Formosan Entomologist

Visionary Words and Realistic Achievements: One Hundred Years of Cecidology[§]

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ABSTRACT

Insect-induced plant galls were known to humans for long, mostly for use as drugs and for extracting ink-like material used in writing and painting. Until the early decades of the 19th century, those who studied galls and their inhabitants referred to these plant abnormalities as galls only. Friedrich Thomas first used the term 'cecidium' in 1873, deriving it from *kékis* (Greek), which means 'something abnormal with an oozing discharge'. Consequently, the study of galls came to be known as Cecidology. One significant name in cecidology is Alessandro Trotter (1874~1967). He founded *Marcellia*, a journal dedicated to cecidology, in 1902, which serviced science until the 1980s.The inaugural issue of *Marcellia* features his article 'Progresso ed importanza degli studi cecidologici' (Progress and importance of cecidological studies). This article includes many thought-provoking statements. In the present article, I have reflected on a few selected passages from the Trotter article, evaluating the progress we have made in the last *c*. 100 years. We have brought to light scores of unknown gall systems and their inducing agents. Between the 1930s and 1980s, the European School of Cecidology established by Ernst Küster in Gießen, Germany, followed by Henri-Jean Maresquelle and Jean Meyer in Strasbourg, France blazed new trails in interpreting galls and their relationships with the inducing and associated arthropods, using an autecological approach. In the late 1970s. Peter Price and Warren Abrahamson in America paved a new approach to gall studies and associated arthropods using a demographic, synecological approach. It has to be noted that Helmut Zwölfer in Bayreuth, Germany simultaneously started investigating arthropod-induced galls using population and community ecological approach. Irrespective of the tremendous advances we have made in the demographic ecology of gall-inducing arthropods and their specialized niche of galls, our efforts to characterize the mechanism of gall development has been rather meagre. Currently we have been reasonably successful in clarifying the steps in the physiology of gall growth and differentiation with the characterization of auxin and cytokinin precursors in the involved arthropod's saliva. However, we have not been able to precisely clarify the earliest step involved — the triggering factor — which usually occurs within the first 24 h of attack of plant tissue by the inducing arthropod. While acknowledging the explanations, the present article highlights the gap that occurs in the triggering of galls. This article concludes with a reminder of insights demonstrated in pathogenic fungus–plant interactions, and how the value of these insights are worthy of exploration in the context of arthropod-induced galls.

[§] This article will commemorate the lives and works of Odette Rohfritsch, Evelyn Westphal, and Roberte Bronner, with whom I trained in gall studies in early 1980s.

Introduction

Insect-induced plant galls were known to humans for long, mostly for use as drugs (Fig. 1) and for extracting writing and painting material (https://irongallink.org/ index.html, accessed on 3 February 2018). Early documents written using gall extracts of different species of *Quercus* (Fagaceae) induced by various species of Cynipoidea on papyrus date back to the 1st century AD. Because of the indelibility, gall extracts were the material of choice for writing documents from the Middle Age until early decades of the 20th century. Pliny the Elder (Gaius Plinius Secundus, 23~79 AD) has referred to using an iron-salt solution on papyrus, pre-soaked in *Quercus*-gall extract. Centuries later, this extract was developed in producing ink, which, however, was corrosive to paper and thus, gradually over time, fell into disuse (Bülow-Jacobsen 2009). That the use of iron-gall ink in the official documents of the Government of Germany was urged until the 1970s is notable (Eusmann 1998).

Konrad Böhner's *Geschischte der Cecidologie* [*History of Cecidology*] (1933~1935) provides a detailed history of insect-induced galls, mostly building on the then-known European works. Evidences indicate that insect-induced galls were used in medicine in ancient India. The encyclopaedic treatise *Amarakôśã* (Amarasimha, *c*. 4th century AD) includes references to the use of galls, which we know today as induced by *Dixothrips onerosus* (Thysanoptera: Phlaeothripidae), on the leaves of *Terminalia chebula* (Fig. 2) for treating stomach ailments (Raman 2013). Recent investigations (*e.g.*, Eshwarappa *et al*. 2016) on *D. onerosus*-induced galls on *T. chebula* show that they include lipoxygenase inhibitors relevant in the management of some of the chronic auto-immune illnesses in humans. William Roxburgh (1751~1815), a medical doctor, who contributed to the botany of southern India, has recorded these galls on *T. chebula* in southern India in his 18th century volume *Plants of the Coast of the Coromandel* (Roxburgh 1798, pp. 52-53). Roxburgh recognized these galls as insect induced. However, he erroneously
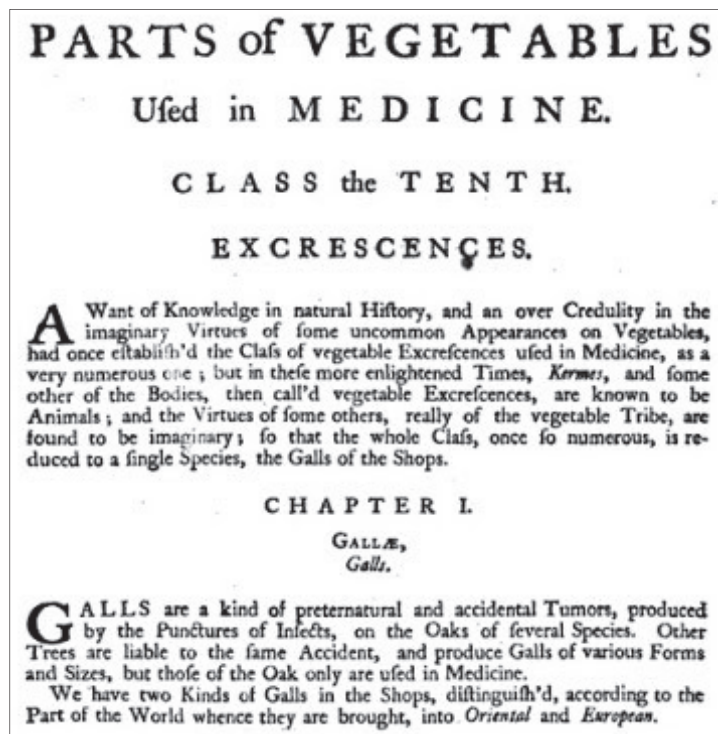

Fig. 1. A page from Hill's *History of the Materia Medica* (1751) that refers to plant galls.

indicated the inhabiting (inducing?) insect is either a species of *Chermes*[1] or that of *Coccus* (Hemiptera). While writing on fabric and fibre materials of the 19ᵗʰ century India, Edward Bancroft (1813, pp. 370-371) refers to the usefulness of *Dixothrips*-induced galls on *T. chebula* in dyeing cotton fabric:

'*I have already noticed the Terminalia chebula, or yellow myrobalan of the shops and the galls produced on its leaves, as being employed in the East Indies to give a yellow colour on cotton; … Their colouring matter is, however, capable of being rendered highly useful in giving a permanent black with an iron basis, especially upon cotton …*'.

Fig. 2. *Dixothrips onerosus* (Thysanoptera: Phlaeothripidae) induced galls on the leaves of *Terminalia chebula* (Combretaceae) known in India from *c*. 4ᵗʰ Century AD.

Galls, cecidia, and cecidology

A gall arises out of the perturbation of normal growth, because of an insect's (either an individual or a colony) intercepting and stimulatory action. Such an action entails two fundamental, altered metabolic events in the plant: inhibition of normal morphogenesis and triggering of new differentiation processes that include the constitution of a specialized tissue of nutrition for the inducing insect (Meyer 1987). Verification of this explanation made using hundreds of galls arising on different plants (mostly dicotyledons) through the world has clarified that insect-induced galls follow a morphogenetic pattern resulting in a defined shape (see Rohfritsch 1971, 1977, 1992a). An elegant symmetry — either radial or bilateral — in external shape is a striking characteristic of galls of insect origin, whereas amorphy characterizes the tumours of bacterial and fungal origin (Fig. 3) (Raman 2011). The root knots induced by different Nematoda also are amorphous, but they include a special tissue of nutrition (giant nurse cells, *sensu* Wyss 1997), similar to those induced by insects and mites in their galls.

Until the early decades of the 19ᵗʰ century, those who studied galls and their inhabitants referred to these plant abnormalities as galls only (gall — English; *galle* — French, Italian; *Galle* — German). This term has been in use from the time of Pliny the Elder (Küster 1911). Friedrich Thomas (1873) first used the term 'cécidium' deriving it from *kékis* (Greek), which means 'something abnormal with an oozing discharge'. This term gave rise to the study of galls as cecidology. The online Merriam–Webster dictionary site (https://www.merriam-webster.com/dictionary/cecidium, accessed on 3 February 2018) explains cecidium:

'Cecidium (plural cecidia\-ēə|) — gall; especially one caused by insects or mites — used especially in combinations, *acarocecidium, zoocecidium.*'

American botanist Melville T. Cook (1910) comments on the terminological confusions in gall studies in 1910:

'*Both botanist and entomologist are continually confusing the cecidia caused by fungi and insects, and the confused state of the literature has led to the neglect or abandonment of many interesting problems. The fact that most of the work has been done by the entomologist has made the literature somewhat inaccessible to the botanist, and has also given the younger botanists a misconception of the character of the subject.*'

Various plant abnormalities, which could generically be termed as excrescences, arise because of the action of parasitic animals. Examples would include bullhorns on *Acacia*-s due to the action of various species of *Pseudomyrmex* (Hymenoptera: Formicidae) and

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[1]   *Chermes* in the 19ᵗʰ century referred to species of Psylloidea (*sensu* Linnaeus 1758).
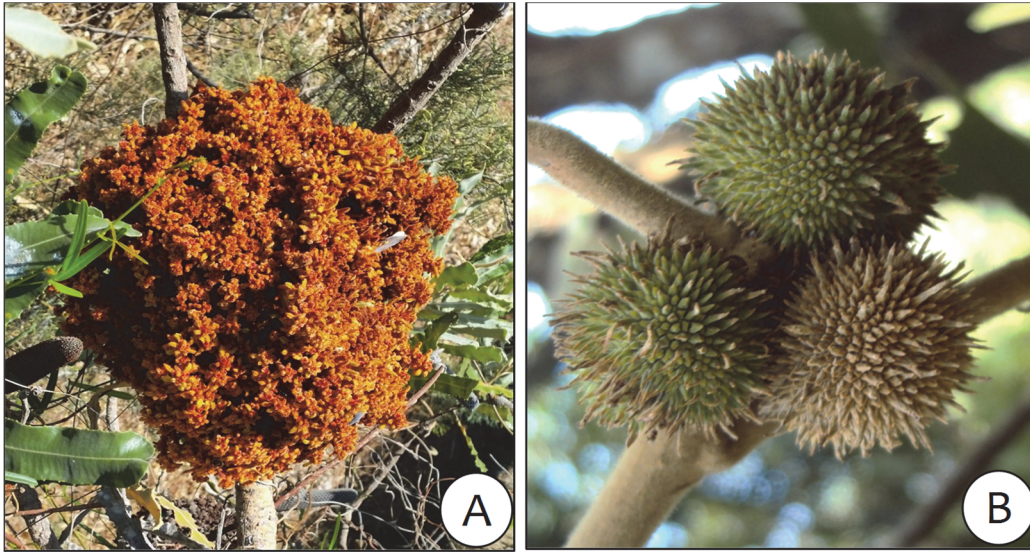
Fig. 3. Plant excrescences. (A) A witches' broom on the shoots of a species of *Banksia* (Proteaceae). (B) Galls induced on the shoots of *Hopea ponga* (Dipterocarpaceae) by *Mangalorea hopeae* (Hemiptera: Coccoidea: Beesoniidae).

domatia induced by different species of the Formicidae and Eriophyidae (*e.g.*, *Asetilobus hodgkinsi*, Acari). Other commonly occurring plant excrescences are the witches' brooms, fasciations, virescences, and phyllodies. These excrescences, we know, are induced by phytoplasmas and similar microbes, and are transmitted by arthropods (e.g., *Aceria proteae, A. cladophthirus,* Acarina: Eriophyoidea). While referring to various types of plant excrescences and in distinguishing galls among them, we need to, therefore, exercise caution.

Alessandro Trotter and *Marcellia*

One significant name in cecidology is Alessandro Trotter (1874~1967), who was the professor of Plant Pathology at the University of Naples, Italy, until 1944 (Fig. 4A). His lifelong contributions to arthropod-induced plant galls are substantial. Although trained as a botanist–plant pathologist, he initially worked on gall-inducing Eriophyoidea and later, on gall-inducing Cecidomyiidae (Diptera) and the Cynipidae (Hymenoptera), describing many of them. Trotter enabled cecidology to blossom as a

refined, sophisticated scientific discipline. Many of his papers refer to insect- and mite-induced galls and inducing arthropods of Italy and adjacent regions, such as Asia Minor (today, Anatolia) and Morocco (Cappelletti, 1969). His *Cecidotheca Italica* (1900~1917), co-authored with Giocomo Cecconi, a forest entomologist of Italy, is a prominent contribution to cecidological literature. He founded *Marcellia*, a new professional journal in 1902, naming it after Marcello Malpighi[2] and dedicating it to publishing papers in cecidology (Fig. 4B). From the inaugural issue, every issue of *Marcellia* included a novel and useful section *Bibliografia e recensioni* (Recent Literature), compiled by Trotter himself. This feature persisted as a significant component until *Marcellia*'s end in the early 1980s. Donald Leatherdale, a British botanist–mycologist, contributed to this feature between the 1950s and 1970s. When *Marcellia* had a new lease of life, with the Pergamon Press of London taking over its publication, this feature was managed by Françoise Jauffret *née* Dreger, a research scientist of the *Laboratoire Cecidologie* (*l'Équipe de Centre National de la Recherche Scientifique*) of *l'Institut de*

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[2] Marcello Malpighi (1628-1694), an Italian biologist and physician, who contributed significantly to microscopical anatomy, histology, physiology and embryology. Malpighi will be remembered in cecidology because of his pioneering work on plant galls — *De Gallis* in 1679 (see Redfern *et al*. 2008).
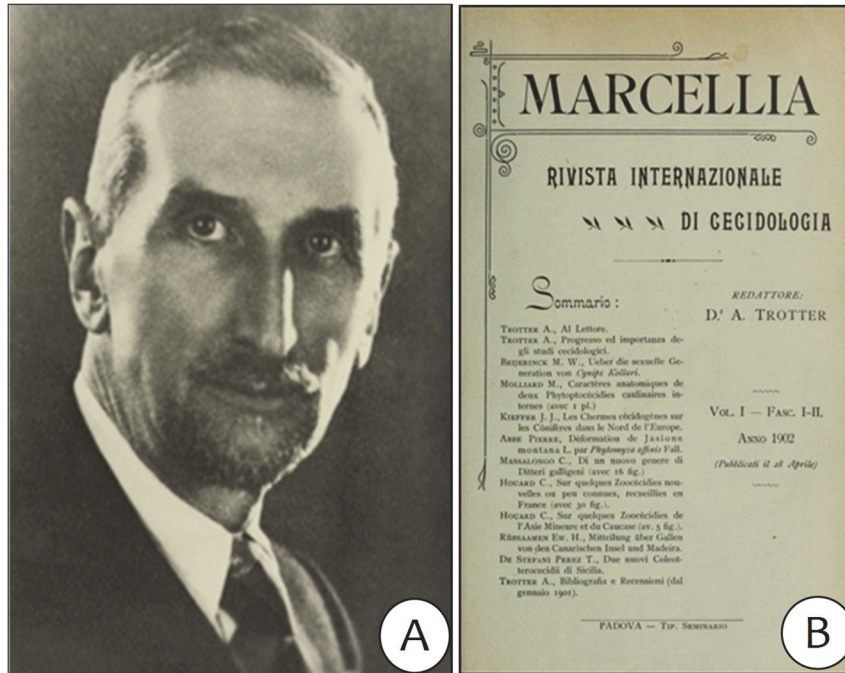
Fig. 4. (A) Alessandro Trotter. (B) Cover of the inaugural issue of *Marcellia*.

Botanique, l'Université Louis Pasteur, Strasbourg, France. Five issues of *Marcellia* were published by Pergamon Press of London and due to poor circulation, the journal folded up in the early 1980s. At the Cecidology meeting held during the 17th International Congress of Entomology, Hamburg, Germany, in August 1984, an attempt was made to sustain *Marcellia*, because the Pergamon Press of London declined to publish it. Prabha Grover and S. Prasad (University of Allahabad, India), who were publishing *Cecidologia Indica*, a cecidological journal from Allahabad, India, as the official organ of the Cecidological Society of India, volunteered to publish *Marcellia*. For a couple of years *Marcellia* appeared from India, under a new title *Cecidologia Internationale,* which indicated on the cover that it incorporated *Marcellia* and *Cecidologia Indica*. However, this journal too ceased publication in later years.

The section 'Current Literature in Cecidology: An Annotated Bibliography' was a popular feature in those days, since it supplied summaries of almost every available article in Cecidology and related disciplines from published literature, along with the names and postal addresses of authors throughout the world. Amazing to think of the effort that would have gone into producing this section in every

issue of *Marcellia*, given that no desktops, laptops, and Internet existed for use by general public.

Keeping the above in context, this article aims to highlight some elements of progress made and yet-to-be-clarified aspects in cecidology referring back to a few of Alessandro Trotter's remarks made in 1902.

Trotter's vision of cecidological studies

The inaugural issue of *Marcellia* (1902) features the article, 'Progresso ed importanza degli studi cecidologici' (Progress and importance of cecidological studies) by Trotter (pp. 5-12), which includes several thought-provoking remarks. To me, they appear visionary. For readers' convenience, the selected segments of Trotter's remarks are reproduced below as such, each followed by an English translation.

Floristics and faunistics of galls

'Ma la Cecidologia, oltre questi tre gruppi quasi naturali di cecidozoi, possiede non poche altre specie galligene disseminate negli altri ordini e famiglie della Classe degli insetti. Non

passa giorno si può dire che gli studiosi, in seguito all'allevamento delle galle, non ci segnalino qualche Cuculionide tra i Coleotteri, qualche Afidino tra gli Emitteri, qualche Tentredinide od Isosoma tra gli Imenottteri, qualche Tortricide o Tineide tra i Lepidotteri, tutti quanti produttori di galle.'

[*Besides the(se) three groups of almost natural cecidozoa (i.e., Eriophydoidea, Cecidomyiidae, and Cynipidae), cecidology includes many other galligenous species scattered in other orders and families of Insecta. We are getting to know of new reports of the Curculionidae among Coleoptera, some Aphidoidea among the Hemiptera, some Tenthredinidae or Isosoma among Hymenoptera, some Tortricidae or Tineidae among the Lepidoptera, which induce galls.*]

Scores of papers and monographs have appeared, since these remarks of Trotter, bringing hundreds of galls and the inducing taxa to light. Prominent examples would be the works of Clodimir Houard (earlier with the University of Strasbourg and later with the University of Paris), who published massive volumes on the gall flora of Africa, Asia, and the Oceania (1922~1923), Central and South America (1933), and North America (1940). Another remarkable Dutch husband-wife team was Willem Marius Docters van and Leeuwen and Jane Docters van-Leeuwen-Reijnvaan, who catalogued the galls of the Indonesian islands (1926). Several groups of arthropods — previously unknown as gall-inducing taxa — too have been brought to light in recent times. I will cite the specific examples of *Cecidonius pampeanus* (Lepidoptera: Cecidosidae) inducing galls on the stems of *Schinus weinmannifolius* (Anacardiaceae) in Pampa, Brazil (Moreira *et al*. 2017) and *Scenergates viridis* (Hemiptera: Cicadellidae) on *Alhagi maurorum* (Fabaceae) in Bukhara (Uzbekistan) (Rakitov and Appel 2012). The larvae of *Cecidonius pampeanus* induce complex, multitrophic galls on the stems of *S. weinmannifolius*. Several species of *Lyrcus* (Hymenoptera: Pteromalidae) parasitize *C. pampeanus* larvae. Galls of *C. pampeanus* include inquilinous taxa belonging to *Allorhogas* (Hymenoptera: Braconidae). In the second example, the feeding action of young instars of *S. viridis* induces the young foliage of *A. maurorum*

to fold along their midribs; subsequent development of *S. viridis* occurs within the tightly folded leaves, which grow as thickened, pod-like structures. Rakitov and Appel indicate the leaf folds as galls. Gravid females insert eggs beneath the inner epidermis of the gall. The ovipositing adults remain within the pod-like structures, as an effort to protect the brood. The walls of folded leaves, which include eggs are approximately three times thicker than the leaves uninfested by *S. viridis*. In these two examples, the excrescences on the stems of *S. weinmannifolius* impress as galls, whereas those induced by *S. viridis* need closer examination. Thickened and folded leaves, occasionally rolled as well, are common among the Phlaeothripidae (Thysanoptera, e.g., *Gynaikothrips uzeli*) and among many Aphidoidea. The explanation for such behaviour in these insects is that the folded (or rolled) leaf 'protects' its brood living within (Mound 2005). Many Auchenorrhyncha are known as the inducers of similar plant abnormalities: e.g., *Philaenus spumarius* (Hemiptera: Aphrophoridae) on the leaves of *Oenothera biennis* (Onagraceae) (Maresquelle 1935) and *Copium teucrii* (Hemiptera: Tingidae) in the flowers of *Teucrium montanum* (Monod and Carayon 1958). Another curious claim in recent years are the galls on *Mourera fluviatilis* (Podostemaceae) induced by *Polypedilum mehinaku* (Diptera: Chironomidae) (Jäger-Zürn *et al*. 2013). I use the term 'curious' here, since we know that in the Diptera, the best-known gall-inducing families are the Cecidomyiidae, Chloropidae, and Tephritidae. Of course, we also refer to the Agromyzidae in this context mainly because we see the tunnelling habit of the Agromyzidae as a precursor of gall-inducing habit.

Biogeography of galls and inducing arthropods, biological diversity, and diversification

'Come si vede i progressi, dal lato semplicemente sistematico, e benchè non riguardanti che una piccola parte dell' emisfero boreale, sono considerevoli e lusinghieri per la Scienza. Io non dubito che quando le regioni tropicali dell'emisfero australe saranno

convenientemente esplorate, ne usciranno fatti di minore importanza, e che altre famiglie naturali di cecidozoi, non si rivelino. Già un sentore lo abbiamo con l'estremo Oriente e l'Australia che ci forniscono galle interessanti e svariate [3] di Cocciniglie e di Psillidi, insetti che invece in Europa, nei reguardi della Cecidogenesi, sono di assai esigua importanza.'

[From a systematic perspective, the progresses made so far, although concerning only a small part of the boreal region of the Northern hemisphere, are remarkable. No doubt when the tropical regions of the Australian continent will be thoroughly explored, realities of less significant elements of galls and their inducing agents will come to light and many other natural cecidozoa will be unveiled. A prediction can be made here based on the scattered knowledge we have is the variety of Coccoidea and Psyllidae (Psylloidea today) in the Orient and Australia. Similar insects (viz., Psylloidea and Coccoidea) from Europe are, as far as cecidogenesis is concerned, of scarce relevance.]

Trotter's specific reference to Australia and the Orient merit further elucidation. Several key findings of gall-inducing Coccoidea and Psylloidea and their galls have been added to literature in the last one-hundred years from these biogeographical regions. Thomas Dobson, Walter Froggatt, Leonard Tuthill, Keith Taylor in the earlier decades of the 20th century, and Penny Gullan (*e.g.*, Gullan 1984) and Gary Taylor (*e.g.*, Taylor 1990) in recent past have clarified taxonomic and ecological details of many Australian Coccoidea and Psylloidea. In the Orient, particularly in the Indian subcontinent, Mahadeva S. Mani (Fig. 5) made significant contributions to the gall flora of the Indian subcontinent through his *Zoocecidia and cecidozoa from India* (1948). He updated this publication in later years as the *Plant Galls of India* (2000). Mani left his indelible footprint in cecidology with his *Ecology of Plant Galls* (1964). In this volume he emphasized the mutual relationship between the inducing insect and the susceptible plant. This emphasis has indeed

been a critical turning point in cecidology. His words (p. xi)

Fig. 5.   Mahadeva S. Mani.

'Plant galls represent a unique and complex interspecific interaction and mutual adaptation between the plant and the gall-inducing organism. The nature and origin of the inter-relation, the role of the gall-inducing organism and the reaction of the plant, the cytological, histogenetic and morphogenetic processes involved in gall formation are essentially ecologic problems that need further investigations.'
capture succinctly the new trail he blazed in studying galls and their inhabitants. Mani's central argument in this book was that a gall represents a specific plant response, more as an effort of protection of itself by isolating the gall-inducing organism in time and space. His 45-years of study of scores of Indian gall-inducing Cecidomyiidae[4] and their galls enabled him to advance this explanation. He considered the sclerenchyma that wrapped the larval chamber as a physiological response of the plant in isolating and insulating the gall-inducing insect (the Cecidomyiidae) and protecting itself (the plant) from the 'damage' and 'stress' caused by the insect (Mani 1933). Mani's interpretation reflects Theodore Cockerell's explanation (1890) on the purpose of galls. Cockerell's short letter (1890) to the editor of *Nature* was in response to the debate on this topic provoked by George Romanes (1889) and St George Mivart (1889) in *Nature*. Cockerell (1890) argued that plants

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[3]   The term 'biological diversity' was first used by Raymond F. Dasmann in 1968, where he advocated conservation. The term 'biodiversity' was first used by Edward O. Wilson in 1988.

[4]   For several years Mani continued to use the term Itonididae in his articles, even after the establishment of the term Cecidomyiidae.

would not enhance their survival values by developing galls for the benefit of the gall-inducing insects. Rather, plants developed galls to protect themselves against the invading insects. Today we know that differentiation of sclerenchyma around the larval chamber does not commonly occur in several galls induced by other insects, *e.g.*, the Sternorrhyncha. If the sclerenchyma in galls facilitated the isolation and insulation of the inducing arthropod, then that should materialize in galls induced by different species of arthropods.

The Strasbourg School of Cecidology led by Jean Meyer and his mentor Henri-Jean Maresquelle[5] challenged this explanation. This does not surprise, since Maresquelle trained in cecidology with Ernst Küster at the University of Gießen (Germany) as a post-doctoral student in 1930~1931 (Maresquelle 1931) and, therefore, was influenced by Küster's thoughts on plant galls. Küster explained that gall-inducing insects depend on specific plants for nutrition (Maresquelle 1954). An articulate explanation of the Küsterian thinking is available in the chapter entitled 'The gall as a host response, which is beneficial to the parasite' (pp. 253-254) in Meyer (1987). This explanation can be referred as the Küster-Maresquelle-Meyer legacy in cecidology.

Our clarity today about gall-inducing insects being highly specialized plant feeders is far greater than what we knew in the first half of the 20th century. We know that a majority of gall-inducing insects remain tied to specific host plants, and that complex mechanisms related to their use of plant tissues result in gall induction. This is one critical reason why gall-inducing arthropods being currently being widely explored in the biological management of weeds (Harris and Shorthouse 1996, Muniappan and MacFadyen 2005). I will recall the classical paper 'Gall midges (Diptera, Cecidomyiidae) as plant taxonomists' by Eric Sylvén of Sweden (1979) here. The extensive volume of literature

that has accumulated in the recent past (see different chapters in Raman *et al*. 2005 for extensive bibliographies) explains how varied the behaviours in different groups of gall-inducing insects can be and yet remain specific to certain species of plants. Some species demonstrate the 'escape from interspecific competition' hypothesis, a few others the 'minimal exposure to predators' hypothesis, and still others the 'increased efficiency of detoxifying plant allelochemicals' and 'increased efficiency in host finding' hypotheses (Schoonhoven *et al*. 1998).

Biogeographical assessments made across the world show that the gall-inducing insects are a highly evolved group with sophisticated biology and physiology that enable them to utilize their host plants more efficiently and effectively than their non-gall-inducing relatives (Shorthouse *et al*. 2005). Nevertheless, some of the recently explained behaviours of quite a few gall-inducing insect taxa reveal diverse and complex patterns and mechanisms of adaptive radiation, with many new and diverse adaptive zones occupied. Recognition of several sibling species in the recent past indicates that radiation, has been, and is, occurring in a dynamic evolutionary state (Price 2005). Demonstrated host shifts in naturally occurring gall-inducing Tephritidae (Diptera) populations in North America and Europe explain the evolution of sympatric host races — due to changes either in the preference in feeding and/or oviposition sites or by evolving 'new' physiological adaptations to new host-plant taxa or through assortative mating. Patterns of radiation among the gall-inducing Cecidomyiidae appear more complex than those that are known in gall-inducing Tephritidae, because of the complex host-plant relationships and the host-plant range traversing diverse biogeographical regions. Although a majority of Cecidomyiidae induce galls on specific host-plant genera (Gagné 2004; Yukawa *et al*. 2005), some of them, such as

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5   Henri-Jean Maresquelle (1898-1977) was associated with the University of Strasbourg as a full professor, and after retirement as *le Doyen Honoraire*. Further to being a stimulus for gall studies in Strasbourg, he was a strong force behind the establishment of *l'Société Francophone de Biologie Théorique* (the French-speaking Society for Theoretical Biology), which held several meetings involving scientists from different fields. In later years these meetings were popularly referred as the 'Maresquelle Club of Theoretical Biology' (Champagnat and Baillaud 1981).

Asphondylia, Contarinia, Dasineura, and *Lasioptera,* display a host range across different, unrelated plant families (Yukawa and Rohfritsch, 2005). Species of *Rabdophaga, Hartigiola, Rhopalomyia,* and *Daphnephila* (Diptera: Cecidomyiidae) in Japan live mainly on *Salix* (Salicaceae)*, Fagus* (Fagaceae)*, Artemisia* (Astraceae)*,* and *Machilus* (Lauraceae)*,* respectively. *Phyllocolpa, Pontania,* and *Euura* (Hymenoptera: Tenthredinidae) occur on different host-plant taxa indicating that the newly diversified sawfly genera explore and occupy new adaptive zones (*sensu* Mitter *et al*. 1988). At least some species belonging to large genera of gall-inducing insects are capable of colonizing diverse plant species and invading new plant organs, indicating shifts into varied ecological niches and adaptive zones. Host-plant shifts, and consequent speciation, among the gall-inducing insects occur because of host-plant traits (*e.g.*, host-plant chemistry), competitive interactions of the gall inducer for the 'best' host resources, and seeking the potential for escape from natural enemies. The Middle-eastern Aphididae inducing galls on *Pistacia* (Anacardiaceae) have been shown to have radiated into many adaptive zones, similar to the European Cynipidae and North American Tenthredinidae, although the radiation level in the Middle-eastern Aphididae is less extensive than what has been shown in European Cynipidae and Tenthredinidae. The Oriental and eastern Palearctic Cecidomyiidae are speciose and include many genera, but their adaptive radiation is more strongly evident in species of Asphondyliini, Alycaulini, and Lasiopterini that are closely linked to fungi in ambrosia galls.

Gall-inducing arthropods, associated arthropods and fungi

'*E sin qui io non ho detto altro che degli animali propriamente galligeni. Il cecidologo, specialmente poi se entomologo, non può non considerare anche l'altra numerosissima falange di insetti a cui fanno capo più o meno i commensali, i parassiti, i parasitti di questi e di quelli, i successori e via dicendo.*'

[Up to this point I have only articulated about truly galligenous animals. A cecidologist, especially when also entomologist, needs to consider another large group of insects such as the commensals, parasites, visitors and successors, that occupy the galls.]

'*Nè gl'insetti sono i soli organismi gallicoli. Ho mostrato in un mio lavoro di come sulle galle, specialemente di Quercia, viva proficuamente una piccola flora micologica, composta da svariate specie, molte delle quali sembrano essere fino ad ora solo proprie delle galle. Altre notizie, benchè più scarse, ci lasciano intravedere un orizzonte vasto e curioso anche per i micromiceti parassiti e simbiotici della galle o del cecidozoo o di ambedue ad un tempo.*'

[Insects are not the only galligenous organisms. I have illustrated in one of my works how within galls, and oak galls in particular, mycological flora, composed by a variety of species, successfully lives. Many of these species appear to be only specific to galls. Other resources, although scarcer, offer a glimpse of a broad and intriguing future also for the study of the parasitic and symbiotic micromycetes either within the galls or with the inducing agents, or concurrently on both.]

In the late 1970s, a new approach to gall studies dawned with investigations of Peter W. Price (earlier in Illinois and later in Arizona) and Warren G. Abrahamson III in Pennsylvania. Both Price and Abrahamson considered insect-induced galls from a synecological perspective: from the population- and community-ecology dimension. Price used gall-inducing Tenthredinidae (Hymenoptera), whereas Abrahamson used gall-inducing Tephritidae (Diptera). Population- and community-ecological investigations led by these American biologists have opened new vistas in understanding gall-inducing arthropod ecology and evolution.

Investigations of Price and group on the galls induced by the Tenthredinidae address the macroevolutionary theory and macroecological patterns testing plant-insect interactions, multiple-trophic-level interactions, population dynamics, and abundance and distribution of insects. Price et al. built their argument on the premise that evolved characters of organisms, such as morphology, behaviour, and life history influence their ecological relationships, including the way populations fluctuate in time

and space. Their long-term population studies using *Euura lasiolepis* (Hymenoptera: Tenthredinidae) which induces galls on *Salix lasiolepis* (Salicaceae) have unequivocally demonstrated that the interactional dynamics are driven by bottom-up effects, from precipitation to host-plant growth and quality, to the ovipositional preference for vigorous plant modules (*sensu* Harper 1980) and to larval performance. A strong ovipositional preference for vigorous plant modules appears to bear a general relationship for many Tenthredinidae and other gall-inducing groups. Details of the fascinating publications of Peter Price and group made on the *E. lasiolepis — S. lasiolepis* gall system are available in http://jan.ucc. nau.edu/pwp4/research.html (accessed on 17 February 2018).

Abrahamson and group explored *Eurosta solidaginis* (Diptera: Tephritidae), which induces ball galls on the stems of *Solidago altissima* (Asteraceae), and associated species of parasitoids, to explain ecology and evolution. The key themes they explored are host-race formation, tritrophic interactions, and natural selection. For example, by exploring host-race formation, the Abrahamson group has intently clarified potential pathways of sympatric speciation, illustrating the evolution of 'new' species from geographically connected populations. Abrahamson and group have clarified through several publications that the host races of *E. solidaginis* mate, lay fertile eggs, and their larvae develop on different species of *Solidago*. However, what remains here is the resolution of possible cryptic species. Because *E. solidaginis* populations nearly always mate on their own specific taxon of *Solidago*, the Abrahamson group indicates that each host race of *E. solidaginis* is reproductively isolated. Details of the highly fascinating publications of Abrahamson and group made on the *E. solidaginis — S. altissima* gall system are available in http://www.facstaff.bucknell.edu/abrahmsn/solidago/gallresearch.html (accessed on 17 February 2018).

Concurrently, Helmut Zwölfer (earlier at Delemont, Switzerland and later at Bayreuth, Germany) explored the community- and population-ecological relationships of gall-inducing and non-gall-inducing Tephritidae pitching on the host specificity of the gall-inducing Tephritidae as an instrument in the biological management of invasive plants that were either deliberately or naturally introduced into new environments. His paper 'Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls' (1979) reports a pioneering interpretation highlighting multiple subtleties and intricacies of in the behavioural ecology of various species of Myoptini (Tephritidae) interacting with different species of European Carduinae (Asteraceae). Later papers of Zwölfer and group at Bayreuth have indeed clarified many a subtle dimension of the synecology and autecology of gall-inducing arthropods and their galls (see Arnold-Rinehart 1989, Zwölfer and Arnold-Rinehart 1993).

One impressive discovery is sociality demonstrated among gall-inducing Aphidoidea by Shigeyuki Aoki in Japan (Aoki 1977), which is continuing to blaze brilliant trails in the ecology and evolution of these insects. These insects exist as dense clonal groups in the galls they induce, which amazingly include specialist soldier nymphs (the *samurai*-s, *sensu* Moffett 1989), which defend the brood from predatory arthropods. Aoki and group have demonstrated the central importance of kin selection in social evolution as well as the decisive roles played by various ecological regulatory factors, such as predation. Bernard Crespi (earlier in the US and later in Canada) has shown similar behaviour in several gall-inducing Phaleothripidae (Thysanoptera) (*e.g.*, Crespi 1992).

Today we have a reasonable knowledge of fungal associates in insect-induced galls. The most striking and significant association occurs in the galls induced by certain taxa of the Cecidomyiidae (Batra and Lichtwardt 1963). The taxa belonging to the Lasiopterini and Asphondyliini generally do not induce nutritive tissue as part of gall development (Rohfritsch 1992b). The 'ambrosia galls' induced by these Cecidomyiidae include fungal mycelia that line the interior perimeter of larval chambers, and the fungal mycelial reticulation subserves the developing larvae as the tissue of nutrition. The fungi not only nourish the inhabiting

Lasiopterini, they also penetrate the stems, induce the lysis of the middle lamella of host cells, and thus open up a channel to the vascular tissues (see Rohfritsch 2008 for an extensive list of cross citations). However in the instance of fungi associated with gall-inducing Cynipidae — previously thought as of pathogenic — have been, actually, found to be associated with the unaffected parts of the host plant as endophytic organisms. In the galls induced by Cynipoidea, the endophytic fungus grows from the host organ (*e.g.*, leaf) into the gall and infects the gall tissue, but does not directly kill the gall-inducing Cynipoidea. The insect, however, dies as a result of gall tissue degenerating due to fungal infection. In the gall system, the fungus functions as an inquiline (Wilson 1995). This explanation is debatable since endophytic fungi are known for not killing host tissue (Raman *et al*. 2012, Raman and Suryanarayanan 2017). The fungal association in Cynipoidea-induced galls needs re-evaluation.

Gall induction

'E la formazione delle galle non è forse tuttora un problema della più alta importanza? Quanti si sono affaticati intorno a ciò, col pensiero o con l'esperienza, da Malpighi in poi? Ed il problema è forse risolto? Una sostanza chimica, un' enzima, si dice; sta bene, è possibile, anzi quanto mai probabile, ma fino ad ora è sempre un'ipotesi e non potrà divenir legge finchè qualche fortunato per ingegno e pazienza non avrà isolato dalle larve la sostanza cecidogenetica od avrà saputo fabbricarla lui stesso, per ripodurre, se non la galla nei suoi particolari, almeno un'ipertrofia od iperplasia notevole che la ricordi.'

[Is not the induction of galls a problem of high relevance? How many have explored this question from Malpighi onwards? Has the problem been resolved? They say it is caused by a chemical substance, an enzyme. That is possible, or at least probable, but so far it is still only a hypothesis that will become law only when a cecidologist will get to the point of characterizing the cecidogenenic substance from the larvae or will successfully produce it ex-situ to 'reproduce' a gall in all its details or at least a hypertrophy

or a hyperplasia that resemble it.]

One significant question that has been troubling us all these years is how galls are induced. This question gains in prominence, because not every plant-feeding insect induces a gall. The leaf-mining habit evident in the Agromyzidae was considered the precursor of gall-inducing habit (Hering 1951). But this explanation is currently disputed (Dempewolf 2005). We need to recognize that the capacity to induce galls occurs only in certain groups of the Insecta. Even within the same order, many families do not include gall-inducing taxa. For example, among the recognized 35 extant families within the Nematocera of the Diptera, only the Cecidomyiidae include gall-inducing species. In the Coccoidea, gall-inducing capacity has evolved multiple times, repeatedly, with the Eriococcidae which includes the most gall-inducing species (Hardy and Gullan 2010).

Several efforts to induce galls artificially on diverse plants have been made over decades. Most of the early trials were based on Trotter's comment (translation supplied in an earlier page),

'..., ma fino ad ora è sempre un'ipotesi e non potrà divenir legge finchè qualche fortunato per ingegno e pazienza non avrà isolato dalle larve la sostanza cecidogenetica od avrà saputo fabbricarla lui stesso, per ripodurre, se non la galla nei suoi particolari, almeno un'ipertrofia od iperpalsia notevole che la ricordi ...'.

Those efforts involved the injection of 'extracts' from the inducing insects into host plants to observe changes that resembled gall growth (Martin 1942, Hough 1953). One innovative trial in this direction was the bioassay by McCalla *et al*. (1962), which involved the application of extracts from the accessory glands of gall-inducing adult Cynipoidea to early stages of developing galls after the removal of the inhabiting larvae. McCalla *et al*. could demonstrate that the accessory-gland extracts effectively substituted larval stimulus required for gall growth, which went to indicate that the accessory glands of adult Cynipoidea included substances similar to those in the saliva of larvae. They also showed the incidence of IAA, adenine, and kinetin which maintained gall growth in their bioassays. McCalla *et al*. (1962)

detected two adenine derivatives in gland extracts, which additionally included uridine, uric acid, and glutamic acid.

Contrary findings have been reported on galls induced by hemipteran insects. Specific free amino acids, such as lysine, histidine, and tryptophan are the implicated trigger factors in gall induction in Hemiptera systems (Anders 1958, 1960, Rilling *et al.* 1974). The most widely explored system was that of the gall on *Vitis vinifera* induced by *Dactulosphaira vitifoliae* (Hemiptera: Phylloxeridae). Unfortunately understanding of galls induced by the Hemiptera are not as advanced as in the Hymenoptera, Tenthredinidae, especially.

A general model of gall development involves newly initiated and activated features (steps) that can be seen as follows: (1) induction, (2) growth involving cell enlargement, cell division, and special tissue differentiation, and (3) ageing and senescence (Rohfritsch 2010, Raman 2011). Each of these steps is distinct in its physiology, although the steps tend to overlap. Several papers have explored the role of plant-growth regulators, such as auxins and cytokinins, which explain the second step, *viz.*, growth. Artificial injection of auxins resulted in gall-like structures (Schäller 1968). Several experiments have indicated the role of auxin precursors in the inducing insects (see Hori 1992). Use of instrumentation such as GC–MS lately, has offered clear and definitive incidence of auxin material in inducing insects (Tooker and De Moraes 2011). These details clarify that the inducing inhabitants of galls (the larvae) are a source of auxins. Towards this end, Yamaguchi *et al.*'s work (2012) on *Pontania-Salix* gall sheds significant light.

In the *Pontania* sp. (Hymenoptera: Tenthredinidae) – *Salix japonica* (Salicaceae) gall system, Yamaguchi *et al.* (2012) indicate the ability of *Pontania* larvae to synthesize IAA from tryptophan. They also show that *Pontania* larvae include high levels of IAA and *t*-zeatin. The accessory glands of adult *Pontania* include high levels of *t*-zeatin riboside. Transcript levels of some auxin- and cytokinin-responsive genes are significantly greater in gall-bearing than in non-gall bearing leaves. The abnormally high concentration of *t*-zeatin riboside in the

accessory glands, Yamaguchi *et al.* implicate that *Pontania* can synthesize cytokinins as well as IAA. Gene expression profiles indicate high levels of auxin and cytokinin activities in growing galls. Yamaguchi *et al.* (2012) suggest that the two undetermined adenine derivatives found by McCalla *et al.* (1962) are '*t*-zeatin riboside' and 'isopentenyl-adenosine' found by them, which are signallers of cytokinin biosynthesis in plants. That is an excellent development in the context of step 2 in gall development, as outlined in the previous paragraph.

Conclusion

We can see three distinct phases in the progress of cecidology made throughout the world in the last one hundred years. In the first phase, up to the 1940s, by and large people explored novelties in terms of gall-bearing plants and inducing arthropods and many useful catalogues appeared (*e.g.*, Felt 1940, and others already cited). From the 1940s to the 1980s, the Strasbourg School pioneered in exploring the developmental physiology of galls induced by the Cecidomyiidae, Cynipidae, Eriophyidae, and Eriococcidae (presently those reclassified under the Beesoniidae, see Takagi 2007). This School approached the gall problem with the nutrition hypothesis as the underpinning factor, testing various galls induced by arthropods of different orders experimentally and keeping the role of the inducing arthropod in the architecture of galls in focus. An autecological approach emphasizing on the individual plant and the associated animal, representative units of biological organisation, was the fundamental driver of the philosophy of the Strasbourg School. A synecological approach commenced in America, which I would refer to as the American School, in the late 1970s, by validating the interactions between the plant and gall-inducing and gall-associated arthropod communities and examining them in varied spatial and temporal scales. The aim of the American School sits on the interactions between populations as determined by specific genotypic and phenotypic characteristics. Incidentally this approach inspired many ecologists using gall systems as

study materials in the 1990s and 2000s, to explore evolutionary relationships using molecular tools (*e.g.*, Nyman *et al*. 2000, Dorchin *et al*. 2015). Helmut Zwölfer in Germany approached the gall problem integrating both synecological and autecological approaches.

I have reflected, in this article, on selected remarks of Alessandro Trotter made c. 120 years ago. It is gratifying to note that we have progressed substantially in the context of his first and second remarks referred in this article. Hundreds of unknown gall systems and their inducing arthropods have been discovered and described. New regional catalogues of arthropod-induced galls across the globe are continuing to appear enlightening us on the variety of the inducing arthropods and their curious, nourishing shelters, *viz*., galls. New directions in the evolutionary ecology of these specialist organisms have been enchantingly brought to light, thanks to Peter W Price, Warren G Abrahamson, Helmut Zwölfer, and Shigeyuki Aoki. Nonetheless, our progress in answering the question 'how galls are induced' has been tardy.

The most critical step in gall development is induction, which occurs within the first 24–48 h of attack on the plant by the inducing arthropod. In the instance of elongate-pouch gall induced on the leaves of *Fagus sylvatica* (Fagaceae) by *Hartigiola annulipes* (Diptera: Cecidomyiidae) in Europe, Rohfritsch (1980~1981) has clarified the dynamic changes that occur on *F. sylvatica* leaf between zero and 24 h at the site where the galls would grow in the following few days. Similar changes occurring between zero and 24 h of attack by *Daktulosphaira vitifoliae* (Hemiptera: Phylloxeridae) on *Vitis vinifera* (Vitaceae) too have been shown, but observed under synthetic conditions (Raman *et al*. 2009). The < 24 h changes in the physiology of host-plant cells have been indicated as cell metaplasia (Maresquelle and Meyer 1965). The chemical and molecular influences that occur during this earliest phase of insect attack, *i.e.,* < 24 h, need resolution.

For a comparison I believe that it would be but appropriate to consider how pathogenic fungi access plant cells. Spores of pathogenic fungi first invade and attack 1-2 cells of the host plant by applying a battery of cell-wall degrading enzymes (*e.g.*, cellulases, hemicellulases, pectinases, cutinases, and proteases). High levels of production of reactive-oxygen-species, induction of necrosis- and ethylene-inducing proteins, and a range of other secondary metabolites such as salicylic acid usually eventuate at this stage of infection (Arenas *et al*. 2010). For example, *Botrytis cinerea* (Ascomycota: Heliotiales: Sclerotiniaceae) produces a strain-specific virulent sesquiterpene — botrydial — (Siewers *et al*. 2005) that induces toxicity in its host tissue (*e.g.*, *Vitis vinifera*, Vitaceae). The establishment of the fungal pathogen and the level of infection depend on the capacity of the fungus to detoxify the phytoalexins and suppress the plant's innate immunity levels. For example, wyerone acid progressively increases and accumulates in the lesions caused by *B. cinerea*, whereas in *B. fabae* caused lesions the wyerone acid levels rise rapidly initially, but decline subsequently. The greater ability of *B. fabae* to colonise *V. faba* tissues is related to its capacity to detoxify *V. faba*'s phytoalexins and to reduce their toxic effects (Madeira *et al*. 1993).

I strongly suspect that a similar phenomenon occurs in the <24 h of interaction between gall-inducing arthropods and plants. Plant pathologists explain that the plant-cell surface is enabled with various metabolic receptors that are functionally linked with diverse intra- and intercellular signal pathways, which readily and rapidly 'recognize' and 'respond' to the invading fungi. This phase of a pathogenic fungus depends on the apoplastic perception of microbe-associated molecular patterns (MAMPs) by pattern recognition receptors (PRRs) expressed by the plant (Mott *et al*. 2014). This response, usually, does not rely only on the perception of MAMPs, which is indicated as PRR-triggered immunity (PTI). Additionally plants have evolved a system through which they indirectly 'monitor' pathogens *via* the perception of the products that arise during the pathogen's segment of the life-cycle on the plant. This occurs when subcellular debris of the cell wall accumulate in cells due to the action of the lytic enzymes secreted by the fungus and wall degeneration in host-plant cells

in the neighbourhood of fungal attack. Specific components of these subcellular debris act as elicitors in the plant, provoking a series of metabolic changes (Agrawal *et al*. 2011). Successful pathogens overcome this immunity and establish an active infection. Many pathogenic fungi have evolved mechanisms to inhibit PTIs through the translocation of effector proteins into host cells (Dou and Zhou 2012). The ability of pathogenic fungi to overcome the host's immunity and establish is the most significant step here.

That the mandibles of gall-inducing arthropods play a vital role by discharging chitin, which acts as an elicitor in arthropod–plant interactions is well demonstrated (Bronner *et al*. 1989). During early phases of feeding, *i.e.*, <24 h, the chitinous chelicerae of *A. cladophthirus* perforate the epidermal cell walls of *S. dulcamara*. Around these perforations, the epidermal cells react by accumulating callose. Within the first hour of *A. cladophthirus*'s feeding action, the nuclei of the injured cells enlarge and appear optically empty, but with a concurrent and gradual loss of DNA — diagnosed as chromatin dispersion — in these cells. Westphal (1982) demonstrated various other subcellular changes, such as vacuolar alkalinization increasing to >8 pH, in the epidermal cells of plants attacked by different species of gall-inducing Eriophyoidea within the first 24 h of attack. The surrounding cells differentiate into nutritive cells on which *A. cladophthirus* feed. Chitosan, a polymer of β-1,4-linked glucosamine residues, with a strong affinity for DNA, manifests in the nuclei of the perforated cells within one hour of attack by *A. cladophthirus*. We need to recall that a high affinity between chitosan and DNA is an established phenomenon in the interactions between plants and pathogenic fungi (see el-Ghaouth *et al*. 1992).

Explanations offered in plant pathology empower us to construct a reasonable context for induction of galls — especially during the earliest phases — by arthropods. Wounding of plant tissues by either feeding (*e.g.*, the Cecidomyiidae) or oviposition (*e.g.*, the Cynipidae) action results in a rapid alteration of the subcellular environment, leaving the target

plant cells in a state of chemical shock. This shock evokes osmotic changes in attacked cells, resulting in the earliest recognizable stage in gall induction, *viz*., the first 24 h of attack. Wounded cells as well as a few adjacent cells get activated due to the action of effector proteins discharged from the saliva of the inducing arthropod, which trigger the activation of elicitors in the attacked cells. Similar to pathogenic fungi, the insects are able to induce galls by overcoming a modest, innate immunity of host plants. Metaplasia of some cells in the 'conquered' plants materializes. The resulting metabolic changes triggered by alterations in the vacuolar pH — expressed as possible novel chemicals — diffuse from these dedifferentiated cell(s) into the immediate neighbourhood, but never throughout either the involved plant organ or the entire plant. Osmotic-change related stress builds up when these specialist insects attack plant cells, which activates a train of events in the immediate environment of the perforated plant cells, including alterations in gas exchange and synthesis of growth promotors. Osmotic stress alters electrical properties of the plasma membrane and impacts on IAA synthesis and activity, which, in turn, alters the H^+-transport.

The physiology of insect-induced galls, on maturation, *i.e.*, when the arthropod ceases to feed and thus provide no further stimulus to the gall to grow, is broadly similar to the physiology of normally developing fruits, although the proportions of production, transport, and storage (and utilization by the inhabiting larva) of various primary and secondary metabolites vary with the species involved. Photosynthesis, for instance, is intensely altered in gall systems, but the sugar transport from other parts of the same plant that bear no galls occurs *via* both symplast and apoplast. Dehiscence of galls and dehiscence of fruits display involve similar physiological processes. Both systems — normally dehiscing fruits and dehiscing galls — include newly differentiated specialized cells and a tight coordination of molecular and biochemical events that lead to cell separation freeing seeds in fruits and the larva (or adult in some instances) in galls.

Gall-hosting plants employ varied strategies

to neutralize the stress that arise subsequent to gall induction, more particularly in the immediately following gall growth and differentiation phase. Although the neutralizing strategies seem to be a part of the genetic constitution of plants, their responses are mediated by novel molecular changes, which obviously vary with the kind of insect involved. In the context of gall induction, susceptible plants generally use a flexible, short-term strategy to respond to stress. Inherited traits also play a role in providing a specific shape to the induced gall, co-ordinated by the innate correlating morphogenetic factors that operate normally in the plant. Verification of my prompts should enable the realization Trotter's vision in its entirety.

One other purpose of this article is to highlight to biologists interested in exploring plant galls induced by arthropods as their study materials that we need not ignore old literature simply because they are old. Many of them include brilliant observations and fascinating interpretations made some tens of years ago, when modern biological tools and methods were unknown.

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現況及未來展望：百年來的癭學研究

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摘　　要

　　人類發現昆蟲引發植物癭已有相當一段時間，最為人知的是作為藥用或是提煉墨水的材料，用於書寫或繪畫。直至 19 世紀初期，研究蟲癭及其造癭者也僅以 gall（癭）稱呼這類植物不正常的生長。Cecidium 一詞則是由 Friedrich Thomas 於 1873 年最早使用，由希臘文的 *kékis* 衍生而來，意指具有滲漏產出的不正常物，此後 Cecidology 一詞便成為癭學的專有名詞。癭學中的另一巨擘是 Alessandro Trotter（1874-1967），他在 1902 年創辦了癭學的專刊 Marcella（1902-1980s），Marcella 的第一篇文章即是由他本人撰寫的《Progresso ed importanza degli studi cecidologici》(癭學研究的重要性與進展)，其中包含許多具有啟發性的陳述。在本文中，我選錄了 Trotter 文章中的部分段落，從而評估過去百年的癭學發展。此期間的研究幫助我們在未知的蟲癭體系與造癭者研究帶來了一道曙光。在 1930-1980 年代，Ernst Küster 於德國的 Gießen 開創了歐洲癭學派，後繼的 Henri-Jean Maresquelle 與 Jean Meyer 等在法國的史特拉斯堡首先以個體學的角度探討癭及其造癭節肢動物。在 1970 年代後期，美國的 Peter Price 與 Warren Abranhamson 運用群落生態學及人口統計學的研究方法簡化了癭學的研究方法。同一時期，Helmut Zwölfer 也在德國的拜羅伊特開始用族群及群落生態學的方式進行癭的調查。相對造癭節肢動物的個體統計及棲位研究方法的豐碩成果，在癭形成機制的研究進展就略顯薄弱。近來我們已能依據生理的改變，將癭的生長與分化劃分出不同的階段，並歸納出節肢動物唾液中的植物生長素及細胞激素的前驅物，然而，我們仍無法釐清最初始的階段所涉及的部分-啟動因子-通常於造癭節肢動物攻擊植物組織後的 24 小時內。在認知目前的狀況下，本文即著重於癭的形成初期的研究缺口，並輔以具有致病力之真菌與植物交互作用之實例，最終以這些洞見提供在節肢動物癭方面的研究潛力與價值作結。

關鍵詞：Alessandro Trotter、Henri-Jean Maresquelle、Jean Meyer、Mahadeva Mani、Helmut Zwölfer、Peter Price、Warren Abrahamson、個體生態學及群落生態學研究法