Review Article

Parasitoid Guilds of *Agrilus* Woodborers (Coleoptera: Buprestidae): Their Diversity and Potential for Use in Biological Control

Philip B. Taylor,¹ Jian J. Duan,¹ Roger W. Fuester,¹ Mark Hoddle,² and Roy Van Driesche³

¹Beneficial Insects Introduction Research Unit, USDA-ARS, Newark, DE 19713, USA

²Department of Entomology, University of California Riverside, Riverside, CA 92521, USA

³ Department of Plant, Soil and Insect Sciences, University of Massachusetts, Amherst, MA 01003, USA

Correspondence should be addressed to Jian J. Duan, jian.duan@ars.usda.gov

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Literature studies in North America (US and Canada), Europe, and Asia (particularly Russia, China, Japan, and the Korean peninsula) were reviewed to identify parasitoid guilds associated with *Agrilus* woodborers. There are at least 12 species of hymenopteran parasitoids attacking eggs of *Agrilus* beetles and 56 species (36 genera), attacking *Agrilus* larvae infesting various host plants in North America, Asia, and Europe. While most of the egg parasitoids (9 species) belong to the family Encyrtidae, a majority of the larval parasitoids are members of five families: Braconidae (24 species/11 genera), Eulophidae (8 species/4 genera), Ichneumonidae (10 species/9 genera), and Eupelmidae (6 species/5 genera). The highest rate of *Agrilus* larval parasitism (>50%) was exerted by encyrtid wasps (4 species) in North America, Asia, and Europe. In contrast, the highest rate of *Agrilus* larval parasitism (>50%) was caused by species in two genera of braconids: *Atanycolus* (North America) and *Spathius* (Asia), and one eulophid genus, *Tetrastichus* (Asia and Europe). Reported rate of *Agrilus* larval parasitism ichneumonids was frequent in North America, but generally low (<1%). Potential for success in biological control of emerald ash borer (*Agrilus planipennis* Fairmaire) in the USA with North American native parasitoids and old-association Asian parasitoids is discussed.

1. Introduction

Agrilus is the largest genus within the family Buprestidae (Coleoptera), with nearly 3,000 described species worldwide [1]. Generally, *Agrilus* spp. only attack angiosperms and do not develop in conifers [2]. Moreover, they tend to be specialists, most species being confined to a single genus or species of host plant. While most *Agrilus* species are not considered to be serious pests of agriculture or forests, at least two species have recently become seriously damaging in forests in their newly invaded areas in North America: the emerald ash borer (EAB), *A. planipennis* Fairmaire, and the gold spotted oak borer (GSOB), *A. auroguttatus* Shaefer. EAB was accidentally introduced to Michigan in late 1990s from its native range (northeast Asia, in parts of China, Russia, and Korea) possibly via wooden crates or pallets for

cargo shipment [3]; it has since spread to 14 additional US states and two Canadian provinces and killed millions of North American ash (Fraxinus spp.) since its detection in 2002 [4, 5]. By contrast, GSOB is native to the oak forests of southwestern Arizona, and while its damage to oak trees in its invaded range has been on a smaller scale, it has killed more than 25,000 oaks in the oak savannahs of California since first discovered there in 2002 [6–8]. A few other exotic Agrilus species have also been recently detected in the United States (e.g., soapberry borer-A. prionurus Chevrolat in Texas [9]) and Canada (e.g., European oak borer-A. sulcicollis Lacordaire in Ontario [10]). Although some of the recently detected, exotic Agrilus species have not become as widespread or damaging as EAB and GSOB, the pest status of Agrilus borers as a whole along with other woodborers appears to have increased in recent years [11].

Search database	Years searched	Agrilus hits	Search hits combined with parasitoid (parasite, natural enemy, or biological control)		
Agricola	1970-date	302	38		
BioAbstracts (BIOS)	1926-date	507	43		
Biological and Agricultural Index Plus	1983-date	30	2		
Biological Sciences Set	1982-date	273	23		
CSA Illumina		265	22		
CAB Abstracts	1985-date	354	94		
ISI Web of Science	1900-date	211	25		
	No duplicates ^a		-105		
	Total publications	1,942	142		

TABLE 1: Summary of online database search for Agrilus and associated parasitoids.

^aWe did not review all 1,942 to exclude duplicates.

Management for the invasive (exotic) Agrilus woodborers (EAB and GSOB) in the United States initially focused on attempted eradication but changed to integration of several approaches when eradication failed to reduce the pests' populations in infested areas and slow spread of the pests to the noninfested areas [12, 13]. In some cases, control methods being used include delimitation of infested areas, regulatory restriction of movement of pest-infested wood or plant materials, insecticide treatment or physical destruction of infested trees [12-14], and biological control via introduction and release of natural enemies collected from pests' native ranges [7, 15–18]. Although none of these approaches individually is adequate, biological control, which relies on self-propagating and dispersing natural enemies, has potential to reduce invasive pest populations, particularly in forests [19-21].

Agrilus adults normally lay their eggs under loose bark or in crevices of host plant tissues and rarely cause significant damage; in contrast, Agrilus larvae typically bore into the living tissue (stems, trunks, branches, or roots) of their host plants, interrupt the translocation of water and nutrients as they feed, and can kill plants within one or a few years of infestation (e.g., EAB [22]; GSOB [6]; A. prionurus [9]). In their native habitats, Agrilus populations are generally suppressed by a diverse group of natural enemies and/or host tree resistance and only occasionally become serious pests. However, when introduced into ecosystems where host plants lack coevolutionary resistance, or where appropriate specialized natural enemies are absent, they can become severe pests. The recent invasions of North America by EAB from northeast Asia and GSOB from southwestern Arizona are excellent examples of this. For example, EAB is considered a sporadic pest of ash stands in its native range in Asia [23-26] but has become a serious pest threatening the existence of North American ash trees since it was accidentally introduced there [22]. Similar observations have been made for GSOB in its home range. Field studies in Asia found that a complex of natural enemies (primarily parasitoids) and host plant resistance by Asian ash trees appear to be the factors responsible for suppressing EAB

populations and preventing them from frequently causing ash mortalities [15, 19].

Deliberate efforts have been recently undertaken in the United States to achieve biological control of EAB and GSOB through introduction of natural enemies (parasitoids) from the native ranges of these pests [7, 17]. These classical biological control efforts for EAB have led to the discovery and introduction of several egg and larval parasitoids that have the potential to establish and suppress the pests' populations in the newly introduced regions [19-21, 27]. Similar programs for GSOB commenced in 2010 and are too immature to reach tentative conclusions about natural enemy diversity and impacts. In reviewing the literature, we found that many groups of parasitoids and other natural enemies have reported attacking Agrilus beetles. An overview of the composition of the parasitoid guild attacking this group of woodborers will contribute to the current and future development of biological control programs to manage these pests, particularly those Agrilus that have invaded new regions or environments. In the present study, we first review the diversity of natural enemy complexes in particular, hymenopteran parasitoid guilds associated with egg and larval stages of Agrilus species, and then discuss the potential of those parasitoids for use as agents of classical biological control against this group of pests.

2. Literature Reviewed

We searched seven major online data bases using the key word "*Agrilus*" either alone or in combination with any of the key words "parasitoid," "parasite", "natural enemy", or "biological control" to locate relevant literature. Databases examined were (1) Agricola, (2) BioAbstracts (BIOS), (3) Biological Sciences Set, (4) Biological and Agricultural Index Plus, (5) CSA Illumina, (6) CAB Abstract, and (7) ISI Web of Sciences set. The key word "*Agrilus*" alone resulted in 1942 articles (Table 1), of which 142 articles remained when combined with "parasitoid or parasite, natural enemies, or biological control." It must be noted that database searches concluded in March 2011. For this paper, we included only

Parasitoid guilds	Order: Family	Species	Recorded <i>Agrilus</i> host	Habitat	Native range in distribution	Level of parasitism	Reference sources
Egg Hym: parasitoids Aphelinidae Hym: Encyrtidae Hym: Signiphoridae Hym: Eulophidae	/	Ablerus sp.	A. anxius	Birch trees	Northeastern USA/Canada	<0.2%	[28]
		Avetianella sp.	A. anxius; A. subcinctus	Birch trees; ash trees	Northeastern USA/Canada	<3.5%	[28, 34]
	Coccidencyrtus sp.	A. liragus	Poplar trees	Northeastern USA/Canada	~55%	[35]	
	/	Ooencyrtus erionotae	A. sexsignatus	Eucalyptus trees	Southeast Asia (Philippines)	32-57%	[31, 32]
	Encyrtidae	tidae <i>Ooencyrtus</i> sp.	A. anxius	Birch trees	Northeastern USA/Canada	<2.4%	[28]
		Oobius agrili	A. planipennis	Ash trees	China/northeast China-Jilin province	>50%	[15, 36]
		Oobius agrili	A. planipennis	Ash trees	United States/Michigan	Not reported	[19]
		Oobius zahaikevitshi	A. viridis and A. planipennis	Hazelnut and ash trees, resp.	Northern Italy/Russian	8 – 58%	[37, 38]
		Orianos brazai	A. sexsignatus	Eucalyptus trees	Southeast Asia (Philippines)	0-47%	[39]
		Signichorini tribe	A. anxius	Birch trees	Northeastern USA/Canada	<1%	[28]
		Ptinobius magniflcus	A. ruficollis	Raspberry, Blackberry, Dewberry	North America	Not reported	[40, 41]
	/	<i>Thysanus</i> sp.	A. liragus	Poplar trees	Northeastern USA/Canada	~12%	[35]
		Pediobius sp.	A. planipennis	Ash trees	United States/Michigan	Not reported	[42]
Larval Parasitoids	Hym: Braconidae	Atanycolus charus	<i>A. anxius</i> and <i>A. liragus</i>	Birch and poplar trees	Northeastern USA/Canada	0.3–52%	[29, 35]
		Atanycolus cappaerti	A. planipennis; A. liragus and A. bilineatus	Ash trees; poplar and chestnut trees	Northeastern USA/Canada	9–71%	[33]
		Atanycolus disputabilis	A. planipennis and other North American native woodborers	Oak trees	Northeastern USA/Canada	<1%	[43]
		Atanycolus simplex	A. planipennis; A. liragus and A. bilineatus	Ash trees; poplar and chestnut trees	Northeastern USA/Canada	<1%	[35, 44]
		Atanycolus hicorie	A. planipennis and other native Agrilus woodborers	Ash trees	Northeastern USA/Canada	<2%	[45, 46]
		Atanycolus nigropopyga	A. planipennis and other North American native woodborers	Ash trees	Northeastern US/Canada	<3%	JJD (unpublished)

TABLE 2: Parasitoid guilds associated with Agrilus woodborers in North America and Asia.

TABLE 2: Continued.

Parasitoid guilds	Order: Family	Species	Recorded <i>Agrilus</i> host	Habitat	Native range in distribution	Level of parasitism	Reference source
		Atanycolus picipes	A. planipennis	Ash trees	Vladivostok, Russia	<5%	JJD (unpublished), [25]
		Doryctes farthus	<i>A. anxius</i> and <i>A. liragus</i>	Birch and poplar trees	Northeastern US/Canada	<0.1%	[44]
		Doryctes rufipes	<i>A. anxius</i> and <i>A. liragus</i>	Birch and poplar trees	Northeastern USA/Canada	<0.1%	[44]
		Doryctes atripes	A. anxius	Birch tree	Northeastern USA/Canada	<0.1%	[44]
		Iphiaulaz impostor	A. biguttatus	Poplar trees	Europe	~13%	[47]
		Leluthia astigma	<i>A. planipennis;</i> <i>A. difficilis</i> and other <i>Agrilus</i> spp.	Ash trees; honey locust trees	USA	~2.1%	[48, 49]
		Spathius agrili	A. planipennis	Ash trees	China	60–90%	[50-56]
		Spathius agrili	A. planipennis	Ash trees	USA/Michigan	Not reported	[21, 57]
		Spathius agrilivorus	A. planipennis	Ash trees	Vladivostok, Russia	~64%	JJD (unpublished), [25]
		Spathius curvicaudis	A. biguttatus	Oak trees	Europe	~25%	[47, 58]
		Spathius floridanus	A. planipennis and other North American native woodborers A. planipennis	Ash trees	USA	<0.5%	JJD (unpublished)
		Spathius laflammei	and other North American native woodborers	Ash trees	USA	<1%	JJD (unpublished)
		Spathius simillimus	A. anxius and A. liragus/; A. planipennis	Birch and poplar tree; ash trees	USA/Canada	<0.5%	[18]
		Wroughtonia (Helconidea) ligator	A. anxius, A. liragus and A. bilineatus	Birch, poplar and chestnut trees	northeastern USA/Canada	<1%	[29, 44]
		<i>Ecphylus</i> sp.	A. subcinctus	Ash trees	USA	Not reported	[34]
		Heterospilus sp.	A. subcinctus	Ash trees	USA	Not reported	[34]
		Pareucorystes varinervis	A. viridis	Hazelnut	Europe/Russia	Not reported	[59]
		Monogonogastra agrili	A. arcuatus	Hickory, pecan	North America	Not reported	[60]
		Microbracon xanthostigmus	A. ruficollis	Raspberry, blackberry, dewberry	North America	Not reported	[40, 41]
	Hym: Chalcididae	Phasgonophora sulcata	A. anxius, A. bilineatus and A. liragus; A. planipennis	Birch, chestnut and poplar tree; ash trees	USA/Canada	2-20%	[28–30, 35]

Parasitoid Recorded Level of Native range in Habitat Order: Family Species Reference sources guilds Agrilus host distribution parasitism A. anxius and Birch and Hym: Tetrastichus USA/Canada A. liragus; poplar trees; < 0.1% [29, 35] Eulophidae nr.rugglesi A. planipennis ash trees Pear trees and Tetrastichus A. sinuatus and raspberries, Europe 55-75% [61-63] heeringi A.aurichalceus resp. Tetrastichus Not A. ribesi [64] Black current Europe heeringi reported Eucalyptus Southeast Asia Tetrastichus sp. A. sexignatus 2-50% [31, 32] trees (Philippines) Northeastern Tetrastichus China/Russian A. planipennis Ash trees 22-40% [15, 65, 66] planipennisi Far East Tetrastichus 0.80% USA Michigan A. planipennis Ash trees [27, 57, 67] planipennisi Baryscapus Not A. aurichalceus Raspberry Europe/Hungary [62, 68] agrilorum reported near Not A. subcinctus Ash trees USA [34] Hadrotrichodes reported Entodon Not China [69] A. surorovi/ Poplar epicharis reported Not Entodon zanara A. surorovi China [69] Poplar reported A. planipennis and other Asia Southeast Hym: Balcha indica and North Ash trees Asia/North <4% [70-72] Eupelmidae American America woodborers Calosota USA/Mexico 15% [6] A. auroguttatus Oak trees elongata Ash trees and Eupelmus pini A. planipennis North America < 0.2% [70] weevils Not Metapelma sp. A. subcinctus Ash trees USA [34] reported Europe/Poland Not Willow Calosota agrili A. salicis [73, 74] and Russia reported Pentacladia Not Agrilus sp. Fig Turkey [75] hatayensis reported Hym: **Bephratoides** A. anxius Birch trees North America <1% [29] Eurytomidae agrili A. rubicola and Rose and Not Eurytoma rosae A. bilineatus chestnut trees reported Eurytoma sp. A. anxius Birch trees North America <1% [29] Not A. subcinctus North America Eurytoma sp. Ash trees [34] reported Hym: Ash trees-to Cunocephalus sp. A. planipennis North America < 0.2% [70] Ichneumonidae be confirmed Dolichomitus A. anxius and Birch trees North America [29] $<\!0.4\%$ messorperlongus A. liragus A. planipennis and other Dolichomitus Ash trees North America < 0.2% [70] vitticrus native woodborers A. anxius and Ephialtes sp. Birch trees North America $<\!0.4\%$ [35] A. liragus

TABLE 2: Continued.

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Parasitoid guilds	Order: Family	Species	Recorded <i>Agrilus</i> host	Habitat	Native range in distribution	Level of parasitism	Reference sources
		Glypta sp.	A. anxius	Birch trees	North America	<1%	[44]
		Ichneumon sp.	A. anxius	Birch trees	North America	<1%	[44]
		Olesicampe sp.	A. anxius	Birch trees	North America	<1%	[44]
		Unknown spp.	A. suvorovi- populneus	Poplar trees	Europe/Hungary	4-5%	[76]
		Orthizema sp.	A. anxius; A. planipennis	Birch trees; ash trees	North America	<1%	[44, 70]
		Pimploterus sp.	A. anxius	Birch trees	North America	<1%	[44]
		Labena apicaulis	A. arcuatus	Hickory, pecan	North America	Not reported	[60]
	Hym: Stephanidae	Foenatopus sp.	A. sexsignatus	Eucalyptus trees	Southeast Asia (Philippines)	2–50%	[31, 32]
	Hym: Pteromalidae	Zatropus sp.	A. arcuatus	Hickory, pecan	North America	Not reported	[60]
i cromar	i teromandae	<i>Oodera</i> sp.	A. subcinctus	Ash trees	USA	Not reported	[34]
	Hym: Bethylidae	Sclerodermus pupariae	A. planipennis	Ash trees	China	Not reported	[77]

those original research articles that provide information on parasitoid identity at the family, genus, or species levels (Table 2).

In addition to searching databases, we contacted colleagues who work on invasive EAB and GSOB beetles and their biological control in the United States and Canada for information on parasitoid guilds of these species. All relevant studies were read and analyzed for mention of *Agrilus* species, associated parasitoids, known host associations, host plants, and geographic distributions. If available, parasitism rates by each group, guild, or species of parasitoids were noted.

3. Results and Discussion

At the genus level, the guilds of egg and larval parasitoids of Agrilus species were similar in North America, Europe, and Asia. While several families of North American parasitoids (including Braconidae, Chalcididae, Ichneumonidae, and Eupelmidae) are capable of utilizing larvae of the newly introduced emerald ash borer (A. planipennis) as a novel host, some Asiatic species of parasitoids appear to be more specific and only utilize Asian Agrilus species as hosts. From the geographic distribution point of view, it appears that there is more diversity in the parasitoid complex associated with Agrilus beetles in North American than in Asia and Europe. However, this geographic difference in parasitoid diversity may actually reflect different levels of research activities on the subject. For example, the invasion of North America by EAB has certainly resulted in much more research activities on the parasitoid complex of this group of woodborers in North America.

There are at least 12 species of hymenopteran parasitoids that attack eggs of *Agrilus* beetles and 56 parasitoid species that attack *Agrilus* larvae in various plants in North America, Asia, or Europe (Table 2). While most of these egg parasitoids (9 species) belong to the family Encyrtidae, a majority of the larval parasitoids are members of five families: Braconidae (24 species/11 genera), Eulophidae (8 species/4 genera), Ichneumonidae (10 species/9 genera), and Eupelmidae (6 species/5 genera). One species of larval parasitoid (*Phasgnophora sulcata* Westwood) (Chalcididae) is frequently associated with native *Agrilus* woodborers in North America [28–30]. In addition, there is one larval parasitoid (*Foenatopus* sp.) in the family Stephanidae that was reported attacking *A. sexsignatus* (Fisher) infesting Eucalyptus trees in southeast Asia [31, 32].

The highest rates of *Agrilus* egg parasitism (>50%) occurred with four species of encyrtid wasps reported in North America, Asia, and Europe (Table 2). In contrast, the highest rates of *Agrilus* larval parasitism (>50%) were caused by two groups of braconid wasps: *Atanycolus* spp. (in North America) and *Spathius* spp. (in Asia), and three species of eulophid wasps (in Asia and Europe). Although ichneumonid wasps were frequently reported attacking *Agrilus* woodborers in North America, the reported rate of parasitism was very low (<1%) for all the ichneumonid species.

It is interesting to note that several species of North American native parasitoids, *Atanycolus* spp., *Spathius floridanus* Ashmead, *S. laflammei* Provancher, *S. simillimus* Ashmead, *Phasgonophora sulcata* Westwood, and one accidentally introduced Asiatic wasp *Balcha indica* (Mani and Kaul), have been recently reported attacking the invasive emerald ash borer. One group of native parasitoids, *Atanycolus* spp., has recently become the dominant mortality factor associated with emerald ash borer, attacking >50% of *A. planipennis* larvae at some forest sites in Michigan (USA) [19, 33]. The potential of both the native (new-association) parasitoids and the introduced (old-association) parasitoids (e.g., *Oobius agrili* Zhang and Huang, *Tetrastichus planipennisi* Yang, and *Spathius agrili* Yang) for biological control of EAB, in the USA, needs further investigation.

A diverse group of hymenopteran parasitoids attacks eggs and larvae of Agrilus woodborers in North America, Asia, and Europe. Literature review of this genus, in regards to its parasitoid guild, has interest due to the introduction of two species in North America (GSOB and EAB). In biological control, parasitoid species of invasive pests are often introduced from the land of origin, if proved to be safe (not become a pest themselves). In addition, new-association parasitoids that inhabit the region prior to the pest introduction sometimes exert pressure on this newly arrived pest and offer opportunity for research and augmentation of indigenous parasitoid populations. Our literature review has provided documentation of research activities for 12 egg parasitoid species and 56 larval parasitoid species. These parasitoids are identified from 19 species of Agrilus, a small representation of almost 3000 described, that attack 18 recorded plant types (13 hardwoods, 5 shrubs). Being a diverse genus, these results show a wealth of research opportunities for further work on Agrilus parasitoids worldwide. Nearly two thirds (64.3%) of the literature found was published after year 2000. Twentyseven of 83 entries (32.5%), in Table 2, reference A. planipen*nis*. These findings are results of EAB postdetection in 2002.

Although *Agrilus* species are relatively host specific, because of larvae's concealed nature, early stages and damage are difficult to assess and take much effort to obtain. This has implications on finding and identifying parasitoid complexes for biocontrol and may be a reason for so little literature. Of those parasitoid species found in association with EAB, some are ectoparasitoids and known to attack woodborers in different families (e.g., Cerambycidae). While data from the current literature do not show any particular relationship between host specificity and mode of parasitization (endoversus ectoparasitoids), further research is needed to investigate such relationship.

Some species occur on multiple Agrilus spp., such as egg parasitoid Oobius zahaikevitshi. Atanycolus cappaerti is known to attack A. planipennis, A. liragus, and A. bilineatus, while Leluthia astigma attacks A. planipennis, A. difficilis, and other Agrilus spp. These may provide better access of parasitoids where poplar, chestnut, honey locust, and ash occur together.

The parasitoid guild of *Agrilus* in China, Russia, and North America and EAB distribution may provide species for introduction or augmentation. Though most of the parasitism rates are low (<10%), a few worthy candidates not yet used for introduction or augmentation include egg parasitoid, *O. zahaikevitshi* from Russia, and larval parasitoids *Atanycolus cappaerti, Spathius agrilovorus*, and *Spathius floridanus*. These species in the USA have not yet been reared in large numbers, and further studies on rearing methods need pursuing. It appears also that braconids and eulophids have provided the best potential for biological control, and the number of studies the last five years bear this out. It also indicates that species size and morphology (ovipositor length) for accessing the host from outside the host plant are important for success. Finally, parasitoid work in biological control efforts often lack taxonomic expertise to provide accurate identifications. Some of these newly known parasitoid species are not well understood. Egg parasitoids are often disregarded due to size and inaccessibility of host eggs. These hamper ongoing biological control of invasive or cyclic native pest populations. A concluding question is should work be done now on conspecifics that have the potential to be invasive (e.g., *A. coxalis* attacks oaks in Mexico—California has a history of acquiring pests from MX, could *A. coxalis* be another threat to CA's besieged oaks forests?).

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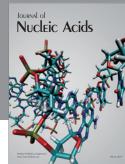
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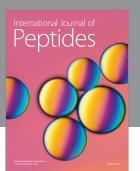
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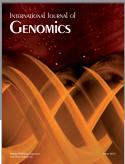
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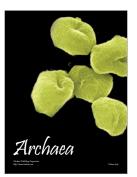








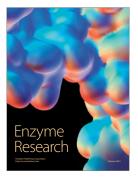








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