

台灣昆蟲專刊

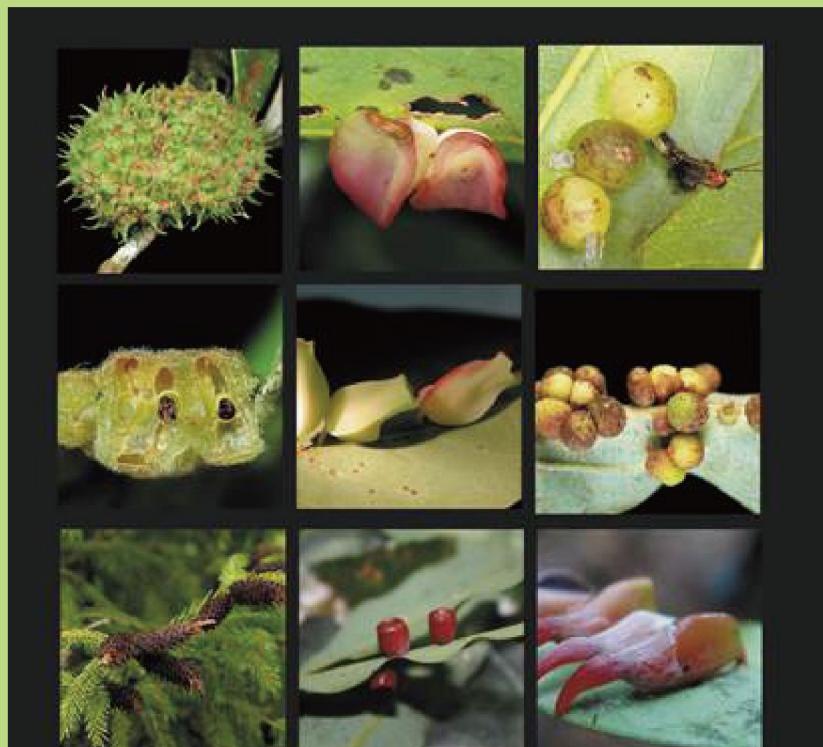


Formosan Entomologist Special Issue

造瘤節肢動物的生態與演化 Ecology and Evolution of Gall-Inducing Arthropods

Edited by Kuang-Hui Lu

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Let's Gall Taiwan
The 7th International Symposium of Cecidology



Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

Preface

This special issue of *Formosan Entomologist* (*FE*) is the result of an international symposium on gall-inducing arthropods held at the Huisun Experimental Forest Station, Nantou, Taiwan, between the 3rd and 8th of March 2018. It was organized as the 7th International Symposium on Cecidology: Ecology and Evolution of Gall-Inducing Arthropods. The slogan of the symposium was *Let's Gall Taiwan*. Pertinent information can be found in the weblinks: <http://www.letsgall.tw>, <https://www.facebook.com/lets.gall/>. It is close to 25 years since the first symposium of this series was held in Siberia in 1993. A concise historical review of the previous symposia, including the presently referred seventh, is provided after this preface.

Although the previous symposia of this series were known as ‘gall symposia’ in short, specific titles given to each of them varied. The word ‘Cecidology’ is introduced into the title of the symposium for the first time, due to its historical popularity of the term cecidology. This special issue starts with Dr. Raman’s review of cecidology in the past one hundred years, followed by Dr. Yukawa’s methodological paper depicting how good galls are useful to us in providing us with ecological information. The other five papers cover ecological, biodiversity, invasive themes. A review of the book, *Let's Gall Taiwan—A Guide Book on Insect Galls* published in March 2018 during the symposium held at Huisun Experimental Forest Station.

Since these symposia are held every four

years, this special issue of *FE* will update our knowledges on gall-inducing arthropods and their associates. We believe that this issue of *FE* along with other presentations made during the symposium will contribute to the development of cecidological studies in future.

We thank the International Union of Forestry Research Organizations (IUFRO) working group, 7.03.02, Gall-Inducing Insects, which has been working closely in holding this series of gall symposia, the Taiwan Entomological Society for accepting to publish this special issue in *FE*, National Chung Hsing University (NCHU) for supporting us variously in the organization and conduct of the symposium in March 2018, and several international colleagues for timely reviews of the published manuscripts. We also acknowledge our laboratory members and many Taiwanese colleagues interested in and working on insect-induced galls for helping us organize the symposium and contributing to insect-induced gall research of Taiwan. Special thanks to Sheng-Feng Lin, Yi-Chang Liao, Yi-Ming Chao, Yu-Chun Lin, and Hsuan Chang who assisted in translating the English abstracts into Chinese. Finally we thank all the participants of the symposium for spirited contributions.

Man-Miao Yang
Gene-Sheng Tung
Taiwan, December 2018





Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

History of the Gall Symposium

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The concept of an international gall-inducing arthropod symposium was developed by William Mattson (USDA Forest Service and Michigan State University, USA) and Yuri Baranchikov (Siberian Branch of the Russian Academy of Sciences, Russia) in 1992. The meeting was organized under the guidelines of the International Union of Forestry Research Organizations (IUFRO). **The first symposium**, entitled as “International Symposium on Gall-Forming Insects: Ecology, Physiology and Evolution of their Relationships with Host Plants”, was held at the Sukachev Institute of Forest and Wood, Siberian Branch of the Russian Academy of Sciences, with support from

IUFRO at Krasnoyarsk, Siberia, with Yuri Baranchikov and Peter Price as organizers, between the 9th and 13th of August of 1993. The proceedings of the symposium were published as *The Ecology and Evolution of Gall-Forming Insects* edited by Peter Price, William Mattson, and Yuri Baranchikov (1994) by the United States Department of Agriculture’s Forest Service, North Central Forest Experiment Station General Technical Report NC-174. This publication includes 22 papers written by 45 contributors. Treated themes include ecology and population dynamics, effects of the physical environment on gall-inducing arthropods, biodiversity and distribution, genetic variation

in host-plant resistance, and evolutionary perspectives. These themes have prevailed in subsequent meetings and a field excursion in exploring galls was included during the meeting. Price and a few other participants at this symposium took the Trans-Siberian train before and after the symposium. Their travel turned out to be an adventure which has left unforgettable experiences and indelible stories.

The success of the first symposium prompted future symposia in different nations. **The second symposium**, entitled as “Biology of Gall Inducing Arthropods”, was held in Mátrafüred, Hungary, organized by György Csóka of the Hungarian Forest Research Institute, from the 14th to the 19th of August of 1997. The meeting included 32 oral presentations and 12 posters. Participants were from around the world representing 20 countries: Australia, Belgium, Brazil, Canada, Czech Republic, England, Finland, France, Germany, Hungary, Israel, Poland, Russia, Scotland, South Africa, Spain, Sweden, Taiwan and the USA. The proceedings of the symposium were published as *The Biology of Gall-Inducing Arthropods*, edited by György Csóka, William Mattson, Graham Stone, and Peter Price (1998), as North Central Research Station General Technical Report NC-199 from the United States Department of Agriculture Forest Service. The book “Plant galls” written by György Csóka, which was published right before the symposium, was given as a gift to the participants. Like the first one, an excursion trip to the field for collecting was organized during the symposium which becomes a distinguishing feature of all the following symposia.

The third symposium, entitled as “Biology of Gall-Inducing Arthropods”, was held in Stellenbosch, South Africa, from the 15th to the 18th of January of 2002. The meeting was organized by Schalk Louw, Jeanne Stoltz and Jan Giliomee, which attracted 49 participants. A field trip to a conservation area of Fynbos vegetation near Hermanus on the south coast, east of Cape Town occurred. No publication resulted from this meeting.

The fourth symposium, entitled as “Biodiversity of Galling Arthropods and Their Associates”, was held in Kyoto, Japan from the 5th to the 9th of September of 2005. The

organizers were Junichi Yukawa, Takayuki Ohgushi, and Kenichi Ozaki. The meeting included 30 oral presentations and 27 posters. Following the tradition, a day of collecting excursion was organized during the meeting period. The proceedings were published as a book, *the Galling Arthropods and their Associates: Ecology and Evolution* edited by Kenichi Ozaki, Junichi Yukawa, Takayuki Ohgushi, and Peter Price (2006) and published by Springer-Verlag, Tokyo. This publication includes 26 papers written by 75 authors.

The 5th symposium, entitled as “Biology of Gall-Inducing Arthropods”, was held in Serra do Cipó in Brazil from the 9th to the 14th of August of 2009. The organizers were Wilson Fernandes, Peter Price, and Heikki Roininen. There were 66 presentations (31 oral presentations and 35 posters) by 52 participants in the event. The studies focused on various themes and were distributed among the sections of (1) Natural History and Biology, (2) Host Relationships, (3) Tri-Trophic interactions, (4) Spatial Ecology and Biodiversity, (5) Genetics and Molecular Biology, (6) Phylogeny and Evolution, and (7) Current and Novel Issues. The country participants were from Brazil, Finland, United States, Australia, Taiwan, Japan, Costa Rica, Mexico, England, Israel, Peru, and Canada. An award was created for the first time in the symposia series and the award was given to Peter Price in recognition of his outstanding work on galling studies and in insect ecology in general. A field trip into the cerrado vegetation of Serro do Cipó provided a great opportunity to this area with exceptionally high diversity of gall-inducing arthropods. No proceedings were published from this symposium but all abstracts were distributed in a CD to all participants.

The next symposium, entitled as “**the 6th International Symposium** on the Biology and Ecology of Gall Inducing Arthropods and Related Endophytes”, was held in O'Reilly's Rainforest Retreat, Queensland, Australia, from the 4th to the 8th of August 2013. The organizers were Robin Adair, Gary Taylor, Anneke Veenstra, and Peter Kolesik. There were 10 sessions with about 50 oral presentations plus 22 posters. The award for significance in gall study was given to Wilson Fernandes. Following the tradition, an excursion

trip was included and the first time for the symposia series, a workshop on the gall midges of mango tree was held during this symposium. A proceedings was published in Plant Protection Quarterly.

The current symposium, entitled as “**the 7th International Symposium** on Cecidology: Ecology and Evolution of Gall-Inducing Arthropods” with a slogan “Let's Gall Taiwan!”, was held from the 3rd to 8th of March 2018 in the Huisun Experimental Forest Station, Nantou County, Taiwan. The organizers were Man-Miao Yang and Gene-Sheng Tung. There were 101 participants from 15 countries (Australia, Brazil, Canada, Czech Republic, Hungary, Israel, Japan, Korea, Poland, Romania, South Africa, Sweden, Taiwan, Turkey, and USA). The total number of presentations were 55, including 35 oral and 20 posters. The research significance award was given to Junichi Yukawa in recognition of his

outstanding research in gall midges and life history strategies of gall-inducing insects. A workshop on the invasive gall-inducing insects and several special events, such as self-designed dye of silk scarf using aphid gall nuts and experience of making edible Aiyu jelly from fig galls, were held within the framework of the event. The book “Let's Gall Taiwan: A Guide Book on Insect Galls” edited by Gene-Sheng Tung and Man-Miao Yang, which was published right before the symposium, was given as a gift to the participants. The proceedings of the symposium is here published as a special issue of the “Formosan Entomologist”, journal of the Taiwan Entomological Society.

The **8th symposium** will be held in the United States organized by Donald Miller and Matthew Buffington in 2022. Let's Gall, then!

Man-Miao Yang
Gene-Sheng Tung



Group photo of participants taken on the first day of the 7th International Symposium on Cecidology: Ecology and Evolution of Gall-Inducing Arthropods at the Huisun Experimental Forest Station.



Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

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

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Received: 11 April 2018 Accepted: 30 August 2018 Available online: 3 June 2019

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 *kékes* (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.

Key words: Alessandro Trotter, Henri-Jean Maresquelle, Jean Meyer, Mahadeva Mani, Helmut Zwölfer, Peter Price, Warren Abrahamson, Odette Rohfritsch, autecological and synecological approaches

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://irongalllink.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 *Geschichte 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 *Amarakōśā* (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

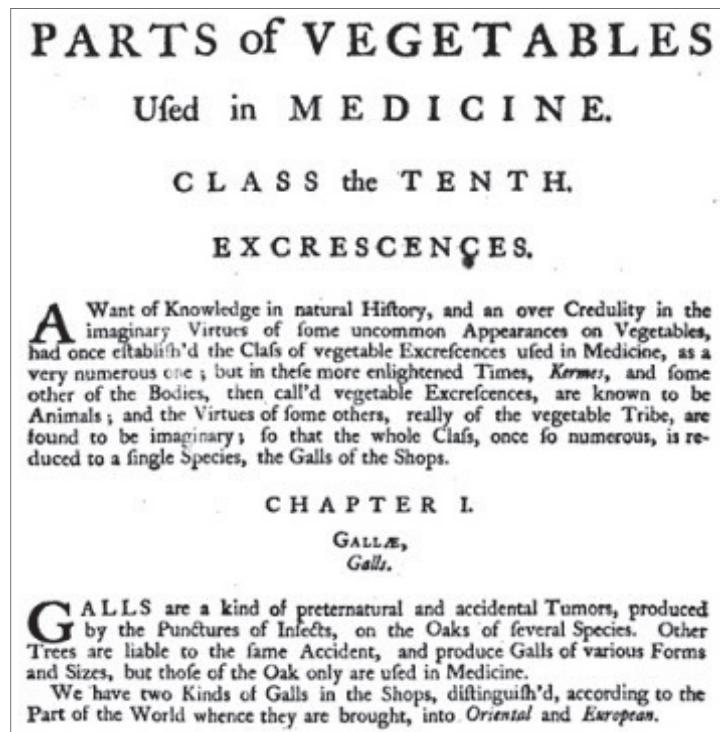


Fig. 1. A page from Hill's *History of the Materia Medica* (1751) that refers to plant galls.

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 amorphousness 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\-ēəl) — 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

¹ *Chermes* in the 19th century referred to species of Psylloidea (*sensu* Linnaeus 1758).

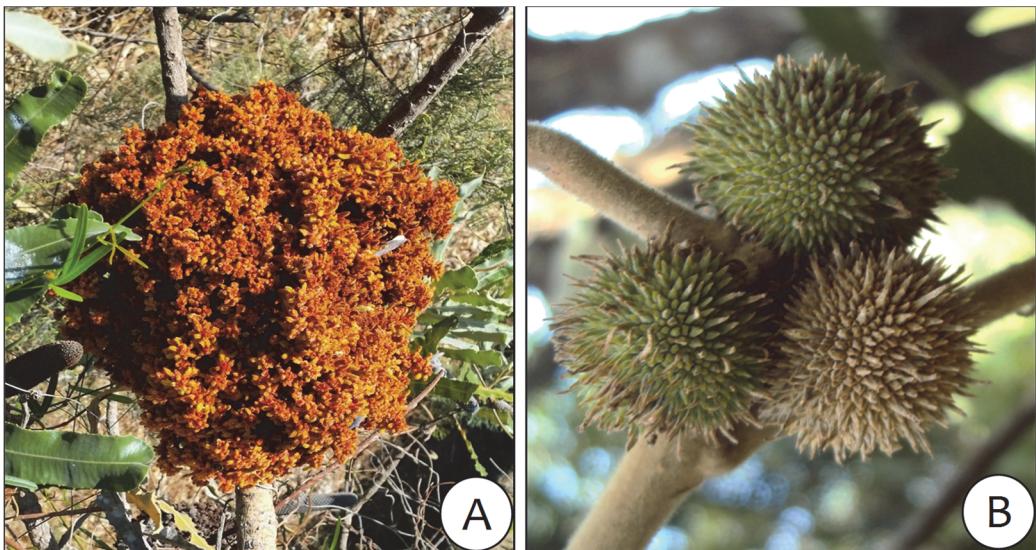


Fig. 3. Plant excrescences. (A) A witches' broom on the shoots of a species of *Banksia* (Proteaceae). (B) Galls induced on the shoots of *Hopea ponga* (Dipterocarpaceae) by *Mangalorea hopeae* (Hemiptera: Coccoidea: Beessoniidae).

domatia induced by different species of the Formicidae and Eriophyidae (e.g., *Asetilobus hodginsi*, 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 Malpighi² 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-mycolologist, 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*

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).

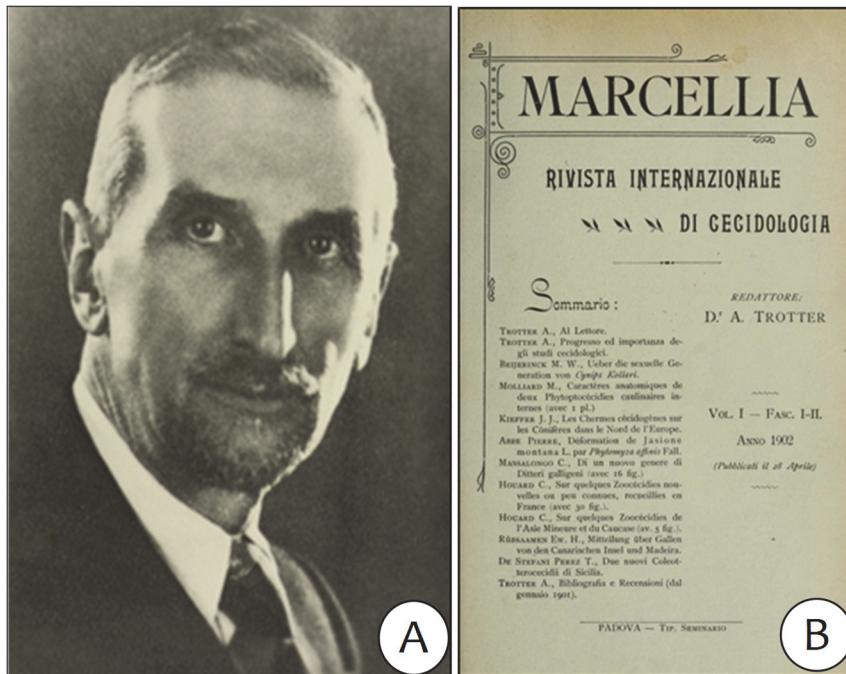


Fig. 4. (A) Alessandro Trotter. (B) Cover of the inaugural issue of *Marcellia*.

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 Cucujionide tra i Coleotteri, qualche Afidino tra gli Emitteri, qualche Tentredinide od Isosoma tra gli Imenopteri, qualche Tortricide o Tineide tra i Lepidotteri, tutti quanti produttori di galle.

[Besides the(se) three groups of almost natural cecidozoa (i.e., Eriophyoidea, 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 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 *Cecidonioides 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 *Cecidonioides 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 svariate³ di Cocciniglie e di Psillidi, insetti che invece in Europa, nei regardi 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)

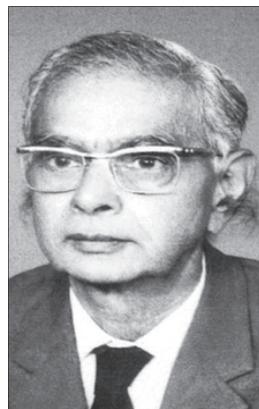


Fig. 5. Mahadeva S. Mani.

'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 interrelation, 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 Cecidomyiidae⁴ 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

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 Maresquelle⁵ 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

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 parassiti 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 gli insetti sono i soli organismi gallicoli. Ho mostrato in un mio lavoro di come sulle galle, specialmente 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 micromicetici 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 Myopinae (Tephritidae) interacting with different species of European Cardinae (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 riprodurre, se non la galla nei suoi particolari, almeno un'ipertrfia 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 cecidogenetic 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 riprodurre, se non la galla nei suoi particolari, almeno un'ipertrfia od iperplasia 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 signalers 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 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: Helotiales: 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.

Acknowledgements

I am thankful to Junichi Yukawa (Kyushu University, Kyushu), Donald Miller (California State University, Chico, California) and S. Raghu (CSIRO, Brisbane) for reading through the final draft. I am obliged to Massimo Maffei (University of Turin, Turin, Italy) for supplying me copies of Alessandro Trotter's biography by C. Cappelletti and Trotter's article in *Marcellia* (1902). My young colleague Marco Lupoli helped me verifying the English translations of selected passages from Trotter (1902). I remain grateful to Marco. Another young colleague of mine, Anamika Sharma, organized the images used in this article and my thanks go to her as well.

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現況及未來展望：百年來的癟學研究

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收件日期：2018年4月11日 接受日期：2018年8月30日 線上刊登日期：2019年6月3日

摘要

人類發現昆蟲引發植物癟已有相當一段時間，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，研究蟲癟及其造癟者也僅以 gall (癟) 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 一詞便成為癟學的專有名詞。癟學中的另一巨擘是 Alessandro Trotter (1874-1967)，他在 1902 年創辦了癟學的專刊 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》(癟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癟學發展。此期間的研究幫助我們在未知的蟲癟體系與造癟者研究帶來了一道曙光。在 1930-1980 年代，Ernst Küster 於德國的 Gießen 開創了歐洲癟學派，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癟及其造癟節肢動物。在 1970 年代後期，美國的 Peter Price 與 Warren Abrahamson 運用群落生態學及人口統計學的研究方法簡化了癟學的研究方法。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癟的調查。相對造癟節肢動物的個體統計及棲位研究方法的豐碩成果，在癟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，將癟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-通常於造癟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，本文即著重於癟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癟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



Galls Provide Us with Good Information for Ecological Studies - Methods of Practical Field Survey and Data Analysis

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Received: 22 April 2018 Accepted: 13 August 2018 Available online: 3 June 2019

ABSTRACT

Galls provide us with various ecological data in a convenient way. To facilitate ecological studies of gall midges benefiting from this convenience, methods of field survey to obtain ecological data regarding adult activities, host plant phenology, life history patterns, and life tables are explained based on practical data of my colleagues and myself. In addition to field surveys, the importance of occasional gall dissection is emphasized. To analyze the life table data, the method of key-factor/key-stage analysis is recommended, instead of the conventional key-factor analysis, to detect density-dependent and independent forces operating on gall midge populations and to assess the relative strength of top-down and bottom-up effects.

Key words: Cecidomyiidae, life table, key-factor/key-stage analysis, adult behavior, mortality factor

Introduction

Galls provide life table data in a convenient way (e.g. Redfern and Cameron, 1978). The number of galls can be easily counted continuously from early to final stage of the gall and the galler's development because of their outstanding features and immobility (e.g., Yukawa, 2000). Therefore, population dynamics of gall-inducing cecidomyiids has been relatively intensively studied (e.g., Redfern and Cameron, 1978, 1993; Keller and Schweizer, 1994; Redfern and Hunter, 2005). In recent years, the method of key-factor/key-stage analysis (Yamamura, 1999) has been used (Yamamura, 2012; Yukawa *et al.*, 2016b), instead of the conventional

key-factor analysis (e.g., Morris, 1959; Varley and Gradwell, 1960, 1968), to detect density-dependent and independent forces operating on gall midge populations at different developmental stages and to assess the relative strength of top-down and bottom-up effects. At the same time of field surveys of gall midges, we can obtain phenological data of host plants, such as seasons of bud burst, shoot-extension, leaf- and flower-openings. These data enable us to analyze the degree of synchronization between gall midge emergence and host plant phenology. Synchronization is a critical event for such short-lived insects as gall midges. Galls also show us patterns of life history strategies of gall midges, including long-term diapause. I provide

some known examples for these topics to facilitate further ecological studies of gall midges and their host plants.

The purposes of this paper are (1) to provide methods of practical field survey, particularly for leaf gall-inducing cecidomyiids on evergreen broad-leaved trees and (2) to show analytical methods of field data. These methods have been practiced and shown in recent papers by my colleagues and myself (Yukawa and Akimoto, 2006; Yukawa *et al.*, 2006, 2013, 2016b, c, 2018).

This paper will be useful for students who plan to begin field surveys for ecological studies of gall midges in evergreen broad-leaved forests in subtropical and tropical regions. Taiwan is one of the most appropriate places for such field surveys because of extremely rich gall midge fauna in the forests (Tung and Yang, 2018).

Field survey

Adult gall midge activities

Prior to field surveys of population dynamics, we need to gather information on adult gall midge activities, such as emergence, mating, swarming, flight ability, oviposition and longevity, together with data of sex ratio and the number of ovarian eggs (Yukawa *et al.*, 1976; 2013). Information on these behavioral traits can be obtained mostly by direct observation in the field and partly by laboratory experiments. For direct observation, we need to select 10 to 20 census host trees in the field.

Gall midges are roughly divided into two groups in terms of daily activities (Barnes, 1930). Diurnal gall midges emerge early or late in the morning. Sometimes males emerge several hours before females (Yukawa *et al.*, 2013). Males usually swarm around host plants from which they emerged and then mating takes place during the morning on the host leaves where emerged females are located (e.g., Yukawa *et al.*, 1976; 2013). Females leave the host plant to lay their eggs in or on newly emerged host organs.

Nocturnal gall midges, such as many species of *Asphondylia*, emerge in the evening or after dark. Swarming and mating take place during the nighttime. Frequently, some individuals emerge during the daytime under

cloudy conditions.

Hourly emergence pattern can be determined for diurnal gall midges by direct observation in the field and for nocturnal species by rearing experiments under natural lighting conditions in outdoor cages. Field surveys of daily emergence pattern are essential in referring to synchronization between gall midge emergence and host plant phenology. Because the daily emergence patterns fit well to the gamma distribution pattern (Yukawa and Akimoto, 2006), the number of adults emerged can be surveyed at intervals of three to four days, instead of everyday observation, to determine the daily emergence pattern. The emergence of gall midges is distinguishable from that of parasitoids by the exit holes that are larger in gall midges and frequently retain pupal exuviae.

Swarming and mating should be observed in the field (e.g., Mishima *et al.*, 2014). The number of females that were not detected by swarming males can be evaluated. Because the observable number of females that are waiting for males on the host leaves is limited for one person in a day, several co-observers are needed to obtain ample data of the rate of females mated. Flight ability can be measured with a strain gage transducer (Kanmiya, 1994). Estimation of flight ability is needed to evaluate dispersal of gall midges, particularly those that exhibit host alternation. If possible, we need to record the daily number of females that visit the host organs for oviposition. With this data we can estimate the rate of females that survive factors operating on adults although identification of the factors is rather difficult.

Sometimes the sex ratio is female-biased and daily emergence patterns are different between sexes. Therefore, at least 50 individuals are needed to determine sex ratio. Because ovarian eggs are matured at the time of emergence, the eggs are countable under a binocular microscope by dissection of female abdomens. Yukawa *et al.* (1976) found 59 eggs on average left in the ovaries of females of *Pseudaspheondylia neolitsea* Yukawa. The females fastened on the host buds in the evening and stopped ovipositing after fulfilling their duty. Thus, they calculated that 189 (76%)

of 248 initial ovarian eggs were laid during oviposition on average per female. The number of adults emerged, their sex ratio, and the average number of ovarian eggs are used to estimate the initial number of eggs of the following generation.

Host plant phenology

First we need to count the number of host organs, such as extending shoots or the current year leaves on the census trees selected. Then, we determine, by observing ovipositing females, the condition of host organs that are suitable for oviposition. In the case when shoots are targets of oviposition, we measure the length of shoots with a scale and regard shoots within the range of suitable length as those available for oviposition. Because shoots extension curve available for oviposition fits well to the normal distribution pattern (Yukawa and Akimoto, 2006), the shoot length can be measured in the field at intervals of three to five days. When eggs are laid on the half opened leaves, we count un-, half- and full-expanded leaves. Usually asynchrony between gall midge emergence and host plant phenology is expressed as time lag in days between 50% emergence date and 50% date in the number of host organs that are available for oviposition. In addition to the time lag, Yukawa and Akimoto (2006) took the amount of resources into the degree of synchrony, with which density-dependent effects was evaluated.

Life history patterns

Life-history patterns of gall midges are closely linked to their host plant phenology (Yukawa and Rohfritsch, 2005). In temperate areas, most trees produce new shoots and flowers once a year, and therefore tree-inhabiting gall midges are inevitably univoltine. In contrast, gall midges on herbaceous plants that produce new shoots repeatedly can be multivoltine. Even on trees, gall midges can become multivoltine particularly in the subtropics and tropics, where new shoots are available in seasons other than spring. Some species have two or more generations a year by alternating between different organs of the same host or different species of host plants.

To determine voltinism, periodical dissection of galls is necessary. The galls should be collected from sampling trees that were selected differently from census trees. If necessary, we need to determine the lower development threshold temperatures (LDT) of gall midges and the thermal constants from egg or first instar to adult, with which the number of generations per year can be estimated for multivoltine gall midges (Yukawa *et al.*, 2016).

Bergant and Trdan (2006) argued that LDT and thermal constants based on laboratory experiments commonly suffer from a great amount of uncertainty. They emphasized that a sufficient temperature range should be covered in the experiment to approach the borders of the linear response as closely as possible. My colleagues and I reared gall midge larvae under various temperature conditions that could decrease the uncertainty in determining LDT around the borders (see Ohtani *et al.* 1983; Okuda and Yukawa 2000; Yukawa *et al.* 2013, 2016a; Kim *et al.* 2015 for details of the rearing experiments).

Life table data

Life table enumeration provides is one of the most appropriate data sets to detect density-dependent and independent forces operating on gall midge populations at different developmental stages and to assess the relative strength of top-down and bottom-up effects. For this purpose, we select some census trees for field surveys or some lower branches in cases when trees are too tall. In addition, some sampling trees should be selected to collect galls for dissection.

Usually life tables start from the egg stage of the first generation (Table 1). The number of eggs can be directly counted when eggs are laid on the host leaf surface or scars of the oviposited position can be recognized after larval hatching. For example, we can find such scars made on the under surface of *Machilus* leaves by larvae of *Daphnephila* that hatched and sank into the leaf tissue. When eggs are laid inside plant tissue, we have to estimate the number of eggs of the first generation (E_n) by the following equation:

Table 1. A simplified example of life table data for an imaginary gall midge

Developmental stage	Season	Mortality factor	<i>Lx</i>	<i>Dx</i>	% <i>Lx</i>
Eggs on the leaf surface	April		1200		100.00
		Predation by ants		700	
1st instars in young galls	July		500		41.67
		Galls fed by moth larvae		100	
1st and 2nd instars in young galls	September		400		33.33
		Fall of galled leaves by typhoon		350	
3rd instars and pupae in mature galls	March		50		4.17
		Parasitism by <i>Bracon</i> sp.		40	
Adults emerged	April	(Sex ratio: 0.6)	10		0.83
Females emerged	April		6		
Potential number of eggs for the following generation	April	(6 × 150 ovarian eggs/female)	900		0.75*

Lx: the number of living individuals, *Dx*: the number of dead individuals caused by each mortality factor, %*Lx*: survival rate from the initial number of *Lx* (1200).

* Reproductive rate in comparison with the number of eggs in the previous generation (1800/1200).

$$E_n = A_{n-1} \times S \times O$$

A_{n-1}: The number of adults emerged from the census trees in the preceding generation

S: Sex ratio (the ratio of females among adults emerged)

O: The number of ovarian eggs before oviposition. If possible, the number of realized eggs after oviposition is more appropriate.

Immediately after galls become conspicuous, we need to record the initial number of early-stage galls that contain first instars. At the same time, we record the number of galled and ungalled host organs such as leaves or young fruit. On the way to the maturity of galls, we need to monitor galls that survived optional feeding by cecidophagous lepidopteran larvae and fall of galled organs caused by physical reasons such as strong wind, by biological reasons related to gall density or to lepidopteran leaf feeders. In addition, we count galls that could not mature because of larval death in the galls by unknown factors. Later in the season (in October-November or in the following March in the case of univoltine gall midges), we need to count mature galls remaining on the census trees. During the growth of galls, we should collect some galls from the sampling trees occasionally (once or twice) and dissect them

under a binocular microscope to know: (1) the developmental stadium of larvae, (2) presence or absence of ectoparasitoid larvae and their developmental stadium, and (3) presence or absence of inquilines and their developmental stadium. About two weeks before emergence, we dissect mature galls again to record the aforementioned items. At this time, we can find endoparasitoids, if any, which pupate in the host larval skin. At every time of gall sampling, we record the number of host organs remaining on the census trees. Thus, we can obtain data regarding rates of the eggs, larvae and pupae that survived age specific mortality factors.

In the survey of fruit gall midges, special attention should be paid to the following facts (Yukawa *et al.*, 2016): (1) The first instars inhabiting flower buds or flowers drop to the ground and die because of flower abortion, which is tremendous in rate. However, the abortion of flowers is a normal event and is not caused by larval infestation. (2) Frequently galled fruit cannot be distinguished from normal fruit in size and color until late autumn. In the light of the aforementioned two facts, occasional dissection of flower buds, flowers and young fruit is more important than direct field observation.

Table 2. Stage specific mortality factors and the calculation of survival rates

The life-table of an imaginary gall midge is divided into 4 developmental stages. N_t is the potential number of eggs on the host leaf surface at the t th year. S_t is the rate of generation change of N_t , that is, N_{t+1}/N_t . Then, S_t can be given by the multiplication of the survival rate (or rate of change) at each developmental stage:

$$S_t = s_{1t} s_{2t} s_{3t} s_{4t} s_{5t}, \quad (1)$$

$$900/1200 = 500/1200 \times 400/500 \times 50/400 \times 10/50 \times 900/10 \quad (\text{actual data})$$

where s_{it} is the survival rate in the population entering the i th life stage at the t th year. The survival rate at each life stage is defined as follows:

s_{1t} : proportion of eggs that survived the predation by ants,

s_{2t} : proportion of first instars that survived lepidopteran larval feeding on galls,

s_{3t} : proportion of first and second instars that survived the fall of leaves by typhoon,

s_{4t} : proportion of third instars and pupae that survived parasitism by *Bracon* sp.

s_{5t} is regarded as the rate of change caused by the oviposition of one female, which is calculated from the sex ratio and the mean number of ovarian eggs per female.

Equation 1 is expressed in common logarithms as follows:

$$\log_e(S_t) = \sum_{i=1}^5 \log_e(s_{it}) \quad (2)$$

$$(6.80-7.09) = (6.21-7.09) + (5.99-6.21) + (3.91-5.99) + (2.30-3.91) + (6.80-2.30)$$

Life tables covering all developmental stages from egg to adult are ideal for analysis, but partial life tables covering a part of the life history (only larval stage, for example) are available for analysis when there are some difficulties in the field survey. The partial life table data during the larval stage tell us about density-dependent and independent forces operating on the gall midge larvae at different developmental stadia. It is much better than nothing.

Data analysis

Yamamura (1999) proposed a key-factor/key-stage analysis by integrating the conventional key-factor analyses (e.g., Morris, 1959; Varley and Gradwell, 1960, 1968) and ANOVA, emphasizing the importance of discriminating between the key-factor and the key-stage. This analysis can identify the key-factor, the key-stage, and the combination of factor and stage that is most influential in determining the fluctuation of total mortality. By discriminating factors and stages, we can avoid all problems raised by Royama (1996) about the conventional analyses (Yukawa *et al.*, 2016b). The effectiveness of the key-factor/key-stage analysis is demonstrated in Yamamura

(1999, 2012), Yukawa *et al.* (2016b). Thus, key-factor/key-stage analysis is most recommended to detect density-dependent and independent forces operating on gall midge populations at different developmental stages and to assess the relative strength of top-down and bottom-up effects.

For this analysis, we need to provide multiple life table data sets. The number of data sets should be more than the number of parameters (= factors going to be evaluated), such as the initial number of eggs, temperature, the amount of precipitation, intensity of typhoons and other biotic or abiotic factors, otherwise key-factor/key-stage analysis (and ANOVA) does not work (e.g., Yukawa *et al.*, 2018). Multiple data sets can be obtained by long-term surveys in one census field or short-term surveys in several different census fields.

In the analysis, we need to define developmental stages on which stage specific mortality factors operate. Table 2 shows the definition of stages and the calculation method for the survival rates based on the life table data for an imaginary gall midge (Table 1). Then, we define biotic and abiotic factors. Actual equations are indicated in Yukawa *et al.* (2016b) and an 'R' function to perform key-factor/key-stage analyses is available from the following

web site (Yamamura, 2015, personal information):
http://cse.niae.saffrc.go.jp/yamamura/Key-factor_analysis_program.html

Yukawa *et al.* (2018) used key-factor/key-stage analysis for the first time to analyze long-term data on leaf longevity of *Neolitsea sericea* (Blume) Koidzumi (Lauraceae), a host plant of *P. neolitseae*. The term “stage” was used for “leaf age”, as has been used in life table studies of other insects. In this analysis, Yamamura (2018, personal information) recommended to use log_e instead of log₁₀ when actual survival rates are converted into logarithms. An “R” function to perform key-factor/key-stage analyses is available from the following web site:

http://cse.naro.saffrc.go.jp/yamamura/Key-factor_analysis_program.html

Acknowledgments

I would like to express my hearty thanks to Prof. MM Yang (National Chung Hsing University, Taichung) and Dr. GS Tung (Taiwan Forestry Research Institute, Taipei) for their kind invitation to the 7th International Symposium of Cecidology and for giving me an opportunity to contribute this manuscript to the Proceedings of the Symposium. My thanks are also due to Dr. KM Harris (former Director of the International Institute of Entomology, UK) for his critical reading of an early draft.

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蟲癟為生態學研究提供了良好的資訊-田野調查及數據分析方法

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收件日期：2018年4月22日 接受日期：2018年8月13日 線上刊登日期：2019年6月3日

摘要

蟲癟以易取得的方式提供我們多元的生態資訊，為了使蟲癟生態研究的便利性更加優化，在此我與其他研究同仁以實際的數據為基石，闡明獲得相關生態資訊的田野調查方法，包括成蟲活動、寄主植物的物候、生活史模式以及生命表。除了田野調查之外，隨機蟲癟解剖調查也十分重要。分析蟲癟研究的生命表數據，建議使用主導因子/主導時期 (key-factor/key-stage) 的分析方式來取代慣用的主導因子分析，並檢測作用於癟蚋族群的密度應變或非密度應變因子的作用力，進而去評估生態系中由上而下 (top-down) 或由下而上 (bottom-up) 的相對影響強度。

關鍵詞：癟蚋科、生命表、主導因子/主導時期分析、成蟲行為、致死因子



Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

Invasive Pest Species of Gall-Inducing Cecidomyiidae (Diptera) in Japan

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Received: 29 April 2018 Accepted: 20 September 2018 Available online: 3 June 2019

ABSTRACT

Certain pest species of gall midge (Diptera: Cecidomyiidae) have invaded Japan in recent decades. *Contarinia maculipennis* Felt probably came to Japan from Southeast Asia, and it is now an exceedingly problematic pest for *Dendrobium* orchids (Orchidaceae) in Okinawa. Molecular phylogenetic analyses have revealed that *C. maculipennis* is a polyphagous species infesting more than eight plant families, including *Momordica charantia* (Cucurbitaceae), a chief vegetable crop in Okinawa. A similar *Contarinia* species was found to induce leaf-fold galls on roses (Rosaceae) cultivated in greenhouses in various prefectures of Japan. A molecular phylogenetic analysis detected geographical variations in the gene sequences of this gall midge, suggesting that this *Contarinia* species is a native to Japan, in contrast to *C. maculipennis*. However, wild host(s) of this gall midge have never been found. *Procontarinia mangicola* (Shi) that attacks the leaves of *Mangifera indica* (Anacardiaceae) was found in Okinawa Prefecture in 2000, on Amami Island, Kagoshima Prefecture in 2008 and the Bonin Islands, Tokyo in 2016. In July 2015, *Dasineura oxyccocana* (Johnson), native to North America, was found to have infested new leaves of cultivated blueberry *Vaccinium* spp. in Honshu, Japan. In addition, three alien species *Stenodiplosis sorghicola* (Coquillett), *Obolodiplosis robiniae* (Halderman), and *Oligotrophus betheli* Felt are known to occur in Japan.

Key words: invasive pest, gall midge, *Contarinia*, *Dasineura*, *Procontarinia*

Introduction

Biological invasions are one of the most serious global concerns critically affecting ecosystems and biodiversity (e.g. Sax and Gaines, 2008; Bellard *et al.*, 2016; Paini *et al.*, 2016).

International trade expansion and globalization trends have increased potential invasion risks, as well as actual invasions by alien species (Kiritani, 1998; Hurley *et al.*, 2016).

The influence of invasive gall-inducing insects on natural and agricultural ecosystems is

also of global concern (e.g. Branco *et al.*, 2016; Csóka *et al.*, 2017). For example, *Quadrastrichus erythrinae* Kim (Hymenoptera: Encyrtidae) probably originated from eastern Africa and has been reported to feed on coral and ornamental trees of the genus *Erythrina* (Fabaceae) in Taiwan, China, Japan, India, Thailand, the Philippines, Singapore, American Samoa, Guam, Hawaii, and Florida (Li *et al.*, 2006; Uechi *et al.*, 2007a; Howard *et al.*, 2008; Rubinoff *et al.*, 2010; Yang *et al.*, 2014; Csóka *et al.*, 2017). The species has rapidly broadened its range and heavily infested *Erythrina* trees in these areas. Another eulophid wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera), which feeds on *Eucalyptus* (Myrtaceae) and is native to Australia, has expanded its range globally to most localities where *Eucalyptus* trees are planted (Mendel *et al.*, 2004; Tung and La Salle, 2010; Csóka *et al.*, 2017).

The chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Encyrtidae) is indigenous to China and spread to East Asia in the 1940s (Moriya *et al.*, 2003) then to eastern North America in the 1970s (Rieske, 2007). The recent invasion of European countries by *D. kuriphilus* has seriously harmed chestnut production (EFSA Panel on Plant Health, 2010; Matošević *et al.*, 2014, 2015; Csóka *et al.*, 2017).

This review summarizes invasive gall-inducing cecidomyiids (Diptera) in Japan and their current status.

***Contarinia maculipennis* Felt**

The blossom midge *Contarinia maculipennis* Felt is a typical polyphagous gall midge infesting the flower buds of *Dendrobium* orchids as well as various plant species from other families (Tokuda, 2012; Gagné and Jaschhof, 2017). In Japan, *C. maculipennis* was first discovered in 1989 in several orchid greenhouses in Nago City, Okinawa Prefecture and subsequently in Kita-Nakagusuku Village and Ozato Village in Okinawa by 1993 (Yasuda and Uehara, 1994; Tokuda *et al.*, 2002). Orchid flower buds infested by this gall midge usually remain closed and fall from the plant (Fig. 1) (Tokuda *et al.*, 2002; Yukawa *et al.*, 2004), and some growers in Okinawa have stopped cultivating orchids due to

heavy infestation by *C. maculipennis* in addition to various economic factors (Uechi *et al.*, 2007b). The description of *C. maculipennis* was originally based on Hawaiian specimens obtained from hibiscus (Felt, 1933), and this species was believed to have invaded from Southeast Asia (Gagné, 1995). Morphological examination revealed it to be a polyphagous pest feeding on at least seven plant families (Jensen, 1946; Nakahara, 1981; Gagné, 1995). It was confirmed by Uechi *et al.* (2003) through molecular analysis.



Fig. 1. *Dendrobium* flower buds infested by *Contarinia maculipennis*.

In 2005, *C. maculipennis* was found to have infested the flower buds of bitter gourd *Momordica charantia* (Cucurbitaceae), which is a major cash crop in Okinawa (Uechi *et al.*, 2007b). During the same year, this species was discovered on *Dendrobium* spp. (Orchidaceae) in Fukuoka and Miyazaki Prefectures, Kyushu (Uechi *et al.*, 2007b); and in 2008, in Mie Prefecture, Honshu (Uechi *et al.*, 2011). *Contarinia maculipennis* was the most frequently intercepted species among Cecidomyiidae in Japanese plant quarantine inspections from 2000 to 2006 (Iwaizumi *et al.*, 2007). Uechi *et al.* (2007b) warned orchid growers, international traders, and inspection officials against the potential risks of transporting infested plant materials and emphasized the urgency of investigating the host range of this gall midge in Japan.

Uechi *et al.* (2011) reported *Pseuderanthemum laxiflorum* (Acanthaceae) as a new host plant for

C. maculipennis. At present, at least 16 species belonging to eight plant families are regarded as host plants of *C. maculipennis* (Uechi *et al.*, 2011).

Two natural enemies of *C. maculipennis*, endoparasitoids of the genus *Synopeas* (Hymenoptera: Platygastriidae), are known to occur in Okinawa (Uechi *et al.*, 2007c). Because *C. maculipennis* has developed resistance to various insecticides, including organophosphorus, synthetic pyrethroid, carbamate, and other major insect growth regulator chemicals (Tokuda *et al.*, 2002), alternative management techniques to chemical applications are required. However, at present, the parasitism rates of *Synopeas* species are low in orchid greenhouses as well as on bitter gourd in fields (Uechi *et al.*, 2007c).

***Contarinia* species on cultivated roses**

In 1998, a *Contarinia* species that induces leaf-fold galls on cultivated roses in greenhouses was found in Yamaguchi and Fukuoka Prefectures (Tokuda and Yukawa, 2004). This gall midge has subsequently been detected in various prefectures from northern Honshu to Kyushu, Japan (Tokuda and Yukawa, 2004).

In Europe and North America, *Dasineura rosae* (Bremi) and *Dasineura* sp. are known to infest cultivated roses, and they induce similar leaf-fold galls to those induced by the Japanese *Contarinia* species (Barnes, 1948; Gagné, 1989; Tokuda *et al.*, 2009; Gagné and Jaschhof, 2017). In Japan, such leaf-fold galls are found on the native roses *Rosa multiflora* and *Rosa rugosa*, and their inducers have been identified as a species of *Dasineura* (Tokuda *et al.*, 2009). To date, *Contarinia* species have been observed inducing leaf-fold galls on *Rosa* only on greenhouse-cultivated roses in Japan (Tokuda and Yukawa, 2004; Tokuda *et al.*, 2009).

According to Iwaizumi *et al.* (2007), gall midges associated with *Rosa* species were not intercepted by Japanese plant quarantine inspections between 2000 and 2005. By contrast, *C. maculipennis* was frequently captured (476 times during this period). In addition, preliminary molecular analyses of the mitochondrial cytochrome oxidase I (COI) region

have detected sequence variations in the *Contarinia* species collected from Japanese cultivated roses that reflect the geographical differences among populations (M. Tokuda *et al.*, unpublished). These analyses imply that the *Contarinia* species is not alien but native species to Japan. However, wild hosts of this gall midge have not yet been found, nor has the invasion pathway to rose-cultivation greenhouses in Japan been ascertained. Otherwise, the species might have invaded Japan multiple times. Further studies are required to reveal the origin of the *Contarinia* species.

***Procontarinia mangicola* (Shi)**

At present, 15 species of *Procontarinia* are known to infest mango plants, *Mangifera indica* (Anacardiaceae). Among them, *Procontarinia mangicola* (Shi) was discovered in 2000 on Okinawa Island and subsequently on seven other islands in Okinawa Prefecture by 2001 (Fig. 2) (Uechi *et al.*, 2002; Yukawa *et al.*, 2004). The species was previously known to occur in China and in Guam (Uechi *et al.*, 2002). This gall midge induces circular blister galls on young leaves. In mango orchards, leaves heavily galled by *P. mangicola* fall prematurely, and most of the remaining galled leaves suffered from anthracnose inoculum (Uechi *et al.*, 2002). Notably, heavily infested shoots do not produce inflorescences, resulting in low mango yields (Uechi *et al.*, 2002). This gall midge invaded Amami Island, Kagoshima Prefecture in 2008 (Kagoshima Plant Protection Office, 2009) and, most recently, the Bonin Islands (Chichijima and Hahajima Islands), Tokyo, in 2016 (Tokyo Metropolitan Plant Protection Office, 2017).

***Dasineura oxyccocana* (Johnson)**

The blueberry gall midge *Dasineura oxyccocana* (Johnson) is native to North America and infests new leaves of the blueberry plant, *Vaccinium* spp. (Ericaceae). In Europe, *D. oxyccocana* was first detected in Italy in 1996 and was subsequently found in other countries such as the United Kingdom and Latvia (Collins *et al.*, 2010; Gagné and Jaschhof, 2017). In Asia, the gall midge was first found in Korea in 2008



Fig. 2. (A) *Procontarinia mangicola* larva and (B) *Procontarinia mangicola* pupa..

and has caused a severe pest problem in blueberry cultivation there (Kim *et al.*, 2015). In Japan, *D. oxycoccana* was first found in July 2015 in Gunma Prefecture, Honshu (Yoshida *et al.*, 2017) and subsequently in Shizuoka, Toyama, and Aichi Prefectures during 2016 (Shizuoka Plant Protection Office, 2016; Toyama Plant Protection Office, 2016; Aichi Plant Protection Office, 2016). Females lay their eggs in the growing point of shoots, and the larvae develop in leaf galls at the shoot tips, causing leaf distortion and blackening of buds (Fig. 3) (Sampson *et al.*, 2002; Roubos and Liburd, 2013; Rhodes *et al.*, 2016). In North America, two genetically distinct strains, one feeding on highbush blueberry, *V. corymbosum*, and the other on cranberry, *V. macrocarpon*, are known to occur (Mathur *et al.*, 2012). These strains produce different sex pheromones (Fitzpatrick *et al.*, 2013). Phylogenetic analysis based on mitochondrial COI sequences revealed that the

Japanese population belongs to the blueberry clade (Yoshida *et al.*, 2017).

Other invasive species

The sorghum midge *Stenodiplosis sorghicola* (Coquillett) is an important pest of *Sorghum bicolor* (Poaceae) and its congeners worldwide (Harris, 1970). Although the time of invasion is unclear, *S. sorghicola* is known to occur in Honshu and Kyushu, Japan, where it was sometimes regarded as a pest from the 1950s until the 1970s (Yukawa and Tanaka, 1976). Studies of this gall midge have not been conducted during the past three decades in Japan.

Obolodiplosis robiniae (Halderman) induces leaf-margin galls on *Robinia pseudoacacia* (Fabaceae), which is one of the nectar-source trees for honeybees in Japan (Fig. 4). Heavy infestation by this gall midge can cause leaf drying and premature abscission (Csóka *et al.*, 2017). This species was found in 2002 in Korea and in 2003 in Japan (Kodoi *et al.*, 2003; Woo *et al.*, 2003). In Japan, this species is distributed from Hokkaido to Kyushu (Uechi *et al.*, 2005; Hara, 2010). A parasitoid *Platygaster robiniae* (Hymenoptera: Platygastridae) that was possibly introduced, together with *O. robiniae*, to Europe and Asia from North America has been known to occur in Japan, but detailed parasitism rates have not been surveyed (Buhl and Duso, 2008).

Oligotrophus betheli Felt causes discoloration in the young twig tips of *Juniperus*

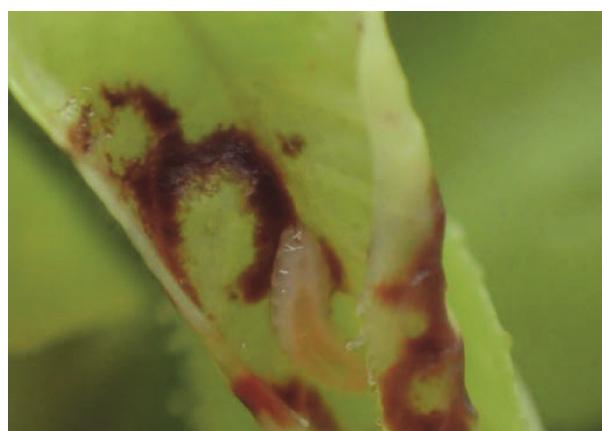


Fig. 3. *Dasineura oxycoccana* larva.



Fig. 4. Leaf-margin galls and a mating pair of *Obolodiplosis robiniae*.



Fig. 5. Galls induced on young twig tips of *Juniperus horizontalis* by *Oligotrophus betheli*.

horizontalis (Cupressaceae), an ornamental plant used for hedge and garden trees in Japan (Fig. 5). This gall midge was first found in 2013 in Japan (Yukawa *et al.*, 2017). A parasitoid *Aprostocetus* sp. (Hymenoptera: Eulophidae) and several predators (spiders and a big-eyed bug) were reported by Yukawa *et al.* (2017).

Conclusion

Iwaizumi *et al.* (2007) reported that gall midges were intercepted at Japanese seaports and airports more than 2,000 times from 2000 to 2005, approximately one discovery per day. To reduce the risk of biological invasion and promote the management of invasive species, international information sharing and cooperation are crucial. For example, Iwaizumi *et al.* (2007) found through plant quarantine

inspection a *Contarinia* species associated with *Alstroemeria* (Alstroemeriaceae) that was imported from Australia and New Zealand. Although these countries had no records of gall midges associated with *Alstroemeria*, this species was later found in Australia and in several other countries. Then it was described as new to science by Kolesik *et al.* (2017). Information about gall midges intercepted through plant quarantine inspections is useful for discovering species in the original distribution areas. Taxonomic and ecological studies in the native ranges can promote the development of control measures for the pest species.

We hope this review promotes international collaboration and contributes to reducing the risk of future biological invasions by gall-inducing insects.

Acknowledgments

We thank T. Aizawa, K. Matsunaga, and H. Yoshimura for providing us with photographs of a *D. oxycoccana* larva, *O. robiniae* adults, and galls induced by *Oligotrophus betheli*, respectively. This study was partly supported by JSPS KAKENHI Grant No. 15K07330.

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入侵日本的造癟癟蚋

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收件日期：2018年4月29日 接受日期：2018年9月20日 線上刊登日期：2019年6月3日

摘要

近數十年間，數種癟蚋害蟲入侵日本。蘭花癟蚋 *Contarinia maculipennis* Felt 推測由東南亞入侵，為目前琉球地區嚴重危害的石斛蘭屬園藝作物的害蟲物種。分子分析顯示蘭花癟蚋為一多食性物種，危害超過八科的植物，包含沖繩地區一重要瓜科栽植作物 *Momordica charantia*。*Contarinia* 屬一近似物種於日本多個縣的玫瑰栽植溫室造成葉片捲曲蟲癟，相對於 *C. maculipennis* 而言，分子分析反映該物種的分子序列有地區變異性，顯示危害玫瑰的 *Contarinia* 屬癟蚋是一原生物種，然而其野外寄主仍待釐清。危害檸果葉片的 *Procontarinia mangicola* (Shi) 於 2000 年發生於沖繩縣，後於 2008 年記錄於鹿兒島縣的奄美群島及 2016 年記錄於東京小笠原群島。於 2015 年 7 月，原生於北美的 *Dasineura oxyccanca* (Johnson) 於日本本州記錄其危害栽植藍莓—越橘屬植物新葉。此外，另三種外來物種 *Stenodiplosis sorghicola* (Coquillett)、*Obolodiplosis robiniae* (Halderman) 及 *Oligotrophus betheli* Felt 亦發生於日本。

關鍵詞：入侵害蟲、癟蚋、*Contarinia*、*Dasineura*、*Procontarinia*



Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

Diversity of Arthropod Galls in Taiwan

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Received: 6 August 2018 Accepted: 30 November 2018 Available online: 3 June 2019

ABSTRACT

A synthesis of a long-term gall faunal study covering Taiwan Island, Kinmen Islands, Penghu Islands, Green Island, and Orchid Island, which was conducted between 1995 and 2018, is presented. A total of 4,328 of arthropod-induced galls were collected, with 96.0% of the gall-inducing arthropods being monophagous. Among the seven orders of gall-inducing arthropods in the region, **DIPTERA** (42.2%) and **HEMIPTERA** (22.8%) were the two dominant gall-inducing groups. The dominant host-plant families were **LAURACEAE** (17.6%) and **FAGACEAE** (16.2%). Enclosed types of galls (65.8%) were more abundant than the open types (32.2%). Most host species (44.7%) harbored two or more, occasionally up to 11, shapes of galls. Galls were mostly found on leaves (55.6%) compared with other parts of plants. Among all gall-inducing taxa, **CECIDOMYIIDAE** was the most diverse group in terms of abundance, richness, and host use.

Key words: Gall flora, biodiversity, gall shape, host plant, gall-inducing arthropods

Introduction

Taiwan is an island nation covering an area of 35,980 km² and is situated along the southeastern Pacific off mainland China between Japan and the Philippines. More than 73% of the landscape is hilly and covered by forest (2,186,002 ha, covering c. 61% of the total landscape). Because of the unique climate, humidity, and altitude, the forests in Taiwan are highly diverse and classified under tropical, subtropical, temperate, and alpine forests (Su, 1984 a, b; Li *et al.*, 2013). Approximately 6,000

species of vascular plants reportedly occur in Taiwan (Taiwan Biodiversity Information Facility, 2018).

Gall-inducing organisms interact intimately with plants. The rich and diverse flora has supported the evolution and diversity of a range of gall-inducing arthropods. Attempts to understand the arthropod-induced gall flora and the inducing faunal elements in Taiwan were first made by Yang and Tung (1998). Subsequent guidebooks were prepared by Yang *et al.* (2000) and Tung *et al.* (2018). Tung *et al.* (2006) analyzed the patterns that manifest in the

interacting plants and gall-inducing insects. The work listed 331 species of plants that were susceptible to gall-inducing arthropods out of a documented 4,698 species of known plants. **CECIDOMYIIDAE (DIPTERA)** (36.5%) and **PSYLLOIDEA (HEMIPTERA)** (33.9%) were the dominant groups, while **LAURACEAE** and **FAGACEAE** were the plant families harboring galls. Other works on galls in Taiwan have focused on specific gall-inducing taxa (Huang, 2003; Huang, 2007; Yang and Raman, 2007; Tung *et al.*, 2008; Yeh, 2009; Yang *et al.*, 2009, 2013; Aoki *et al.*, 2013; Tang, 2015; Liao *et al.*, 2016; Lin *et al.*, 2018a) or galls living on specific host plants (Su, 2002; Yang *et al.*, 2002; Tang, 2008; Tokuda *et al.*, 2008; Melika *et al.*, 2010; Chiang, 2011; Lin, 2011; Tsai, 2012; Su, 2013; Pan *et al.*, 2015a, b; Yang *et al.*, 2014; Lin *et al.*, 2018b, c).

The present study aimed to update the results of long-term research on gall fauna in Taiwan as of 2018. We inventoried the diversity of gall-inducing arthropod and host-plant species richness. Key characteristics of galls in Taiwan and patterns of host specificity were also analyzed.

Materials and Methods

From 1995 to 2018, galls were collected from Taiwan Island, Kinmen Islands, Pescadores Islands, Green Island, and Orchid Island. The plant organs with galls were cut, stored in polyethylene bags, and transported to Taiwan Forestry Research Institute (Council of Agriculture, Taipei) and the Department of Entomology, National Chung Hsing University (Taichung). The samples were either dissected immediately or refrigerated at 5°C for later handling in order to determine the inducing agents and their developmental stages. The gall-inducing agent, host plant, locations, and gall shapes were recorded. Host plants were identified according to the Editorial Committee of the Flora of Taiwan, Second Edition (1993~2000) and APG IV (Chase *et al.*, 2016). Insects were identified according to Möhn (1955), Yukawa (1971), McAlpine (1981), Yang (1984), Mamaev and Krivosheina (1993), Gagné (1994), Melika and Abrahamson (2002), Tokuda

(2004), Tokuda *et al.* (2008), Yeh (2009), Yang *et al.* (2009, 2013), Melika (2006), Melika *et al.* (2010), Tang *et al.* (2011), Melika *et al.* (2013), and Tang *et al.* (2016). For the gall-inducing species that were yet to be described, our use of "species" was closer to the idea of "morphospecies", in which we combined information on the morphology of gall inducers, host-plant species, plant part attacked, and morphology of galls. Gall-bearing plant organs and gall shapes were recorded. Different galls were divided into 10 types as curling, folding, pit, blister, swollen, filz, pouch, rosette, covering, and mark galls according to Küster (1911), Mani (1964), and Dreger-Jauffret and Shorthouse (1992). We recorded the gall-inducing species as "monophagous" when they induced galls on a single plant species only, and as "oligophagous" when they induced galls on closely related plant taxa.

We used the Pearson's Chi-square test and Cramer's V coefficient in R version 3.4.0 (R Core Team, 2017) to analyze the correlations among gall-inducer orders, host-plant classes, host-plant groups, gall-bearing organs, gall shapes, and gall types. To investigate gall inducer and plant richness, we determined gall-inducing species per total plant species and per host-plant species according to the method of Espírito-Santo and Fernandes (2007).

Results

A total of 4,328 galls were collected between 1995 and 2018. Among them, 157 Acarina-induced and 975 insect-induced galls were found on 526 plant species belonging to 91 families. Among the plants, 125 species were endemic.

Gall-inducing arthropods

DIPTERA (42.2%) and **HEMIPTERA** (22.8%) were the major gall-inducing groups (Table 1). A majority of the gall-inducing arthropods (96.0%) were monophagous and thus induced galls on a single host (Table 2). Within the monophagous group, 55.7%, 20.1%, 13.0%, 4.1%, 3.3%, 3.0%, and 0.2% of the galling organs were on leaves, stems, buds, petioles, fruits, flowers, and roots, respectively. By contrast, only 4% of the gall-inducing arthropods were

Table 1. Number of gall-inducing species in Taiwan

	Acari	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Thysanoptera	Total
Described species	21	0	9	48	37	0	0	115
Morphological species	136	19	469	210	121	40	22	1017
Total	157	19	478	258	158	40	22	1132
	13.9%	1.7%	42.2%	22.8%	14.0%	3.5%	1.9%	

Table 2. Specificity of gall-inducing species in Taiwan

	Acari	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Thysanoptera	Total
Monophagous	155	19	458	248	145	40	22	96.0%
Oligophagous	2	0	20	10	13	0	0	4.0%
Total	157	19	478	258	158	40	22	1132

Table 3. Species richness of host species, gall-inducer species, and gall shapes

Host species number within each plant family	Number of Host families	Name of host families	Number of host species within the host family	Number of gall-inducing species within the host family	Number of gall shapes within the host family
above 20	4	Fagaceae	51	183	37
		Lauraceae	47	199	30
		Compositae	23	38	16
		Rosaceae	22	42	21
15-20	7	Theaceae	20	29	14
		Euphorbiaceae	19	38	13
		Moraceae	17	37	15
		Myrtaceae	17	28	11
		Fabaceae	17	26	12
		Rubiaceae	15	24	10
		Verbenaceae	15	28	11
10-14	4	Symplocaceae	13	29	13
		Aquifoliaceae	12	20	10
		Urticaceae	11	15	8
		Caprifoliaceae	10	14	8
5-9	15				
bellow 5	61				

oligophagous (Table 2, Appendix 1). The oligophagous species induced galls on different plants. For example, *Asphondylia* sp.4 were found living on the fruits of *Solanum americanum* and *S. nigrum* (**SOLANACEAE**), *Pitydiplosis puerariae* on the leaves of *Pueraria lobata* and *P. montana* (**FABACEAE**), and *Lasioptera* sp.1 on the petioles of *Zehneria mucronata* (**CUCURBITACEAE**) and the stems of *Achyranthes aspera* var. *rubro-fusca*

(**AMARANTHACEAE**) and *Z. mucronata*. Among the oligophagous gall-inducing arthropods, 48.0% were found on leaves, 19.2% on petioles, 12.3% on stems, 12.3% on buds, 5.5% on flowers, and 2.7% on fruits.

A total of 199 species of gall-inducing taxa (the highest number of gall-inducing taxa in the region) occurred on 183 species of **LAURACEAE** and **FAGACEAE** (Table 3, Appendix 2). **CECIDOMYIIDAE** constituted 42.2% of the

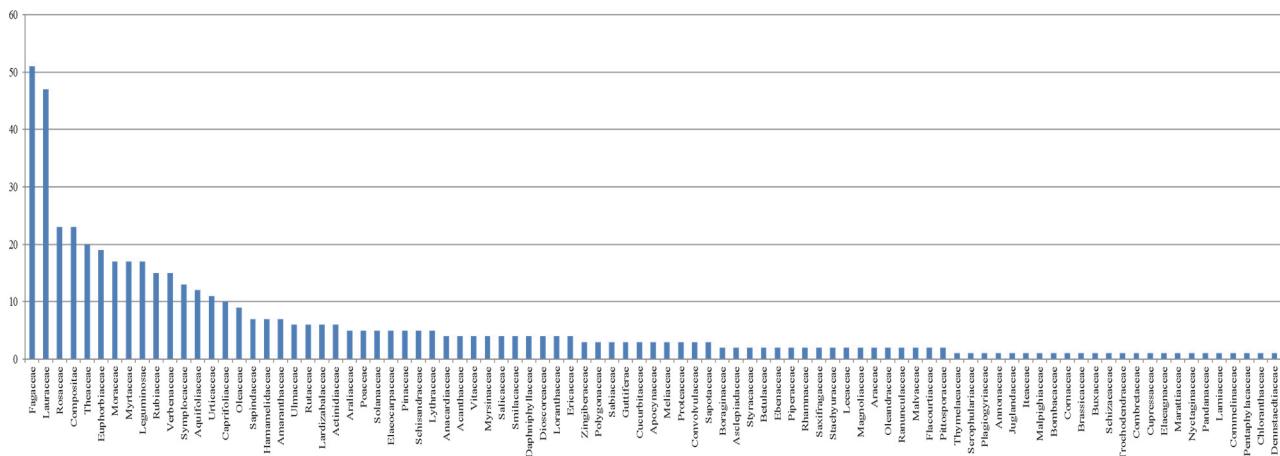


Fig. 1. Distribution of gall-inducing arthropod species among host families arranged from high to low.

gall flora. In addition, 18 species of gall-inducing **ACARI**, 107 of **DIPTERA**, 65 of **HEMIPTERA**, and four of **THYSANOPTERA** were associated with the species of **LAURACEAE**, while 123 species of the Hymenoptera-induced galls were found on **FAGACEAE**. Ten species of **COLEOPTERA** occurred on the species of **MYRTACEAE** and **LYTHRACEAE** (five each). Moreover, 15% of the galls induced by six species of **LEPIDOPTERA** occurred on **EUPHORBIACEAE**.

Host plants

FAGACEAE topped the list of host plants, hosting 51 species of gall-inducing arthropods, followed by **LAURACEAE** and **ASTERACEA**, which hosted 47 and 23 species, respectively (Fig. 1, Table 3). We observed that most of the host plants (71.7%) had gall-inducing inhabitants that belonged to the same order (Table 4). One hundred and forty-nine plant species out of the total 526 host plants hosted more than one order of gall-inducing arthropod. *Cinnamomum subavenium* (**LAURACEAE**) hosted six gall-inducing orders, including three **HEMIPTERA** species, three **DIPTERA** species, two **THYSANOPTERA** species, one **ACARI** species, one **COLEOPTERA** species, and one **LEPIDOPTERA** species (Table 4, Appendix 3).

A majority of gall-inducing arthropods (95.3%) were associated with dicotyledons. Less than 3% of the gall-inducing arthropods were found on monocotyledons, 1.3% were found on gymnosperms, and 0.7% were found on

pteridophytes. Among the different gall-inducing orders, **DIPTERA** was the major order, making use of 41.4% of the recorded dicotyledonous hosts, 62.5% monocotyledonous hosts, and 73.3% of gymnosperms in contrast to the host use of other insect orders. The ratio of galled plant species to the total flora of Taiwan was 0.09, while the average number of gall-inducing species per plant species was 0.19. For the correlation analysis, gall-inducing arthropod orders were both highly and poorly correlated with host-plant families ($p < 0.001$, Cramer's V = 0.53), host-plant groups ($p < 0.001$, Cramer's V = 0.21), and host-plant class ($p < 0.001$, Cramer's V = 0.12). Among the host-plant classes, gall-inducing **DIPTERA** and **ACARI** arthropods had wider host ranges in **PTERIDOPHYTA**, **GYMNOSPERMAE**, dicotyledons, and monocotyledons, in contrast to other gall-inducing agents on the plant taxa (Table 5). There were only few records of galls on **PTERIDOPHYTA** induced by **ACARI** and **DIPTERA**, including three species of **ERIOPHYIDAE** on *Nephrolepis biserrata* (**OLEANDRACEAE**), **ERIOPHYIDAE** sp.16 on *Lygodium japonicum* (Schizaeaceae), **ERIOPHYIDAE** sp.90 on *Angiopteris lygodiifolia* (**MARATTIACEAE**), **ERIOPHYIDAE** sp.105 on *N. auriculata*, **CECIDOMYIIDAE** sp. 124 on *Plagiogyria falcata* (**PLAGIOGYRIACEAE**), and **CECIDOMYIIDAE** sp. 370 on *Pteridium revolutum* (**DENNSTAEDTIACEAE**).

Rosids and asterids were the two major correlated host-plant groups (Table 5). Gall-

Table 4. Gall-inducing order richness in each host species

Number of gall-inducer within each host species	Order	Number of host species	Example taxa	%
6		1	<i>Cinnamomum subavenium</i>	0.2
5		1	<i>Cyclobalanopsis glauca</i>	0.2
4		7	<i>Cinnamomum osmophloeum</i> etc.	1.3
3		28	<i>Bischofia javanica</i> etc.	5.3
2		112	<i>Actinidia latifolia</i> etc.	21.3
1		377	<i>Acer kawakamii</i> etc.	71.7

Table 5. Number of gall-inducing species on host-plant classes and host-plant groups in Taiwan

	Gall-inducing species on host-plant classes				Gall-inducing species on host-plant groups					
	Pteridophyta	Gymnospermae	Dicotyledons	Monocotyledons	Magnoliids	Asterids	Rosids	Monocots	Commelinids	NA
Acari	6	1	147	3	19	41	77	2	1	17
Coleoptera	0	0	18	1	1	3	13	0	1	1
Diptera	2	11	447	20	115	137	150	3	16	66
Hemiptera	0	3	254	1	65	82	81	0	1	29
Hymenoptera	0	0	155	3	1	7	146	1	0	3
Lepidoptera	0	0	39	1	3	10	19	0	1	7
Thysanoptera	0	0	19	3	7	7	4	0	0	4
Total	8	15	1079	32	211	287	490	6	20	127

Table 6. Richness of gall-inducing species and host plants of different orders in Taiwan

	Acari	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Thysanoptera	Total
Number of host family	49	10	56	48	20	20	13	91
Number of host species	136	16	262	183	73	34	20	526
Gall-inducing species/ host species	1.15	1.19	1.82	1.41	2.16	1.18	1.10	2.15

inducing arthropod orders, including **ACARI** (77 species), **COLEOPTERA** (13 species), **DIPTERA** (150 species), **HYMENOPTERA** (146 species), and **LEPIDOPTERA** (19 species) induced galls on different rosid species. Similarly, 7 **THYSANOPTERA** species and 82 **HEMIPTERA** species induced galls on different asterid species.

Among the 91 host-plant families, **DIPTERA** (56), **ACARI** (49), and **HEMIPTERA** (48) were recorded on more than 50% of the host plants (Table 6). There were 269 species of host plants (51.1%) supporting only single species of gall inducers (Table 7). However, *Cyclobalanopsis glauca* (**FAGACEAE**) hosted galls induced by 14 species of **CYNIPIDAE** (e.g., *Cyclocynips*,

Cycloneuroterus, *Dryocosmus*, and *Plagiotrochus*), three species of **CECIDOMYIIDAE**, one species of **ERIOPHYIDAE**, one species of **CURCULIONIDAE**, and one species of **PSYLLOIDEA** (Appendix 3).

Position of galls on plant organs

Galls induced on leaves (55.6%) were more frequent than those on other plant organs (Fig. 2, Table 8). Within each category of gall-inducing taxa, **ACARI** (88.5%, 139/157 species), **DIPTERA** (45.2%, 216/478), **HEMIPTERA** (77.9%, 201/258), **HYMENOPTERA** (47.5%, 75 /158), and **THYSANOPTERA** (90.9%, 20/22) occurred on leaves. **COLEOPTERA** (63.2%, 12/19) and **LEPIDOPTERA** (55.0%, 22/40)

Table 7. Distribution of gall-inducing species per host-plant species in Taiwan

Number of gall-inducing species per Host-plant species	Number of Host-plant species	%
20	1	0.2
14	1	0.2
13	1	0.2
12	2	0.4
11	4	0.8
10	1	0.2
9	3	0.6
8	5	1.0
7	4	0.8
6	17	3.2
5	14	2.7
4	31	5.9
3	54	10.3
2	119	22.6
1	269	51.1

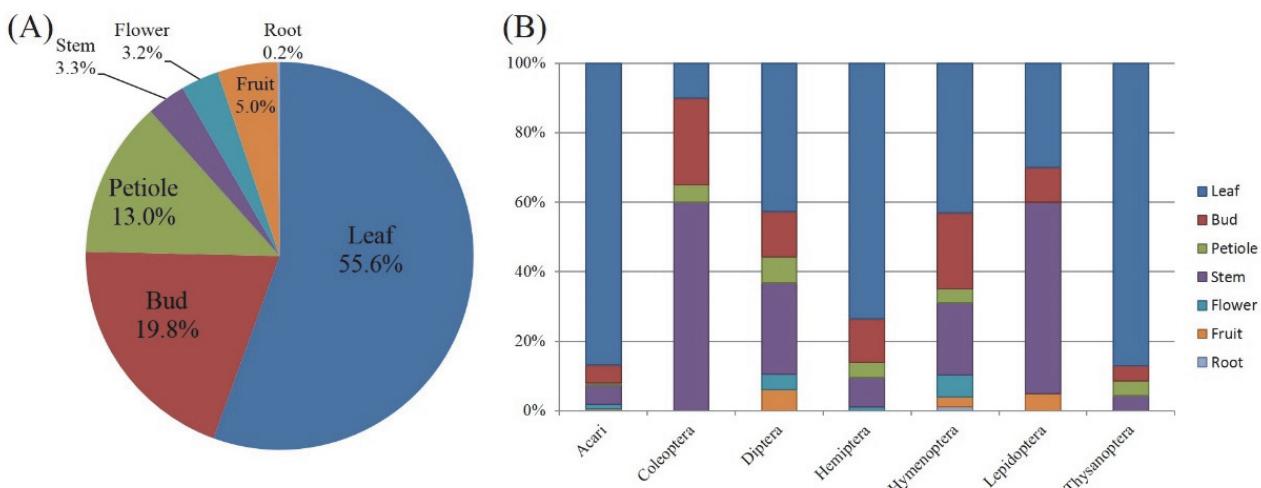


Fig. 2. Positions of galls on plant organs. (A) Positions of galls for all gall inducers. Galls were more frequently found on leaves than on other parts. (B) Positions of galls induced by different orders of gall-inducing arthropods.

induced galls more often on stems.

Shapes of Galls

A total of 66 morphologically varied shapes of galls were recorded (Appendix 1, Appendix 4). Some of the gall shapes were more abundant on specific plant organs. For example, pouch galls were common on leaves (142 species of gall inducers), and spindle-shaped galls were common on stems (87 species). The swollen galls, which only had swollen tissues with no special

shapes were common on buds (32 species), flowers (8 species), and petioles (16 species). With regard to fruit galls, 14 species of gall inducers induced galls of the same fruit shape and were difficult to record. Only spindle-shaped and swollen galls were observed on roots.

Some host plants bore several galls of diverse shapes; these galls were induced by different insects. For example, *Machilus pseudolongifolia* (LAURACEAE) had at least 11 morphologically varied shapes in the covering

Table 8. Number of gall-inducing species on different host-plant organs

Fauna of gall-inducer	Leaf	Bud	Petiole	Stem	Flower	Fruit	Root
Acari	139	9	8	1	2	1	0
Coleoptera	2	12	5	0	0	1	0
Diptera	216	134	66	31	22	38	0
Hemiptera	201	23	34	0	3	12	0
Hymenoptera	75	36	38	5	11	7	2
Lepidoptera	12	22	4	2	0	0	0
Thysanoptera	20	1	1	0	0	1	0
Total	665	237	156	39	38	60	2

and mark galls induced by seven species of **CECIDOMYIIDAE**, three species of **PSYLLOIDEA** (pouch and covering galls), one species of **ACARI** (blister gall), and one species of **THYSANOPTERA** (leaf roll). *Machilus zuihoensis* had 11 different types of blister and mark galls induced by 11 species of **CECIDOMYIIDAE** and two species of **PSYLLOIDEA** (pouch and pit galls). The occurrence frequencies of different gall shapes, from the most to the least, were mark gall (40.3%), covering gall (21.6%), pouch gall (14.9%), curling (5.9%), pit gall (4.9%), blister gall (3.6%), folding (3.5%), swollen (2.7%), filz gall (1.4%), and rosette gall (1.4%).

Types of Galls

Among the 10 gall types, mark and covering galls represent the two dominant gall types in the present study. Gall types were moderately correlated with the order of gall inducers ($p < 0.001$, Cramer's V = 0.44). There were more enclosed types of galls (65.8%) than open types (32.2%). Within each gall-inducing group, the major gall types induced by **ACARI** (58.6%, 92/157 species) and **HEMIPTERA** (29.8%, 77/258) were pouch galls, whereas those induced by **COLEOPTERA** (100%, 19/19), **HYMENOPTERA** (91.1%, 144/158), **DIPTERA** (57.5%, 275/478), and **LEPIDOPTERA** (45.0%, 18/40) were mark galls. **THYSANOPTERA** (54.5%, 12/22) typically induced leaf curls.

Galls induced on leaves and buds were highly correlated with pouch galls (17.8%, 161/902 species of gall inducers), covering galls (23.1%, 208/902), and mark galls (33.4%,

301/902) ($p < 0.001$, Cramer's V = 0.51). The major gall type that was induced on stems (79.3%, 188/237), fruits (89.7%, 35/39), flowers (76.3%, 29/38), and roots (100%, 2/2) was mark gall. Galls on petioles were typically covering galls (63.3%, 38/60). In addition, gall types were highly correlated with the plant clades ($p < 0.001$, Cramer's V = 0.14). We recorded 85 gall inducer species inducing mark galls on 63 species of asterids, 13 on 7 species of commelinids, 98 on 34 species of magnoliids, and 213 on 103 species of rosids.

Discussion

The major host-plant families of gall-inducing arthropods are varied in different areas throughout the world. **FAGACEAE** has been observed to be the dominant host family in Europe and North America (Felt, 1940; Mani, 1964), while **FABACEAE** is the most dominant in Africa (Mani, 1964), India (Mani, 1964; Mani, 1973), and South America (Houard, 1933; Dreger-Jauffret and Shorthouse, 1992; Gonçalves-Alvim and Fernandes, 2001; Maia and Fernandes, 2004). In addition, **ROSACEAE** is more commonly attacked by **HEMIPTERA** in Japan (Yukawa and Masuda, 1996). In the descending order of abundance, **LAURACEAE** (17.6%), **FAGACEAE** (16.2%), and **ROSACEAE** (3.7%) are the principal gall-bearing families in Taiwan.

We recorded 347 species of arthropod gall inducers (30.7%) on 125 endemic host plants (23.8%), whereby **DIPTERA** represented the predominant gall-inducing order (Table 9). The

Table 9. Number of gall inducers found on endemic host plants

Fauna of gall-inducing arthropods	Endemic host-plant species		Gall-inducer species		Number of gall-inducer species in 2006
	species	percentage	species	percentage	
Acari	30	15.6%	34	9.2%	-
Coleoptera	2	1.0%	4	1.1%	1
Diptera	79	41.1%	179	48.2%	83
Hemiptera	57	29.7%	105	28.3%	51
Hymenoptera	12	6.3%	35	9.4%	13
Lepidoptera	7	3.6%	9	2.4%	7
Thysanoptera	5	2.6%	5	1.3%	2
Total	125		371		157

Table 10. Comparison of the gall-inducing faunas of Taiwan and Japan

	Acari	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Thysanoptera
Taiwan	157	19	478	258	158	40	22
Japan	171	20	647	292	222	58	10
Ratio	1.09	1.05	1.35	1.13	1.41	1.45	0.45

endemic host-plant species of *Machilus* sp. and *Cinnamomum* sp. hosted 55 (15.9%) and 38 species (11.0%) of gall-inducing arthropods, respectively (Appendix 3). The endemic *Machilus* spp. were most preferred by DIPTERA, and the endemic *Cinnamomum* spp. were most preferred by the HEMIPTERA. *Machilus* and *Cinnamomum* species are also dominant groups in low and intermediate altitude forests in Taiwan (Su, 1984a, b, 1985). The larger plant families were not expected to host more gall-inducing species in Taiwan (Tung *et al.*, 2006), and the results did not support the plant family size hypothesis, which was suggested by Fernandes (1992). However, the influence of gall-inducing species richness was similar to the effect of presence of hosts such as *Qualea* spp. (Vochysiaceae) in Brazil (Araújo *et al.*, 2013) and *Terminalia sericea* (Combretaceae) in South Africa (Veldtman and McGeoch, 2003). Such endemic host-plant taxa provide diverse local gall-inducing species and represent keystone resources in different localities.

In the Sino-Japanese region, the gall-inducing arthropod fauna is relatively well studied in Japan (Yukawa and Masuda, 1996). In

general, Taiwan and Japan share 1,677 common plant species (Hsieh, 2002). Because gall-inducing arthropods are usually closely limited with regard to host plants, we contrasted host-plant flora and gall-inducing orders between Taiwan and Japan. ASTERACEAE, CAPRIFOLIACEAE, FAGACEAE, LAURACEAE, FABACEAE, and ROSACEAE are preferred by gall-inducing arthropods, which constitute a considerable proportion of DIPTERA, HEMIPTERA, and HYMENOPTERA (Table 10).

In many regions, CECIDOMYIIDAE is the predominant gall-inducing arthropod family (Mani, 1964; Price *et al.*, 1998; Espírito-Santo and Fernandes, 2007). Hanson and Gómez-Laurito (2005) studied gall diversity in Costa Rica, which has a warm temperature, and reported that cecidomyiid species accounted for 70% of the gall inducers. Taiwan has 197 cecidomyiid species/1,000 km² and 1,676 plant species/1,000 km² (Table 11). We compared the proportions of cecidomyiid species to plant species among Costa Rica, Taiwan, and Japan, and approximately similar patterns were observed.

Table 11. Taxonomic distribution of gall inducers in Taiwan, Japan, and Costa Rica

	Gall-inducers in Costa Rica	Gall-inducers in Taiwan	Gall-inducers in Japan
Regions	Neotropical	Tropical to Temperate	Subtropical to Temperate
Latitudes	8° and 12°N	22° and 25°N	24° and 54°N
Acari	6.8%	13.9%	12.0%
Coleoptera	1.4%	1.7%	1.4%
Diptera	71.7%	42.2%	45.6%
Hemiptera	7.1%	22.8%	20.6%
Hymenoptera	6.8%	14.0%	15.6%
Lepidoptera	5.7%	3.5%	4.1%
Thysanoptera	0.6%	1.9%	0.7%
Number of plant species per 1,000 km ²	3368	1676	1366
Number of cecidomyiid species per 1,000 km ²	290	197	143

The complete faunal study is a long-term project, and the data is still dynamic by further research. We observed a positive relationship between gall-inducing arthropod orders and host-plant families in Taiwan. In the present study, the types of galls were influenced by many factors such as the orders of gall inducers, positions of galls on plant organs, and plant groups.

Acknowledgments

We thank Taiwan Forestry Research Institute, Forestry Bureau of Taiwan, and the Ministry of Science and Technology for funding support. We thank Dr. Raman Anantanarayanan (Charles Sturt University, NSW Australia) for valuable and constructive comments and reviewing the manuscript. We also thank Chia-Chin Hsu, Chin-Jung Liu, Sheng-You Lu, Hsin-Ting Yeh, Ya-Ling Lin, Pei-Jung Lin, Chia-lung Huang, Yi-Shyr Chung, Li-Ping Ju, Chih-Sheng Wu, Wen-Yu Wang, Chia-Chun. Hsu, Min-Kuan Chu, Hsiao-Ling Lee, Te-Pin Chang, Tsung-Yu Hung, Yi-Der Lin, Sz-Yi Tsai, Cheng-Te Hsu (Taiwan Forestry Research Institute, Council of Agriculture, Taiwan), Gwo-Ing Liao (Department of Life Sciences, National Cheng Kung University, Taiwan), Shau-Ting Chiu (Division of Biology, National Museum of Natural Science,

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台灣造癟節肢動物之多樣性

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收件日期：2018 年 8 月 6 日 接受日期：2018 年 11 月 30 日 線上刊登日期：2019 年 6 月 3 日

摘要

根據 1995 至 2018 年於台灣、金門、澎湖、綠島與蘭嶼的植物癟普查，共採集到 4,328 種由節肢動物所造的癟，其中有 96.0% 的造癟節肢動物為單食性。已記錄的七目造癟節肢動物中，雙翅目 (42.2%) 與半翅目 (22.8%) 為主要的兩個造癟類群。產癟的寄主植物則以樟科 (17.6%) 與殼斗科 (16.2%) 為本地優勢的寄主植物。這些植物癟中，封閉式癟 (65.8%) 種類較開放式癟 (32.2%) 多。多數寄主植物 (44.7%) 被造癟節肢動物引發 2 種以上的癟，最多達到 11 種外形的癟。若比較寄主植物的造癟部位，葉片為較常被造癟的器官 (55.6%)。在所有造癟的分類群中，癟蚋科在造癟種類數、蟲癟豐富度與寄主植物產癟部位都是最多样化的類群。

關鍵詞：植物癟相、生物多樣性、癟形態、寄主植物、造癟節肢動物



Biology of a Gall-inducing Species of *Anselmella* (Hymenoptera: Eulophidae) within the Fruits of *Syzygium samarangense* (Myrtaceae)

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Received: 21 August 2018 Accepted: 24 December 2018 Available online: 3 June 2019

ABSTRACT

Gall-inducing insects develop within the galls they induce, and generally remain undetected. In recent years, many instances of gall-inducing insects turning into invasive organisms internationally have come to light. *Anselmella miltoni* induces seed-like galls within the fruits of *Syzygium samarangense* was found in Taiwan recently, thus impacting severely on the country's earnings made out of the export of fresh fruits of *S. samarangense*. Biological details of *A. miltoni* are sparsely known, thus limiting an effective management. We studied *A. miltoni* populations from an orchard in Jhongpu, Chiayi and report in this paper its biology, including notes on field populations, synchronization between fruit development in *S. samarangense* and gall development, emergence, and adult longevity. *Anselmella miltoni* lays eggs during the anthesis stage of fruit phenology of *S. samarangense*. The egg stage of *A. miltoni* overlaps with the petal fall stage in *S. samarangense*. Immature stage of *A. miltoni* develops through the rapid stage to middle fruit stage. *Anselmella miltoni* enters into pupal stage and adults emerge, when the fruits of *S. samarangense* in mature stage. A gall inside the fruit includes many compartments, each compartment with one individual of *A. miltoni* inside. Average number of gall compartments within a fruit is 20.08 ± 11.5 . The emergent adults leave its fruit unsynchronized and the period of adult emergence from one gall last for 3~7 days. Adult longevity is 2.36 ± 1.16 days. Based on biological details, we offer suggestions for the management of *A. miltoni*.

Key words: gall, invasive species, ovule, phenology

Introduction

Gall-inducing insects such as *Orseolia oryzae* (Diptera: Cecidomyiidae) and *Leptocybe invasa* (Hymenoptera: Eulophidae) can damage economically useful plants, such as *Oryza sativa* (Poaceae) and different species of *Eucalyptus*

(Myrtaceae), which are presently treated as 'invasive' organisms (Rajamani *et al.*, 2004; Mendel *et al.*, 2004). Gall-inducing insects remain concealed within galls, rendering their management difficult. Moreover, depending on the morphology of gall-bearing plant organs, some of the gall-inducing insects are hard to

detect during early stages of growth. In such cases, spread and outbreaks occur easily through exporting and trading of host plants (Mendel *et al.*, 2004; Li *et al.*, 2006; Csóka *et al.*, 2017).

Gall-inducing insects, such as *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae) on various species of *Castanea* (Fagaceae), *Procontarinia robusta* (Diptera: Cecidomyiidae) on *Mangifera indica* (Anacardiaceae), *Litchiomyia chinensis* (Diptera: Cecidomyiidae) on *Litchi chinensis* (Sapindaceae), *Leptocybe invasa* (Hymenoptera: Eulophidae) on different species of *Eucalyptus*, *Quadrastichus erythrinae* (Hymenoptera: Eulophidae) on various species of *Erythrina* (Fabaceae) have been known as invasive organisms in Taiwan in recent years (Kim *et al.*, 2004; Yang *et al.*, 2004; Tang *et al.*, 2015). They induce galls on either the foliage or young shoots and damage the plant by affecting either photosynthesis or bud growth.

A majority of the known gall-inducing Hymenoptera lives on stems, buds, and leaves, whereas those attacking fruits are few. However, a few instances of seed-gall-inducing Eulophidae, such as species of *Quadrastichodella*, *Leprosa*, and *Moona* are known (Ikeda, 1999; Doğanlar and Doğanlar, 2008; Kim and Salle, 2008). *Quadrastichodella nova* develops on *Eucalyptus resinifera* and *E. umbellatus* and induces galls within seed capsules (Doğanlar and Doğanlar, 2008). *Moona spermophaga* Kim & La Salle induces galls on the seeds of two *Corymbia* species (Myrtaceae) (Kim *et al.*, 2005). *Anselmella miltoni* induces galls within the seed chamber of the fruits of *S. samarangense*. It has emerged as a serious quarantine problem (Fig. 1) (Xiao *et al.*, 2006; Huang *et al.*, 2008).

Anselmella includes four species (*A. kerrichi*, *A. malacia*, *A. miltoni*, and *A. oculata*) and mainly distributed in Malaysia, India, the Philippines, Fiji, and in the state of Queensland (Australia) (Bouček, 1988; Xiao *et al.*, 2006). All the four species of *Anselmella* induce seed galls within the fruits of various *Syzygium* species (Xiao *et al.*, 2006). Knowledge of *Anselmella* is limited to taxonomic reports only. Its status as an invasive was not known until it was trapped in port-quarantine stations. In 2003, at the airport quarantine control of Zhengzhou, China, galls within the fruits of *S. samarangense* from a

passenger from Malaysia. The emergent adult from the gall was named three years later as *Anselmella malacia* (Xiao *et al.*, 2006; Chao *et al.*, 2007). Tsai *et al.* (2013) reported another similar instance in Hainan, China that the airport quarantine office intercepted *A. malacia* from fruits of *S. samarangense* carried by a passenger from Vietnam. Curiously, *A. malacia* was trapped only in the customs office of China, never known in its place of origin. Whether it is a pest of Malaysia and Vietnam presently remains unclear. Fruits of *S. samarangense* exported from Taiwan to China were examined by quarantine officials and found a species of the *Anselmella*, which was different from *A. malacia* and was determined as *A. miltoni* in 2005 and 2007 (Huang *et al.*, 2008). The incidence of *A. miltoni* strongly affects export of *S. samarangense* from Taiwan to China. *Anselmella miltoni* are recognized as quarantine-restricted insects, since the Government of PR China claims that they have no record of *Anselmella* associated with the fruits of *S. samarangense* (Chao *et al.*, 2007; Huang *et al.*, 2008; Tsai *et al.* 2013).

Syzygium samarangense Merr. et Perry. (Myrtaceae), commonly known as wax apple tree, is indigenous to Malaysia and Andamans (Republic of India). This is often planted as crop, ornamental, and shade tree (Lin *et al.*, 2004; Chen *et al.*, 2012). In Taiwan, *S. samarangense* is an important crop tree, cultivated over 5,500 ha in southern and central Taiwan, with the average production exceeding 5,500 t/y (Chen *et al.*, 2012). *Syzygium samarangense* flowers from January to April, and the fruit is usually harvested between May and July in Taiwan (Lan, 2004; Lin *et al.*, 2004; Chen *et al.*, 2012). Harvesting of the fruits would usually occur during wet season (May to September) in Taiwan, during when high humidity and temperature would induce cracking of fruit skin, which acts as a port for pathogens, such as *Pestalotiopsis eugeniae* (Melanconiales: Melanconiaceae), *Phytophthora palmivora* (Peronosporales: Peronosporaceae), and *Botryodiplodia theobromae* (Botryosphaeriales: Botryosphaeriaceae) (Tsai, 2012). Therefore, *S. samarangense* remains stressed and resulting in low-quality fruits during its natural season in Taiwan. Most

farmers used various cultivation practices, such as pruning branches, covering the whole tree with black net or inducing stress by injuring root and trunk, which allows farmers to successfully adjust the time of harvesting *S. samarangense* whole year round according to the area condition (Lan, 2004; Chen *et al.*, 2012), and highly promotes profit in price and quality (Huang, 1993; Lee, 2010).

The internal feeding habit with minimal external symptoms on the infested fruits of *S. samarangense* explain why little is known about this insect. Lack of detailed biological knowledge impede developing strategies for its effective management, especially when *A. miltoni* is a newly emerging invasive insect on *S. samarangense* in Taiwan. Not until August 2007, fruits of *S. samarangense* planted in Jhongpu, Chiayi of central Taiwan, were found attacked by *A. miltoni*. Many questions remain to be answered. How does *A. miltoni*'s life cycle match with host-plant phenology? How long do adults survive? Do they extend the longevity by consuming honey from the flowers of *S. samarangense*? At what stage do they initiate galls? How many individuals exist within one fruit? Do they reproduce sexually? If so, what is the sex ratio? Keeping these questions in full view, this study aimed at investigating the biology of *A. miltoni* on *S. samarangense* in Taiwan by answering the above questions with an intent to manage these populations.

Materials and Methods

Phenology of *S. samarangense* and *A. miltoni*

Our sampling orchard was at Jhongpu, Chiayi ($23^{\circ}24'47.2''N$, $120^{\circ}33'41.2''E$), Taiwan where large areas suffer production loss because of *A. miltoni* infestation. Collections of *A. miltoni* were made weekly from May to August in 2014 and different developmental stages of the fruits of *S. samarangense* was obtained. Phenological stages was recorded according to the Manual of Plant Protection, Council of Agriculture, Government of Taiwan (Lin *et al.*, 2004) which classified that into eight stages: middle bud stage (豆粒期), full white stage (白肚期), anthesis stage (盛花期), petal fall stag (胚仔期), rapid

stage (合臍期), young fruit stage (幼果期), middle fruit stage (中果期), mature stage (熟果期) (Fig. 2). As the blooming of flowers on the tree is unsynchronized, quantitative recording of the presence of different phenological stages became necessary and we followed the sampling method of Peduzzi *et al.* (1996). In each field observation, we randomly selected different branches of sampling trees in the orchard to count the number of each developmental stages on each branch of *S. samarangense*. Phenological counting is completed when accumulated number of every developmental stage has reached ten. The ratio of each developmental stage to total number of sampling was recorded. In case all branches had been observed but some developmental stages remained less than ten, the ratio of developmental stages was counted directly using all the available samplings.

We collected adults of *A. miltoni* using both sticky traps and net sweeping. We suspended 20 yellow sticky traps in the sample site. Each trap was at least two *S. samarangense* trees apart (c. 10~30 m) and replaced every week. Collections of *A. miltoni* ceased when no flower and fruit could be observed for at least two weeks, which is around September. Samples from sticky traps and net sweeps were examined under stereo binocular microscope (Leica EZ4, Wetzlar, Germany). Adults of *A. miltoni* were separated and stored in 70% alcohol.

Gall development in relation to phenology of *S. samarangense*

Flowers and fruits of *S. samarangense* collected from the sample site were dissected to determine the developmental stages of the gall and *A. miltoni*. The *A. miltoni*-induced gall tissue of *S. samarangense* usually will include one gall, but may occasionally comprise up to three (Fig. 1), inside one single fruit chamber. Every gall consisted of several compartments, each with one individual larva of *A. miltoni*. Forty to 50 fruits of *S. samarangense* were collected weekly in March-September 2014 and were dissected in laboratory to determine the stage of insect development and corresponding phenology. The galls that included the pupae were placed in a circular plastic cage (diameter: 7.5 cm, height: 4 cm) to obtain adults. Emerging

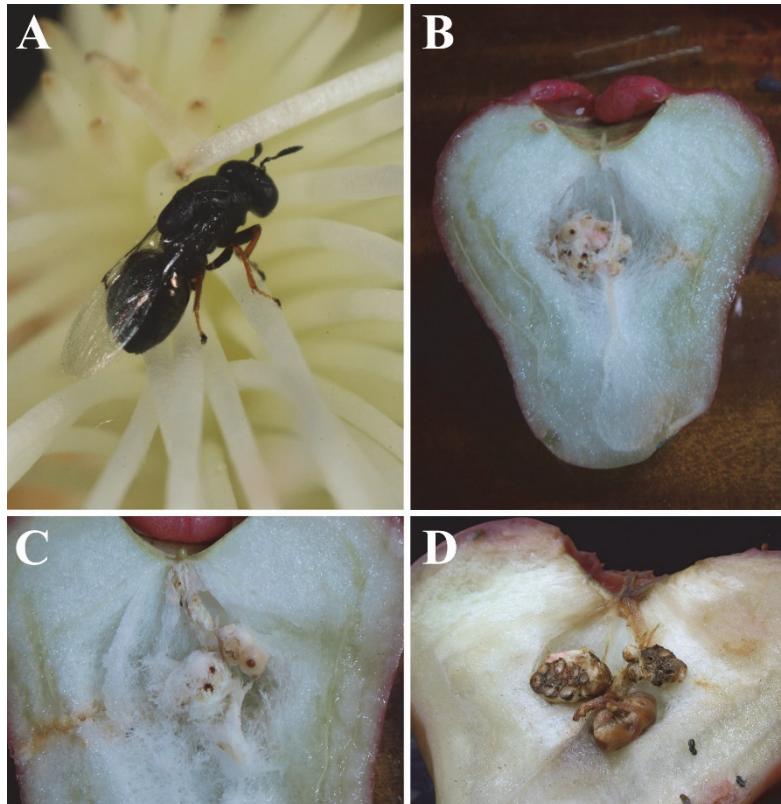


Fig. 1. A, Adult of *Anselmella miltoni* visiting flower of *Syzygium samarangense*. B, infected *S. samarangense* by *Anselmella miltoni* with one gall. C, D, two and three galls in one infected *S. samarangense* respectively. Adult emergence holes on the galls and a tunnel on the left of the fruit could be seen in C. The three galls in D had the upper two already being dissected the inside compartments could be seen while the bellow one remained intact.

adults were stored in 70% alcohol and all voucher specimens were deposited in the National Chung Hsing University.

Number of gall compartments and adult emergence span

Newly emerged *A. miltoni* adults were collected and counted daily from 10-12 am. We determined the sex and date of newly emerged adults. The period from first to the last adult emergence from the gall of a fruit was recorded as 'adult emergence span'. If no *A. miltoni* emerged from the gall for three days, we then dissected them to count their numbers and measure the gall-compartment diameter.

Galls with adult emergence > 50% were included for the analysis of relationship between number of compartments/gall and emergent adults using a simple linear regression. The linear regression model was performed using the program PAST 3 (Hammer *et al.*, 2001) and the tests of significance were verified at $P < 0.05$.

Adult longevity of *Anselmella miltoni*

We reared the newly emergent adults from the adult-emergence span experiment in round plastic cages for measuring adult longevity. Adults were reared individually in each of the following three treatments which provided either 10% honey solution (treatment 1) or water (treatment 2), or none (treatment 3). In treatments 1 and 2, cotton balls were soaked in appropriate solution (honey and water) and placed in a plastic dish (diameter 5 mm) which was placed within the plastic cage stored in a growth chamber at $25 \pm 2^\circ\text{C}$. The soaked cotton balls were renewed daily. The dead adults were checked and removed, and stored in 70% alcohol daily. Data were analyzed using PAST 3, and nonparametric statistics were performed. Significant differences were accepted at $P < 0.05$.

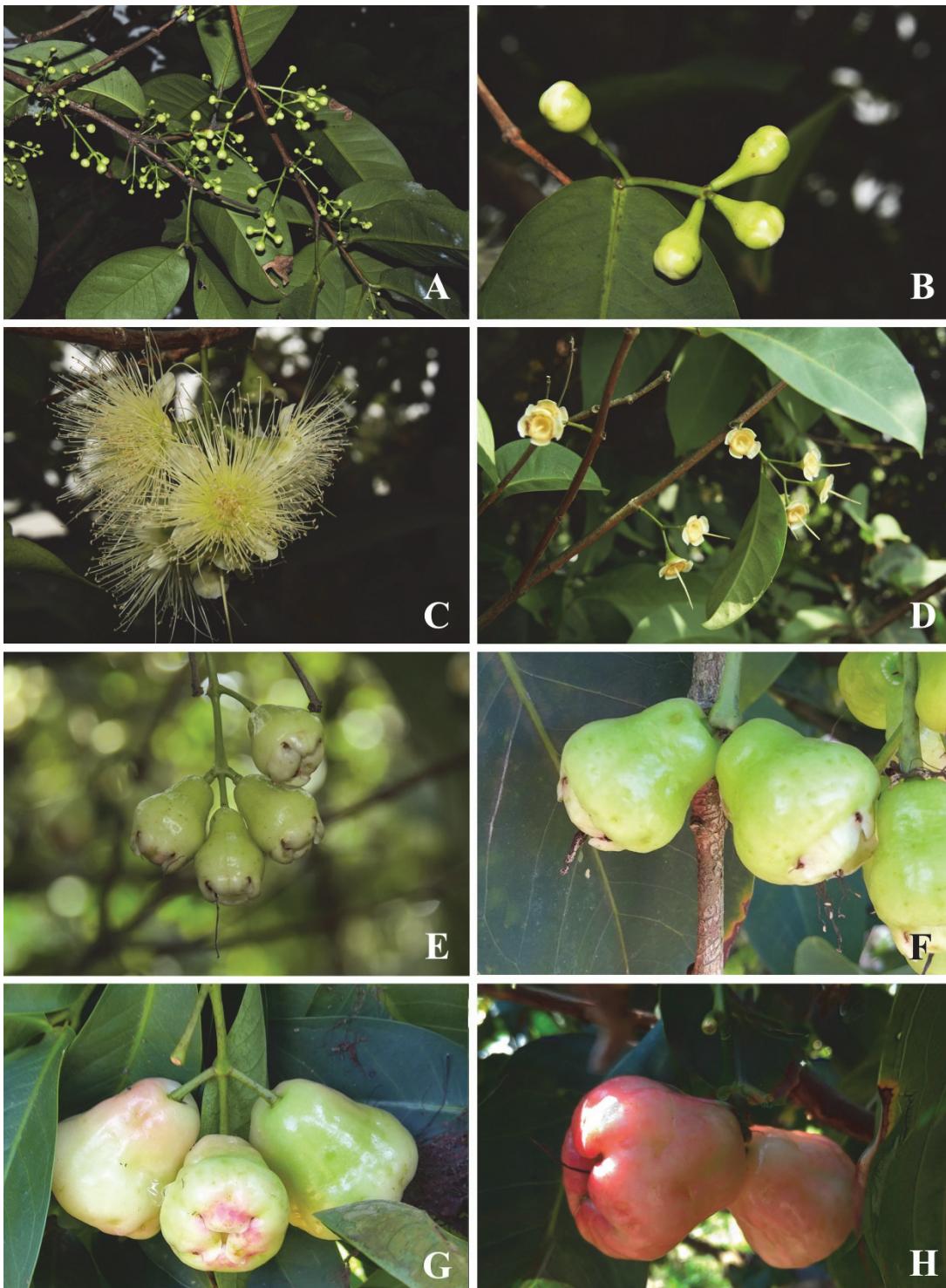


Fig. 2. Development stage of *Syzygium samarangense* based on Lin et al. (2004). A, Middle bud stage (豆粒期). B, Full white stage (白肚期). C, Anthesis stage (盛花期). D, Petal fall stage (胚仔期). E, Rapid stage (合臍期). F, Young fruit stage (幼果期). G, Middle fruit stage (中果期). H, Mature stage (熟果期).

Results

Phenology of *S. samarangense* and investigation of *A. miltoni* populations in orchard

The reproductive phase of fruits of *S.*

samarangense in the sampling area lasted from May to August and two growing cycles occurred in the same year (Fig. 3). In mid-May, *S. samarangense* was in the middle bud stage. Fully blooming of flowers, at anthesis stage, were first observed on 19 May 2014, which

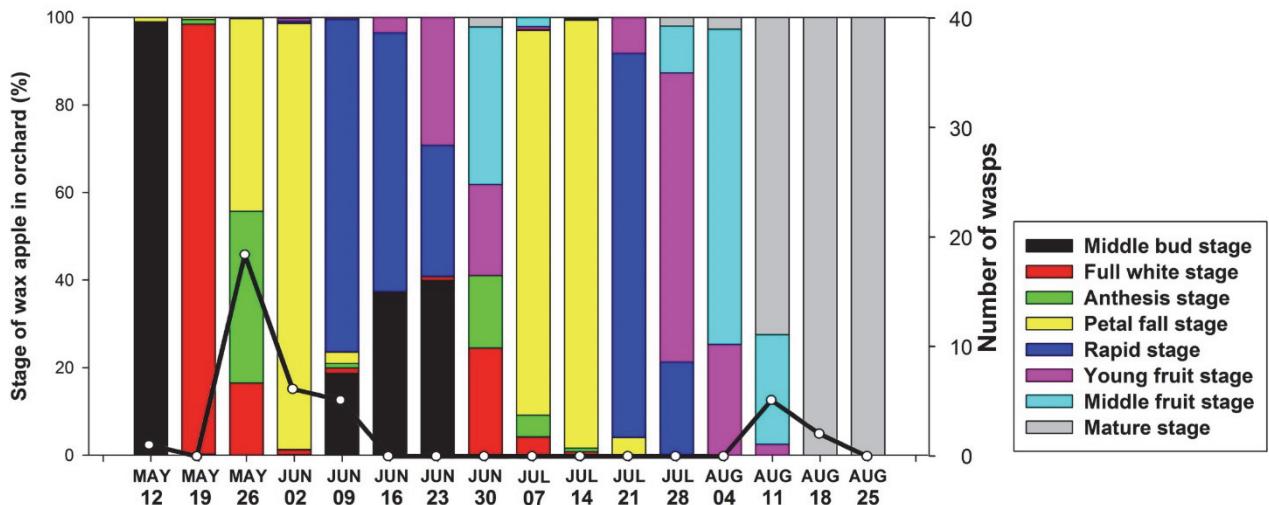


Fig. 3. The developmental stage of *Syzygium samarangense* fruit phenology and number of *Anselmella miltoni* adults collected by sweeping and sticky paper in orchard. Different colors indicate different growing stage of *S. samarangense*.

peaked at 39.2% of phenology in orchard in late May. Young fruits of the first growing cycle appeared in mid-June and by this time, the second middle bud stage also began. Mature stages of the first growing cycle did not occur because most of the fruits had dropped in late June. The second anthesis stage of *S. samarangense* also occurred in late June and through the next six weeks, mature stages occurred.

Using sweep nets and sticky papers, *A. miltoni* were collected when *S. samarangense* were at the anthesis stage and the petal fall stage during the first growth cycle, and a few individuals of *A. miltoni* were collected during mature stage of *S. samarangense* in their second growing cycle. The ratio of infestation in the two growing cycle were 28.6% ($n = 406$) and 7.5% ($n = 268$), respectively, and there were significant differences in the infestation rate between the two growing cycle (Chi-square test, $p < 0.001$).

Gall development in relation to phenology of *S. samarangense*

A fruit chamber with galls induced by *A. miltoni* included 20.8 ± 11.5 compartments ($n = 57$). Each compartment was circular (as in cross-sections) and the diameter was 2.55 ± 0.46 mm ($n = 31$). As the minute (< 0.1 mm) and transparent larvae of *A. miltoni* at the initial stage is generally hard to distinguish from the

floral tissue of *S. samarangense*, characteristics of both insect and gall development were used to categorize their development. The six developmental stages (Fig. 4) were as follows: 'Ea' stage: eggs visible on host ovules with no obvious changes in the host-plant tissues; 'Eb' stage: sponge-like tissue developing around eggs, eggs still visible; 'La' stage: galls evident and the neonate larvae as well, inner wall of the gall moist and soft; 'Lb' stage: galls mature and the larvae obvious, inner wall of gall firm and no more moist; 'P' stage: larvae have turned into pupae; and 'PA' stage: both pupae and adults occur at the same time, one individual in one compartment, some adult may have chew a hole leaving the fruit

The life cycle of *A. miltoni* and developmental stage of *S. samarangense* were shown in Fig. 5. The Ea stage of *A. miltoni* occurs during petal fall stage of *S. samarangense*. During 'rapid stage', 21% and 38% *A. miltoni* develop to Eb and La stage. During young fruit stage, 82 *A. miltoni* (56.6%) were in La stage. Then, 46 individuals (46.9%) get into Lb stage and 33 individuals (33.7%) in P stage when *S. samarangense* reached the mid fruit stage. In mature stage of *S. samarangense*, 80% individual of *A. miltoni* grow to P stage and 20% have emerged. The *A. miltoni* adult stayed inside gall compartment for several days before exit the fruit (see next section). Overall, it takes about 35

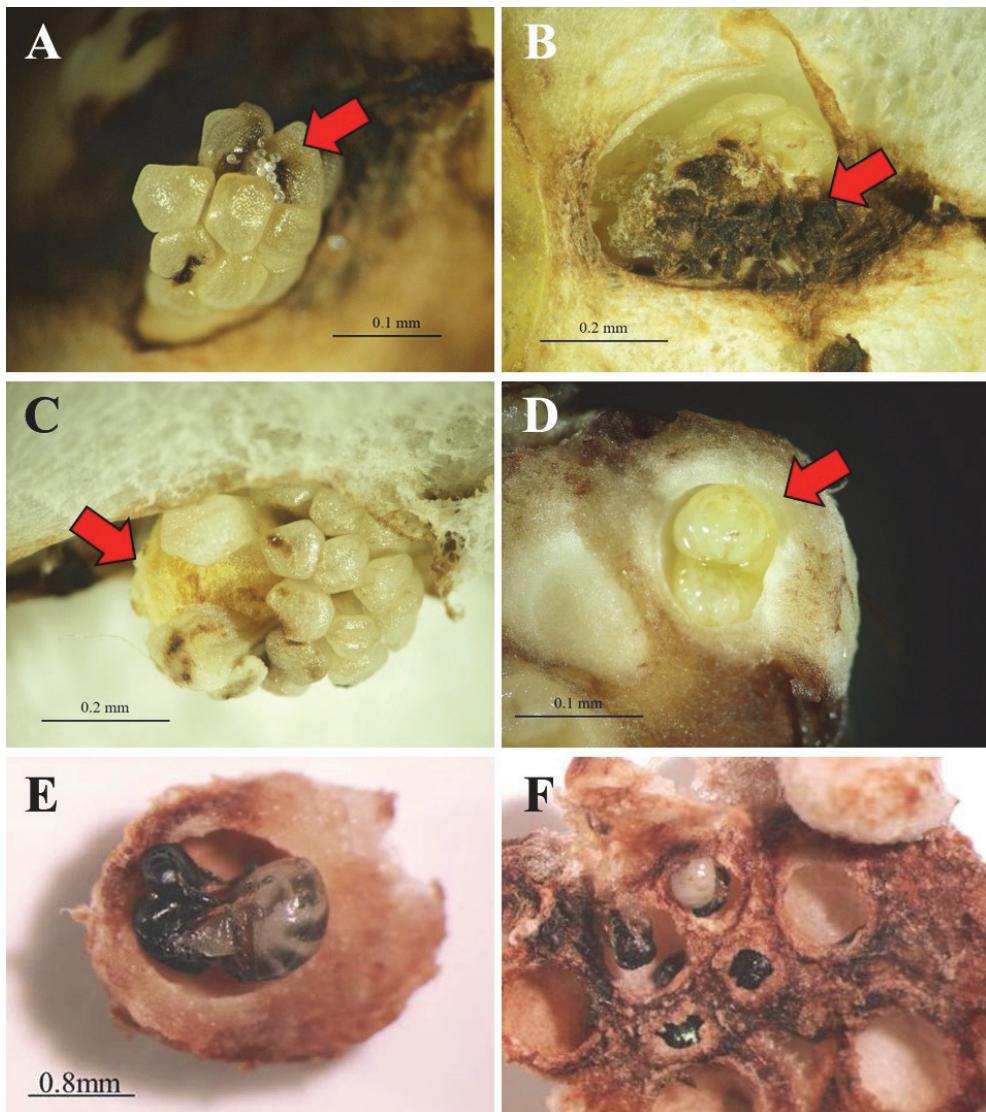


Fig. 4. Developmental stage of gall of *Anselmella miltoni*. A, Ea-eggs visible on ovules with no obvious changes in the host-plant tissues. B, Eb-sponge-like tissue developing around eggs, eggs still visible. C, La-galls evident and the neonate larvae as well, inner wall of the gall moist and soft. D, Lb-galls mature and the larvae obvious, inner wall of gall firm and no more moist. E, P-larvae have turned into pupae. F, PA-both pupae and adults occur at the same time; adults within gall compartments.

days from egg stage to adult.

Adult emergence span

Population of *A. miltoni* from galls did not emerge simultaneously. The time for all adults emerging from a gall may last from 3 to 7 days. The emergent period was spread over seven days and more males than females emerged in the first day (Fig. 6). The number of compartments positively correlated with adult emergence ($y = 0.09153x + 0.2160$, $R^2 = 0.8178$, $P < 0.001$) (Fig. 7). More the number of compartments in a galled fruit, the more number of days necessary for *A. miltoni* populations to emerge. The sex ratio

(male/female) is 1: 0.66. Some galls included more of adult females than males.

Adult longevity of *A. miltoni*

The longevity of adult *A. miltoni* revealed no significant differences among 10% honey solution, water, and no food treatments (Kruskal-Wallis test, $X^2 = 0.0019$, $P = 0.99$, Fig. 8), and also no significant differences between genders (Mann-Whitney test, $U = 213$, $P = 0.8558$). Longevity of adult *A. miltoni* reared by 10% honey solution was 2.21 ± 0.86 d ($n = 56$). Water treatment was 2.62 ± 1.67 d ($n = 36$) while

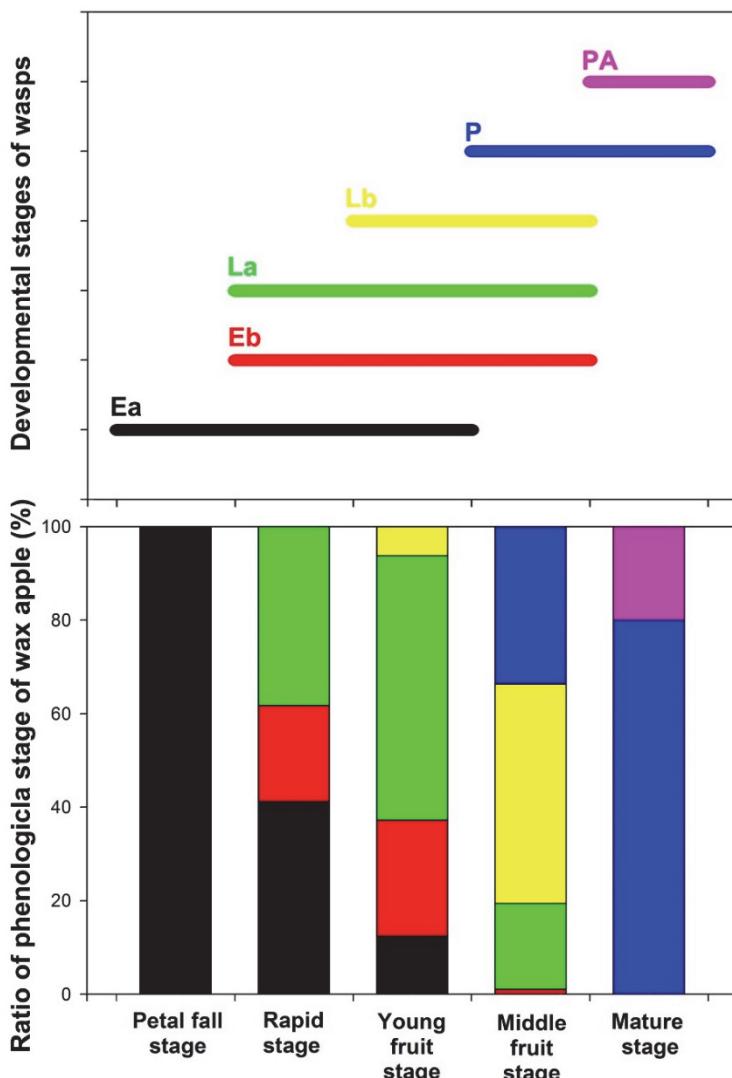


Fig. 5. The developmental stage of gall and *Anselmella miltoni* related to the phenological stage of *Syzygium samarangense*. Colors indicate different developmental stage of *A. miltoni*. Ea, eggs visible on ovules with no obvious changes in the host-plant tissues. Eb, sponge-like tissue developing around eggs, eggs still visible. La, galls evident and the neonate larvae as well, inner wall of the gall moist and soft. Lb, galls mature and the larvae obvious, inner wall of gall firm and no more moist. P, larvae have turned into pupae. PA, both pupae and adults occur at the same time; adults within gall compartments.

no food treatment was 2.36 ± 0.96 d ($n = 34$). Adult longevity of male and female were 2.7 ± 1.3 d ($n = 73$) and 2.3 ± 1.3 d ($n = 53$), respectively (Fig. 8), while the average of total individuals was 2.36 ± 1.16 d ($n = 126$).

Discussion

Anselmella miltoni is a newly emerging invasive living on the fruits of *S. samarangense* in Taiwan. Although this species does not induce either an immature fruit drop or decay in pulp in *S. samarangense* as would populations of *Bactrocera dorsalis* (Diptera: Tephritidae) do,

the Taiwanese horticultural industry sees *A. miltoni* as an issue of deep concern. Traditionally farmers growing *S. samarangense* wrap the branches bearing young fruits with a paper bag to avoid infestations by *B. dorsalis* and other pestiferous arthropods (Lin *et al.*, 2004). However, this practice does not work for *A. miltoni* because *A. miltoni* lay eggs much earlier, during anthesis and petal fall stages in flowers, much before bagging done by farmers.

Agriculturally relevant gall-inducing insects are often neglected because of two reasons. First is that the host usually does not display obvious

symptoms during early stages. Second, gall-inducing insects live most of life endophytically, i.e., remain embedded, concealed within host-plant tissues, which makes it all the more difficult to manage using contact insecticides (Xu *et al.*, 2009; Csóka *et al.*, 2017). These reasons also caused barriers in the present study. Attack by populations of *A. miltoni* did not result in apparent damage to fruits. Most likely *A. miltoni* will not emerge as a key pest of *S. samarangense* compared with *B. dorsalis*. However, the export of *S. samarangense* fruits from Taiwan to countries such as People's Republic of China are declared pest-free areas which made it a matter of deep concern. The *A. miltoni* is listed as a quarantine pest by the Chinese Quarantine Authority, and therefore, any inspected fruits including the infestation at the harbor will result in the destruction of the commodity and the estimated overall damage would cost USD 8.6 million annually to Taiwan (COA, 2017). An effective management, therefore, is necessary to prevent this economic loss. Because of the embedded nature of *A. miltoni*, an integrated pest management would be the practice of choice, since the biology and bionomics of *A. miltoni* supplied in this paper would be useful.

As adults of *A. miltoni* emergence from a mature fruit of *S. samarangense* would take ca. 7 days (Fig. 6), some of the early emerging individuals can flag early signs of insect emergence to farmers. If the paper bags tied around young fruit-bearing branches are endowed with transparent windows, periodical inspection for the *A. miltoni* could be made easily. For reducing the export loss, we propose that farmers should inspect early emerging population using the transparent window of paper bags during cultivation. In spite of *A. miltoni* population, no obvious symptom may occur on the infested fruits of *S. samarangense*. Once an individual adult found inside a certain bag, all fruits in that paper bag should be excluded from exporting and inspection on other bags should be done more carefully.

Gall-inducing insects require particular host stage to induce galls. Therefore, they always synchronize with specific phenological stages in their host plants (Yang and Tung, 1998; Yukawa, 2000). Adults of *A. miltoni* do not emerge

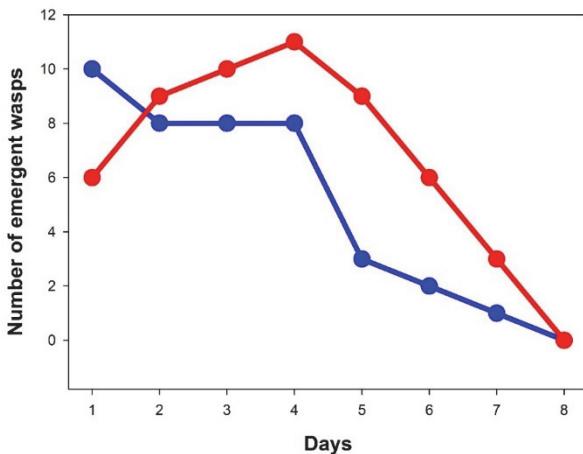


Fig. 6. The emergence frequency of two genders of *Anselmella miltoni* from 15 galls. Blue: male; red: female.

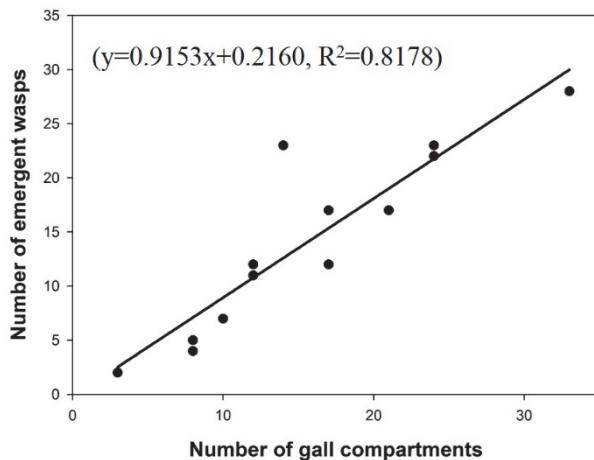


Fig. 7. The relationship of number of gall compartments and emergent adults of *Anselmella miltoni*.

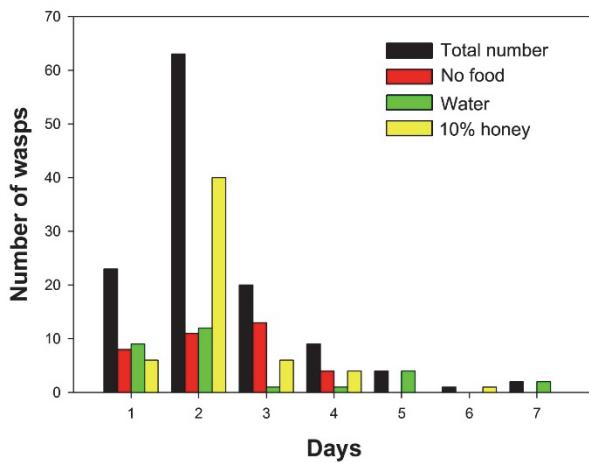


Fig. 8. Adult longevity of *Anselmella miltoni* of different rearing treatments. Black: total number in three treatments; red: no food; green: water; yellow: 10 % honey.

simultaneously. Flowering time in *S. samarangense* lasts for 7~10 days in January-May each year. Reproductive period of *S. samarangense* extends between 90 and 160 days, the remaining is vegetative period. Adults of *A. miltoni* live only for 2~3 days. However, the unsynchronized emergence time of adults from a gall, usually last for 7 days, may extend the appearance of the population in the field. *Syzygium jambos* (L.) Alston (Myrtaceae) is also reported as host of *A. miltoni* in Taiwan forming seed-like galls similar to those known in *S. samarangense* (Yang and Lin, 2016). Although both of the hosts bloom in March to April, however, the time span of flowering is not quite the same and varies with different cultivation areas. How this short-lived insect completes its life cycle needs further research.

The adult emerging trait of *A. miltoni* also emphasizes the importance of field sanitation. According to this study, one seed gall includes 20.8 ± 11.5 compartments. The maximum emerging period for *A. miltoni* could up to seven days and the more gall compartments the longer emerging period. No matter whether the emerging holes appear, the dropped infested fruits must be removed and burned, since they could be source of new infestations.

There is no previous record of *A. miltoni* of Taiwan until Huang *et al.* (2008) reported it from the fruits of *S. samarangense* imported at the Fu-Chien Harbor (China) during routine quarantine inspection. However, examination of the specimens will find that some head characters do not fit the original description of *A. miltoni* Girault 1926 and the species status appears to be dubious. As the known hosts of this species are exotic to Taiwan, when and where this species of *Anselmella* wasp get into Taiwan and how it becomes an invasive pest remained to be answered.

Acknowledgments

We thank the Bureau of Animal and Plant Health Inspection and Quarantine for supporting the project (103-救助調整-檢-01). We also thank Mr. Bo-Han Kao offered the orchard for collecting, and farmers in the 16th Agricultural Production and Marketing class of

Meishan Township to share the information about *S. samarangense* and *Anselmella miltoni* in field. We thank Chi-Cho Huang, Fengshan Tropical Horticultural Experiment Branch, Taiwan Agricultural Research Institute, Council of Agriculture and Shao-Ting Chiu, National Museum of Natural Science, for providing useful phenological information. We appreciate Chun-I Chiu, Jen-Ruei Lin, Cyuan-Chen Jhong and other members in the Laboratory of Insect Systematics and Evolution, National Chung Hsing University, for collecting and dissecting the sample.

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於蓮霧（桃金娘科）果實內部造癟的 *Anselmella* 紬小蜂（膜翅目：紬小蜂科） 生物學

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收件日期：2018 年 8 月 21 日 接受日期：2018 年 12 月 24 日 線上刊登日期：2019 年 6 月 3 日

摘要

造癟昆蟲生活於植物組織形成的癟內，隱匿式的習性不易被偵測，近年來不乏成為國際入侵性害蟲的例子。危害蓮霧的米爾頓紬小蜂在果實空腔內形成類種子癟，近年於台灣發現，嚴重影響台灣蓮霧的外銷收益，然而關於此物種的生物學資料仍相當缺乏，影響防治效率。因此本研究以嘉義中埔之蓮霧園作為樣區，針對米爾頓紬小蜂進行基礎生物學研究，包含田間發生、蓮霧物候及蟲癟發育之同步性、羽化形式以及成蟲壽命，結果顯示小蜂在田間主要於蓮霧盛花期前來產卵，小蜂卵期與蓮霧胚仔期同步，幼期發育則歷經合臍期至中果期且主要於熟果期化蛹並羽化為成蟲，單一果實蟲癟具有 20.8 ± 11.5 個癟室，一蟲一癟室，成蟲不取食，且壽命為 2.36 ± 1.16 天，本研究也依據其生物學特性提供相關的防治建議。

關鍵詞：蟲癟、入侵物種、胚珠、物候學



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Communal Gall Sharing Enables Interspecific Brood Parasitism in *Tamalia* Gall Aphids

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Received: 1 March 2018 Accepted: 4 September 2018 Available online: 3 June 2019

ABSTRACT

I sought to evaluate the hypothesis that primitive social behavior, in the form of aphids sharing gall space, facilitates the evolution of specialized inquilines exploiting this behavior. Because gall-inducing *Tamalia* aphids reproduce parthenogenetically, gall-mates are, potentially, clonally related, theoretically reducing conflict within the gall. Consequently, mean levels of relatedness were estimated for foundresses sharing galls. Phylogenies of gall-inducing *Tamalia* aphids and their inquilines were generated to pinpoint the origins of the inquiline clade. Further, I evaluated the hypothesis that maintenance of inquiline populations is a function of density dependence in the host aphid species. Field trials were carried out to compare modes of dispersal of gall-inducers and inquilines within and between host plants. The abundance and density of both gall-inducers and inquilines were monitored on populations of host plants. The presence of inquilines appears to depend on the abundance of the host aphid. The high tolerance of gall-inducing females for others in the gall appears to enable its exploitation not only by additional gall-inducers but also by *Tamalia* inquilines, close relatives acting as obligate social parasites of gall-inducers. The origin and maintenance of *Tamalia* inquilines may be consistent with a pattern of density dependence, but the ecological factors associated with this remain unclear.

Key words: gall, aphid, inquiline, *Tamalia*

Introduction

Unlike the majority of gall-inducing insects, the aphids (Hemiptera) and thrips (Thysanoptera) are distinctive in that they occupy hollow, rather than solid galls on their host plants. Thus these insects undergo development and reproduction within an arena in the confines of the gall, potentially setting the stage for social behavior as well as its

exploitation by social parasites. Because all aphids reproduce through parthenogenesis for at least a portion of their life histories, aphid reproduction may occur clonally as well as sexually. Thus selection acts upon the entire aphid clone (Janzen 1977), which comprises a set of distinctive *morphs*, each specialized for some aspect of the species life history (Dixon, 1998, Abbot, 2011).

The life history of a typical species of gall

aphid involves a sessile, gall-inducing generation alternating with alate (winged) morphs adapted for dispersal from the gall. The gall-inducing progenitor of the clone, or stem mother, is apterous (wingless), with greatly reduced legs and sensory organs; she is highly fecund as well. (In this paper, I refer to all apterous gall-inducing morphs as *foundresses*.) By contrast, the dispersive, asexual morph is winged, with relatively well-developed legs, eyes, and antennae; she is proportionately less fecund, owing to the physiological constraints of investment into wing musculature and associated locomotory apparatus (Dixon and Kindlmann, 1999). A series of parthenogenetic generations culminates in an annual sexual generation yielding novel genotypes (Wool, 2004, Simon et al., 2002).

Tamalia aphids and their host plants, woody shrubs in the Ericaceae, are restricted to North America, with centers of biological diversity in California and Mexico. Upwards of six gall-inducing species of *Tamalia* have been described, including at least one inquiline species (*Tamalia inquilinus*); additional species of inducers and inquilines await description (Miller et al., 2015). *Tamalia* aphids constitute a distinct taxon, only distantly related to other gall-inducing Aphidoidea; hence, they represent an independent origin of gall induction (Remaudière and Stroyan, 1984). The evidence strongly suggests that inquilines and gall-inducers are sister taxa, inquilines having originated from a common gall-inducing ancestor, perhaps in conjunction with a host-plant shift (Miller and Crespi, 2003).

Here I argue that the permeability of the *Tamalia* aphid gall, together with the high level of tolerance among foundresses for sharing gall space, facilitates or *enables* its exploitation by conspecific gall-inducers and, by extension, congeneric inquilines. This remarkable circumstance arises as a consequence of the variably clonal structure of aphid populations, as well as the tolerance for intruders by foundresses. First-instar *Tamalia* foundresses have three options for gaining access to critical gall space for development and reproduction: they may locate a suitable site for gall induction on the host plant, join another foundress in

establishing a gall, or (especially if they are late-comers) invade a gall and share it. Co-occupation of galls is frequent and widespread in *Tamalia* aphids: of 143 populations surveyed between 1993~2017, inspection of 13,700 galls indicates at least 74 of these populations show some level of gall co-occupation (unpublished results). This striking form of elementary sociality is distinctive of *Tamalia* aphids (Miller, 1998a). By contrast, numerous examples exist of agonistic behavior in other gall aphids, ranging up to gall usurpation or even lethal combat (Whitham, 1979, Inbar, 1998, Foottit and Maw, 2018).

When foundresses share gall space, they do so at a significant cost *per capita*: survival rates are highest for foundresses occupying galls singly, declining with increasing numbers of foundresses sharing galls. Similarly, *per capita* rates of reproduction vary inversely with the number of foundresses per gall, although this is not necessarily true for *total* numbers of foundresses and offspring produced in jointly-occupied galls (Miller, 1998b). Mutual tolerance among co-foundresses occurs in many social insect systems, such as ants (Heinze et al., 2017) and wasps (Hunt and Toth, 2017), and may be regarded as a critical enabling mechanism for the origins of sociality in animal groups (Krafft et al., 1994, Prokopy and Roitberg, 2001), but it seems puzzling in the case of *Tamalia* aphids, given its negative fitness consequences. This apparent paradox may find a resolution within the context of group kinship considerations. Because *Tamalia* and other aphids reproduce clonally for at least a portion of their life cycle, the possibility is raised that clonal groups of foundresses may share gall space, reducing to zero any theoretical conflict among them. Hence natural selection acts on the entire genotype, which comprises multiple animals in the case of clonal societies (Janzen, 1977, Stern and Foster, 1996). There is no evidence for kin discrimination between *Tamalia* foundresses, as is true of other taxa investigated for this behavior (Aoki et al., 1991, Miller, 1998b).

As with gall-inducers, *Tamalia* inquilines must occupy galls to complete development and reproduction. Unlike their host aphids, inquilines are unable to initiate galls, acting as obligate parasites. The early stages of gall

induction offer the best opportunities for access by intruders. Inquilines may, alternatively, enter mature, desiccated galls that have opened and released their occupants (the winged, dispersing generations of the host aphids) (Miller, 2004). Typically, inquilines are borne by winged morphs, either hatching from eggs or produced live; but inquilines differ from their gall-inducing hosts by possessing additional flexibility in their life history. Rather than undergoing a strict sequence of sessile gall occupation alternating with a winged, dispersing generation, adult inquilines may produce additional apterae either remaining within their natal gall, or dispersing on foot seeking additional galls to invade.

Genetic evidence from mitochondrial, nuclear, and endosymbiont DNA markers reveals differential rates of evolution in *Tamalia* gall-inducers and their inquilines. Three lines of data support this assertion: 1) the rates of base-pair substitution in mtDNA are 2.5-3 times faster in the genomes of inquilines than that of gall-inducers, 2) haplotype network analysis of populations suggests greater structure in those of inquilines, and 3) host-associated differentiation (HAD) is stronger in inquilines than in gall-inducers (Miller and Crespi, 2003, Miller et al., 2015). The causes of accelerated evolution and HAD in inquilines are not clear, but are likely ecological in nature (Turcotte et al., 2011). These may include greater population viscosity and structure arising from important life history differences, including distinct modes of dispersal. Reduced population sizes of inquilines, relative to those of their host aphids, may cause genetic bottlenecks resulting from greater dynamics of inquiline populations across years. These, in turn, can yield increased population structure and accentuate genetic drift, potentially causing substantial evolutionary change in populations (Wright, 1931, Akimoto, 1988, Funk et al., 2001). Greater population densities of gall-inducers and host plants may engender the origin and maintenance of inquilines, as a consequence of density-dependent processes (Brown and Brown, 1986, Savolainen and Vepsäläinen, 2003). In this paper I explore some ecological and life-history aspects of *Tamalia* aphids potentially sufficient

to promote rapid evolution in inquilines. Specifically, I evaluate the hypothesis that gall-inducers and inquilines employ contrasting strategies of dispersal, reflecting their differing life history patterns.

Materials and Methods

Overview

My research program has combined investigative methods in the laboratory, including standard molecular genetics applications, with original observations and experimental trials in wild populations of aphids and their host plants. Because the biology of *Tamalia* aphids remains, to a considerable degree, imperfectly understood, I have undertaken detailed studies of the natural history and ecology of aphid populations on three principal species of host plant, *Arctostaphylos patula*, *Arctostaphylos viscida*, and *Arctostaphylos manzanita* (Ericaceae), in the Sierra Nevada and Cascade mountain ranges of California, USA, beginning in 1993 and continuing to the present. One of my primary goals was documenting the occurrence and frequency of communal gall occupation in *Tamalia coweni*, and this I accomplished by sampling galls randomly along transects of the host plants, then dissecting and examining the gall contents under a stereoscopic microscope (Miller, 1998a). In a second, experimental field study, I investigated the consequences of communal gall occupation, as well as the potential for kin discrimination among gall foundresses (Miller, 1998b). To reveal kin structure of communal foundresses, galls were sampled and aphids genotyped using amplified fragment length polymorphism (AFLP) protocols (Taylor and Miller, 2014).

Tamalia inquinatus was previously unrecognized, suggesting it existed as a cryptic species (Hebert et al., 2004) until its formal description by Miller and Sharkey (2000). In a prior field-based investigation of inquiline ecology, I estimated survival and reproduction rates by gall-inducers sharing galls with inquilines, comparing those against galls containing gall-inducers only (Miller, 2004).

Construction of *Tamalia* phylogenies has

been carried out using a variety of molecular markers, including aphid mtDNA, nDNA, and DNA of the aphid endosymbiont *Buchnera* (Miller and Crespi, 2003, Miller et al., 2015). This work was performed to 1) establish that the inquiline clade composed a monophyletic group; 2) situate inquiline *Tamalia* within the context of the entire genus, to pinpoint their origins; 3) elucidate patterns of diversification and host-race formation between *Tamalia* aphids and their host plants.

Ecological study of *Tamalia* populations

In this long-term project with my colleague, Colleen Hatfield, we have investigated *Tamalia* aphid populations and their host plants at the Big Chico Creek Ecological Reserve, at California State University, Chico. Specifically, our study populations comprise a 1-hectare mosaic of scrub and oak-pine forest at 550 meters elevation in the Cascade-Sierra foothills. A significant element of this community are the approximately 600 *Arctostaphylos* shrubs, including 400 individuals of *A. manzanita* and 200 of *A. viscida*. Like many fire-adapted plants, *Arctostaphylos* spp. require fire for sexual reproduction (Anacker et al., 2011).

Wildfires in 1999 yielded a highly patchy distribution of surviving trees and shrubs: this irregular pattern of burning opened bare ground in which new *Arctostaphylos* could be established during the following growing season (the year 2000). I estimate that 152 of the total 155 shrubs classified as “juveniles” germinated in 2000, implying that the surviving juvenile plants comprise a single cohort precisely 16 years old (as of 2016). The approximately 350 remaining plants in the study are classified as “mature” individuals, their origins dating back to earlier episodes of fire. Beginning in 2008, all juvenile plants were assigned unique three-digit identities; a randomly drawn subset of mature plants (25 of each species) was similarly coded. The lack of galls on juvenile *Arctostaphylos* shrubs prior to 2008 provided a natural experiment in which arrival rates of gall-inducers and inquilines putatively originating from galls on nearby mature shrubs could be compared, to estimate their relative rates of dispersal and colonization.

Monitoring study plants

Starting in 2008, I inspected all juvenile plants during each growing season, for the presence of any *Tamalia* galls. Up to two galls were collected annually from each plant, representative of different portions of the shrub. I stored sample galls at 4°C until dissection under the microscope. Inspection of fresh galls permitted detection of active gall-inducers as well as any inquilines present. In addition to sampling galls during the growing season, all remaining galls were counted at the conclusion of the growing season in an annual *gall census*. Care was taken to count only those galls produced in a given year: this was verified by including galls only on new branch growth. In addition to counting all new galls on study plants, estimates were made of maximum dimensions of height and breadth, to the nearest cm. These metrics were then used to estimate shrub volume, approximating the surface area of a cone. Gall density was estimated as the mean number of galls/m² of shrub surface area. The annual gall census and shrub measurements were performed as a class activity involving undergraduate students in my general ecology course at California State University, Chico.

Dispersal trials

In this experiment, I tested the hypothesis that inquilines exit their natal galls to seek additional galls in which to develop and reproduce (*gall-exit trials*). Hence I predicted first-instar inquilines would be captured leaving galls disproportionately more often than gall-inducers. In May-Jun 2003, Jun 2006, and Jun 2008, a total of 83 galls (designated “source galls”) on *A. viscida* approaching maturity were selected systematically and marked with flagging. The adhesive material Tanglefoot (Scotts Miracle-Gro, Marysville, Ohio, USA) was then applied to the entire petiole supporting the leaf, potentially trapping any insects exiting the gall on foot. Galls were monitored every three days until aphids were thus trapped on petioles, or for a maximum of 2 weeks. I then collected all trial galls, and, under a stereoscopic microscope, recorded the identity and number of all trapped insects, before dissecting the presumed source galls to record their contents. First-instar gall-

inducers and inquilines are readily distinguished by the presence of capitate setae on the gall-inducers only; setae on inquilines are tapered (Miller and Sharkey, 2000).

In a second experiment, I quantified differences in dispersal rates between gall-inducers and inquilines (*inter gall dispersal trials*). Specifically, I predicted that inquilines were the more likely to exit galls on foot and appear in neighboring galls. Clusters of newly-mature *A. viscida* galls (from which developing alates had dispersed) were selected haphazardly. With a laboratory pipettor (Eppendorf, Hamburg, Germany) about 100 µl of fluorescent insect tracking powder (Exosect Ltd, Winchester, UK) were injected into a gall, designated the “donor gall.” After monitoring for 1-2 weeks, the donor gall and all neighboring mature galls on the same branch tip (“potential recipient galls”) within 0.5 m walking distance were collected and their contents examined under an ultraviolet lamp. Minimum walking distance was estimated (to the nearest 1 cm) between donor galls and all potential recipient galls, which were then collected and their contents examined for evidence of aphid movement between galls.

Results

For the purposes of this study, I established as useful plants only those juveniles surviving long enough to have produced galls, or which were still alive as of 2016 (i.e., had not yet been colonized): this totaled 127 plants (Figure 1). Of these, 96 juvenile plants had been colonized at least once by 2016; 31 plants had never had galls within the time frame of this study. The estimated mean lag between first appearance of galls on juvenile host plants and first detection of inquilines was 2.56 years (SEM 0.3 years, n = 59). This is likely an overestimate of the true value, as plants were sampled only during the growing season, and generally once per year. In 18 of 59 cases, gall-inducers and inquilines first appeared in sample galls on identical dates, indicating a high efficiency rate of inquilines locating host aphid galls. Once plants had been colonized by gall-inducers and inquilines, the frequency of inquilines in galls stabilized at ~10%. Based on data for the 2016 season, a

preliminary linear regression analysis showed no significant association between inquiline abundance and gall density ($F = 0.135$, $n = 66$, $p = 0.716$).

I completed a total of 83 gall-exit trials. As expected, all aphids trapped were first-instar larvae. The number of trials with inquilines trapped was 19; by contrast, only 3 trials captured gall-inducers, in spite of the greater abundance of gall-inducers in *Tamalia* populations generally. The total number of inquilines trapped (82) likewise exceeded that of gall-inducers (5), reflecting greater activity of inquilines presumably seeking galls to enter. A test of independence indicated the appearance of inquilines in Tanglefoot traps was highly dependent on the presence of adult inquilines within donor galls, under the assumption that first-instar aphids arose from adults present within adjacent galls ($X^2 = 60.52$, with Yates's correction for continuity ($n = 107$, $P < 0.001$)). Corroborating this was the observation that in 5 of 6 instances of the inquilines trapped by Tanglefoot, the donor gall was found to contain adult inquilines.

I completed 70 inter-gall dispersal trials, inspecting a total of 313 potential recipient galls. Ten galls showed evidence of inter-gall dispersal, in the form of either marked larvae or their exuvia. In nine of these, first-instar inquilines were detected; in one instance, a first-instar gall-inducer was identified, suggesting that marked aphids appearing in potential recipient galls are more likely to be inquilines than gall-inducers. In nine of ten cases, I found marked animals in the nearest neighbor gall. Mean distance of dispersal was 3.3 cm (± 2.8 cm SD).

Discussion

Tamalia gall-inducers and inquilines show striking differences in dispersal patterns within host plants and gall occupation rates, apparently reflecting their distinct life history strategies. These may be considered at two spatial scales: a coarse-grained scale (movement in meters or tens of meters) for colonization of new plants, by alate adults; and a fine-grained scale (movement in cm) for dispersal between galls on the same host plant, by ambulatory first-instars.

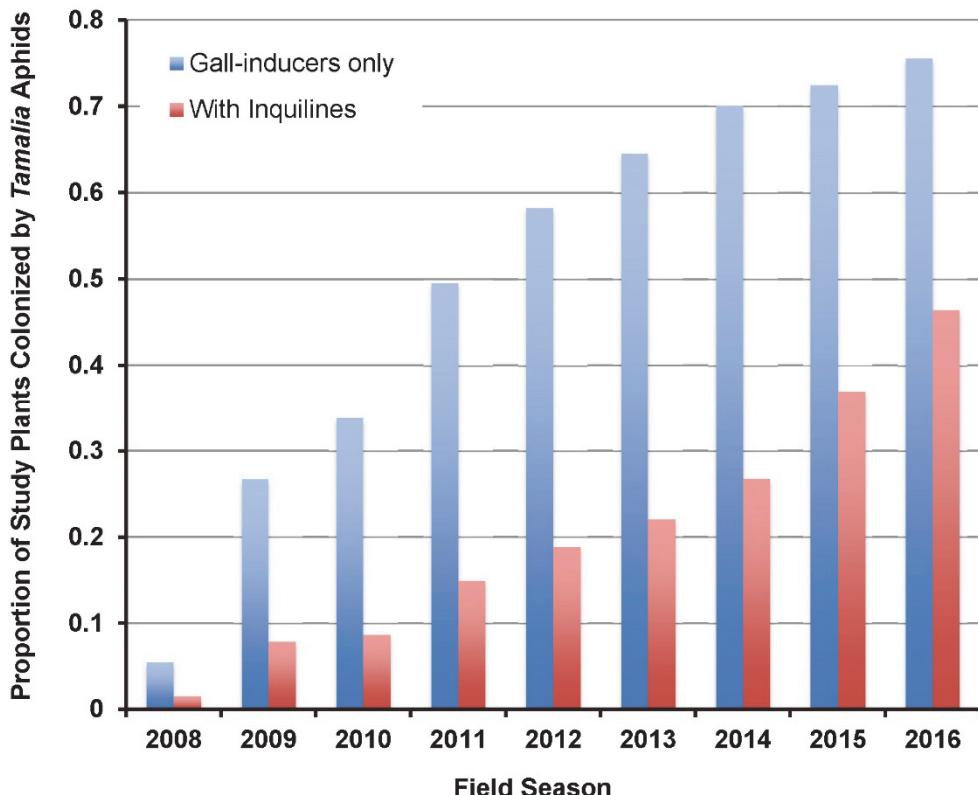


Fig. 1. Cumulative colonization by *Tamalia* aphid gall-inducers and inquilines, as a proportion of the total set of juvenile *Arctostaphylos viscida* and *Arctostaphylos manzanita* plants in the study population at the Big Chico Creek Ecological Reserve, 2008-2016.

The juvenile plants in my study population were first colonized in 2008, nine years following the 1999 wildfire. Figure 1 demonstrates an increasing rate of colonization of plants, which begins to attenuate in 2012 until 2016, the most recent year for which data are available. By contrast, the frequency of inquilines in galls increases only gradually at first, then accelerates in 2014~2016, suggesting inquiline colonization of plants proceeds according to properties spatially different from those of the gall-inducers. These trends indicate that, at some point, inquiline colonization rates will reach an asymptote approaching that of the proportion of plants colonized by gall-inducers. Because the detection probabilities (Mackenzie et al., 2006) of inquilines are lower than that of gall-inducers, colonization rates by inquilines are likely underestimates. A minimum dispersal-distance hypothesis, as has been proposed for benthic marine propagules, may best explain aerial patterns of dispersal in

relatively weak fliers such as aphids (Dixon, 1998, Shanks et al., 2003).

According to my experimental evidence, first-instar *Tamalia* inquilines were significantly more likely to appear in Tanglefoot traps than were gall-inducers, and more likely to move between galls. This pattern of activity is consistent with the hypothesis that inquilines readily seek and occupy gall space (Miller, 2004). A minority of first-instar gall-inducers may also act as opportunists by invading established galls (unpublished data). Alternatively, first-instar inquilines may develop inside their natal gall rather than exiting. Both patterns of behavior may be a function of density dependence, such that crowding within a gall promotes inter-gall dispersal. Another important biological aspect of *Tamalia* inquilines is the reproductive flexibility of adult apterae within the gall: these females may invest differentially in apterous or alatoid (pre-winged) offspring, perhaps owing again to conditions of density (Gilbert, 1980, May et al.,

1981) but this hypothesis remains to be documented in detail. Such a pattern would be consistent with the general flexibility of aphid clones making investment decisions in offspring as a function of crowding (Dixon and Kindlmann, 1999, Shiba et al. 2010), as well as the hypothesis that the interspecific inquiline strategy originated from an intraspecific, opportunistic one.

In a broader, ecological context, *Tamalia* gall-inducing aphids and their inquilines are characteristic of xeric plant communities in North America, where periodic fire plays a critical role in maintaining host plant populations of these specialist insects. The spatial and temporal aspects of ecological succession following wildfire have evidently provided an evolutionary backdrop in which gall induction by *Tamalia* aphids has originated; opportunistic strategies employed by *Tamalia* inquilines may well be derived from similar intraspecific behaviors in *Tamalia* gall-inducers. The precise roles of density dependence on colonization rates, reproductive investment decisions, and dispersal both within and between galls remain to be elucidated, but hold promise for future investigations. For example, high-precision global positioning system technology (Trimble Inc., Sunnyvale, California, USA) may be applied to develop detailed maps revealing the patterns of colonization and dispersal by both *Tamalia* gall-inducers and inquilines. These, in turn, can facilitate evaluating whether inquiline populations are indeed highly structured and more subject to genetic bottlenecks than those of the gall-inducers. Such data may additionally test the hypothesis that alate *Tamalia* aphids act as “aerial plankton” by moving randomly among host plants according to a minimum-dispersal model (Shanks et al., 2003, Williams et al., 2005).

Acknowledgments

This work was supported in part by a David W. and Helen E.F. Lantis University Chair Award at California State University, Chico. The author appreciates the continued support of the staff at the Big Chico Creek Ecological Reserve,

for access to study populations of host plants and aphids. I am grateful for the collective efforts of General Ecology students at CSU, Chico in conducting an annual census of *Tamalia* galls on host shrubs. Colleen Hatfield kindly read the manuscript and offered constructive feedback. The CSU, Chico Center for Water and the Environment provided funding and laboratory space for this work.

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***Tamalia* 屬造癟蚜蟲的蟲癟空間共享習性致使種間的巢寄生行為**

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收件日期：2018年3月1日 接受日期：2018年9月4日 線上刊登日期：2019年6月3日

摘要

本研究藉由蚜蟲可共享蟲癟空間的習性進而促使客居者特化出利用蟲癟之行為，檢測原始的社會昆蟲行為假說，因造癟蚜蟲 *Tamalia* 屬行孤雌生殖，癟室內成員應皆為同胞近親，理論上可減少癟內的衝突，故可藉由分析共存於蟲癟內的各幹母的親緣關係，建構 *Tamalia* 屬癟蚜及其客居者的系統發生來瞭解客居者的起源。本研究也進一步探討客居者維持族群與寄主蚜蟲之間有無符合密度應變假說，比較野外造癟者及客居者於寄主植物的種內及種間散佈模式，並監測造癟者及客居者在寄主植物上的豐度及密度，結果顯示客居者存在與否取決於蚜蟲寄主的豐度。造癟蚜蟲對於其他物種可並存於癟內的高度容忍性，促使其他造癟者及 *Tamalia* 客居者利用此一習性，這些與造癟者近緣的客居者也演化為專一性的群居寄生者。*Tamalia* 客居者的演化起源及族群維持可能與寄主的族群密度關聯，但相關的生態因素則仍有待發掘。

關鍵詞：蟲癟、蚜蟲、客居者、*Tamalia*



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The Relationship between Gall Size and Sizes of Selected Inhabitants of the Ball Gall of *Eurosta solidaginis* on *Solidago altissima*

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Received: 30 April 2018 Accepted: 15 October 2018 Available online: 3 June 2019

ABSTRACT

The purpose of this study was to determine if there is a correlation between final ball gall mass and the mass of the gall inducing larva of *Eurosta solidaginis* and/or the mass of the adult fly that emerges, and to determine if there is a correlation between gall mass and the mass of the parasitoid *Eurytoma obtusiventris*. Another goal was to determine if there was a correlation between ball gall size and the sex of the adult fly that emerges. Adult flies were sexed and weighed as were the associated galls. Larval dry masses and dry masses of ball galls, with or without exit tunnels, were also determined. No correlation was found between ball gall mass and the mass of the adult fly that emerged from the gall. Adult female flies were of greater mass than male flies, but there was no correlation between gall mass and the sex of the gall former. Results indicate no biologically significant correlation between dry masses of the gall formers and dry masses of the galls. Furthermore, no biologically significant correlation was found between ball gall size and the size of the parasitic wasp *Eurytoma obtusiventris*. Interestingly, larger ball galls do not typically yield larger larvae or adults of *Eurosta solidaginis*.

Key words: Diptera, Tephritidae, *Eurosta solidaginis*, *Solidago altissima*, ball gall

Introduction

Ball gall formation (Figure 1A) on the tall goldenrod (*Solidago altissima* L., Asteraceae) is induced by the fly *Eurosta solidaginis* (Fitch) (Diptera: Tephritidae). Adults emerge from galls, mate and then the adult female fly deposits its fertilized egg into the terminal bud of *S. altissima* during late spring (Figure 1B). Once the larva hatches and tunnels into the stem, gall initiation begins. By the middle of September,

both the larva and gall are considered full size. In autumn, larvae begin to scrape exit tunnels just up to the outer surface of the gall. The successful larva overwinters in the gall (Figure 1C), and then in spring, pupation occurs (Figure 1D), with the adult emerging in May in the northeastern United States (Uhler, 1951).

Larvae of *Eurosta solidaginis* may be jeopardized by the parasitoids *Eurytoma gigantea* Walsh (Hymenoptera: Eurytomidae) and *Eurytoma obtusiventris* Gahan

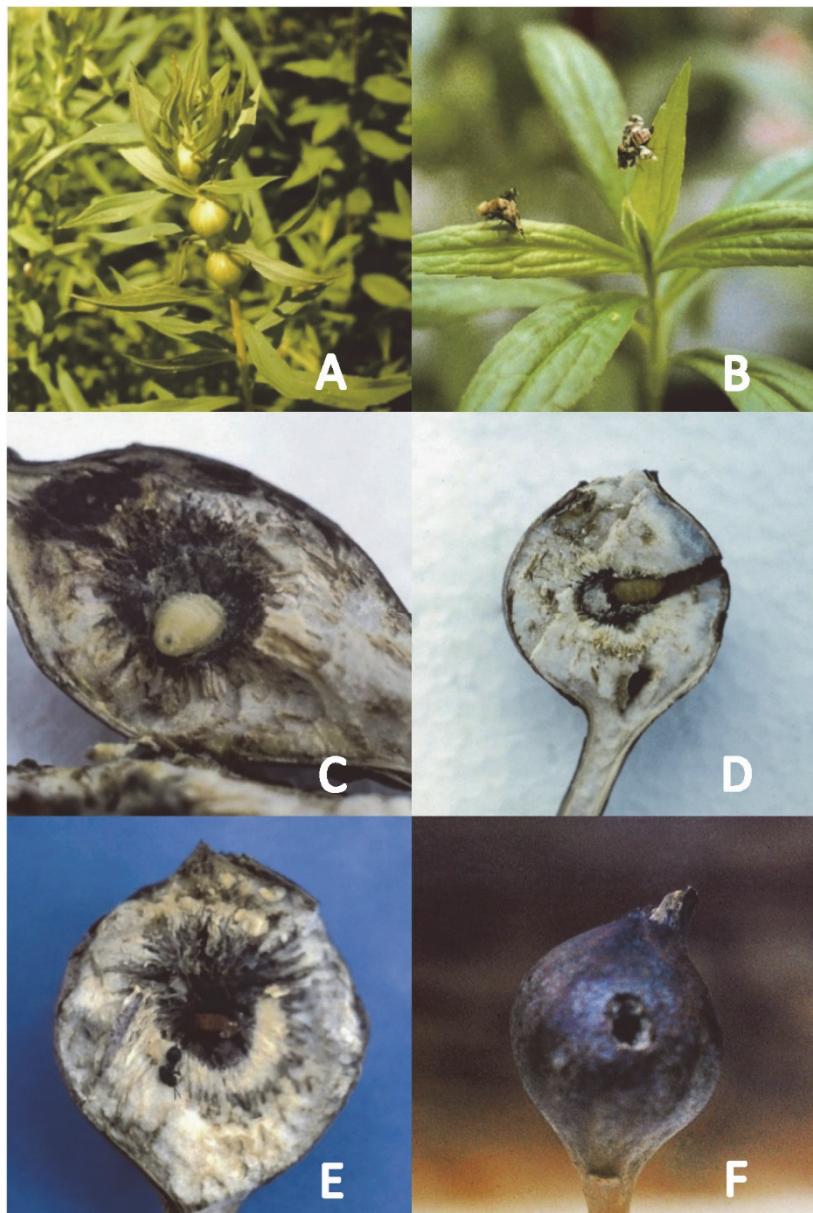


Fig. 1. A, goldenrod ball galls caused by *Eurosta solidaginis*; B, *Eurosta solidaginis* adults on *Solidago altissima*; C, third instar larva of *Eurosta solidaginis* inside ball gall; D, puparium of *Eurosta solidaginis* in ball gall with a completed exit tunnel; E, adult of *Eurytoma obtusiventris* that emerged from a premature puparium in a ball gall; F, goldenrod ball gall with a bird predation hole.

(Hymenoptera: Eurytomidae) (Figure 1E), by a beetle inquiline/predator *Mordellistena convicta* LeConte (Coleoptera: Mordellidae), bird predation (Abrahamson and Weis 1989) (Figure 1F), or predation by squirrels (Shealer *et al.* 1999). Typically, the parasitoid *Eurytoma gigantea* is found in smaller galls (Cane and Kurczewski 1976, Shealer *et al.* 1999). It has been shown that *E. gigantea* tends to be found in smaller galls because the adult wasps preferentially deposit eggs into smaller galls given the limited sizes of their ovipositors (Weis

et al. 1985).

Downy woodpeckers, *Picoides pubescens* (Linneaus), and black-capped chickadees, *Poecile atricapillus* (Linneaus), are predators of *Eurosta solidaginis* during the winter months (Schlichter 1978). Bird predators have a tendency to seek out larger ball galls (Confer and Paicos 1985, Abrahamson and Weis 1989, Shealer *et al.* 1999). Abrahamson and Weis (1989) found that the combined effect of predatory birds preferentially seeking out larger ball galls and *Eurytoma gigantea* preferentially

attacking smaller galls had a stabilizing effect on selection, causing *Eurosta solidaginis* in intermediate sized galls to have the highest survivorship. Similar findings have been reported for galls caused by *Diplolepis rosae* (Linneaus) on roses. Vertebrate predation frequency increased with gall size, while smaller galls had higher rates of attack by parasitoids (László *et al.* 2014).

Eurytoma obtusiventris is an internal parasite of *Eurosta solidaginis* (Uhler 1951) and it attacks *E. solidaginis* during the egg stage (Abrahamson and Weis 1997). *Eurytoma obtusiventris* causes the gall-former to make a premature puparium in late summer, and then it consumes its host and overwinters as a larva within the puparium prior to its pupation the next spring (Weis and Abrahamson 1985).

Given that birds preferentially seek out larger ball galls and that larger galls have the potential to provide more nutrition for the inhabitants, one might hypothesize that larger ball galls contain larger larvae of *Eurosta solidaginis*. The purpose of this study was to determine if there is a correlation between the sizes of ball galls and the sizes of fully developed *E. solidaginis* larvae within the galls as well as the sizes of *Eurytoma obtusiventris* inhabitants within ball galls. An additional goal was to determine if there is a correlation between the sizes of ball galls and the sizes of the *Eurosta solidaginis* adult flies that emerge from the galls. We aimed to answer the question as to whether larger ball galls contain larger *E. solidaginis* larvae, yield larger *E. solidaginis* adults, and contain larger *Eurytoma obtusiventris* inhabitants.

Materials and Methods

Goldenrod ball galls were collected from eleven *Solidago altissima* fields in Berks and Lehigh counties in Pennsylvania, USA over three different stages: late summer/early autumn (September 23~October 16, 2017), late autumn (November 11~December 7, 2017), and overwintering (February 24~April 28, 2017). Galls from the late summer/early autumn were collected prior to exit tunnel completion (pre-tunnel galls), and galls collected in late autumn

had completed exit tunnels (galls with exit tunnels). The pre-tunnel galls and galls with exit tunnels were cut open, and inhabitants were identified. Galls and the respective inhabitants were dried in a Fisher Scientific Isotemp oven at 60°C for a minimum of 7 days, and dry masses of galls and inhabitants were determined using an ED244S Sartorius balance.

Eurosta solidaginis adults were reared from overwintering galls that were placed in mesh covered mason jars or *Drosophila* culture tubes fitted with foam inserts and incubated in a Conviron E7/2 growth chamber at 22°C under a 14-hour photoperiod. *E. solidaginis* flies were sexed, and fresh masses were determined using an ED244S Sartorius balance within 24 hours of emergence. Adult flies and their respective galls were dried in a Fisher Scientific Isotemp oven for 7 days, and dry masses were also recorded.

Once the dry masses for galls and inhabitants had been recorded, these masses were plotted using Microsoft Excel, and linear regressions were performed to determine if there was a correlation between gall sizes and sizes of gall inhabitants. Regression analyses were also used to determine if results were statistically significant. Means and standard errors were calculated to make comparisons of the sizes of *E. solidaginis* larvae, adults, and ball galls. Two-sample independent t-tests were conducted to determine if the mean dry masses of *E. solidaginis* larvae for pre-tunnel galls and exit tunnel galls were significantly different. Two-sample t-tests were also used to determine if the mean sizes of female and male adult *E. solidaginis* flies were significantly different and to determine if their associated galls were significantly different in mass. F-tests were run prior to all t-tests to determine whether or not there was equality of variances.

Results

There was no significant relationship between the dry masses of fully formed pre-tunnel ball galls and the dry masses of their respective *Eurosta solidaginis* larvae ($R^2=0.0319$, $F_{1,41}=1.35$, $p=0.25$); larger galls did not yield larger larvae for the late summer/early autumn time period (Figure 2). There was a very

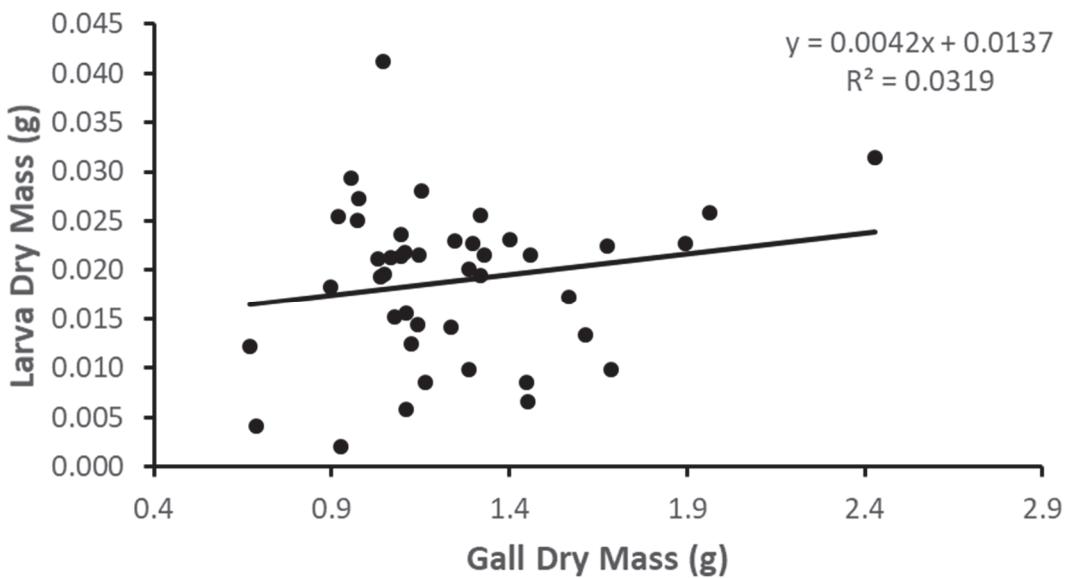


Fig. 2. The gall dry mass and respective larval *Eurosta solidaginis* dry mass for the late summer/early autumn time period showed no significant relationship ($R^2=0.0319$, $F_{1,41}=1.35$, $p=0.25$). These larvae had not started their exit tunnels.

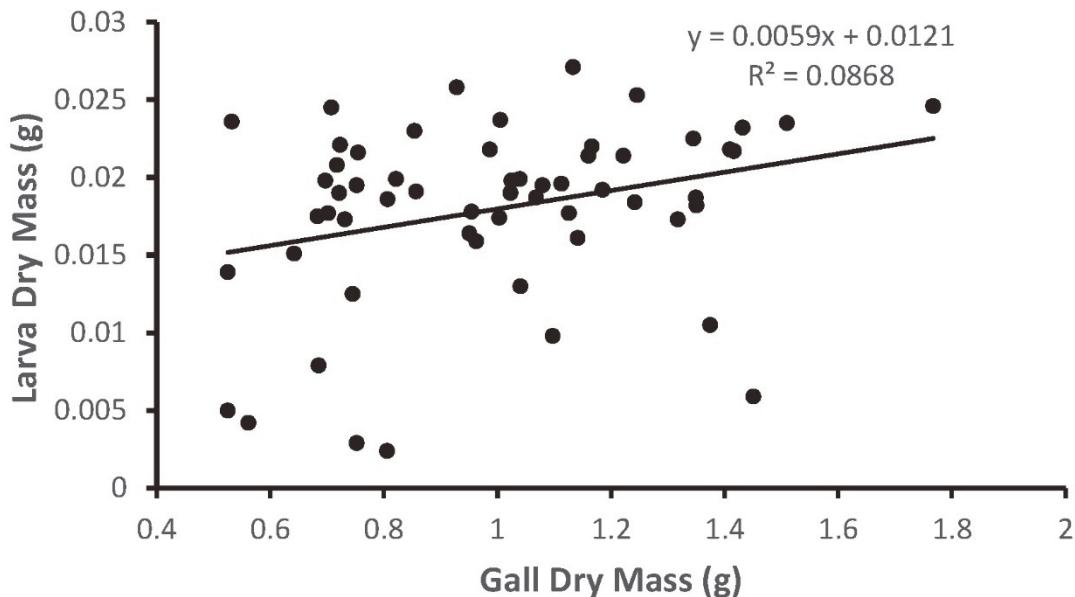


Fig. 3. The gall dry mass and respective larval *Eurosta solidaginis* dry mass for the late autumn collection showed a very weak positive correlation ($R^2=0.0868$, $F_{1,56}=5.32$, $p<0.05$). At this collection stage, larvae had completed exit tunnels.

weak, but statistically significant, positive relationship between the dry masses of galls with completed exit tunnels and the dry masses of the associated *E. solidaginis* larvae for the late autumn time period ($R^2=0.0868$, $F_{1,56}=5.32$, $p<0.05$; Figure 3). The mean dry masses of the *E. solidaginis* larvae from fully formed pre-tunnel

galls was 18.9 ± 1.2 mg ($n=43$) while the mean dry masses of the larvae from the galls with exit tunnels was 18.0 ± 0.8 mg ($n=58$), showing no significant difference ($t=0.67$, $df=73$, $p=0.25$).

No relationship was found between the dry masses of the adult *E. solidaginis* flies and the dry masses of their respective galls ($R^2=0.0154$,

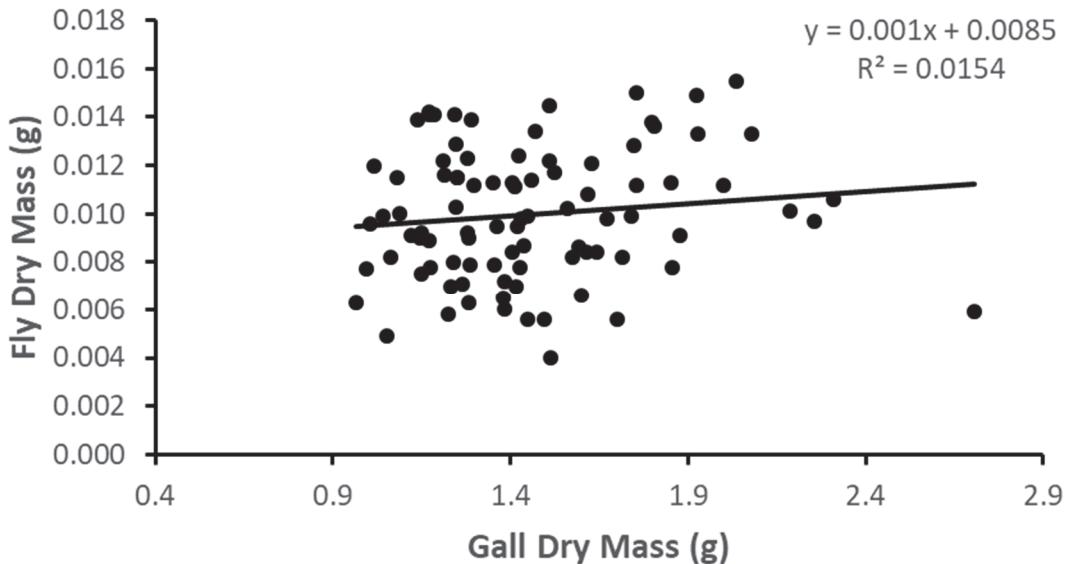


Fig. 4. The gall dry mass and the adult *Eurosta solidaginis* fly dry mass exhibited no significant relationship ($R^2=0.0154$, $F_{1,88}=1.38$, $p=0.24$).

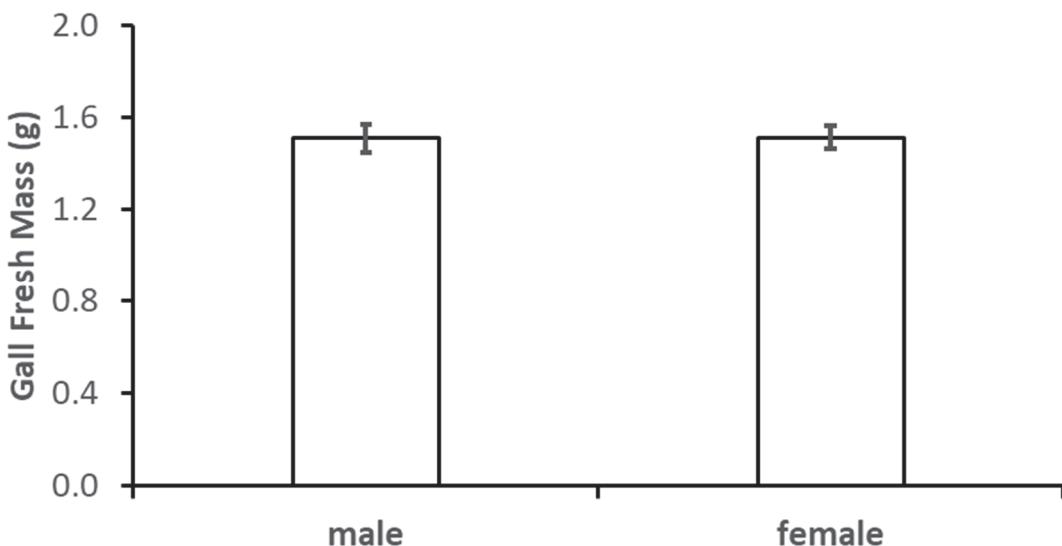


Fig. 5. The mean fresh masses of galls caused by male *Eurosta solidaginis* flies ($n=51$) and female *E. solidaginis* flies ($n=43$). Standard error bars and a two-sample independent t-test indicated that results were not significantly different ($t=-0.06$, $df=92$, $p=0.48$).

$F_{1,88}=1.38$, $p=0.24$; Figure 4). The mean fresh mass of female *E. solidaginis* flies was significantly greater at 29.8 ± 0.8 mg ($n=54$) compared to males flies with a mean of 24.7 ± 0.7 mg ($n=57$) ($t=4.77$, $df=109$, $p<0.01$). However male galls and female galls were not statistically different in mass ($t=-0.06$, $df=92$, $p=0.48$; Figure 5).

The late autumn collection of galls parasitized by *Eurytoma obtusiventris* showed a weak, but statistically significant, positive

relationship between the dry masses of the galls and the dry masses of *E. obtusiventris* ($R^2=0.1792$, $F_{1,27}=5.89$, $p<0.05$; Figure 6).

Discussion

For pre-tunnel galls, there was no relationship between ball gall dry mass and *Eurosta solidaginis* larval dry mass, while for galls with exit tunnels, there was only a very weak positive relationship between ball gall dry

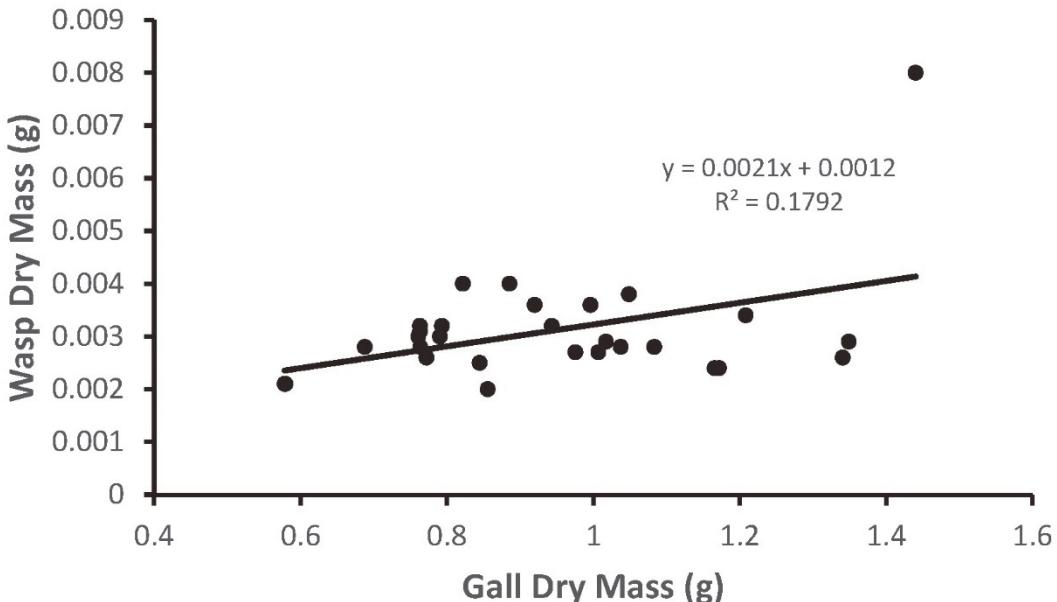


Fig. 6. The gall dry mass and the dry mass of the parasitoid *Eurytoma obtusiventris* showed a slightly positive correlation for the galls collected in late autumn ($R^2=0.1792$, $F_{1,27}=5.89$, $p<0.05$).

mass and larval dry mass with an R^2 of 0.0868. This suggests that gall size is not a reliable predictor of the size of the *E. solidaginis* larval inhabitant. Fully formed ball galls were collected at the two different stages, before and after exit tunnel completion. If gall size were an important factor affecting *E. solidaginis* larval size, one might have predicted that ball galls with exit tunnels would be more likely to show a strong correlation between gall size and larval size. If the larvae gain nutrition during the process of scraping exit tunnels through the gall tissue, larger ball galls would have more tissue that would need to be removed/consumed in the process of exit tunnel completion resulting in larger larvae. Instead the results of this study did not show a strong correlation between ball gall size and *E. solidaginis* larval size for galls with completed tunnels. Interestingly mean larval mass did not increase or change from the pre-exit tunnel collection to the completed exit tunnel collection time suggesting that *E. solidaginis* larvae do not gain mass during exit tunnel completion. Any nutrition that is gained may be used to provide energy for the exit tunnel completion process as there was no loss of mass in the larvae as well.

How *et al.* (1993) reported a significant positive correlation between *E. solidaginis* larval

dry mass and ball gall dry mass with an R^2 of 0.284 when doing a combined analysis of fully developed ball galls found on *S. altissima* and *S. gigantea* from Minnesota and Pennsylvania. It is not clear whether these galls had completed exit tunnels at the time of collection but the regression presumably included a mix of what is now known as two host races of *E. solidaginis* (Abrahamson and Weis 1997). It is interesting that there was a stronger positive correlation between gall size and *E. solidaginis* larval size than what was obtained in this study in which we report no correlation for pre-tunnel galls and only a weak positive correlation with an R^2 of 0.0868 for galls with completed exit tunnels. Perhaps *S. gigantea* host race galls show more of a correlation between *E. solidaginis* larval masses and ball gall masses. Cane and Kurczewski (1976) indicated they found no significant correlation between the diameters of ball galls and the *E. solidaginis* larvae within, but did not provide data to support their statements.

The results presented here show a weak positive correlation between the dry masses of *Eurytoma obtusiventris* and the dry masses of their associated ball galls (Figure 6). Given that *E. obtusiventris* is an internal parasite of *Eurosta solidaginis* during the entire

development of the ball gall, it is not surprising that the results are similar to those that we report for *E. solidaginis* in showing, at most, a weak positive correlation between ball gall mass and inhabitant mass. Cane and Kurczewski (1976) indicated they found no significant correlation between the diameters of ball galls and *Eurytoma obtusiventris* larvae within, but did not provide any supporting data.

There was no correlation between the dry masses of the galls and the dry masses of the adult *E. solidaginis* flies that emerged from the galls in this study. Contrary to what one might have expected, larger ball galls did not yield larger *E. solidaginis* adults. The findings reported here are in contrast to those of Stille (1984) who found a correlation between the sizes of adults of the gall former *Diplolepis rosae* and the sizes of the rose galls from which they emerged.

Female *Eurosta solidaginis* adults were shown to be of greater mass than male *E. solidaginis* adults in this study in corroboration with findings of Hess *et al.* (1996). Despite their larger size, the females did not emerge from larger galls. This is unlike some gall systems where females produce larger, morphologically distinct galls (Goncalves *et al.* 2005).

Results presented here indicate that larger ball galls did not yield larger adults of *Eurosta solidaginis*. In addition, gall size is not a good predictor of the sizes of *E. solidaginis* larvae or the sizes of the parasitoid *Eurytoma obtusiventris*. While one might have assumed that larger galls produce larger *Eurosta solidaginis* larvae and yield larger adults, this was not clearly shown in this study. These results could be explained by considering that larvae of *E. solidaginis* do not consume all of the surrounding gall tissue, and that the wasps of *Eurytoma obtusiventris* are internal parasitoids of the gall former and do not consume any gall tissue. As a result, larger galls do not act as a source of a larger amounts of food for these inhabitants.

Birds such as woodpeckers seek out larger *Eurosta solidaginis* galls (Abrahamson and Weis 1997), but the results of this study indicate that the largest ball galls will not always yield the largest larvae of *E. solidaginis*. Shealer *et al.*

(1999) reported that when all occupants were considered, including the parasitoids and gall formers, the masses of ball gall occupants in smaller galls were significantly less than the masses of ball gall occupants in medium and larger ball galls, and small galls were more likely to be empty. Given that *Eurytoma gigantea* more frequently parasitizes smaller ball galls and that *E. gigantea* larvae weigh much less than *Eurosta solidaginis* larvae, bird predators would be more likely to find a larger inhabitant to consume in larger ball galls (Shealer *et al.* 1999). Shealer *et al.* (1999) also found that the eastern gray squirrels (*Sciurus carolinensis* Gmelin) that predated on ball galls did not prefer ball galls of a particular size class, and they were found to consume *E. solidaginis* larvae as well as parasitoids.

While birds are more likely to find an inhabitant in a larger ball gall, and are more likely to find an *E. solidaginis* larva when avoiding smaller galls, the results of this study show that birds that seek out larger ball galls are missing the large *E. solidaginis* larvae that can be found in smaller galls. The results presented here, along with results from other studies, could also have practical implications for ice fishermen. Ball galls are sometimes collected by individuals to remove the *E. solidaginis* larvae to use as bait for ice fishing (Frank Mapes, personal communication). If the goal is to find large *E. solidaginis* larvae, one should not restrict oneself to collecting large galls given that there is not a strong positive correlation between ball gall size and the sizes of *E. solidaginis* larvae.

Acknowledgments

We would like to thank Zachary Huss, Roberta Beard, Julia Falkowski, and Nicoll Lezano for their help with gall collection and sample processing. We would also like to thank Dr. Christopher Sacchi for his assistance with data analysis and would like to thank Dr. Sacchi and Dr. Alex Hernandez for their helpful comments on a draft of the manuscript.

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北美一枝黃花上癟蠅 (*Eurosta solidaginis*) 的球狀蟲癟大小和癟內生物之相關性

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收件日期：2018年4月30日 接受日期：2018年10月15日 線上刊登日期：2019年6月3日

摘要

本研究之目的為瞭解成熟的球狀蟲癟重量是否與癟蠅(*Eurosta solidaginis*)之幼蟲重量及/或與成蟲重量有相關性，及蟲癟重量是否與癟蠅寄生蜂 *Eurytoma obtusiventris* 重量相關，另一目的則為探討蟲癟大小是否與癟蠅成蟲之性別有相關性。首先鑑定成蟲性別，再進行成蟲及蟲癟的稱重，同時記錄幼蟲乾重、蟲癟乾重與是否有羽化通道。結果顯示蟲癟重量和成蟲重量之間無相關性，雌蟲較雄蟲重，但蟲癟重量和性別無相關性。由此顯示癟蠅之造癟者的乾重和蟲癟的乾重無生物學之顯著關聯，再者，蟲癟大小和寄生蜂體型也無生物學中的顯著相關，其中有趣的是，較大的蟲癟並不會孕育出較大的癟蠅幼蟲或成蟲。

關鍵詞：雙翅目、果實蠅科、*Eurosta solidaginis*、*Solidago altissima*、球狀蟲癟



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Let's Gall Taiwan: A Guidebook on Insect Galls

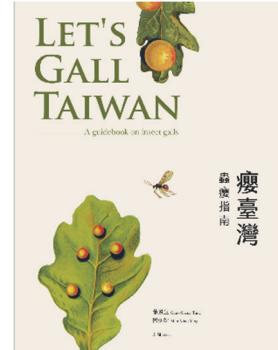
edited by Gene-Sheng Tung and Man-Miao Yang, Published by the Council of Agriculture (Forestry Bureau), and the Taiwan Entomological Society, Taipei, 248 pages, 2018. ISBN: 978-986-05-5346-8 (Hard cover). Price: NTD 460⁰⁰

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Received: 19 November 2018 Available online: 3 June 2019



Taiwan, a 36000 km² island-country, occurs off the coast of south-east Asia, bordered by Fujian Province of the People's Republic of China in the west, South Korea and the Fukuoka Prefecture of Japan in the north, Luzon Province of the Philippines in the south, and the Philippine Sea in the east. Historically a shallow shelf of the Taiwan Strait connected the islandic Taiwan and China. During the interglacial periods of the Pleistocene glacial cycles, this shelf submerged separating China and Taiwan. Repeating topographic changes during the post-Pleistocene glacial cycles enabled the colonization of organisms between China and Taiwan (Chiang and Schaal, 2006). Yet c. 25% of Taiwanese plants are native to this land plate, which have evolved there because of (i) continent-island colonization, (ii) *in-situ* radiation, and (iii) synergy between colonization and radiation. Additionally, the Tropic of Cancer divides Taiwan into a southern tropical and a northern subtropical regions. Thus Taiwan's unique geography, over the years, has enabled the natural build-up of a delightful biological diversity across this island-nation. Additionally the subtropical climate has contributed to the varied demographics of Taiwanese plants and animals (Wu *et al.*, 2006). Because of the high diversity of Taiwanese plants – most of which are

endemic – more than 60% of the described plant-feeding arthropods of Taiwan are endemic as well (Shao *et al.*, 2003). In such a context of a fascinating natural landscape and complex biological diversity, Gene-Sheng Tung and Man-Miao Yang have catalogued several arthropod-induced galls of Taiwan in this c. 250 page colourful and elegant book.

Galls are plant excrescences induced by the action of specific groups of Insecta and Acarina, which manifest as neofomed structures. Insect-induced galls are beautiful objects sculpted by Nature. We require a character – a special one – to admire the beauty of these natural sculptures. American photographer Wilson ‘Snowflake’ Bentley’s (1855~1931, Jericho, Vermont) words,

‘Their (snowflakes) uniqueness is part of their fascination and romance, yet there is undoubtedly something similar about them; they share a ‘six-ness’. Which is more interesting? Perhaps it depends on the character of the observer.’

in *Appletons' Popular Science Monthly* (1898) ring in my ears as I write this section.

Arthropod-induced plant galls are in no way different from what Bentley speaks about snowflakes. The plant galls are stunning and

beautiful, yet each gall type induced by an arthropod species is unique in space. Arthropod-induced galls brilliantly bear witness to Gerald Holton's Ionian enchantment to me, because of their admirable orderliness in chaos in their form. I feel a delicate sense of Ionian enchantment, when I think of the spherical galls induced by *Eurosta solidaginis* (Diptera: Tephritidae) on the stems of *Solidago altissima* (Asteraceae) in North America and the sea-urchin galls induced by *Mangalorea hopeae* (Hemiptera: Beesoniidae) on the stems of *Hopea ponga* (Dipterocarpaceae) in southern India. The gross shape of any arthropod-induced gall, I am confident, will strike a pleasing chord in the minds of those, who look for and study these plant abnormalities. In northern Taiwan, galls of stunning shapes and structures arise on the foliage and stems of *Machilus thunbergii* (Lauraceae) because of the action of *Daphnephila taiwanensis*, *D. sueyенae*, *D. stenocalia*, *D. ornithocephala*, and *D. truncicola* (Diptera: Cecidomyiidae) (Tokuda *et al.*, 2008). The other impressive element in the ecology of gall-inducing arthropods is that they are generally fussy and choosy of host plants. They display a strong level of commitment, which I prefer to describe as 'fidelity' to specific plants. In this context, gall-inducing Insecta and Acarina can be seen as highly reliable plant taxonomists. As a rule of thumb, experienced scientists working on galls and gall-inducing arthropods can easily determine the plant by looking at the inducing organism and the gall, and determine the inducing organism by looking at the plant and the gall.

Several amateur biologists and hobby natural historians passionately pursue these curious natural sculptures, similar to others interested in snakes and other reptiles, birds, butterflies, mushrooms, and ferns. Consequently many handbooks and plain-English guidebooks on plant galls have appeared through the world: e.g., Michael Chinery's *British Plant Galls: A Photographic Guide*, Ronald Russo's *Field Guide to Plant Galls of California and Other Western States*, and Rosalind Blanche's *Life in a Gall*. The *Let's Gall Taiwan* is one of that kind. This book, includes chapters contributed by Sheng-Feng Lin, Chang-Ti Tang, Yi-Chang Liao, Hsin-

Ting Yeh, Chuan-Chan Wang, and Meng-Yuan Huang, further to the editors, Gene-Sheng Tung and Man-Miao Yang. Chien-Chun Hsiao, translator, has generally done a good job in rendering English texts, although certain parts could have been done better. This book's key purpose is to empower amateur biologists, who would be looking for arthropod-induced galls and the inducing arthropods in Taiwan. My commentary offered in the following paragraphs will refer only to the English sections of this book, since I am illiterate with Chinese characters.

First, on the overall quality and get-up of the book. This hard-cover book, elegantly Bradel bound, includes thick-gauge, high-quality A4-size pages. The spine bears a neat imprint of the book name in English and Chinese characters, along with the names of editors and publisher. The front cover is spectacular with attractive water colours of the European red-pea galls on *Quercus* leaves (Fagaceae) and the inducing *Cynips* (Hymenoptera) extracted from the *Alternating Generations: A Biological Study of Oak Galls and Gall Flies* by Hermann Adler (translated from German by Charles Straton, 1894, Clarendon Press, London, 198 pages). The back cover includes beautiful water-colour illustrations depicting the developmental sequence of the architecturally complex, urn-shaped Taiwanese gall arising on the leaves of *Machilus zuihoensis* (Lauraceae) induced by *Daphnephila urnicola* (Diptera: Cecidomyiidae). Several superbly executed water-colour and crayon sketches decorate different pages. The India-ink artworks in pages 24~25 referring to the rollings induced by Coleoptera on *Bischofia javanica* (Phyllanthaceae) and *Rhus chinensis* (Anacardiaceae) are superb. I will applaud the artists, Chu-Yu Quo and Li-Li Tseng, who have provided scientifically accurate artworks that creatively and aesthetically supplement the efforts of Gene-Sheng and Man-Miao.

Chapters 1~3 (pages 8~72) provide notes on the general context of arthropod-induced plant galls, their evolutionary and ecological significance, how the inducing arthropods behave during gall induction, and how galls have been used by humans, as in dyeing and medicine, over millennia, in easily-readable prose. Chapter 2.5, 'Coloration of galls', explains the mechanism

of hyper- and hypo-pigmentation that develop in galls. We need to recall here that the physiology of insect-induced galls 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, of course, would 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 similar physiological processes. In both systems, normally dehiscing fruits and dehiscing galls include newly differentiated specialized cells and a tight coordination of molecular and biochemical events that would lead to cell separation freeing seeds in fruits and the larva (or adult in some instances) in galls, once they mature.

Chapter 4 (pages 74~93) offers insights into the biologies and management of gall-inducing insects that have invaded Taiwan's agri- and horticulture in recent years: *Quadrastichus erythrinae* (Hymenoptera: Eulophidae) on species of *Erythrina* (Fabaceae), *Leptocybe invasa* (Hymenoptera: Eulophidae) on quite a few commercially important species of *Eucalyptus* (Myrtaceae), *Anselmella miltoni* (Hymenoptera: Eulophidae) on *Syzygium samarangense* (Myrtaceae), *Procontarinia mangicola* and *P. robusta* (Diptera: Cecidomyiidae) on *Mangifera indica* (Anacardiaceae), and *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae) on *Castanea mollissima* (Fagaceae). Gene-Tung and Man-Miao, the authors of this chapter, refer to different biological-management efforts trialled and practiced in Taiwan in the last few years. Useful basic information to people and plantation managers in nearby nations and those far away, who grapple with similar problems.

Chapter 5 (pages 96~243) constitutes the main part of this book - the guide to various gall-inducing arthropods, galls, and host plants of Taiwan. In about 135 pages this Chapter refers to 126 galls and associated insects. As in the rest of the world, the Cecidomyiidae top the list with 45 taxa, followed by the Cynipidae with 34. A few

Taiwanese hemipteran gall-inducing taxa from the Homotomidae, Aphididae, Adelgidae, Triozidae, Phacopteronidae, and Tingidae, and six taxa from the less-known gall-inducing groups, *viz.*, Gracillaridae, Sesiidae (Lepidoptera), Phlaeothripidae (Thysanoptera), and Curculionidae (Coleoptera) are also included. Details of all of these taxa are presented in a consistent style with brief notes in both Chinese and English characters, supported by high-quality images of galls and the inducing taxa, each taxon neatly accommodated within a page. Occasional supplementary photographs add value. Overall, this chapter, more-than adequately, fulfils the primary purpose of this volume by supplying images and notes that would substantially help an amateur gall enthusiast.

Two galls, one induced by *Bruggmanniella* sp. (Diptera: Cecidomyiidae) on *Litsea acuminata* (Lauraceae) (page 111) and another by *Daphnephila* sp. (Diptera: Cecidomyiidae) on *Machilus japonica* (Lauraceae) (page 121) reminded me of two Indian galls: *Apsylla cistellata* (Hemiptera: Aphalaridae) on *Mangifera indica* (Anacardiaceae) and *Phacopteron lentiginosum* (Hemiptera: Phacopteronidae) on *Garuga pinnata* (Burseraceae), because of similarities in gall morphologies. I will not attempt to make any comparisons here because the Taiwanese galls are induced by the Cecidomyiidae and the Indian galls by the Psylloidea. However, their apparent external similarity rang a bell of morphological convergence, which may have significant implications in evolutionary ecology.

As I was reading through, for a moment, I paused in page 135, which speaks about the Cecidomyiidae (*Asphondylia* sp.)-induced fruit galls of *Alpinia intermedia* (Zingiberaceae). That was an interesting pause. On an overall scale of gall incidence on angiosperms, the number of galls on monocotyledons is low — immensely low. The best-known examples of galls on monocotyledons are 'silver shoots' on *Oryza* (Poaceae) induced by *Orseolia* (Diptera: Cecidomyiidae) (Gagné, 2010). One other monocotyledon bearing galls is *Phragmites australis* (= *P. communis*, Poaceae) due to the action of *Graudiella inclusa* (Diptera:

Cecidomyiidae) known in Europe (Skuhravý, 1981). Odette Rohfritsch (Strasbourg, France) and Teja Tscharntke (Göttingen, Germany) have published several papers on the physiological ecology and population ecology, respectively, of *G. inclusa*-*P. australis* system in later years. Why so few galls occur on monocotyledons is a million-dollar question. The image in page 135 that details the developmental stage of the inhabiting *Asphondylia* was so good that I felt that this system requires a close investigation, that too soon, given that *Alpinia intermedia* is medicinally important (Amagai *et al.*, 2017). At least >500 secondary metabolites of significant medicinal use are known today in several species of *Alpinia* (Ma *et al.*, 2017). I am confident that the Gene-Sheng—Man-Miao team will study the *Alpinia intermedia*-*Asphondylia* system and come out with detailed bionomical and chemical-ecological data.

The book ends with a short epilogue (pages 245~246) and a list of books and relevant references, which would be of use to the user.

I cannot but avoid saying the following: the book suffers from a few errors. I will cite some as examples: cinipid for cynipid in p. 39, *Qadrastichus* for *Quadrastichus* in p. 76, use of ‘infected’ for ‘infested’ in p. 85 (this error is repeated in different places), *Castanea mollissima* for *Castanea mollissima* in p. 92. Two different subsection theme pages for Hemiptera (pages 144 and 162) confused me. The Aphididae- and the Tingidae-induced abnormalities shown in pages 166, 167, 168, 169, and 182 made me wonder whether these abnormalities could be considered galls! I did applaud the beautiful artworks included in different pages of the book: but in many a page, these artworks have not been suitably annotated with a legend. For example, in page 30, a beautiful water-colour image of a vertical sectional view of a triozidine (Psylloidea) gall exists. Various segments of this beautiful gall, impressively adapted to the needs of the inhabiting immature, have been shown in bright colours. How the intended details of this image would be understood by a hobby natural historian, I am not sure. Similar gaps are glaring in all chapters except Chapter 5. In Chapter 5 the photographs can be interpreted by the reader

because the biological names of plants and insects are supplied in the same page, although not as a legend to the figure. Whether the frequently used terms ‘monothalamous’ and ‘polythalamous’, I doubt, would be understood by the intended readers. A glossary explaining such professional terms would have been helpful. How come no acarine gall has been listed in this book, especially in Chapter 5? The absence of an index (at least an index of binomials), I felt, was prominent. I am hopeful that the editors would address these in the next edition.

Inclusion of a plastic magnifying lens (ϕ 6 cm) with a c. 6 cm long handle that includes the markings of a centimetre ruler, supplied *gratis* with each book copy, is thoughtful. A handy and helpful item in the field! This beautiful book is priced at NTD 460⁰⁰. The price is highly reasonable given the high quality of production. Readers from other countries too, I am sure, can procure a copy of this book with no hesitation, since the international price would be US\$ 16⁰⁰.

When I reached the back cover after my journey through the book, I felt a deep sense of satisfaction. The book is splendidly illustrated with perfect and high-resolution images. I am sure that any gall enthusiast interested in pursuing the beauty of Taiwanese galls will benefit substantially from this handsome volume. In short, this book is as beautiful as the *Daphnephila*-induced galls on *Machilus* in Taiwan are! From all of us — the community of gall enthusiasts and researchers from all over the world — heartfelt thanks go to Gene-Sheng and Man-Miao for this elegantly presented informative book. A splendid and welcome addition to world gall literature.

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