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WHEN A MARINE BIOLOGIST GOES TERRESTRIAL: HENRI DE LACAZE-DUTHIERS AND PLANT GALLS

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GALL
INTERACTIONS
PARASITISM
PLANT
EVOLUTION

ABSTRACT. – Besides his work on marine biology which legacy is undisputed, Henri de Lacaze-Duthiers, as other 19th century zoologists, extended his interests to many fields of natural history. He was generally a keen observer (and very talented illustrator) of the anatomy of complex natural structures. In particular, he initiated studies on insect-induced galls addressed in his article "*Recherches pour servir à l'histoire des galles*" (Lacaze-Duthiers 1853) and illustrated his research on the subject by magnificent drawings. The purpose of this essay is to report this lesser-known aspect of the work of H. de Lacaze-Duthiers. Without judging the value of Lacaze-Duthiers' research, we aim at extending the questions he raised at his time, and attempt to provide answers using recent knowledge on insect-induced gall diversity, ecology and physiology. In the process, we stress how the issues raised by Lacaze-Duthiers are connected to more general questions that apply to all biological associations between species (including parasitism). We will see that H. de Lacaze-Duthiers paper not only constitutes a pioneering work on insect galls but also addresses concepts that are still very relevant in current research, in particular on the genesis and development of galls.

INTRODUCTION

Henri de Lacaze-Duthiers is well known for his work and extensive (and splendid) illustrations of marine invertebrates. He has conducted pioneering studies on the description of red corals (Vielzeuf *et al*. 2022) and he is also the founder of two French marine stations (in Roscoff and Banyuls-sur-Mer) that are still at the forefront of marine biology today. However, as a field naturalist, he extended his interests to many organisms (Jessus *et al*. 2021). He was a keen observer (and a very talented illustrator) of the anatomy of complex natural structures. Quite early in his career, he worked on insects and he undertook studies on gall-making insects addressed in his article "*Recherches pour servir à l'histoire des galles*" (Lacaze-Duthiers 1853). In this article, Henri de Lacaze-Duthiers starts by defining what a gall is and pleads for a collaboration between botanists and entomologists for a better understanding of how these structures can arise from the interactions between insects and the plants that host them. He then questions the genesis of galls and their development. To that aim, he investigates the histology of these structures, identifying which tissues are involved in the formation of the galls and the nutrition of its inhabitants throughout the development of the gall. Doing so, he differentiates different types of galls according to the position of the outgrowths with respect to the plant organs as well as the location of the insects (inside the plant tissues or on their surface). These descriptions reveal a striking anatomical diversity of galls, which potentially gives important clues on the mechanisms underlying their development.

Prior to this essay, there were to our knowledge few studies on the diversity and formation of insect-induced galls that are so well documented. In this article, Henri de Lacaze-Duthiers only cites six authors who have dealt with the study of galls in generalist entomology books. Folliot's (1964) synthesis on galls wasp (Cynipidae) indeed underlines that H. de Lacaze-Duthier's work on the structure of these galls was pioneering. Finally, throughout this work, H. de Lacaze-Duthiers insists on the need for accurate descriptions of the anatomy of galls in order to better understand the involvement of the substances injected by the insects in these plant abnormal growths. This approach is still advocated in the most recent research on galls (*e.g*. Korgaonkar *et al*. 2021).

In this paper, we discuss Lacaze's questioning (in *italics*) from the points of view of an entomologist, Emmanuelle Jousselin, a fish parasitologist, Yves Desdevises, and a naturalist, Joseph Garrigue.

I. WHAT IS A PLANT GALL? DEFINITION AND DIVERSITY

First of all, let's give an updated definition of a plant gall. For Henri de Lacaze-Duthiers, a gall was "*a new,* *abnormal product, developed either on the external surface or in the middle of the plant tissue*" (translated from Lacaze Duthiers 1853) and plant-galls were restricted to the product of animal/plant interactions. Since then the definition has broadened and now includes all abnormal plant growths induced by another organism: "a gall or cecidia is a set of cells or plant tissues, showing a modified development specific to the influence of another organism" (Dreger-Jauffret *et al*. 1992, Harris & Pitzschke 2020). This definition therefore includes galls that are the result of infections by bacteria, fungi, viruses, protozoa, parasitic plants in addition to many types of animals including insects, mites, nematodes (Harris & Pitzschke 2020). Hence, in his 1853 article, Henri de Lacaze-Duthiers only reports on insect-induced galls and his illustrations are restricted to those. They have since fascinated many entomologists and some insect study systems have been the subject of long-term research in evolutionary ecology. We can cite among others: Cynipid wasps that form galls on *Quercus* (Egan *et al*. 2012), aphids that induce galls on poplar and *Pistacia* trees (Inbar *et al*. 2004, Compson *et al*. 2011) and gall midges that can be found on very diverse botanical families (Yukawa *et al*. 2005), all documented by Lacaze-Duthiers in his time (Figs 1, 2 & 3). However, many questions raised in H. de Lacaze-Duthiers' essay probably apply to other gall inducing organisms, and though we restrict our review to insects, as underlined by Harris & Pitzschke (2020), investigating the commonalities between different plant galls would probably enhance our understanding of their genesis. As other galls, insect-caused growths are generally three-dimensional and resistant to flattening; they are known to occur on any plant organs: leaves, twigs, flowers, and buds. Recent work on fossilized flora has shown that they have been around since the Paleozoic (Labandeira 2021).

How can we explain the production of galls by insects?

Henri de Lacaze-Duthiers raised several hypotheses on the process of gall induction: "*What is the cause? In the greatest number of cases, and this is admitted by all, insect bites determine the development of galls; but going further, and breaking down this general cause, it must be asked: is it the wound which, as a lesion only, causes the development of the abnormal tissue? Or is it the action consequent upon the wound, that is, the suction or drawing of the juices into the wound, which produces the burbling of the parenchyma? Or, finally, is it a special fluid deposited in the wound that alone develops the disease?*" (translated from Lacaze-Duthiers 1853). He then argued that galls must be caused by a substance injected by the insects: "*the incision, the wound has in our opinion only a very secondary part in the production of galls*"; "*This is therefore for us the explanation of the production of galls: deposition at the same time as the egg, of a liquid with special properties influencing differently on the plant tissues, from where productions of various pathologies*". He therefore wondered about the quality of the substance emitted by the insect and mentioned "*a morbid product, a venom, a virus*" (Lacaze-Duthiers 1853).

Focusing on the interaction between gall-inducing insects and plants, recent research has indeed investigated whether the production of a gall can be the result of a product injected by the insect that influences the way the attacked plant organ will grow. Phytohormones (*i.e*. auxin, cytokinins, and abscisic, jasmonic, and salicylic acids) have been hypothesized to play a key role in gall production. Early and recent studies indeed suggest that gall-inducing insects might introduce precursors of auxines and cytokinins into the plant tissues through their salivary or accessory-gland (reviewed in Raman 2021), those precursors are called "effectors" (Hogenhout *et al*. 2009). For instance, quite early work by Nysterakis (1947) has shown that auxin was found in the saliva of gall-inducing aphids. However, generally the mode of action of these chemical substances and how they are manipulated or secreted by insects remain unclear (Yamaguchi *et al*. 2012, Bartlett & Connor 2014, Tooker & Helms 2014, Raman 2021). The insects genes that are coding for these "effectors", their expression as well as parallel expression patterns in host plant genes during gall development are under investigation in several study systems (*e.g*. in Cynipids, Cambier *et al*. 2019, Hearn *et al*. 2019, in aphids; Korgaonkar *et al*. 2021). Studies suggest that there is a complete reprogramming of the plant's cellular development under the effect of insect behavior and/or substances. At the molecular level, there could be an activation and a deactivation of plant genes in the cells involved in the gall (Hearn *et al*. 2019). All these studies reveal a complex interplay between insect's effectors/behavior and plant developmental programs. However, as underlined in Raman's synthesis (2021), there are still many unknowns in the processes of gall induction by insects and therefore the question raised by H. de Lacaze-Duthiers on the nature of the insect substance is not fully answered and remain the subject of cutting-edge research in both entomology and botany.

Henri de Lacaze-Duthiers wondered how many plants were likely to produce galls.

"*A German, Mr. Hammerschmidt, found more than fifty different species of galls on oak alone. This suggests an important underestimation of the actual number of galls, which would increase greatly if all these botanical species were studied with the same care as the tree in our forests*" (translated from Lacaze Duthiers 1853). At the time of H. de Lacaze-Duthiers's essay, it was mainly the "nuts" of oak galls that were known and studied thoroughly because they were used as a source of tannin (Redfern 2011). About fifty "species" of galls were known from

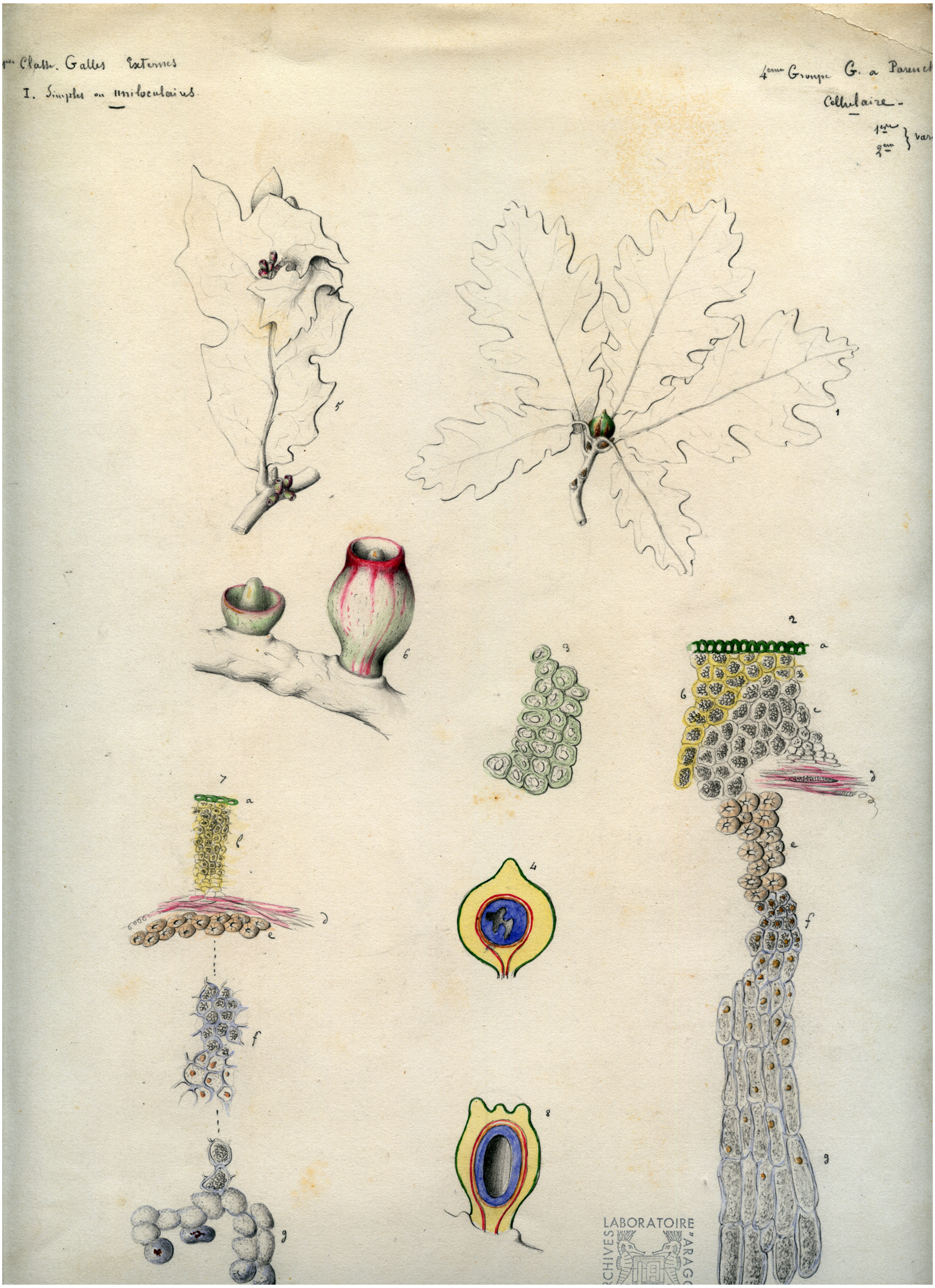

Fig. 1. – Original drawing made by Lacaze-Duthiers representing the gall made by a Cynipid wasp, *Andricus inflator* on oak trees (*Quercus* spp.) (© Archives Laboratoire Arago/Sorbonne Université).

oak trees! Since then, botanists and entomologists have uncovered many more: there are about 1000 species of Cynipini within gall-wasps (Cynipidae) and most of them develop inside the galls they induce on oak trees (Fig. 1) (Ronquist *et al.* 2015). In France, P. Dauphin, in his book *Les Galles de France* published in 1993, mentions more than 1600 "species" of galls occurring on more than 480 different plant genera, and according to this book more than 15,000 cecidogenic species are listed in the world (Dauphin 1993). As an indication, in the small forest of La Massane, about 150 species are listed, occurring on more than 50 plant genera on only 336 hectares.

Those numbers are actually probably beneath the reality. Quite recently it has been estimated that there were about 130,000 species of insects that could be responsible for gall induction (Espírito-Santo & Fernandes 2007). However, the question raised by Lacaze-Duthiers was "how many plants are likely to produce galls?" and not "how many animals are gall inducers?". If there are studies that aim at estimating the number of "gall inducers", at least among insects, we failed to find any study attempting to answer H. de Lacaze-Duthiers' question, *i.e.* estimating the number of "gall makers" among all plants. Maybe any plant, if attacked by the "right" enemy, can alter its cellular development and grow a gall.

How can a botanical species give so many different structures for the same organ, on all organs? *Are gall-makers magicians, manipulators, managing to induce such spectacular structures that are foreign to what the plant usually produces? H. de Lacaze-Duthiers wondered about the diversity of insect galls.*

"When we see an oak tree presenting the ten species of galls that we have been allowed to study on its leaves, what strength and what truth does not take the principle of specificity, of the quality of the venom?" (translated from Lacaze-Duthiers 1853).

As suggested by *Lacaze Duthiers*, depending on the insect species, the type of "*venom*" (if we were to use H. de Lacaze-Duthiers' terminology) injected probably varies and generates a completely different "reprogramming" code for plant growth. The plant organ attacked, the stage of development of the plant organ attacked, also strongly influence the shape of the gall (Favery *et al.* 2020, Isaias & Oliveira 2012). It is not the same to "reprogram" the growth of a leaf in bud as it is to reprogram a leaf that is already well developed, nor is it the same to "reprogram" the growth of a stem as it is to reprogram the growth of a leaf. It is also interesting to note that plants are not necessarily defenseless against gall-inducers. There are many examples of plant resistance. For instance the grape phylloxera, *Daktulosphaira vitifoliae*, a gall inducer that is native of North America which threatened to destroy the French wine industry in mid-nineteenth century, was controlled using resistant grape (Granett *et al.* 2001).

As a conclusion, as underlined by Harris & Pitzschke (2020), many parts of the plant are capable of making galls for many types of organisms. As the result of these multidimensional interactions (*i.e.* plant-species / plant-organ / plant developmental stages / gall inducer species), we can obtain the wide diversity of galls observed and documented by H. de Lacaze-Duthiers.

II. UNDERSTANDING THE EVOLUTION OF GALL INDUCTION STRATEGIES

What are the benefits (and costs) of gall making for inducers (the insects)?

Galls are usually enclosed spaces, protected from the outside, as if the plant was providing shelter and food for its own parasites (Price *et al.* 1987). This dual function of the gall (nourishment and protection) was already underlined by H. de Lacaze-Duthiers: "*The animal germ develops, undergoes all its metamorphoses, and emerges as a perfect insect. This series of transformations requires a suitable food, and a protection especially sufficient to guarantee the larva whose skin is soft and tender*" (translated from Lacaze-Duthiers 1853). Henri de Lacaze-Duthiers made numerous anatomical drawings of the plant tissues of the galls, showing the nourishing part and the protective parts (Fig. 2). They clearly show that, in some cases, the eggs of the gall inducers are entrusted to the plant, which raises them. Has nature already invented surrogate motherhood? At what cost, what risk?

Recent studies suggest that a gall can indeed be seen as surrogate motherhood and also sometimes, a nursery. This phenomenon of entrusting one's offspring to another organism is actually a well-established biological trait that occurs throughout the animal kingdom. In some case, not only does the gall shelter the egg and developing larva but sometimes its offspring. In some gall-making aphids (Hemiptera: Aphididae), galls can sometimes house up to thousands of individuals born from a single foundress that hatched from an egg (Wool 2004, Miller 2005) (Fig. 3). Inside a gall, the developing offspring of gall-inducers are at least partially protected from natural enemies (Stone & Schönrogge 2003). In addition, galls do not only provide a shelter away from predators but the gall itself can form a nourishing tissue, a source of food that has often been shown to be more nutritious than other plant tissues (Price *et al.* 1987, Giron *et al.* 2016). The gall can also probably act as a buffer against environmental hazard such as temperature variations. Hence, for the gall inducer the benefit of gall-making seems high and it probably favors the development of multiple generations as observed in aphids.

However, the secretion of the "effector" by the insects may also generate some cost, but this has seldom been measured and may be negligible. Nevertheless, gall induc-

Fig. 2. – Original drawing made by Lacaze-Duthiers representing the galls made by *Andricus inflator* (1 & 2) a Cynipidae on *Quercus* sp., *Lasioptera rubi* (4), a Cecidomyiidae on brambles (*Rubus* spp.) and *Lasioptera eryngii* (6) an other Cecidomyiidae on *Eryngium campestre*. (© Archives Laboratoire Arago/Sorbonne Université).

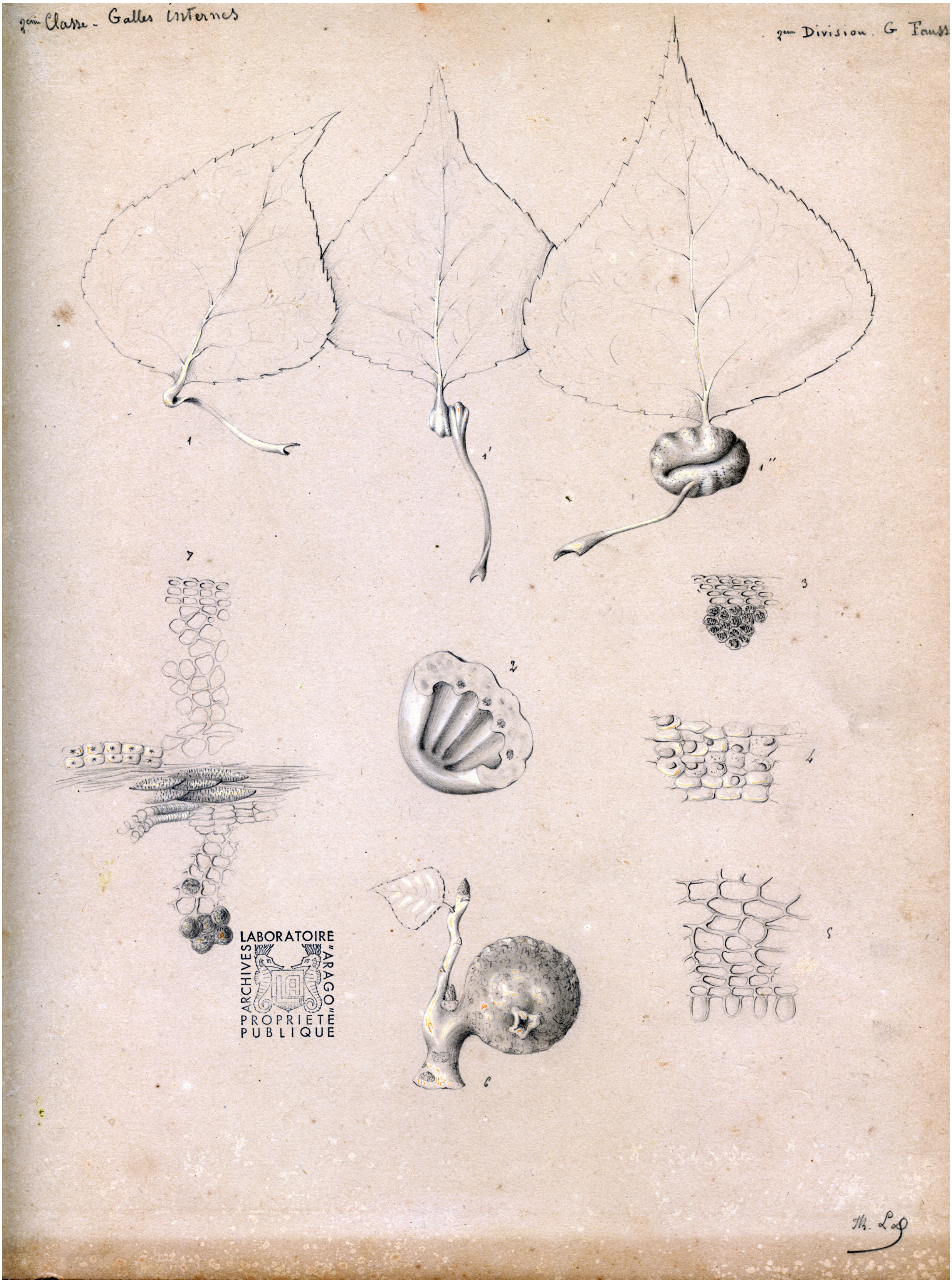

Fig. 3. – Original drawing made by Lacaze-Duthiers representing the gall made by a *Pemphigus spirothecae* (1) and *P. bursarius* (6), galls making aphid on poplar trees (*Populus nigra*). (© Archives Laboratoire Arago/Sorbonne Université).

tion can also be a risky strategy. For the insect, the risk is that life in an enclosed space makes the larva especially vulnerable to a natural enemy that could penetrate the gall. Any breach inside the gall is highly costly in terms of fitness. To prevent such a cost, some galling-aphid species present morphs inside the attacked/lost galls that sacrifice themselves to close the gall by secreting a fluid (Kutsukake *et al.* 2019).The gall can then be a nursery, sometimes with its own security team ready for the ultimate sacrifice to protect all offspring.

The cycle of some gall-makers requires several hosts. What is the point of having such complex cycles and what are the risks?

While complex life cycles involving several hosts are described for numerous animal parasites, it seems to be rarer for herbivorous insects. However, many galling insects such as Cynipidae use several hosts (*e.g.* Schönrogge *et al.* 1999). In such cases, the balance between the costs and the benefits of gall induction can be more difficult to estimate. As in any other biotic interaction where the "symbiont" (parasite or mutualist) uses two hosts, host alternation might be a strategy that optimizes nutrition by using two types of resources, a highly nutritious plant in spring and another more abundant in summer (Moran 1992, Parker *et al.* 2003, Jousselin *et al.* 2010). Changing hosts can also sometimes help to escape predators that are specialized on different host plants. Some complex cycles are also the result of a constraint on certain stages of the cycle. For some parts of the cycle, for example reproduction, it is necessary for the partners to be able to meet, in which case it is better to be on a specific "meeting place" (a plant) (Mackenzie & Dixon 1990, Moran 1992, Parker *et al.* 2003). In the more "vegetative" phase of the insect, it may be valuable to feed on another plant, more interesting regarding nutrition and above all in a more diverse species range than the mating sites.

The more hosts you have to complete your cycle, the more you have to diversify the means of finding and infesting them. What are the mechanisms developed in parasites in general to find and successfully exploit two hosts?

The two hosts must be present and sufficiently abundant. But as mentioned above, there are advantages to diversifying hosts and this is very common in the parasitic world. Having two hosts (or more!) seems at first glance complicated and costly, increasing the chances not to complete a cycle, which is often seen compensated by the production of a great amount of eggs and/or larvae (but see Poulin 2011). However, parasites are so successful, representing very likely the majority of the living world (see Price 1980), even with complex life cycles, that this is certainly not a worthwhile explanation. In their hosts, parasites have an easy access to trophic resources and are protected from predators (Poulin 2011, Parker *et al.* 2015). Moreover, when trophically-transmitted and in an intermediate host, predation of their host will allow them to disseminate and complete their life-cycle by reaching the next host of the cycle, here the predator. Parasites have developed very effective ways to find their hosts, for example they use chemical cues (this is the case in fish monogeneans, see Buchmann & Lindenstrom 2002), and can even manipulate them and favor their life-cycle (*e.g.* Dheilly *et al.* 2015). Therefore, having hosts, even multiple hosts, has advantages that certainly overcome the risks in many environmental situations.

What are the costs and benefits of gall making for the makers (the plants)?

Why is the plant hosting these parasites so comfortably while spending a lot of energy? Is it a diabolical manipulation or a shared benefit? According to some authors, a gall always benefits the gall-inducer but the fitness consequences for the plants are variable and range from highly costly to not harmful and even beneficial (Harris & Pitzschke 2020). The manipulation of plant morphogenesis and physiology for the gall inducers' own sake is necessarily costly for the plant. First of all, there is a risk for the plant, that the gall becomes a "sink" of resources, and that its growth and maintenance over time derives the resources usually allocated to the development of the plant, therefore affecting the general growth of the plant and possibly its investment in reproductive structures (flowers/fruits). Furthermore, in many cases, as stated above, the gall forms a nutritive tissue for the larvae that they shelter, so that gall-inducers can also be considered as plant-feeders. However, when measured, the cost of gall production in terms of fitness is rarely measured and sometimes despite drastically modifying plant shape, gall production does not directly affect fruit production (Kurzfeld-Zexer *et al.* 2010). Finally, the gall can also be fed on by a wide variety of inquiline species which lay their eggs inside the gall and develop at the expense of the gall maker (and therefore the plant), forming a kind of hyper-parasitism (Sanver & Hawkins 2000). This was rightfully noted by Lacaze-Duthiers: "e*ach larva or insect, the cause of the gall, has an enemy that pursues it, even in the depths of these entrenchments so well made, as we shall see, to defend it. It would be interesting to compare each tumour with the parasite of the insect it contains*" (translated from Lacaze-Duthiers 1853). In some cases of extreme proliferation, gall-inducers can affect the survival of the plant it parasitizes, and can transmit pathogens (viruses, bacteria, fungi, etc.) (*e.g.* Meyer *et al.* 2015). These are generally side effects of gall-induction, the gall inducers do not kill their host, this would actually be against their own reproductive interest but they bring in the process phytopathogens that can be deadly.

Hence it seems that, most often, gall-inducers can be seen as parasites that harm their hosts. However, the induction of novel plant phenotypes by insects can also provide some kind of rewards to the host-plants. In this situation, gall-inducers and gall-makers form true mutualistic relationships. This is the case for all nitrogen-fixing root nodules (Oldroyd *et al.* 2011), and gall inducing fungi on Orchids, which become obligate symbioses (Favre-Godal *et al.* 2020). The insects that make galls inside a fig are also pollinators and have become indispensable to the plant for fertilizing its flowers (Jousselin & Kjellberg 2001). In all these mutualisms, coevolution has shaped many traits in both partners that favour the association (*e.g.* chemical signals for recognition) and optimize the benefits that they obtain from the interaction.

As a conclusion to this part, as any other interspecific interactions, gall induction and gall making are on a continuum from parasitism to mutualism and their outcome is dependent on the biological traits of the interactors but it is also highly dependent on environmental variations, *i.e.* availability of resources, predator abundance, predictability of these ecological factors (Bronstein 1994; Sachs *et al.* 2004).

III. GALLS AS A SOURCE OF ECOLOGICAL INNOVATION AND SPECIES DIVERSIFICATION

In oaks, galls are mainly produced by Cynipidae, in willows by Tenthredinidae, and in poplars and pistachio trees by aphids (Aphididae). *Why one group rather than another? Is it linked to competition, affinity?*

This question comes down to interrogating the specificity of interspecific interactions (Futuyma & Moreno 1988). The specificity of the gall-makers towards their host plants was clearly underlined by H. de Lacaze-Duthiers in his essay ("*The Cynip rosae virus has no effect on oak. This fact, true for distant species, does not exist anymore for closer species: thus the oaks of various species of the south of France present, with some exceptions, most of the species of galls*", translated from Lacaze-Duthiers 1853). This specificity of the reaction is actually one of the arguments that led him to conclude on the involvement of a special insect "venom" in gall genesis at the beginning of his essay.

The specificity of an insect lineage for a group of plants is not particular to gall-makers; all phytophagous insects are quite specialized (Jaenike 1990). To feed on a plant, they must: 1) find it, 2) digest it, 3) overcome or bypass its anti-herbivore defenses. Each of these challenges requires adaptations that are the result of a long evolution of insects with plants: specializing on a plant/lineage of plants that share a lot of ecological characteristics makes it possible to be "good" at eating, reproducing and sheltering its offspring on this range of plants; if you do not specialize, you are a bit bad everywhere… "Jack of all trades, master of none".

In Cynipids, midges, aphids, many species are gall-inducers but some are not. How and why such biological diversity in a group?

Gall making insects are indeed highly diversified: they often represent what is known as an adaptive radiation (Price 2005), *i.e.* fast speciation driven by adaptation to different ecological niches.

This species diversification reflects the diversity of ecological niches offered by the galling habit. There are many ways to exploit a plant as mentioned above. Each species does it in its own way. This diversity is no more or less spectacular in gall inducers insects than in any other parasitic group. The fast diversification of Cynipid galls has been well documented and clearly shows that the formation of different type gall types (on different host/plants, different organs) is associated to the formation of new species (Cook *et al.* 2002). Such rapid diversification is also well exemplified in sawflies (Nyman *et al.* 2000). The gall itself can actually be seen as an accelerator of speciation, as population occurring on different types of galls are compartmentalized (spatially and sometimes temporally) and therefore have little chance of mating together (Egan *et al.* 2012) (causing a process called reinforcement in evolutionary biology).

In terms of modes of reproduction, cecidogens are also incredibly diverse. In the case of the Cynipidae alone, we find modalities of the bisexual generation type, arrhenotokous parthenogenesis (without fertilisation, only males), thelytokous parthenogenesis (only females), heterogony (alternation of bisexual generations and agamas), indefinite agamy (which joins thelytokous parthenogenesis). These different phases led past scientists to describe several species for the same species.

How and why can a species take such different forms?

This diversity is called phenotypic plasticity: depending on environmental conditions (resources, temperatures, photoperiod, density of conspecifics), the same genotype does not necessarily produce the same morphotype (West-Eberhard 2003). This is definitely not specific to gall-inducers, many insects show a high degree of plasticity. Plasticity in reproductive modes is well documented in many Hymenopteran groups and also aphids, and does not only apply to gall inducers in these insect groups.

Can gall represent a new ecological niche for non-gall inducers, a new habitat, and therefore promote further ecological diversification besides the gall-inducers?

When breeding galls, most of the species that emerge are not their "rightful owners". Henri de Lacaze-Duthiers was a very good observer and rightly writes about this: "*In addition, there are insects whose larvae feed on the galls without causing them. These are parasites of a new* *species that we should also learn to know*" (translated from Lacaze-Duthiers 1853).

The abandoned galls, or even those that have not yet been abandoned, can give shelter to new inhabitants that dig a deep excavation into the softest part of the parenchyma where they deposit their eggs, in the middle of flies and aphids. Those parasites, or rather inquilines, can even inflict further cost to the plant as mentioned in the previous section of this essay. Their ecology is not always well studied. It would be interesting to find out whether a particular species seeks out a particular gall for the development of its eggs. The specificity of these parasites to the gall-maker species or the gall inducer species is not always known (Sanver & Hawkins 2000; Gobbo *et al.* 2020). Their diversity is also probably not that well described. For instance, the Chalcidian family with more than 23,000 species described and over 500,000 species estimated is still a world away from being well described (Munro *et al.* 2011). Yet, they comprise many gall inducers but also inquilines which biology remains to be studied. In any case, this shows that gall occupation further promotes species diversification. It has actually been demonstrated that these inquilines can even shift to being gall inducers Cynipid wasps (Gobbo *et al.* 2020).

In addition to parasites, within the galls, many other organisms are observed. In many galls, the lodges can be filled with fungi. These fungi can act as gall parasites (Wilson 1995) or feed on the plant and serve as food for cecidogen larvae. This is the case in many Cecidomyiidae diptera (Rohfritsch 2008). The females then have organs for transporting the spores (specialized bristles, pouches, etc.) and thus ensure the "culture" of the fungus. In any case, this shows that galls can be source of ecological innovation for many organisms besides the sole gall inducer. Therefore, it is indeed a biological trait that fuels diversification.

CONCLUSION

So, Henri de Lacaze-Duthiers was right to be interested in insect-induced galls?

Indeed, galling insects have fascinated many entomologists and more generally evolutionary biologists since Lacaze-Duthiers' work. They have attracted the attention of researchers and naturalists because of their unique and variable shapes (they can sometimes be mistaken for fruit of flowers) that raise interesting questions on how a species can manipulate another one for its own benefit. Studying insect galls has shed light on ecological factors that can promote insect species diversification; it has also provided fundamental knowledge on insect-plant coevolution. Elucidating the molecular aspects of gall development has brought interesting results in plant developmental biology. Henri de Lacaze-Duthiers was already arguing for a collaboration between botanists and entomologists to study galls: "*In order to make a complete and useful history of galls, entomology and botany must unite, and it is because they have remained too far apart from each other that this history has made little progress*" (translated from Lacaze-Duthiers 1853). Using the new technological tools that H. de Lacaze-Duthiers did not have (*e.g.* transcriptomics), recent work illustrates how fruitful collaboration allows a better understanding of the interplay between insects and plants and the mechanism involved in the manipulation of plant cell expression. It has allowed exploring new horizons such as the search of candidate gall-inducing effectors from insects (Cambier *et al.* 2019, Eitle *et al.* 2019, Korgaonkar *et al.* 2021). Many of the questions raised by Lacaze-Duthiers at his time remain relevant. Moreover, many of them have not found definitive answers and to paraphrase Harris & Pitzschke in their thorough 2020 review, galls remain "portals of discovery" for plant biologists.

Finally, do these "parasites" have positive or negative effects?

By definition, parasites have negative effects! And though the cost of producing galls in terms of plant fitness has not often been measured, galls do not appear to bring any adaptive benefits to the plants that produce them. However, species interactions are generally much more complex than the definition we would like to fit them into. As exemplified above, galls can have different outcomes that depend on the precise environmental and ecological conditions surrounding a given association (Price *et al.* 1987).

To conclude, galls, through their diversity and the different functions of living organisms to which they appeal, are of great interest to nature, zoology, mycology, botany, biochemistry, genetics, art and education, in their sometimes ancient uses, such as in dyeing, or more recently in biological control, as exemplified on the olive fly by Lecomte (2015). Galls question us about the organization of the living organisms. They bear witness to the complexity and richness of the world around us, which should still and always encourage man to show a little more humility and respect for his environment.

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