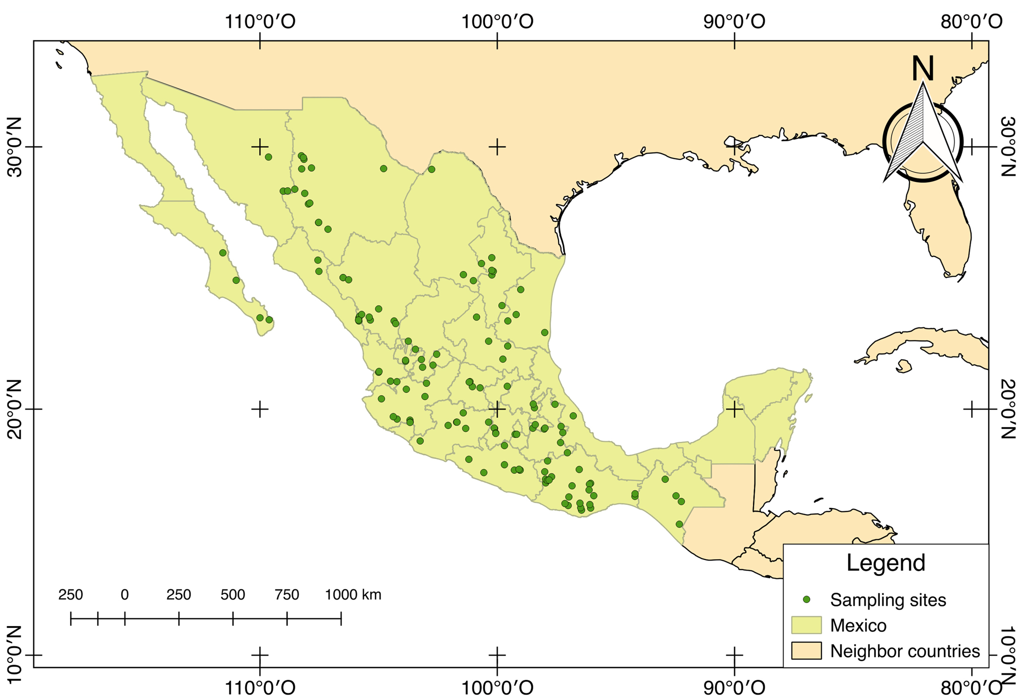

Figure 1. Sampling localities of gall morphotypes of oaks in Mexico.

The collection of cynipids was based on gall morphology and was taken from across the country. A total of 80 oak species that were associated with this guild of herbivores was analyzed. For this study, each distinct gall morph is considered a potentially distinct species. We classified the galls according to the number of larval chambers as unilocular (a single chamber) or multilocular (with several chambers) and with or without ornaments (spines, hairs).

The collected galls were brought to the laboratory for growth and subsequent taxonomic determination. The taxonomy of the species is being determined in collaboration with Dr. José Luis Nieves-Aldrey from the National Museum of Natural Sciences in Madrid, Spain.

Results

A total of 224 distinct gall morphotypes induced by cynipids was found in 73 of the 80 oak species under analysis, of which 40 correspond to the *Lobatae* section (red oaks) and 33 to

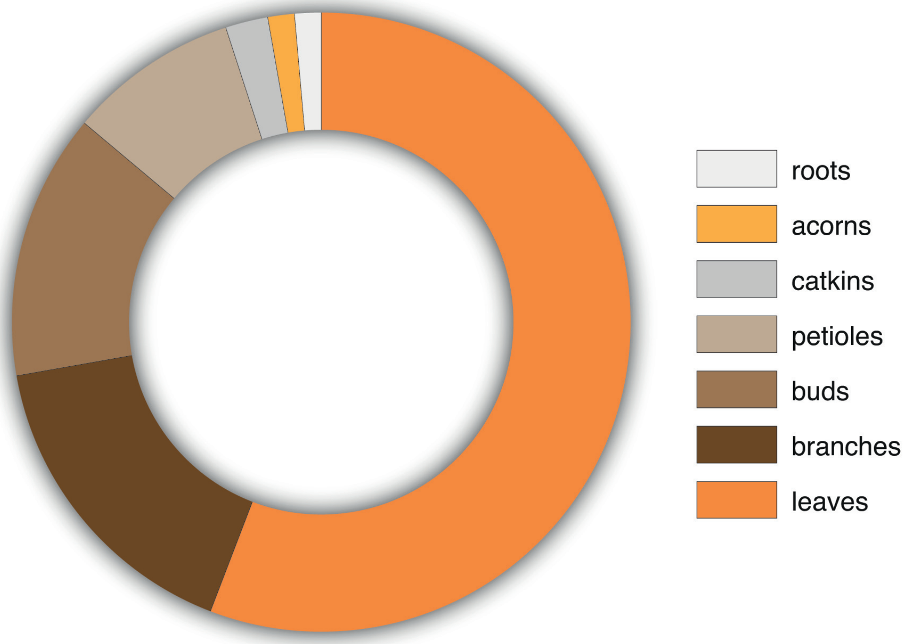

Figure 2. Number of gall morphotypes in each plant organ of oaks. Total number of galls = 224. 1 = leaves (125 galls; 55.8%); 2 = branches (37; 16.5%); 3 = buds (31; 13.8%); 4 = petioles (20; 8.9%); 5 = catkins (5; 2.2%); 6 = acorns (3; 1.3%); and 7 = roots (3; 1.3%).

the *Quercus* section (white oaks). Galls were not found in the following seven oak species: *Q. canbyi*, *Q. gentryi*, *Q. crispifolia* and *Q. hypoleucoides* from the Lobatae section and *Q. glabrescens*, *Q. glaucoides* and *Q. lancifolia* from the *Quercus* section. The largest number of morphotypes was found in leaves (125), followed by branches (37), buds (31), petioles (20), catkins (5), acorns (3) and roots (3) (Figure 2). A total of 126 gall morphotypes were found in the *Quercus* section, and 113 were found in the *Lobatae* section.

The number of gall morphotypes associated with each oak species, their taxonomic section, and the amplitude of geographical distribution and whether they are endemic to Mexico is summarized in Table 1. In the *Lobatae* section (red oaks), the species with the greatest number of morphotypes are *Quercus crassifolia* (11), *Q. castanea* (10) and *Q. mexicana* (7). The remaining species have one to five distinct morphotypes (Figure 3). In the *Quercus* section (white oaks),

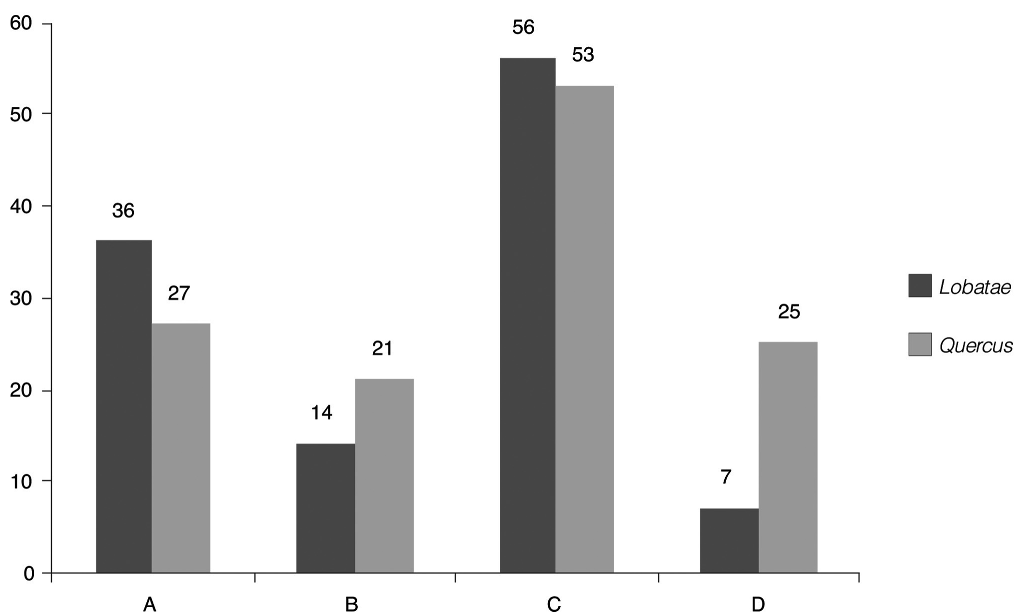

Figure 3. Number of gall morphotypes according to the morphology in the two sections of oaks (*Lobatae* and *Quercus*). **A)** Unilocular without ornaments. **B)** Unilocular with ornaments. **C)** Multilocular without ornaments. **D)** Multilocular with ornamentes.

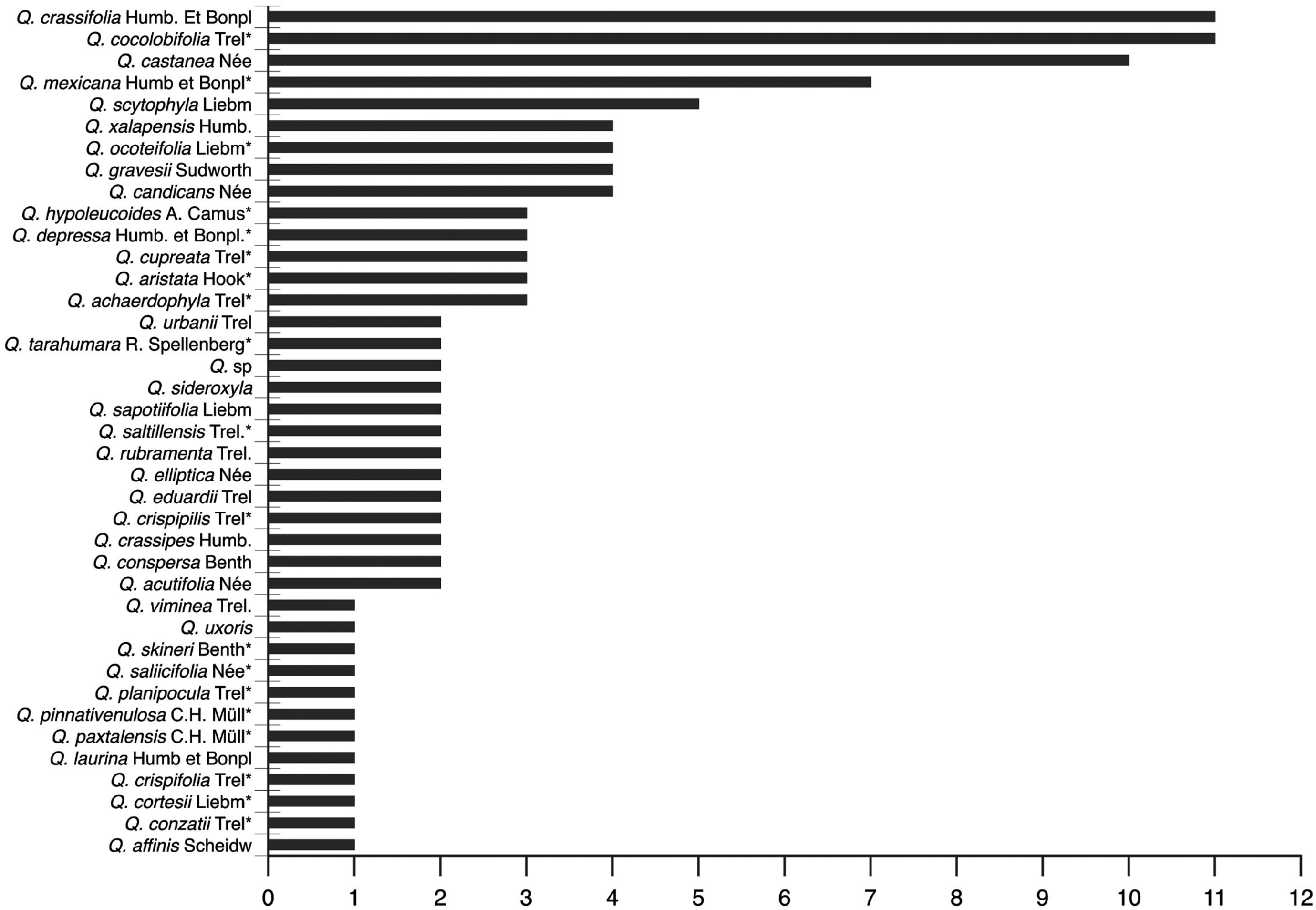

Figure 4. Number of gall morphotypes associated to each oak species in the Section *Lobatae*.

the oak species with the greatest number of gall morphotypes were *Q. microphylla* (20 morphotypes), followed by *Q. resinosa* (17) and *Q. magnoliifolia* (14). The remaining species have one to five distinct associated morphotypes (Figure 4). As in the case of section *Lobatae*, the species with the greatest number of morphotypes are those with a wide geographical distribution.

Only 31.5 % of the 73 oak species (13 red oaks and 10 white oaks) had only a single associated gall morphotype; 24.7 % (12 red and 6 white oaks) had two gall morphotypes, 16.4 % (6 red and 6 white oaks) had three gall morphotypes, and the remainder (27.4 %) had more than 4 morphs. Of the 13 species of red oaks with a single gall morphotype, 9 are endemic to Mexico, and of the 10 white oaks, 6 are endemic.

We found 63 galls with a single larval chamber (unilocular) with smooth surface (without ornaments) (36 in *Lobatae* and 27 in *Quercus*), 35 unilocular with ornaments (14 *Lobatae* and 21 *Quercus*), 109 multilocular without ornaments (56 *Lobatae* and 53 *Quercus*) and 32 multilocular with ornaments (7 *Lobatae* and 25 *Quercus*) (Figure 5).

Discussion

In this study, we found a great diversity of galls induced by wasps on oaks as host species (Figure 6). The assumption that gall-inducing wasps from the Cynipidae family exhibit a high degree of specialization to their host plants in the *Quercus* genus (Weld 1960, Ronquist 1995, Liljeblad & Ronquist 1998, Nieves-Aldrey 2001, Stone *et al*. 2002, Csóka *et al*. 2005) should be reviewed based on the results of this study. Most of the oak species studied here had more than one gall morphotype, and in some cases, they had an unexpectedly high number of gall morpho-

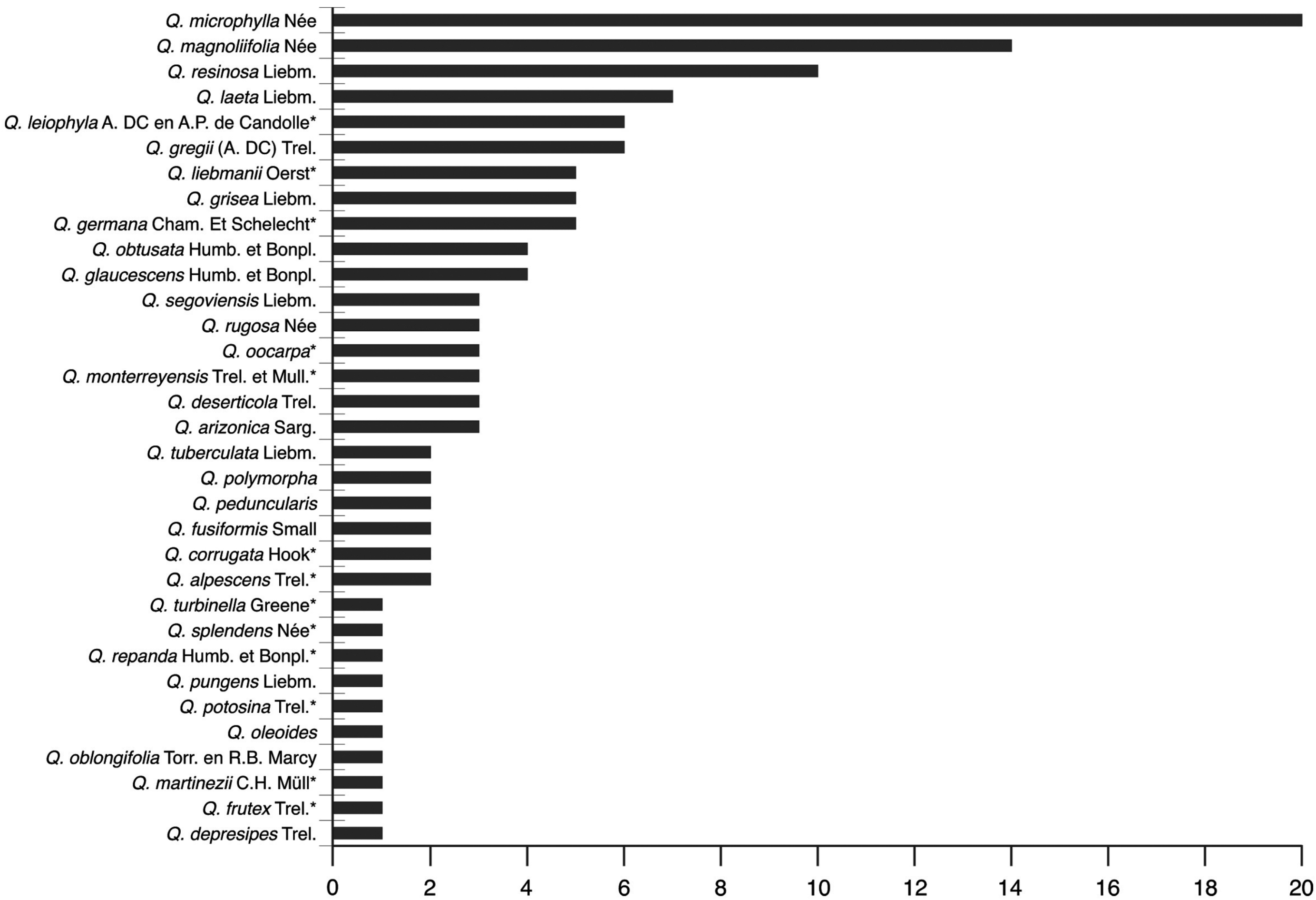

Figure 5. Number of gall morphotypes associated to each oak species in the Section *Quercus*.

types throughout their geographical distribution. In particular, three species of white oaks [*Q. microphylla* (20 morphotypes), *Q. resinosa* (17) and *Q. magnoliifolia* (14)] and three red oaks [*Q. crassifolia* (11), *Q. coccolobifolia* (11) and *Q. castanea* (10)] had a considerable number of galls collected from throughout their broad distribution in Mexico. These oak species have a wide range of geographic distribution occurring in different environmental conditions that could represent diverse ecological niches occupied by different gall wasps. It is also necessary to study the degree of host specialization of these galls through their entire geographic range in future studies.

In these cases, in particular, these oak species could be considered super hosts, since they have galls throughout their entire distribution and because galls occur over the entire structure of the tree. They also have morphotypes that are specific to certain localities, which may indicate endemism.

In the case of the endemic oak species, many have only a single morphotype, and even similar morphotypes had variations in bark texture or the inside the gall itself. It can therefore be assumed that they are distinct species and probably endemic and a detailed ecological and taxonomic study would need to be conducted for each of them.

By contrast, very unique morphs were discovered, which were only found on the leaves of oaks in the *Quercus* section, for example, *Q. magnoliifolia*, *Q. resinosa*, *Q. laeta*, *Q. deserticola*, *Q. rugosa* and *Q. obtusata*. According to Pujade-Villar *et al*. (2010), there is a new genus called *Kinseyella*, although confirming it would require a thorough review of both the gall and the gall inducers to know whether it is the same genus and a distinct species, or whether it is the same species of gall inducer in all the hosts listed here.

Figure 6. Photos of gall morphotypes in different oak species in Mexico. 1. *Quercus conzati* (petiole) Jal. 2. *Q. sideroxyla* (branch) Chih. 3 y 4. *Q.magnoliifolia* (leaves) Gro. 5. *Q. resinosa* (catkin) Mich. 6. *Q. crassifolia* (bud) Chis. 7. *Q. ocoteifolia* (yema) Oax. 8. *Q. uxoris* (leaf) Oax. 9. *Q. sp.* (branch) Ver. 10. *Q. castanea* (branch) Mich. 11. *Q. segoviensis* (catkin) Chis. 12. *Q. polymorpha* (leaf) NL. 13. *Q. arizonica* (leaf) Coah. 14. *Q. segoviensis* (leaf) Chis. 15. *Q. cupreata* (root) NL. 16. *Q. obtusata* (leaf) Dgo. 17. *Q. microphylla* (acorn) Gto. 18. *Q. laurina* (branch) Hgo. 19. *Q. gregii* (leaf) Dgo. 20. *Q. laeta* (bud) Mich. 21. *Q. rugosa* (bud) Jal. 22. *Q. conspersa* (branch) NL. 23. *Q. frutex* (leaf) Pue. 24. *Q. viminea* (bud) Dgo. 25. *Q. deserticola* (leaf) Sin. Abbreviations of each locality (state) as indicated in Table 1.

In the case of *Q. magnoliifolia* and *Q. resinosa*, recent studies showed that these oak species form hybrids in regions where their geographic distributions overlap (Albarrán-Lara *et al*. 2010), generating new adaptive zones for the formation of new species of gall insects (Pérez-López *et al*. 2016). These zones are also suggested by the *Q. crassifolia* × *Q. crassipes* complex (Tovar-Sánchez & Oyama 2004) in which three gall morphotypes were exclusively associated with the hybrid individuals found there (Tovar-Sánchez & Oyama 2006). However, this pattern cannot be generalized, since in another hybrid complex formed by *Q. affinis* × *Q. laurina* (González-Rodríguez *et al*. 2004, González-Rodríguez & Oyama 2005, González-Rodríguez *et al*. 2005), only one gall morphotype was found in each of the species in this study (see Table 1).

The galls induced by cynipids can be classified according to the number of larval chambers (*e.g.*, unilocular and multilocular) and their ornamentation (*e.g.*, without ornamentation and a

Table 1. Number of gall morphotype associated to each oak species in the section Lobatae (red oaks) and section ***Quercus*** (white oaks). Oak endemic species to Mexico is indicated by an asterisk. The type of gall morphotype: U = unilocular, M = multilocular, s/o = without ornaments and c/o = with ornaments.

Section	Species	Collected states	Number of gall morphotypes	Unique gall in a population	Type of gall morphotype
Lobatae	*Q. acutifolia* Née	Mich., Oax., Jal.	2		Ms/o(2)
	Q. acherdophylla Trel. *	Hgo., Pue.	3		Us/o(1), Ms/o(2)
	Q. affinis M.Martens & Galeotti.	Gto., Pue., Hgo., Ver., S.L.P.	1		Ms/o
	Q. aristata Hook & Arn*	Jal., Nay.	3		Us/o(1), Ms/o(2)
	Q. candicans Née	Chih., Chis., Dgo., Gro., Jal., Mich., Nay., Oax	4		Us/o(1), Ms/o(3)
	Q. castanea Née	Chis., Col., Dgo., Gto., Gro., Hgo., Jal., Mich.,Oax.	10	Us/o (2)	Us/o(3), Ms/o(3), Uc/o(2), Mc/o(2)
	Q. coccolobifolia Trel.*	Chih., Jal., Nay.	11		Us/o(4), Ms/o(4), Uc/o(2), Mc/o(1)
	Q. conspersa Benth.	Chih., Gro., Jal., Mich., N.L.	2		Ms/o(2)
	Q. conzattii Trel.*	Dgo., Jal., Oax., Zac.	1		Ms/o
	Q. cortesii Liebm.*	Chis., Oax., Ver.	1		Ms/o
	Q. crassifolia Bonpl.	Chih., Chis., Dgo., Mich., Oax.	11		Us/o(4), Ms/o(4), Uc/o(2), Mc/o(1)
	Q. crassipes Bonpl.	Col., Gto., Hgo., Mich.	2		Ms/o(2)
	Q. crispifolia Trel.*	Chis., Oax.	1		Ms/o
	Q. crispipilis Trel.*	Chis.	2		Uc/o(1), Ms/o(1)
	Q. cupreata Trel. & C.H.Mull.*	N.L.	3	Us/o(1)	Us/o(1), Ms/o(2)
	Q. depressa Bonpl.*	Hgo.,Oax., Ver.	3		Us/o(1), Ms/o(2)
	Q. eduardi Trel.	Chih., Dgo., Mich., Ver.	2		Us/o(1), Ms/o(1)
	Q. elliptica Née	Chis., Jal., Mich., Sin.	2		Us/o(1), Ms/o(1)
	Q. gravesii (Sarg.) Sudw.	Coah.	4		Us/o(1), Uc/o(1), Ms/o(1)
	Q. hypoleucoides A.Camus*	Chih., Coah., Dgo.	3		Us/o(1), Ms/o(2)
	Q. laurina Bonpl.	Gro., Gto., Hgo., Mich., Pue., Tlax., Ver.	1		Ms/o
	Q. mexicana Bonpl.*	Coah., Hgo., N.L., Tamps., Tlax., Ver.	7	Uc/o(1)	Us/o(2), Ms/o(3), Uc/o(1), Mc/o(1)
	Q. ocoteifolia Liebm.*	Chis. , Oax.	4	Uc/o(1)	Us/o(1), Uc/o(1) Ms/o(2)
	Q. paxtalensis C.H.Müll.*	Chis.	1		Us/o
	Q. pinnativenulosa C.H.Müll.*	N.L. ,Ver.	1		Us/o
	Q. planipocula Trel.*	Mich, Gro., Sin.	1		Us/o
	Q. rubramenta Trel.	Gro., Oax.	2		Us/o(1), Ms/o(1)
	Q. salicifolia Née*	Gro., Jal., Mich.	1		Ms/o
	Q. saltillensis Trel.*	Coah., N.L.	2		Us/o(1), Ms/o(1)
	Q. sapotifolia Liebm.	Chis., Hgo., Oax., Ver.	2		Uc/o(1), Ms/o(1)
	Q. scytophylla Liebm.	Gro., Jal., Mich., Pue.	5		Us/o(2), Ms/o(2), Mc/o(1)
	Q. sideroxyla Bonpl	Ags., Chih. Coah., Dgo., Jal., Zac.	2		Us/o(1), Ms/o(1)
	Q. sp.	Tamps., Ver.	2		Us/o(1), Ms/o(1)
	Q. skinneri Benth.*	Chis., Oax.	1		Us/o
	Q. tarahumara R. Spellenb., J.D. Bacon & Breedlove*	Chih, Sin, Dgo.	2		Us/o(1), Mc/o(1)
	Q. urbanii Trel.	Dgo., Gro., Sin.	2		Us/o(1), Ms/o(1)
	Q. uxoris McVaugh	Col., Jal., Oax.	1	1 Uc/o	Uc/o
	Q. viminea Trel.	Ags., Dgo., Gto., Nay.	1		Ms/o
	Q. xalapensis Bonpl.	Hgo., Ver.	4		Us/o(1), Uc/o(1), Ms/o(2)
Quercus	*Q. alpescens* Trel.*	Hgo., N.L.	2		Ms/o (2)
	Q. arizonica Sarg.	Chih., Coah., Dgo.	3		Us/o (1), Mc/o (2)
	Q. corrugata Hook*	Chis, Gro., Ver.	2		Uc/o(1), Ms/o(1)
	Q. depressipes Trel.	Chih., Zac.	1		Ms/o(1)
	Q. deserticola Trel.	Gto., Jal., Mex., Mich., Oax., Qro., Sin.	3		Uc/o(1), Ms/o(2)
	Q. frutex Trel.*	Hgo., Mex., Oax., Pue.	1		Uc/o(1)
	Q. fusiformis Small	Coah., N.L.	2		Ms/o (2)

Table 1. Continuation.

Section	Species	Collected states	Number of gall morphotypes	Unique gall in a population	Type of gall morphotype
	Q. germana Schltdl. & Cham. *	Oax., Pue., Ver.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. glaucescens Bonpl.	Gro., Jal., Mich., Sin.	4		Us/o(1), Ms/o(3)
	Q. greggii (A.D.C) Trel.	Coah., Dgo., N.L.	6		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(2)
	Q. grisea Liebm.	Ags., Chih.,Coah., Gto., Jal.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. laeta Liebm.	Ags., Coah., Dgo.,Gto., Hgo., Jal., Mex., Mich., Zac	7		Us/o(1), Uc/o(2), Ms/o(2), Mc/o(2)
	Q. leiophylla A.D.C. *	Oax., Pue.	6		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(2)
	Q. liebmannii Oerst ex Trel*	Gro.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. magnoliifolia Née	Col.,Gro., Hgo., Jal., Méx., Mich., Oax., Pue., Sin.	14	Us/o(1), Uc/o(1), Ms/o(1)	Us/o(4), Uc/o(4), Ms/o(4), Mc/o(2)
	Q. martinezii C.H.Mull*	Gro., Jal., Nay., Mich.	1		Mc/o (1)
	Q. microphylla Née	Ags.,Gto., Nay.	20		Us/o(6), Uc/o(4), Ms/o(6), Mc/o(4)
	Q. monterreyensis Trel. & C.H.Mull.*	N.L.	3		Us/o (1), Mc/o (2)
	Q. oblongifolia Torr.	Chih., Coah., Son.	1		Ms/o(1)
	Q. obtusata Bonpl.	Dgo., Gro., Gto., Jal., Mich.	4		Us/o(1), Ms/o(3)
	Q. oleoides Schltdl. & Cham.	Chis., S.L.P., Oax.	1		Mc/o (1)
	Q. oocarpa Liebm.*	Jal., Nay.	3		Us/o (1), Mc/o (2)
	Q. peduncularis Neé	Chis., Col., Nay.	2		Ms/o (2)
	Q. polymorpha Schltdl. & Cham.	Chis., Hgo., N.L.	2	Us/o(1), Ms/o(1)	Us/o(1), Ms/o(1)
	Q. potosina Trel.*	Ags., Dgo., S.L.P.	1		Ms/o(1)
	Q. pungens Liebm.	Chih.	1		Ms/o(1)
	Q. repanda Michx..*	Hgo., Tlax.	1		Ms/o(1)
	Q. resinosa Liebm.	Ags., Dgo., Gto., Jal., Mich.	10	Uc/o(1)	Us/o(2), Uc/o(2), Ms/o(4), Mc/o(2)
	Q. rugosa Née	Ags., Chis., Col., Gro., Gto., Mich., Mor., N.L., Zac.	3		Us/o(1), Uc/o (1), Ms/o(1)
	Q. segoviensis Liebm.	Chis.	3	Ms/o (1)	Us/o (1), Ms/o (2)
	Q. splendens Née*	Nay., Jal., Mich.	1		Ms/o(1)
	Q. tuberculata Liebm.	B.C., Nay., Son.	2		Us/o(1), Ms/o(1)
	Q. turbinella Greene*	B.C., Son.	1		Ms/o(1)

States abbreviations. Ags.: Aguascalientes; BC: Baja California; Coah.: Coahuila; Col.: Colima; Chih.: Chihuahua; Chis.: Chiapas; Dgo.: Durango; Gro.: Guerrero; Gto.: Guanajuato; Hgo.: Hidalgo; Jal: Jalisco; Méx.: Estado de México; Mich.: Michoacán; Mor.: Morelos; Nay: Nayarit; N.L.: Nuevo León; Oax.: Oaxaca; Pue.: Puebla; S.L.P.: San Luis Potosí; Sin.: Sinaloa; Son: Sonora; Tamps.: Tamaulipas; Tlax.: Tlaxcala; Ver.: Veracruz; Zac.: Zacatecas.

smooth surface, or with hair and spines). The highest numbers of galls for both sections are multilocular galls without ornamentation, and they are usually associated with the branch of the host. According to Ronquist (1995, 1999) and Rokas *et al*. (2003), this gall morphotype is the most primitive, suggesting the colonization of the host by cynipids. Confirming this colonization would require a phylogenetic and comparative biological study to locate these species relative to European species and assess their degree of relationship.

There is, however, a peculiar morph in the *Lobatae* section that is unilocular, globular, with or without ornamentation, and similar to galls from the *Amphibolips* genus (Nieves *et al*. 2012). This finding may indicate that there is a particular association between this endemic group of oaks with a genus of cynipid inducers, an interaction so specific that it could be considered a process of speciation that often occurs in the hosts of this section of oaks (Nieves *et al*. 2012).

The collection effort is a key factor in this type of study. Maldonado-López *et al*. (2015a, b, 2016) recorded up to 40 morphologically distinct galls that were induced by wasps on *Q. castanea* throughout its geographic distribution. This finding suggests that studies with both greater temporal and spatial collection intensity, focused on a single species of oak throughout its entire distribution, can produce this type of result.

Conclusions and perspectives

Gall-forming wasps (Hymenoptera: Cynipidae: Cynipini) represent a very diverse group with ecologically interesting characteristics (Nieves-Aldrey 1998, 2001, Ronquist & Liljeblad 2001, Hayward & Stone 2005). In this study, an important effort to add new records to this guild of insects in Mexico was undertaken. However, it is necessary to continue this type of study to determine the total species richness of wasps in Mexico as well as their phylogenetic relationships, and finally, to establish their patterns of diversification. Mexico represents one of the two most important centers of oak diversification in the world, especially for red oaks (section *Lobatae*). These collection efforts must be accompanied by taxonomic studies that elucidate the discovery of new species (Nieves-Aldrey *et al*. 2012) and even genera as observed in some of the collections made in this study.

One important and characteristic aspect of the cynipids associated with oaks is that they are cyclically parthenogenetic, which has been a source of confusion during their taxonomic classification. Thus, studies should focus on finding both morphological (Hernández-Soto *et al*. 2015) and molecular tools to resolve this problem, in addition to elucidating which processes cause this phenomenon.

At the population level, it is important to determine the dispersal distances of individuals and their patterns of colonization in both themselves and their new hosts through either ecological studies (Schönrogge *et al*. 1994, 1999) or genetic studies using molecular markers (Castillejos-Lemus 2016).

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