Research paper

Examination of Gall Features of an Undescribed *Ophelimus* sp. Gall Wasp and Host Susceptibility of Various *Eucalyptus* Host Species and Hybrid Strains in Taiwan

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【Summary】

An undescribed *Ophelimus* gall wasp species that causes damage to *Eucalyptus* trees was found in Taiwan in a recent investigation. The major hosts of this *Ophelimus* sp. are *Eucalyptus grandis* (Myrtaceae), *E. urophylla*, and *E. camaldulensis*. Analysis by Tukey's test showed no significant difference in mature gall volumes among the 3 host plants, regardless of differences in gall color or shape. An evaluation of galling preferences and host susceptibility of the hybrid strains from the 3 major hosts showed that the most preferred host to galling adults was the (*E. urophylla* × *grandis*) × *E. camaldulensis* hybrid, followed by the (*E. grandis* × *urophylla*) × *E. camaldulensis* hybrid. The (*E. grandis* × *urophylla*) × (*E. tereticornis* × *grandis*) hybrid had the lowest infestation rate, and it was found that mixing non-host species with suitable hosts to build resistant hybrid strains could be a workable management tool for plantation pest control. Previous research on host preferences and host ranges of known invasive wasps on eucalypts was also reviewed in this study, which may help choose ideal strains to alleviate attacks from this *Ophelimus* wasp in the future.

Key words: *Eucalyptus* gall, *Ophelimus*, invasive species, susceptibility test, host preference.

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研究報告

臺灣新發現種桉癭釉小蜂在不同寄主上的蟲癭差異與造癭偏好性

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摘　要

近期調查發現有一種過去在臺灣未曾描述過的桉癭釉小蜂屬 (*Ophelimus*) 造癭釉小蜂會對桉樹植群造成危害。此種造癭蜂主要造癭在玫瑰桉 (*Eucalyptus grandis*, Myrtaceae)、尾葉桉 (*E. urophylla*) 與赤桉 (*E. camaldulensis*) 葉片。以 Tukey's test 進行分析顯示，無論蟲癭顏色或形狀是否有差異，其成熟蟲癭體積在三種寄主植物間無顯著差異。進一步針對此種桉癭釉小蜂進行雜交桉的感染偏好性試驗，結果顯示成蟲最偏好 (尾葉桉×玫瑰桉)×赤桉之雜交品系，(玫瑰桉×尾葉桉)×赤桉雜交品系次之。(玫瑰桉×尾葉桉)×(細葉桉×玫瑰桉) 之雜交品系感染率較低，顯示使用非寄主為親本的雜交桉是可行的蟲害管理方式。此試驗結果可作為育成抗性品種進行造林及蟲害管理時的參考。本研究同時也回顧入侵種桉樹造癭害蟲的寄主偏好與寄主範圍，作為桉樹品種選植的建議，以利減輕桉癭釉小蜂對桉樹造林的危害。

關鍵詞：桉樹蟲癭、桉癭釉小蜂屬 (*Ophelimus*)、入侵種、造癭偏好性試驗、寄主偏好。

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INTRODUCTION

Eucalypts (*Eucalyptus, Corymbia*, and *Angophora*) are exotic trees commonly and widely cultivated for solid timber, paper pulp, ornamental purposes, and oil extraction in many countries (Hill and Johnson 1995, Udovicic et al. 1995, Ladiges and Udovicic 2000, Ladiges et al. 2003, Parra-O et al. 2006, 2009). Among all eucalypt genera, *Eucalyptus* is the largest genus made of about 700 species (Brooker 2000, Slee et al. 2015), with plantation species usually belonging to its largest subgenus *Symphyomyrtus* (Rejmánek and Richardson 2011). *Corymbia* is the second largest genus including 113 species (Parra-O et al. 2009) with plantation eucalypts usually belonging to the subgenus *Blakella* (Rejmánek and Richardson 2011). *Angophora* consists of about 12 species and subspecies which are koala habitat trees and mostly exclusive to eastern Australia (Brooker 2000, Slee et al. 2015, Timber Queensland 2015). *Angophora costata* is a species naturalized through previous afforestation efforts in Hawaii, and is the source of landmark trees or food supplies for koalas in California and New Zealand (GCW 2007, PIER 2010, Ritter 2015). Other *Angophora* species are not well-known forestry species as they are less often used in plantations. Most eucalypts are native to Australia, while some species are endemic to Indonesia (e.g., *E. urophylla*) and New Guinea (e.g., *E. tereticornis, E. pellita,* and *C. tessellaris*) (Hill 1994, Menut et al. 1995, Pepe et al. 2004, ICRAF 2021, POWO 2022).

Many eucalypts have been used for afforestation, with some *Eucalyptus* species, i.e., *E. camaldulensis*, *E. deglupta, E. globulus, E. grandis, E. robusta, E. saligna*, and *E. urophylla*, being major choices for the practice (FAO 2001). In the early days, their many adaptive characteristics, such as the resistance to drought, few infestation by pests, rare infection by diseases, etc., helped promote the rapid expansion of plantation areas. However, the promising productivity of eucalypt plantations has been challenged by increasing instances of invasive gall-inducing pests in the last 20 yr (Hurley et al. 2016). The global homogenization of employing *Eucalyptus* species for afforestation has also helped provide areas for these invasive pests to spread (Garnas et al. 2013, Csóka et al. 2017). Moreover, the successful invasion by these gall-inducing pests can also be facilitated by factors including the absence of parasitoids, the reproductive ability via parthenogenesis, the ability to circumvent host defenses, and suitable climates for the pest (Csóka et al. 2017). In order to fight against these invasive pests, other *Eucalyptus* species, including *E. camaldulensis, E. grandis, E. tereticornis, E. nitens, E. urophylla,* and *E. saligna,* and their paired hybrid strains, such as *E. grandis* × *E. camaldulensis, E. grandis* × *E. urophylla,* or hybrids from multiple species, have thus appeared to have increasing use in forestation (Dessie and Erkossa, 2011, Dittrich-Schröder et al. 2012, Wingfield et al. 2013, 2015, Hurley et al. 2017, Eskiviski et al. 2018).

The Eulophidae (Hymenoptera) is one of the largest and most diverse family in the Chalcidoidea (Burks et al. 2011, Noyes 2019), and is classified into five subfamilies, i.e., the Entedoninae, Entiinae, Eulophinae, Opheliminae, and Tetrastichinae (Burks et al. 2011, Rasplus et al. 2020). Galling pest wasps which induce galls on twigs, leaves, flower buds, and seeds of *Eucalyptus* and *Corymbia* trees belong to the Opheliminae and Tetrastichinae (Mendel et al. 2004, Kim et al. 2005, La Salle 2005, Wylie and Speight 2012, Noyes 2019). They can cause damage to plants and great economic losses. Invasive leaf-galling wasps can cause withering and early defoliation, malformation, and underdevelopment of trees, loss of essential oil production, and even the death of plants (Mendel et al. 2004, Nyeko 2005, Protasov et al. 2007, Franco et al. 2016). Invasive seed-galling wasps may have negative impacts on the number of seeds in seed capsules and the number of viable seeds produced (Kim et al. 2005, Klein et al. 2015). Some seed-galling wasps can stay dormant in a seed for many years and can survive CO_2 fumigation (Kim et al. 2005, Blanche 2012), causing quarantine problems to exporters of eucalypt seeds.

There are around 30 species of eucalypts cultivated in Taiwan today since the first species was introduced in 1896 (Chang 1981, Chen et al. 1995). Among these introduced species, *E. camaldulensis* is the core species subjected to long-term cultivation and research in Taiwan (Chung et al. 2017). These eucalypts showed no records of gall-inducing pests in several studies conducted in 1986, 1991, 1992, and 1994 (Chang and Fan 1989, Chang et al. 1992, Wang 1992, Chao 1995, Chung et al. 2017). The first invasive pest gall wasp on the eucalypt, *Leptocybe invasa* (Tetrastichinae), was recorded in 2010 (Tung and La Salle 2010, Chung et al. 2017). To combat infestations since 2013, susceptible host species were filtered out and changed to hybrid strains for pest control (Hsui et al. 2016, Chung et al. 2017). However, after the first discovery in 2010, there were no new leads of other invasive pest gall wasps on eucalypts until 2017. In 2017, we found a new leaf-galling *Ophelimus* sp. wasp (Opheliminae) that appeared to be an undescribed species in Tainan City, southwestern Taiwan. More investigation details concerning this galling pest species are discussed in a later part of this article. Worldwide invasive galling pests usually present different life cycle patterns and variable ecological attributes in different places they invade. They tend to be easily affected by the environment, and their life cycle may change. But they also have the ability to adjust themselves to adapt to the environment. The galling species, *L. invasa,* is a great example as it may have 2~3 generations per year in Iran, Israel, and Turkey (Mendel et al. 2004) but at least 6 generations per year in Taiwan (Tung et al. 2014). In order to obtain the necessary information as soon as possible to formulate efficient prevention policies to control this new species of *Ophelimus* wasp, we conducted basic biological studies on (1) the gall shape and gall density on different host species in the field, and (2) the galling preferences and life cycle on different *Eucalyptus* hybrid strains, which were formerly used for pest management against *L. invasa*, in the greenhouse. In this research, we also reviewed previous findings on galling preferences, host range, galling site, and invaded areas of known invasive gall wasps on eucalypts, in a discussion to provide useful ideas to help promote effective pest control strategies and plantation management in the future.

MATERIALS AND METHODS

Examination of gall feature variations on 3 natural *Eucalyptus* hosts

A study of gall shape, density, and gall volume of this galling pest species on host leaves of *E. grandis, E. urophylla,* and *E. camaldulensis* was conducted from March to June 2019. These *Eucalyptus* host species were identified according to Slee et al. (2015). Gall samples were collected from plantation sites, urban trees, and botanical gardens in northern Taiwan (Taipei City and Hsinchu City), central Taiwan (Taichung City and Yunlin County), and southern Taiwan (Tainan City and Kaohsiung City). For each chosen infected host specimen, 3 randomly selected twigs 30 cm long were removed from the lower crown. The total number of galls was counted, and the gall density per twig was calculated. Then, 6 galled leaves of each twig were randomly selected, and after that, 10 randomly selected galls per leaf were measured and dissected to examine developmental stages. The gall color was also recorded, and the following formula was applied to calculate the gall volume:

$$V = \frac{4}{3}\pi abc.$$

All results of gall density and gall volume were then analyzed by the Kruskal-Wallis test in PAST (vers. 2.17c). Tukey's test was also used to conduct an interspecies analysis.

Host preferences and susceptibility tests on different *Eucalyptus* hybrid strains

In a further biological study of the new leaf gall-inducer to search for resistant strains or least infested hosts by this gall wasp, the *Eucalyptus* hybrid strains #3702 ((*E. grandis* × *urophylla*) × (*E. tereticornis* × *grandis*) hybrid), #3803 ((*E. grandis* × *urophylla*) × *E. camaldulensis* hybrid), and #3901+3902 ((*E. urophylla* × *grandis*) × *E. camaldulensis* hybrid) provided by Mr. Jia-Bin Tsai (associate researcher, Liukuei Research Center, Taiwan) were used to run these tests. All of these are fast-growing, high-cellulose hybrids, that are resistant to *L. invasa*. Hybrid strain #3702 is a mixed product of a non-host species, *E. tereticornis,* to *Ophelimus* sp. Seedlings were grown in 11.4-cm plastic pots and watered twice daily in nursery garden no. 13 at Taipei Botanic Garden (25.032772N, 121.508537E).

Sample plants were randomly divided into 2 groups. In 1 group, each single plant (from 1 strain) was kept in an insect-rearing sleeve with 20 adult gall wasps, while in the other group, 3 plants (from the 3 strains) were kept in an insect-rearing tent with 60 adults. All of the adults were fed 1:1 honey water, and numbers of eggs produced by the wasps in each rearing sleeve and tent were counted and recorded. After being infested, the plants were observed daily until the larvae hatched and began to induce galls in the initiation stage in the plant leaves. Numbers of galls in different developmental stages and adult offspring were also counted and recorded. Results were first analyzed within species by the Kruskal-Wallis test (PAST, vers. 2.17c), and analysis by the Tukey-Kramer test was then used to assess differences among the different hybrid strains.

RESULTS

Examination of gall feature variations on 3 natural *Eucalyptus* hosts

Galls are regarded as an extended phenotype of gall inducers. Colors and shapes of galls that are heavily influenced by gall inducers and host plants are useful taxonomic characteristics to help identify gall-inducer species. *Ophelimus* sp. galls were collected around Taiwan (Fig. 1). They were green to greenish-yellow on *E. urophylla* and *E. camaldulensis* (Fig. 2A) and reddish to red on *E.*

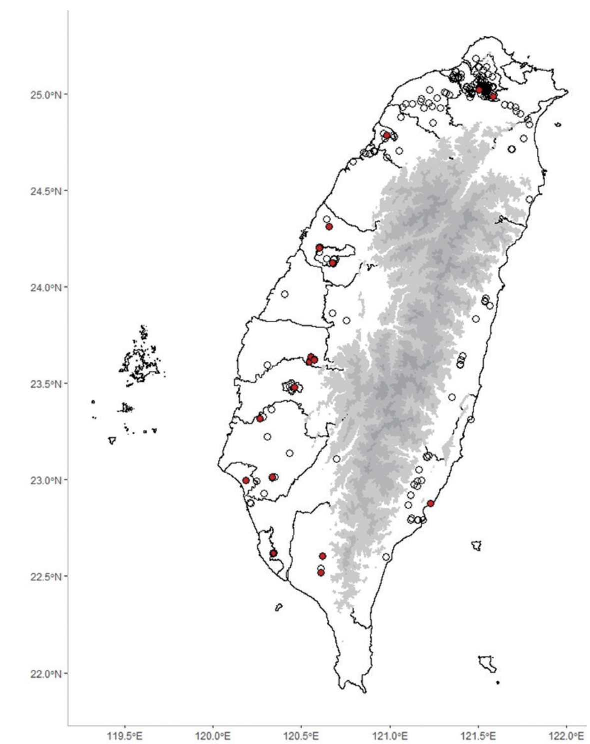

Fig. 1. *Eucalyptus* distribution map of Taiwan. Red dots: *Eucalyptus* trees with galls of *Ophelimus* sp.; white dots: *Eucalyptus* trees without *Ophelimus* sp. galls.

grandis (Fig. 2B). All of the host species were found to have galls induced by this wasp species with either a vertical ellipsoid shape (Fig. 3A) or flattened ellipsoid shape (Fig. 3B). *Eucalyptus grandis* had the highest gall density (282.6±179.1 galls per twig, with a maximum of 863 galls) which was much higher than those of *E. urophylla* (160.6±112.7 galls per twig, with a maximum of 516 galls) and *E. camaldulensis* (161.5±142.5 galls per twig, with a maximum of 579 galls) ($p < 0.001$). The average volume of mature galls was 35.7

Fig. 2. Galls of 2 different colors induced by wasps of *Ophelimus* sp. on different host species. A, *Eucalyptus urophylla*; B, *E. grandis.* Scale bar = 5 mm.

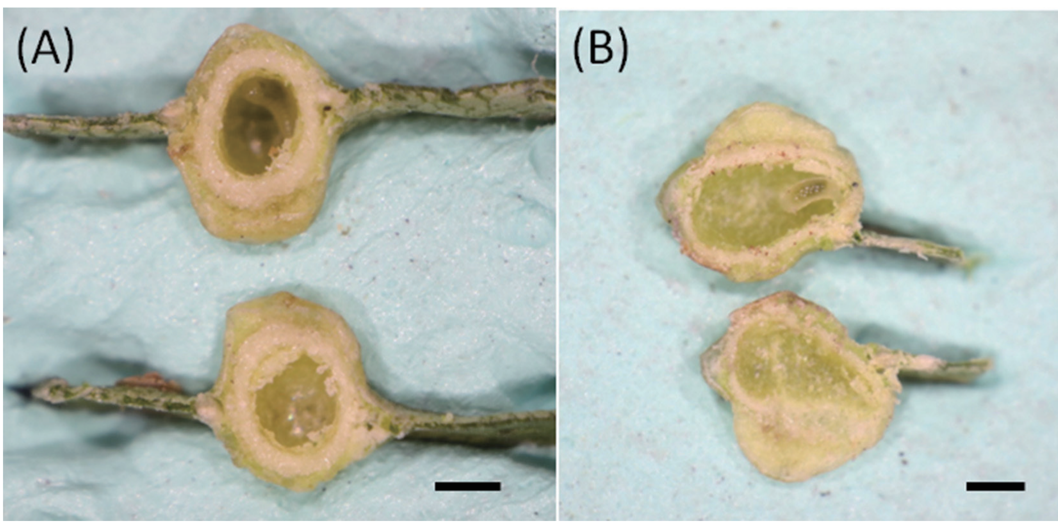

Fig. 3. Leaf galls on *Eucalyptus* hosts. A, Longitudinal section of a gall with a vertical ellipsoid shape; B, longitudinal section of a gall with a flattened ellipsoid shape. Scale bar = 0.5 mm.

mm^3 on *E. grandis* (length: width: height = 1: 0.75: 1), 31.6 mm^3 on *E. urophylla* (length: width: height = 1: 0.78: 0.96), and 36.3 mm^3 on *E. camaldulensis* (length: width: height = 1: 0.75: 0.80). However, regardless of the different colors and shapes, gall volumes of mature galls of *Ophelimus* sp. did not significantly differ among the 3 host species by Tukey's test.

Host preferences and susceptibility tests on different *Eucalyptus* hybrid strains

Unfertilized eggs inserted into host *Eucalyptus* leaves with conspicuous ovipositional marks (Fig. 4A, 4B) were usually laid in rows along the leaf margins or the veins, from the petiole end toward the tip of the leaf. Adults more preferred *Eucalyptus* hybrid strain #3901+3902 than the other 2 hybrid strains. In the single host-choosing test, adults preferred seedlings of *Eucalyptus* hybrid strains #3901+3902 (53.4±37.0 eggs per twig) and #3803 (43.3±14.7 eggs per twig) rather than #3702 (16.8±13.5 eggs per twig) ($p < 0.001$). Analysis of the #3702-#3901+3902 pair revealed a significant difference by the Tukey-Kramer test (α = 0.05, k = 3, df W = 46). While in the multiple host-choosing test, 66.5% of adults chose to lay eggs on #3901+3902 (36.4±21.7 eggs per twig) than the 18.3% of adults on #3803 (21.5±16.6 eggs per twig) ($p < 0.001$). Another 22.2% of adults chose to oviposit on #3702 (24.8±20.8 eggs per twig). Analysis of the #3803-#3901+3902 pair revealed a significant difference by the Tukey-Kramer test (α = 0.05, k = 3, df W =138).

Larvae hatched and began inducing initiation-stage galls on the 6th day after eggs were laid on the twigs (Fig. 4C). Suc-

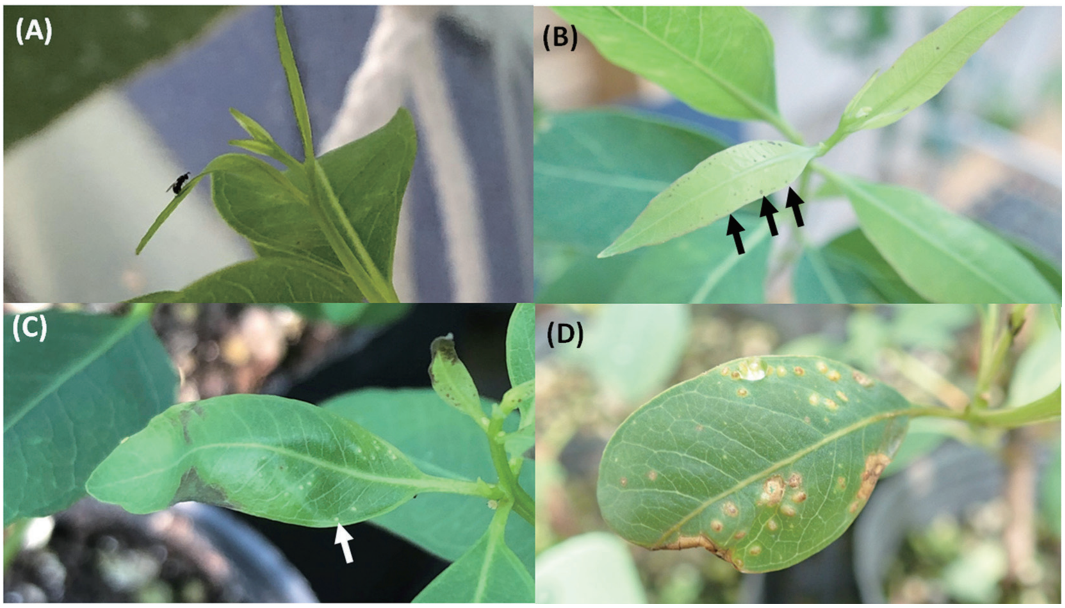

Fig. 4. Developmental stages of galls of *Ophelimus* sp. A, Adult wasp laid eggs on a leaf; B, at 12 h after oviposition, ovipositional marks (black arrow) could usually be found along the leaf margins or veins; C, at 6 d after oviposition, sign of young larvae visible (L1) inside initiation-stage galls (white arrow); D, at 25 d after oviposition, mature larvae or pupae have developed inside galls under the maturation stage.

cessful induction rates of initiation-stage galls on #3901+3902 (75.0±12.9%), #3803 (76.0±12.1%), and #3702 (71.2±18.4%) were similar. All of the galls were green to greenish-yellow on these hybrid strains. Most galls withered before reaching a maturation stage, and we found that larvae also ended up dead within the galls (Fig. 4D). Very low percentages of galls successfully developed to the maturation stage on #3702 (2.5±11.5%), #3803 (0.2±1%), and #3901+3902 (1.8±6.6%) twigs. The health condition of infested twigs could be affected by gall formation. About 10.7% of twigs withered within 1~2 wk after the development of initiation-stage galls (Table 1). Withered twigs appeared to have a higher successful induction rate (85.3±15.3%) than did surviving twigs (73.4±13.6%) ($p < 0.001$) by the Kruskal-Wallis test.

Although this research showed a high mortality rate of gall wasps in their gall development, more than 90% of second-generation adult gall wasps still successfully made it to emergence from the remaining maturation-stage galls on #3702 (97.3%), #3803 (100%), and #3901+3902 (94.7%). The average complete lifespan (from egg to adult emergence) of this new species of *Ophelimus* wasps was 37.8 ± 3.9 d (n = 213). All of the offspring of this wasp species were females. We also found and recorded the second generation offspring that induced third generation galls in the initiation stage on #3901+3902 and #3803 twigs in mid-December (19.2 °C).

DISCUSSION

The Opheliminae and Tetrastichinae are 2 subfamilies that make up of Eulophidae gall-inducing wasps, parasitoids, and inquilines (La Salle 2005, Burks et al. 2011). Fifty-one described *Ophelimus* species are native to Australia, and the majority of them are associated with *Eucalyptus* (Noyes 2019). Four invasive *Ophelimus* species that attack leaves of eucalypts are known to have occurred outside Australia (Table 2). We found 1 *Ophelimus* sp. outside Australia and confirmed that it is a gall-inducing wasp species in this study. This *Ophelimus* sp. wasp will be described and named in our forthcoming paper.

Ophelimus sp. wasps are insects that reproduce by thelytokous parthenogenesis, which means that their asexual reproduction with unfertilized eggs will only produce female offspring, and the entire process can only be done by female adults themselves. Natural host *Eucalyptus* species of *Ophelimus* sp. wasps in Taiwan mostly belong to the *Latoangulatae* section (*E. urophylla* and *E. grandis*). The complete lifespan of this invasive species in the greenhouse was around 38 d, which is shorter than a related species *O. maskelli* (Protasov et al. 2007). This undescribed *Ophelimus* sp. wasp presented different ovipositional behavior from that of *O. maskelli*. This research recorded that *Ophelimus* sp. laid its eggs in rows with visible

Table 1. Resistance ability of *Eucalyptus* hybrid strains to gall wasps

Eucalyptus hybrid strain	No. of killed twigs/no. of induced-gall twigs
3702	8/38
3803	5/36
3901+3902	3/110

Table 2. Galling wasp (Opheliminae)-infected leaves of *Eucalyptus* and *Corymbia* around the world [1] Withers et al. 2000, [2] Raman and Withers 2003, [3] Filho et al. 2004,[4] Kavallieratos et al. 2006, [5] Protasov et al. 2007, [6] Branco et al. 2009, [7] CABI 2011, [8] Dessie and Erkossa 2011, [9] Ghabeish and Araj 2016, [10] Borowiec et al. 2019, [11] Molina-Mercader et al. 2019, [12] Noyes 2019, [13] Dittrich-Schröder et al. 2020.

Eucalyptus		**Pest species**	*Ophelimus maskelli*	*O. eucalypti*	*O. mediterraneus*	*O. migdanorum*	*Ophelimus* sp.
		Invaded area	Worldwide	Asia, Africa, Europe	Europe	South America	Asia
Subgenus	**Section**	**species** / **Galling site**	leaf	leaf	leaf	leaf	leaf
Cruciformes		*Eucalyptus guilfoylei*		-			
Eucalyptus	*Longistylus*	*E. diversifolia*	-				
		E. preissiana	-				
	Longitudinales	*E. moorei*	-				
Eudesmia	*Limbatae*	*E. erythrocorys*	-				
	Reticulatae	*E. miniata*	-				
Idiogenes		*E. cloeziana*	++				
Symphyomyrtus	*Adnataria*	*E. albens*	+				
		E. coolabah	-				
		E. crebra	-				
		E. intertexta	-				
		E. lansdowneana	-				
		E. leucoxylon	-				
		E. melanophloia	+				
		E. melliodora	+				
		E. microtheca	-				
		E. moluccana	-				
		E. polyanthemos	-				
		E. sideroxylon	-				
		E. woollsiana	-				
	Bisectae	*E. astringens*	**NS**				
		E. brockwayi	**NS**				
		E. burdettiana	-				
		E. burracoppinensis	-				
		E. calycogona	-				
		E. campaspe	-				
		E. cornuta	-				
		E. dielsii	-				
		E. dundasii	**NS**				
		E. eremophila	-				
		E. erythronema	-				

Table 2	Continued					
	E. foecunda	-				
	E. gillii	**NS**	+			
	E. goniantha	-				
	E. grossa	-				
	E. kruseana	+				
	E. loxophleba	+				
	E. occidentalis	-				
	E. orbifolia	-				
	E. pachyphylla	-				
	E. platypus	-				
	E. redunca	-				
	E. salmonophloia	-				
	E. salubris	-				
	E. sargentii	-				
	E. spathulata	-				
	E. stricklandii	-				
	E. websteriana	-				
	E. annulata	-				
Bolites	*E. gomphocephala*	+				
Dumaria	*E. angulosa*	+				
	E. cyanophylla	-				
	E. dumosa	-				
	E. forrestiana	-				
	E. kondininensis	-				
	E. lesouefii	-				
	E. tetraptera	-				
	E. torquata	-				
	E. woodwardii	+				
Exsertaria	*E. amplifolia*	++				
	E. camaldulensis	++	++		++	+
	E. rudis	++				
	E. tereticornis	++				
Inclusae	*E. diversicolor*		-			
Latoangulatae	*E. botryoides*	++	++			
	E. deanei		++			
	E. grandis	++	++			++
	E. pellita		-			
	E. punctata		-			
	E. robusta	++	-			
	E. saligna	++	++			
	E. urophylla		++			++
Maidenaria	*E. bridgesiana*	++				

Table 2	Continued						
		E. cinerea	++		++		
		E. cypellocarpa			++		
		E. globulus	++	++	++	++	
		E. gunnii	++		++		
		E. nicholii	++				
		E. parvula			++		
		E. pulverulenta	++				
		E. viminalis	++				
	Platysperma	*E. brevifolia*	-				
	Sejunctae	*E. cladocalyx*	-				
	Similares	*E. longifolia*		-			
	***Eucalyptus* hybrid**						
		E. torwood hybrid *(E. torquata × E. woodwardii)*	**NS**				
		E. trabutii hybrid *(E. camaldulensis × E. botryoides)*	++				
		E. urograndis hybrid *(E. grandis × E. urophylla)*	**NS**	++			
	3702	hybrid *(E. grandis × E. urophylla) × (E. tereticornis × E. grandis)*					+
	3803	hybrid *(E. grandis × E. urophylla) × E. camaldulensis*					++
	3901+3902	hybrid *(E. urophylla × E. grandis) × E. camaldulensis*					++
		hybrid *E. grandis × E. camaldulensis*	++				
Corymbia							
Subgenus	**Section**	**species**					
Blakella	*Maculatae*	*Corymbia citriodora*	-				
		C. maculata	+				
	Naviculares	*C. eximia*	-				
	Torellianae	*C. torelliana*	+				
Corymbia	*Septentrion-ales*	*C. ptychocarpa*	-				
	References		5, 6, 7, 9, 12	1, 2, 3, 4, 7, 8, 12, 13	10	11	

++, with severe gall development; +, infested by wasps but showing only limited gall formation; NS, no specified host, showed signs of oviposition but no galls had developed; -, non infested.

traces (ovipositional marks) in contrast to the ovipositional pattern of *O. maskelli*, which lays eggs randomly on the leaf and leaves no visible signs (Protasov et al. 2007). Unlike *O. maskelli* which ignores mature leaves when producing eggs on a host (Protasov et al. 2007), *the Ophelimus* sp. wasp laid eggs on both immature and mature leaves of a host. These findings showed that this undescribed species has a similar egg-laying distribution pattern to that of *O. maskelli:* it oviposited on 52.5% of leaves, and 86.5% of galled leaves had 1~10 initiation-stage galls per leaf (the maximum was 44 initiation-stage galls on 1 leaf). The color of *Ophelimus* sp. galls was affected by the host species, not by exposure to sunlight. Despite galls having shown a reddish to red color on *E. grandis,* all of the gall colors were green to greenish-yellow on hybrid strains. Abscission of immature leaves can be caused by *Ophelimus* sp., but that phenomenon was not observed with *O. maskelli* (Protasov et al. 2007). As to the withered twigs associated with the new *Ophelimus* sp. gall wasp, they were not the result of being affected by the number of eggs produced on the leaf, but the result of being affected by the successful induction rate of initiation-stage galls.

Understanding the natural history of invasive pests and susceptibility of their specific hosts is fundamental for pest management. It is also important to clarify susceptibility levels of hosts and hybrid strains for authorities to develop more-ideal prevention strategies against specific pests. According to our findings, more-susceptible eucalypt hosts to the Eulophidae gall-inducing wasps were mostly from the *Exsertaria, Latoangulatae*, and *Maidenaria* sections that belong to the subgenus *Symphyomyrtus* (Tables 2-4). These 3 sections contain the most important eucalypt species for commercial afforestation. However, eucalypt species in the section of the *Blakella* subgenus in previous studies presented lower susceptibilities to galling pests (Tables 3, 4). *Eucalyptus* gall wasps established in areas outside of Australia can be divided into 2 groups. One comprises a multiple-host group including the leaf galler *L. invasa* (Table 3), all of the described invasive *Ophelimus* species (Table 2), and the seed gallers *Quadrastichodella nova* and *Moona spermophaga* (Tetrastichinae) (Table 4). The other comprises a single-host group of the leaf gallers *Epichrysocharis burwelli* and *Selitrichodes globulus* (Tetrastichinae) (Table 3). Species of the multiple-host group are usually widespread and can easily cause great damage to host plants and possibly massive economic losses. Based on an analysis of the host species phylogeny on the 3 natural hot species of this new invasive *Ophelimus* sp., *E. grandis* and *E. urophylla* (section *Latoangulatae*) were in a cluster together, and the two were less close to *E. camaldulensis* (section *Exsertaria*) (Steane et al. 2011). Although galls are constituted of plant cells responding to stimuli, gall shapes are commonly seen as one of the extended phenotypes of gall inducers. Since the wasps of *Ophelimus* sp. in this research induced similar gall shapes and sizes on the 3 natural host species of *E. grandis*, *E. urophylla*, and *E. camaldulensis*, it is suggested that all the 3 *Eucalyptus* species are natural hosts of *Ophelimus* sp. wasps. The ability of this *Ophelimus* sp. wasp to adapt itself to multiple hosts could be a potential threat to *Eucalyptus* plantations with adverse economic impacts on the *Eucalyptus* industry.

Cultivation of resistant plant varieties is one of the frequently used methods employed for pest control in forestry industries (Wingfield et al. 2013, 2015), as for example strains developed to combat infestation by *L. invasa,* such as the #U49 strain, # L151x L151, and

Table 3. Galling wasp (Tetrastichinae)-infected leaves of *Eucalyptus* and *Corymbia* around the world [1] Schauff and Garrison 2000, [2] Filho et al. 2004, [3] Mendel et al. 2004, [4] Santana and Anjos 2007, [5] Kim 2008, [6] La Salle et al. 2009, [7] Nyeko et al. 2009, [8] Thu et al. 2009, [9] Nyeko et al. 2010, [10] Nadel and Slippers 2011, [11] Dittrich-Schroder et al. 2012, [12] EPPO 2012, [13] FAO 2012, [14] IPPC 2012, [15] Wylie and Speight 2012, [16] Lin et al. 2014, [17] Franco et al. 2016, [18] Jorge et al. 2016, [19] Noyes 2019, [20] Pujade-Villar et al. 2019, [21] CABI 2021

Eucalyptus		**Pest species**	*Leptocybe invasa*	*Epichrysocharis burwelli*	*Selitrichodes globulus*
		Invaded area	Worldwide	Europe, North America, South America	North America
Subgenus	**Section**	**Galling site** / **Species**	young branch, petiole, vein	leaf	branch, twig, leaf
Alveolata		*Eucalyptus microcorys*	++		
Eucalyptus	*Pseudophloius*	*E. pilularis*	+		
Eudesmia	*Limbatae*	*E. erythrocorys*	**NS**		
Idiogenes		*E. cloeziana*	**NS**		
Symphyomyrtus	*Adnataria*	*E. coolabah*	+		
		E. crebra	-		
		E. leucoxylon	**NS**		
		E. melanophloia	-		
		E. moluccana	+		
		E. polyanthemos	-		
		E. populnea	-		
		E. sideroxylon	**NS**		
	Bisectae	*E. astringens*	-		
		E. dundasii	-		
		E. erythronema	-		
		E. loxophleba	-		
		E. occidentalis	-		
		E. platypus	-		
		E. salubris	-		
		E. sargentii	-		
		E. spathulata	-		
		E. stricklandii	-		
	Bolites	*E. gomphocephala*	**NS**		
	Dumaria	*E. kondininensis*	-		
		E. torquata	-		
		E. woodwardii	-		
	Exsertaria	*E. alba*	**NS**		
		E. amplifolia	+		
		E. camaldulensis	++		
		E. camaldulensis subsp. *camaldulensis*	++		
		E. camaldulensis subsp. *obtusa*	++		

Table 3 Continued

		E. camaldulensis subsp. *simulata*	++	
		E. exserta	+	
		E. rudis	+	
		E. tereticornis	++	
		E. tereticornis subsp. *tereticornis*	++	
	Latoangulatae	*E. botryoides*	++	
		E. deanei	+	
		E. grandis	++	
		E. pellita	++	
		E. propinqua	++	
		E. punctata	-	
		E. resinifera	-	
		E. robusta	++	
		E. saligna	++	
		E. urophylla	++	
	Maidenaria	*E. benthamii*	++	
		E. bridgesiana	++	
		E. cinerea	+	
		E. dunnii	+	
		E. globulus	++	++
		E. globulus subsp. *globulus*	+	
		E. globulus subsp. *maidenii*	++	
		E. gunnii	++	
		E. nicholii	+	
		E. nitens	+	
		E. pulverulenta	**NS**	
		E. smithii	++	
		E. viminalis	++	
	Sejunctae	*E. cladocalyx*	**NS**	
	Eucalyptus **hybrid**			
		E. algeriensis hybrid (*E. camaldulensis* × *E. rudis*)	++	
		E. torwood hybrid (*E. torquata* × *E. woodwardii*)	**NS**	

Table 3	Continued				
		E. trabutii hybrid (*E. camaldulensis* × *E. botryoides*)	++		
		E. urograndis hybrid (*E. grandis* × *E. urophylla*)	++		
		hybrid (*E. grandis* × *E. urophylla*) × (*E. grandis* × *E. urophylla*)	++		
		hybrid (*E. tereticornis* × *E. grandis*) × *E. camaldulensis*	++		
		hybrid (*E. tereticornis* × *E. grandis*) × (*E. grandis* × *E. urophylla*)	++		
		hybrid *E. camaldulensis* × (*E. grandis* × *E. urophylla*)	+		
		hybrid *E. camaldulensis* × *E. camaldulensis*	+		
		hybrid *E. camaldulensis* × *E. grandis*	++		
		hybrid *E. grandis* × *E. camaldulensis*	++		
		hybrid *E. grandis* × *E. nitens*	++		
		hybrid *E. grandis* × *E. tereticornis*	++		
		hybrid *E. nitens* × *E. grandis*	++		
		hybrid *E. saligna* × *E. urophylla*	+		
Corymbia					
Subgenus	**Section**	**species**			
Blakella	*Abbreviatae*	*Corymbia tessellaris*	**-**		
	Maculatae	*C. citriodora*	+	++	
		C. citriodora subsp. *citriodora*	**NS**		
		C. henryi	**NS**		
		C. maculata	+		
	Torellianae	*C. torelliana*	**NS**		
Corymbia	*Septentrionales*	*C. polycarpa*	++		
	References		3, 5, 7, 8, 9, 10, 11, 13, 14, 15, 16, 18, 19, 21	1, 2, 4, 5, 12, 17, 19, 20	6

++, with severe gall development; +, infested by wasps but showing only limited gall formation; NS, no specified host, showing signs of oviposition but no gall had developed; -, non infested.

Table 4. Galling wasp-infected seeds of *Eucalyptus* and *Corymbia* around the world [1] La Salle 1994, [2] Kim et al. 2005, [3] Doğanlar and Doğanlar 2008, [4] Kim 2008, [5] Klein et al. 2015, [6] Noyes 2019, [7] Dittrich-Schröder et al. 2020.

Eucalyptus		**Pest species**	*Quadrastichodella nova*	*Moona spermophaga*
		Invaded area	Worldwide	Africa, South America
Subgenus	**Section**	**Galling site / Species**	seed capsules	seed capsules
Symphyomyrtus	*Exsertaria*	*E. camaldulensis*	++	
		E. tereticornis	++	
	Latoangulatae	*E. resinifera*	++	
Corymbia				
Blakella	*Maculatae*	*C. citriodora*		++
		C. citriodora subsp. *variegata*		++
		C. maculata		++
References			1, 3, 4, 5, 6	2, 7

++, with severe gall development.

#GUT5 strain selected in Taiwan (Lin et al. 2014, Chung et al. 2017), and *E. grandis* × *E. camaldulensis* and *E. urophylla* × *E. grandis* hybrid strains in Argentina (Eskiviski et al. 2018). Similar to those completed implementations, although *Ophelimus* sp. wasp-resistant hybrid programs in Taiwan are still in process, some resistant hybrid eucalypts to this wasp have been successfully selected. In this research, the 3 natural host species *E. grandis*, *E. urophylla*, and *E. camaldulensis* of this *Ophelimus* sp. wasp and 1 non-host species *E. tereticornis* were used experimentally as parent species to develop hybrid strains. After the tests, research showed that the level of host susceptibility to this *Ophelimus* wasp varied in the hybrid strains. Results on hybrid strain #3702 ((*E. grandis* × *urophylla*) × (*E. tereticornis* × *grandis*) hybrid) presented a lower host preference, a lower number of eggs oviposited on the plant, and a lower infestation rate. In contrast to hybrid strain #3702, hybrid strain #3901+3902 ((*E. urophylla* × *grandis*) × *E. camaldulensis* hybrid) presented a higher host preference, a higher adult emergence rate, and continuing infestation in natural situations. These results were similar to those of hybrid host tests on the pest galling wasps *L. invasa* and *O. maskelli*, which indicated that pest wasps cannot successfully develop on specific hybrid hosts generated from wasp-resistant parent species (Mendel et al. 2004, Protasov et al. 2007). Our findings also support that the hybridization between host and non-host parent species has the potential to be a workable pest management tool against the new *Ophelimus* sp. wasp studied in this paper.

CONCLUSIONS

One undescribed thelytokous gall-inducing *Ophelimus* wasp was recently found in Taiwan and has been confirmed to be a new gall-inducing wasp species by this study. Suitable hosts of this *Ophelimus* sp. belong to the section *Latoangulatae* (*E. grandis* and *E. urophylla*) and the section *Exsertaria* (*E. camaldulensis*). We also conducted evaluation tests on host preferences and susceptibility of *Eucalyptus* hybrid strains. Test results showed that the *Ophelimus* sp. wasp presented a high mortality rate during development on all hybrid strains. One hybrid that came from a mix with 1 unsuitable host parent species, *E. tereticornis*, turned out to have a lower host preference, a lower infestation rate, and a lower successful adult emergence rate. This study assumed that *Ophelimus* sp. could be a potential threat with damaging economic impacts on relevant *Eucalyptus* industries as the wasps gradually and successfully adapt themselves to multiple hosts. The study also suggests that mixing host parent species with non-host parent species to build resistant hybrid strains can be a workable pest management tool against this *Ophelimus* sp. in the future.

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LITERATURE CITED

Blanche R. 2012. Life in a gall: the biology and ecology of insects that live in plant galls. Collingwood, Australia: CSIRO Publishing. 80 p.

Borowiec N, La Salle J, Branaccio L, Thaon M, Warot S, Branco M, et al. 2019. *Ophelimus mediterraneus* sp. n. (Hymenoptera: Eulophidae): a new *Eucalyptus* gall wasp in the Mediterranean region. Bull Entomol Res 109:678-94.

Branco M, Boavida C, Durand N, Franco JC, Mendel Z. 2009. Presence of the *Eucalyptus* gall wasp *Ophelimus maskelli* and its parasitoid *Closterocerus chamaeleon* in Portugal: first record, geographic distribution and host preference. Phytoparasitica 37:51-4.

Brooker MIH. 2000. A new classification of the genus *Eucalyptus* L'Hé r. (Myrtaceae). Aust Syst Bot 13:79-148.

Burks RA, Heraty JM, Gebiola M, Hansson C. 2011. Combined molecular and morphological phylogeny of Eulophidae (Hymenoptera: Chalcidoidea), with focus on the subfamily Entedoninae. Cladistics 27:581-605.

CABI. 2011. *Ophelimus eucalypti*. Available at https://www.cabi.org/isc/datasheet/37565. Accessed 1 Oct 2022.

CABI. 2021. *Leptocybe invasa* (blue gum chalcid). Available at https://www.cabi.org/isc/datasheet/108923. Accessed 1 Oct 2022.

Chang CA. 1981. Investigation and research of cultivated *Eucalyptus* in Taiwan. Q J Chin For 14:43-64.

Chang YC, Fan YB. 1989. Surveys on major insect-pests of trees and shrubs in Taiwan. Taipei, Taiwan: Taiwan Forestry Research Institute. Special Bulletin no. 32.

Chang YC, Huang YS, Fan YB, Zhang TR. 1992. Research of *Eucalyptus* pests. Taipei, Taiwan: Council of Agriculture. Forestry Series 41. A compilation of 1991 silvicultural techniques of fast growing trees research project reports, p 93-102.

Chao JT. 1995. The species and potential harms of insect-pest in eastern Taiwan *Eucalyptus* plantation. Taiwan For J 21:2-6.

Chen CF, Yang JC, Chang TY, Horng FW. 1995. Results of the adaptability test of twenty *Eucalyptus* species grown in Taiwan. Bull Taiwan For Res Inst 10:283-92.

Chung JD, Chen ZZ, Tsai JB. 2017. Heavy responsibilities of tree improvement. For Res Newsl 24:20-3.

Csóka G, Stone GN, Melika G. 2017. Non-native gall-inducing insects on forest trees: a global review. Biol Invasions 19:3161-81.

Dessie G, Erkossa T. 2011. *Eucalyptus* in East Africa: socio-economic and environmental issues. Planted Forests and Trees Working Paper 46/E. Available at https://www.fao.org/3/am332e/am332e.pdf. Accessed 1 Oct 2022.

Dittrich-Schröder G, Hurley BP, Wingfield MJ, Nahrung HF, Slippers B. 2020. Invasive gall-forming wasps that threaten non-native plantation-grown *Eucalyptus*: diversity and invasion patterns. Agric For Entomol 22:285-97.

Dittrich-Schröder G, Wingfield MJ, Hurley BP, Slippers B. 2012. Diversity in *Eucalyptus* susceptibility to the gall-forming wasp *Leptocybe invasa*. Agric For Entomol 14:419-27.

Doğanlar O, Doğanlar M. 2008. First record of the eucalyptus seed gall wasp, *Quadrastichodella nova* Girault, 1922, (Eulophidae : Tetrastichinae) from Turkey. Turk J Zool 32:457-9.

EPPO. 2012. *Epichrysocharis burwelli* (EPCRBU). Available at https://gd.eppo.int/taxon/EPCRBU. Accessed 1 Oct 2022.

Eskiviski ER, Schapovaloff ME, Dummel DM, Fernandez MM, Aguirre FL. 2018. Susceptibility of eucalyptus species and hybrids to the gall wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) in northern Misiones, Argentina. For Syst 27:eSC01.

FAO. 2001. Forest plantations thematic papers. Available at https://www.fao.org/3/AC121E/ac121e00.htm#Contents. Accessed 1 Oct 2022.

FAO. 2012. *Leptocybe invasa* Fisher and La Salle. Available at http://www.fao.org/forestry/13569-05912e0e2fe9054c3ed4904ae597e3310.pdf. Accessed 1 Oct 2022.

Filho EB, Costa VA, La Salle J. 2004. Primeiro registro da vespa-da-galha, *Epichrysocharis burwelli* (Hymenoptera: Eulophidae) em *Corymbia (Eucalyptus) citriodora* (Myrtaceae) no Brasil. Braz J Agric 79:363.

Franco JC, Garcia A, Branco M. 2016. First report of *Epichrysocharis burwelli* in Europe, a new invasive gall wasp attacking eucalypts. Phytoparasitica 44:443-6.

Garnas JR, Hurley BP, Slippers B, Wingfield MJ. 2013. Biological control of forest plantation pests in an interconnected world requires greater international focus. Int J Pest Manage 58:211-23.

GCW. 2007. *Angophora costata* (Myrtaceae). Available at http://hear.org/gcw/species/angophora_costata/. Accessed 4 Jan 2023.

Ghabeish IH, Araj SEA. 2016. Population trend, host susceptibility and damage study on the Eucalyptus gall wasp *Ophelimus maskelli* (Ashmead) (Hym., Eulophidae) in Jordan. Jordan J Agric Sci 12:239-48.

Hill KD, Johnson LAS. 1995. Systematic studies in the eucalypts 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). Telopea 6:185-504.

Hill RS. 1994. The history of selected Australian taxa. In: Hill RS, editor. History of the Australian vegetation: Cretaceous to recent. Adelaide, South Australia: University of Adelaide Press. p 390-420.

Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B. 2016. Increasing numbers and intercontinental spread of invasive insects on eucalypts. Biol Invasions 18:921-33.

Hurley BP, Slippers B, Sathyapala S, Wingfield MJ. 2017. Challenges to planted forest health in developing economies. Biol Invasions 19:3273-85.

Hsui YR, Chung JD, Tsai JB. 2016. Study on fast-growing and high-cellulose tree species from afforestation on the plains. In: Chiou JM, editor. 2016 Symposium of Plain

Afforestation Experiment and Monitoring. Taipei, Taiwan: Taiwan Forestry Research Institute. p 9-16.

ICRAF. 2021. *Eucalyptus urophylla*. Available at http://apps.worldagroforestry.org/treedb2/speciesprofile.php?Spid=821. Accessed 1 Oct 2022.

IPPC. 2012. Occurrence of *Eucalyptus* gall wasp *Leptocybe invasa* in Mozambique. Available at https://www.ippc.int/en/countries/mozambique/pestreports/2012/02/occurence-of-eucalyptus-gall-wasp-leptocybe-invasa-in-mozambique/. Accessed 1 Oct 2022.

Jorge C, Martínez G, Gómez D, Bollazzi M. 2016. First record of the eucalypt gall-wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) from Uruguay. Bosque 37:631-6.

Kavallieratos NG, Kontodimas DC, Anagnou-Veroniki M, Emmanouel NG. 2006. First record of the gall-inducing insect *Ophelimus eucalypti* (Gahan) (Hymenoptera: Chalcidoidea: Eulophidae) in Greece. Ann Benaki Phytopathol Inst 20:125-8.

Kim IK. 2008. Evolution of gall inducing Eulophidae (Hymenoptera: Chalcidoidea) on Myrtaceae in Australia [PhD thesis]. Canberra, Australia: Australian National Univ.

Kim IK, McDonald M, La Salle J. 2005. *Moona,* a new genus of tetrastichine gall inducers (Hymenoptera: Eulophidae) on seeds of *Corymbia* (Myrtaceae) in Australia. Zootaxa 989:1-10.

Klein H, Hoffmann JH, Neser S, Dittrich-Schröder G. 2015. Evidence that *Quadrastichodella nova* (Hymenoptera: Eulophidae) is the only gall inducer among four hymenopteran species associated with seed capsules of *Eucalyptus camaldulensis* (Myrtaceae) in South Africa. Afr Entomol 23:207-23.

La Salle J. 1994. North American genera of Tetrastichinae (Hymenoptera: Eulophidae). J Nat Hist 28:109-236.

La Salle J. 2005. Biology of gall inducers and evolution of gall induction in Chalcidoidea (Hymenoptera: Eulophidae, Eurytomidae, Pteromalidae, Tanaostigmatidae, Torymidae). In: Raman A, Schaefer CW, Withers TM, editors. Biology, ecology, and evolution of gall-inducing arthropods. Enfield, NH, USA: Science Publishers, p 507-37.

La Salle J, Arakelian G, Garrison RW, Gates MW. 2009. A new species of invasive gall wasp (Hymenoptera: Eulophidae: Tetrastichinae) on blue gum (*Eucalyptus globulus*) in California. Zootaxa 2121:35-43.

Ladiges PY, Udovicic F. 2000. Comment on a new classification of the eucalypts. Aust Syst Bot 13:149-52.

Ladiges PY, Udovicic F, Nelson G. 2003. Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. J Biogeogr 30:989-98.

Lin YL, Chang TP, Tung GS. 2014. Susceptibility tests of various *Eucalyptus* host species to *Leptocybe invasa* in Taiwan. Taiwan J For Sci 29:65-71.

Mendel Z, Protasov A, Fisher N, La Salle J. 2004. Taxonomy and biology of *Leptocybe invasa* gen. & sp. n. (Hymenoptera: Eulophidae), an invasive gall inducer on *Eucalyptus.* Aust J Entomol 43:101-13.

Menut C, Molangui T, Lamaty GE, Bessiere JM, Habimana JB. 1995. Aromatic plants of tropical Central Africa. 23. Chemical composition of leaf essential oils of *Eucalyptus goniocalyx* F. Muell. and *Eucalyptus patens* Benth. growth in Rwanda. J Agric Food Chem 43:1267-71.

Molina-Mercader G, Angulo AO, Olivares T, Sanfuentes E, Castillo-Salazar M, Rojas E, et al. 2019. *Ophelimus migdanorum* Molina-Mercader sp. nov. (Hymenoptera: Eulophidae): application of integrative taxonomy for disentangling a polyphenism case in *Eucalyptus globulus* Labill forest in Chile.

Forests 10:720.

Nadel RL, B Slippers. 2011. *Leptocybe invasa,* the blue gum chalcid wasp. ICFR. Available at http://www.forestry.co.za/uploads/File/home/notices/2011/ICFR%20IS01–2011gallwasp. pdf. Accessed 1 Oct 2022.

Noyes JS. 2019. Universal Chalcidoidea database. World Wide Web electronic publication. Available at http://www.nhm.ac.uk/chalcidoids. Accessed 1 Oct 2022.

Nyeko P. 2005. The cause, incidence and severity of a new gall damage on *Eucalyptus* species at Oruchinga refugee settlement in Mbarara District, Uganda. Ugandan J Agric Sci 11:47-50.

Nyeko P, Mutitu EK, Day RK. 2009. *Eucalyptus* infestation by *Leptocybe invasa* in Uganda. Afr J Ecol 47:299-307.

Nyeko P, Mutitu KE, Otieno BO, Ngae GN, Day RK. 2010. Variations in *Leptocybe invasa* (Hymenoptera: Eulophidae) population intensity and infestation on eucalyptus germplasms in Uganda and Kenya. Int J Pest Manage 56:137-44.

Parra-O C, Bayly M, Drinnan A, Udovicic F, Ladiges PY. 2009. Phylogeny, major clades and infrageneric classification of *Corymbia* (Myrtaceae), based on nuclear ribosomal DNA and morphology. Aust Syst Bot 22:384-99.

Parra-O C, Bayly M, Udovicic F, Ladiges PY. 2006. ETS sequences support the monophyly of the eucalypt genus *Corymbia* (Myrtaceae). Taxon 55:653-63.

Pepe B, Surata K, Suhartono F, Sipayung M, Purwanto A, Dvorak WS. 2004. Conservation status of natural populations of *Eucalyptus urophylla* in Indonesia and international efforts to protect dwindling gene pools. FAO. Forest Genetic Resources no. 31: 62-64. Available at https://www.fao.org/3/y5901e/Y5901E15.htm. Accessed 1 Oct 2022.

PIER. 2010. *Angophora costata* (Gaertn.) J. Britten, Myrtaceae. Available at http://www.hear.org/pier/species/angophora_costata.htm. Accessed 3 Jan 2023.

POWO. 2022. *Eucalyptus tereticornis.* Available at https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:593412-1. Accessed 1 Oct 2022.

Protasov A, La Salle J, Blumberg D, Brand D, Saphir N, Assael F, et al. 2007. Biology, revised taxonomy and impact on host plants of *Ophelimus maskelli*, an invasive gall inducer on *Eucalyptus* spp. in the Mediterranean Area. Phytoparasitica 35:50-76.

Pujade-Villar J, Díaz-Ramos SG, Rodríguez-Rivas A, Cibrián-Llanderal VD, Askew D. 2019. First record of *Epichrysocharis burwelli* from Mexico, a. New invasive gall wasp attacking *Corymbia* (Myrtaceae). SW Entomol 44:323-5.

Raman A, Withers T. 2003. Oviposition by introduced *Ophelimus eucalypti* (Hymenoptera: Eulophidae) and morphogenesis of female-induced galls on *Eucalyptus saligna* (Myrtacea) in New Zealand. Bull Entomol Res 93:55-63.

Rasplus JY, Blaimer BB, Brady SG, Burks RA, Delvare G, Fisher N, et al. 2020. A first phylogenomic hypothesis for Eulophidae (Hymenoptera, Chalcidoidea). J Nat Hist 54:597-609.

Rejmánek M, Richardson DM. 2011. Eucalypts. In: Simberloff D, Rejmánek M, editors. Encyclopedia of biological invasions. Berkeley, CA: Univ of California Press. p 203-9.

Ritter M. 2014. Field guide to the cultivated eucalypts (Myrtaceae) and how to identify them. Ann Missouri Bot Gard 99:642-87.

Santana DLQ, Anjos N. 2007. Microvespado-eucalipto-citriodora (*Corymbia citriodora*) - *Epichrysocharis burwelli* Schauff (Hymenoptera: Eulophidae). Comunicado Técnico 188:1-4.

Schauff ME, Garrison R. 2000. An introduced species of *Epichrysocharis* (Hymenoptera: Eulophidae) producing galls on *Eucalyptus* in California with notes on the described species and placement of the genus. J Hymenopt Res 9:176-81.

Slee AV, Brooker MIH, Duffy SM, West JG. 2015. EUCLID Eucalypts of Australia Edition 4. Centre for Australian National Biodiversity Research. Available at https://apps.lucidcentral.org/euclid/text/intro/index.html. Accessed 1 Oct 2022.

Steane DA, Nicolle D, Sansaloni CP, Petroli CD, Carling J, Kilian A, et al. 2011. Population genetic analysis and phylogeny reconstruction in *Eucalyptus* (Myrtaceae) using high-throughput, genome-wide genotyping. Mol Phylogenet Evol 59:206-24.

Thu PQ, Dell B, Burgess TI. 2009. Susceptibility of eucalypt species to the gall wasp *Leptocybe invasa* in the nursery and young plantations in Vietnam. Sci Asia 35:113-7.

Timber Queensland. 2015. Timber plantation operations code of practice for Queensland. Available at http://www.timberqueensland.com.au/Docs/Growing-Processing/Timber-Plantation-Operations-Code-of-Practice-Version-1.pdf. Accessed 5 Jan 2023.

Tung GS, La Salle J. 2010. Pest alert-a newly discovered invasion of gall-forming wasps, *Leptocybe invasa* (Fisher & La Salle), on *Eucalyptus* trees in Taiwan. Formosan Entomol 30:241-5.

Udovicic F, McFadden GI, Ladiges PY. 1995. Phylogeny of *Eucalyptus* and *Angophora* based on 5S rDNA spacer sequence data. Mol Phylogenet Evol 4:247-56.

Wang WY. 1992. Survey of *Eucalyptus* diseases in Taiwan. Bull Taiwan For Res Inst 7:179-94.

Wingfied MJ, Brockerhoff EG, Wingfield BD, Slippers B. 2015. Planted forest health: the need for a global strategy. Science 349:832-6.

Wingfield MJ, Roux J, Slippers B, Hurley BP, Garnas J, Myburg AA, Wingfield BD. 2013. Established and new technologies reduce increasing pest and pathogen threats to eucalypt plantations. For Ecol Manage 301:35-42.

Withers TM, Raman A, Berry JA. 2000. Host range and biology of *Ophelimus eucalypti* (Gahan) (Hym.: Eulophidae), a pest of New Zealand eucalypts. NZ Plant Prot 53:339-44.

Wylie FR, Speight MR. 2012. Insect pests in tropical forestry. 2nd ed. Oxfordshire, UK: CABI. 365 p.