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Biology and Control of Emerald Ash Borer



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Chapter 6: Biology of Emerald Ash Borer Parasitoids

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INTRODUCTION

The emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), an invasive beetle introduced from China (Bray et al., 2011), was identified as the cause of ash (*Fraxinus* spp.) mortality in southeast Michigan and nearby Ontario in 2002 (Haack et al., 2002; Federal Register, 2003; Cappaert et al., 2005). Although eradication was attempted for several years after the beetle's discovery, it continued to spread throughout North America, killing ash trees in urban, forested, and riparian areas. In an effort to conserve native species of *Fraxinus*, researchers continue to evaluate integrated pest management methods that include the use of classical biological control, systemic insecticides, and the development of resistant cultivars (Herms and McCullough, 2014).

Surveys of EAB populations in recently invaded areas of North America revealed a low prevalence of native generalist parasitoids, mainly species in *Atanycolus* and *Spathius* (Hymenop.: Braconidae), and *Phasgonophora sulcata* Westwood (Hymenop.: Chalcididae) (Bauer et al., 2004; Lindell et al., 2008; Duan et al., 2009, 2012a, 2013a). In regions of China where EAB is native, specialist EAB parasitoids were recovered (Liu, H-Q. et al., 1996; Liu, H-P. et al., 2003, 2007; Zhang et al., 2005; Yang et al., 2005). The most promising of these parasitoids for EAB biocontrol in North America were *Oobius agrili* Zhang and Huang (Hymenop.: Encyrtidae), *Tetrastichus planipennisi* Yang (Eulophidae), and *Spathius agrili* Yang (Hymenop.: Braconidae).

Following research on the biology, host specificity, and impacts of these parasitoid species on EAB population dynamics in China, researchers proposed their release as EAB biocontrol agents in the continental United States in an Environmental Assessment (Federal Register, 2007). After a public comment period in 2007, regulatory agencies involved in biological control risk-benefit analyses approved trial releases of the three parasitoid species in Michigan, permits were issued, and releases began (Bauer et al., 2008, 2009, 2014, in press). Establishment of the introduced parasitoids was confirmed within a year of their first release, leading to the decision by USDA to initiate the EAB Biocontrol Program, construction of an EAB-parasitoid rearing facility in Brighton, Michigan, and development of an online database where parasitoids can be requested and data on parasitoid releases, recoveries, and mapping are stored (USDA FS, 2009; Bauer et al., 2010ab; MapBioControl, 2014). As a result, EAB biological control agents are being released in other states with known EAB infestations. In addition, another larval parasitoid of EAB from the Russian Far East, *Spathius galinae* Belokobylskij (Hymenop.: Braconidae), is being considered for release in the future (Belokobylskij et al., 2012; Duan et al., 2012b).

To improve the integrated pest management of EAB in forest ecosystems using classical biological control, researchers have been studying the introduced and native natural enemies of EAB populations at long-term study sites in Michigan and other states (Bauer et al., in press; Duan et al., 2010, 2012a, 2013b, 2014a; Jennings et al., 2014). In this chapter, we will review the literature on the biology of key parasitoids known to attack EAB in North America and Asia.

BIOLOGY OF NATIVE OR SELF-INTRODUCED PARASITOIDS ATTACKING EAB IN NORTH AMERICA

Several native parasitoids and one self-introduced exotic species are known to attack EAB larvae at field sites in North America; no native EAB egg parasitoids are known (Table 1). In general, the EAB larval parasitoids reported in North America are parasitoids of *Agrilus* spp., although several species also parasitize the larvae of other groups of wood-boring insects (Gibson, 2005; Duan et al., 2009; Taylor et al., 2012). Rates of larval parasitism by these species are generally low (<5%) during the initial phase of the EAB invasion; however, there are reports in Michigan of increasing larval parasitism by parasitoids of other coleopteran woodborers (Cappaert and McCullough, 2009; Duan et al., 2012a, 2014a).

The most prevalent native parasitoids of EAB are several braconids in the genus *Atanycolus* and

Table 1. List of reported hymenopteran parasitoids attacking emerald ash borer larvae or eggs.

Name	Family	Parasitoid biology	Reported Range
Sclerodermus pupariae	Bethylidae	gregarious larval ectoparasitoid	China
Atanycolus cappaerti	Braconidae	solitary larval ectoparasitoid	Michigan
Atanycolus disputabilis	"	"	Northeastern North America
Atanycolus hicoriae	"	"	Northeastern North America
Atanycolus nigropopyga	"	"	Northeastern North America
Atanycolus nigriventris	"	"	Russian Far East
Atanycolus simplex	"	"	Northeastern North America
Spathius agrili[1]	"	gregarious larval ectoparasitoid	China, Northeastern US
Spathius floridanus[2] (= *Spathius simillimus*)[2]	"	"	Northeastern North America
Spathius galinae[3]	"	"	Russian Far East, South Korea
Spathius laflammei (= *Spathius benefactor*)	"	"	United States
Spathius polonicus	"	"	Europe, Moscow
Leluthia astigmata	"	solitary larval endoparasitoid	United States
Phasgonophora sulcata	Chalcididae	solitary larval endoparasitoid	Northeastern North America
Oobius agrili[1]	Encyrtidae	solitary parthenogenic egg parasitoid	China, United States
Oobius sp.	"	"	Russian Far East
Oencyrtus sp.	"	solitary egg parasitoid	China
Tetrastichus planipennisi[1,4]	Eulophidae	gregarious larval endoparasitoid	China, Russian Far East, North America
Tetrastichus sp.	"	"	South Korea
Balcha indica	Eupelmidae	solitary parthenogenic, larval ectoparasitoid	Southeast Asia, Northeastern United States
Eupelmus sp.	"	solitary ectoparasitoid	Northeastern North America
Cubocephalus sp.	Ichneumonidae	solitary larval ectoparasitoid	Northeastern North America
Dolichomitus sp.	"	"	Northeastern North America
Orthizema sp.	"	"	Northeastern North America

[1] introduced as EAB biological control agents in the United States starting in 2007
[2] recent evidence suggests these are separate species (JPL, J. Strazanac, N. Havill, unpublished data)
[3] in 2015, proposed for release as an EAB biological control agent in the United States
[4] introduced as EAB biological control agent in Canada starting in 2013

the chalcidid *Phasgonophora sulcata* Westwood (Bauer et al., 2008; Duan et al., 2009, 2013a, 2014a). In the genus *Atanycolus, A. cappaerti* Marsh and Strazanac and *A. hicoriae* Shenefelt are the most common species found attacking EAB in Michigan, Ohio, or Pennsylvania, but *A. simplex* Cresson, *A. nigropopyga* Shenefelt, and *A. disputabilis* (Cresson) are also reported (Bauer et al., 2008; Cappaert and McCullough, 2009; Duan et al., 2013a). Other less common parasitoids include (1) several braconid species – *Spathius floridanus* Ashmead, *S. simillimus* Ashmead (see taxonomic changes below in section on *Spathius* biology), *S. laflammei* (= *Spathius benefactor* Matthews), and *Leluthia astigmata* (Ashmead); (2) several unknown ichneumonids in *Dolichomitus, Orthizema,* and *Cubocephalus*; and (3) two eupelmids – *Eupelmus* sp. and *Balcha indica* (Mani & Kaul) (Bauer et al., 2005, 2008; Duan et al., 2009, 2013a, 2014a; Kula et al., 2010). These parasitoids are native except for *B. indica*, which is from Southeast Asia and is self-naturalized in the eastern United States where it attacks a range of wood-boring beetles (Gibson, 2005).

Atanycolus spp. (Braconidae)

Marsh et al. (2009) reports 11 native species of *Atanycolus* in North America, which parasitize the larvae of *Agrilus* species or those of other wood-boring beetles. The five *Atanycolus* species reported from species of *Agrilus* (Taylor et al., 2012) are solitary, ectoparasitic idiobionts of late-stage larvae that complete one or two generations in northern regions of the United States (Fig. 1a-d). Many of the *Atanycolus* adults reared in the laboratory from

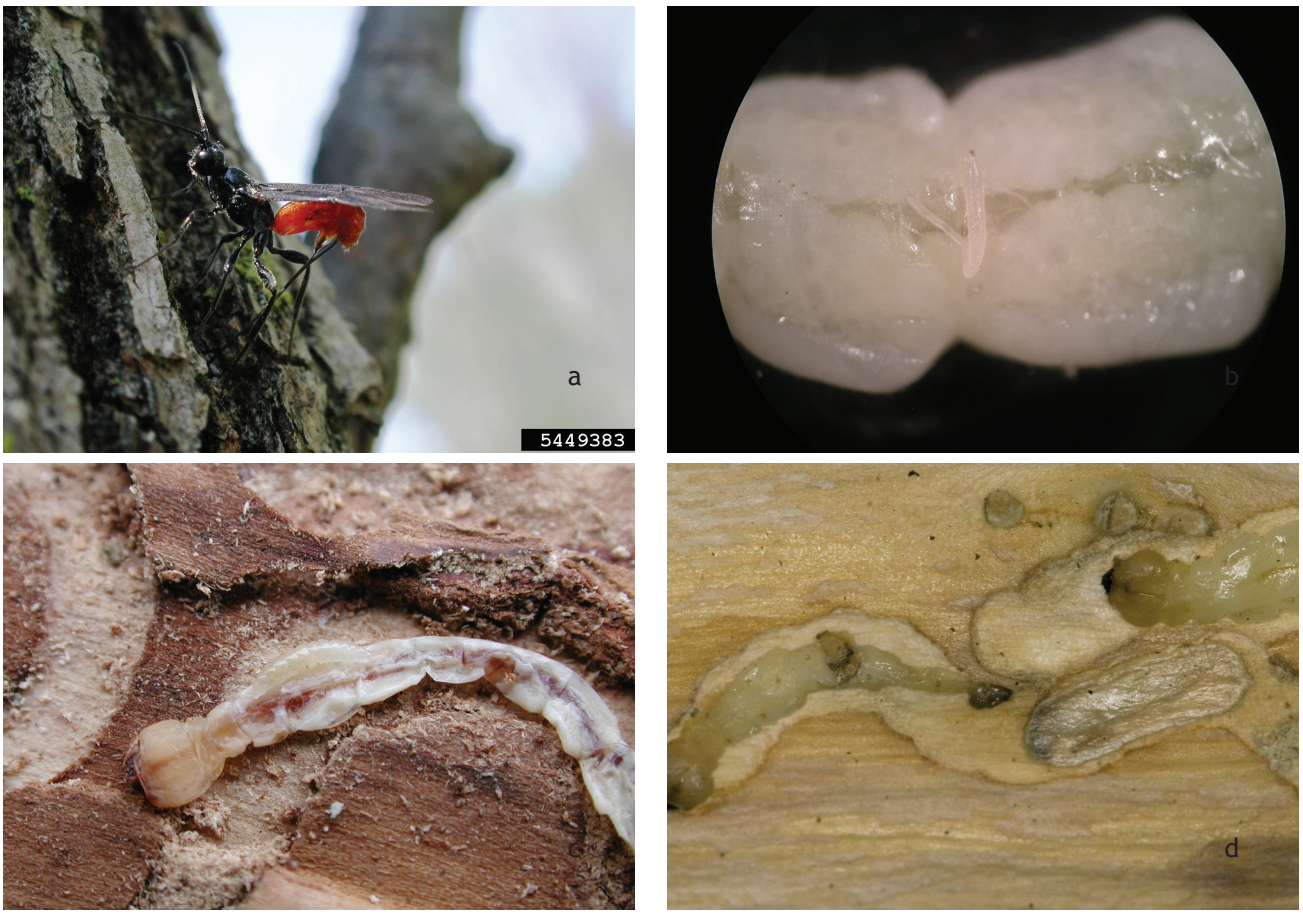

Figure 1. *Atanycolus* species life stages. (a) *Atanycolus* adult ovipositing onto an EAB larva in the trunk of an ash tree. (Photo credit: Houping Liu); (b) *Atanycolus* egg on an EAB larva photographed though a dissecting microscope (45X). (Photo credit: Deborah Miller); (c) *Atanycolus* larva feeding on an EAB larva in its gallery. (Photo credit: Deborah Miller); (d) *Atanycolus* cocoon containing a pupa with the remnant of its EAB larval host (to the left of the cocoon) in an EAB gallery. (Photo credit: David Cappaert)

EAB larvae are relatively large wasps (5-7 mm long) with long ovipositors (4-6 mm) (Marsh et al., 2009). Consequently, they can parasitize EAB larvae in mature ash trees (>57 cm diameter at breast height [DBH]) with thick outer bark (up to 9 mm thick) (Abell et al., 2012). The biology of *A. cappaerti*, a recently described species found parasitizing EAB in Michigan, is best known and is typical of other *Atanycolus* species (Cappaert and McCullough, 2009; Marsh et al., 2009).

The biology of *A. cappaerti* is reported from a field study in southern Michigan in 2007 and 2008 (Cappaert and McCullough, 2009; Tluczek et al. 2010). The life cycle of *A. cappaerti* is generally well synchronized with EAB in Michigan, with increasing numbers of cocoons found throughout the summer and fall from newly developing EAB larval hosts. By the end of October, *A. cappaerti* larvae are found parasitizing medium to large EAB larvae that are still actively feeding in the phloem. *Atanycolus cappaerti* also parasitizes the larvae of *Agrilus liragus* Barter & Brown and *Agrilus bilineatus* (Weber), demonstrating at least a genus-level host range for this parasitoid in Michigan forests (Cappaert and McCullough 2009). Due to similarities in the morphology and biology of *A. cappaerti* and *A. hicoriae,* another parasitoid of EAB larvae in Michigan, these two species are combined as "*Atanycolus* spp." for studies on EAB population dynamics (e.g., Duan et al., 2013a, 2014a).

Species of *Atanycolus* (Fig. 1a-d) overwinter as mature larvae or prepupae inside cocoons spun in EAB galleries during the fall. Adult emergence begins in early June, and these adults parasitize overwintered EAB larvae. Most first generation *Atanycolus* larvae complete their development in about one month, with emergence occurring in early to mid-July. These wasps parasitize the current year's EAB larvae. The longevity of female wasps held in the laboratory averaged 32 days (JJD, unpublished data). As reported for other braconid parasitoids of *Agrilus*, some first generation larvae may enter diapause, overwinter, and emerge as adults the following spring.

Spathius spp. (Braconidae)

Species of the genus *Spathius* are gregarious ectoparasitic idiobionts of various coleopteran families including Cerambycidae, Buprestidae, Scolytinae, Curculionidae, Bostrichidae, and Anobiidae (Marsh and Strazanac, 2009). In North America, several species of *Spathius* are found attacking late-instar EAB larvae (Bauer et al. 2004; Duan et al., 2009) (Table 1).

Spathius floridanus (Fig. 2a,b) and *S. simillimus* are the most common *Spathius* species found attacking EAB in Michigan (Bauer et al., 2004), while *S. laflammei* is the common species in western Pennsylvania (Duan et al., 2009) (Table 1). Following the initial identifications of the two species attacking EAB in Michigan, Marsh and Strazanac (2009) merged these into *S. floridanus*. Current evidence, however, suggests that *S. floridanus* and *S. simillimus* are distinct species (JPL, J. Strazanac, N. Havill, unpublished data). Although published literature is lacking on the biology of these native *Spathius*, laboratory studies in Michigan found *Spathius* adults emerged in late spring and early summer, and completed one or two generations before fall temperatures induced diapause in the remaining larvae; when reared in the laboratory at 25-27 °C, *Spathius* species completed a generation in 28-32 days (JPL, unpublished data).

Phasgonophora sulcata (Chalcididae)

Phasgonophora sulcata (Fig. 3a-d), native to eastern North America, is a solitary endoparasitic koinobiont of *Agrilus* larvae and completes one generation per year. It has been reared from *A. anxius*, *A. bilineatus*, *A. liragus,* and more recently from EAB in the United States and Canada (for review see Taylor et al., 2012). The emergence of *P. sulcata* adults lags about two weeks behind that of EAB adults (Roscoe, 2014). In the field in southern Michigan, these relatively large wasps (~8 mm long) are readily observed during late June through July seeking host larvae in EAB-infested ash trees. By sequential larval dissections throughout the season, we have observed the hatch and slow development of *P. sulcata* eggs and larvae in the posterior region of the host hemocoel. Preliminary studies suggest *P. sulcata* parasitizes first or second instar EAB larvae; pupation occurs the following spring inside host prepupae (LSB, unpublished data).

Figure 2. *Spathius floridanus* life stages: (a) *S. floridanus* adult searching for EAB larvae in a small ash log in the laboratory. (Photo credit: Jian Duan); (b) *S. floridanus* cocoons with pupae in an EAB larval gallery. (Photo credit: Jian Duan)

Figure 3. *Phasgonophora sulcata* life stages: (a) *P. sulcata* adult searching for EAB larva in a small ash log in the laboratory. (Photo credit: Deborah Miller); (b) *P. sulcata* egg dissected from a field-collected EAB larva. (Photo credit: Deborah Miller); (c) *P. sulcata* larva dissected from the posterior hemocoel of a field-collected EAB larva. (Photo credit: Deborah Miller); (d) *P. sulcata* cocoon in an EAB pupal chamber in the trunk of an ash tree. (Photo credit: Leah Bauer)

Balcha indica (Eupelmidae)

Balcha indica (Fig. 4a-c), native to Southeast Asia and naturalized in eastern United States, is occasionally found parasitizing EAB and other wood-boring beetles (Gibson, 2005). It is a solitary, ectoparasitic and parthenogenic idiobiont that parasitizes EAB larvae, prepupae, and pupae (Bauer et al., 2004; Duan et al., 2009). Adult females reared from woodborers in the United States vary in size from 3 to 8 mm long (Gibson, 2005). Duan et al. (2011a) studied its biology in the laboratory at 25 ºC using adult females reared from parasitized EAB larvae collected in Pennsylvania (Duan et al., 2009). They found the generation time of *B. indica* averaged 83 days (range 47-129), which is slow compared to the development time of other EAB ectoparasitoids reared under similar conditions. Female fecundity averaged 36 eggs during an average 59 day life span. These laboratory findings support field observations of one unsynchronized generation per year attacking immature EAB infested ash trees in Michigan, Pennsylvania, and Maryland (Duan et al., 2011a). As an established parasitoid of EAB and other woodborers in the United States, *B. indica* will continue playing a role in suppressing EAB population densities in North America (Duan et al., 2014a).

Figure 4. *Balcha indica* life stages: (a) *B. indica* adult reared from an EAB prepupae in laboratory. (Photo credit: Houping Liu); (b) *B. indica* larva parasitizing an EAB larva in gallery. (Photo credit: Houping Liu); (c) *B. indica* cocoon with remnant of EAB host larva in gallery. (Photo credit: Houping Liu)

BIOLOGY OF PARASITOIDS ATTACKING EAB IN EURASIA

Several hymenopteran parasitoid species attack EAB larvae in Asia, as does one recently discovered attacking EAB in Europe (Table 1). In Asia, rates of EAB larval parasitism are consistently higher than those reported for EAB in North America. *Tetrastichus planipennisi* (Hymenop.: Eulophidae) is the dominant parasitoid of EAB larvae in northeast China (Liu, H-P. et al., 2003, 2007; Yang et al., 2006). This parasitoid was also found attacking EAB in the Khabarovsk and Vladivostok regions of the Russian Far East (Duan et al. 2012b). In South Korea, an unidentified species of *Tetrastichus* was found parasitizing EAB larvae (Williams et al., 2010). Other larval parasitoids of EAB in Asia are in the family Braconidae. *Spathius agrili* is the most

prevalent parasitoid of EAB larvae in the vicinity of Tianjin, China, southeast of Beijing. It is also found sporadically in the northeastern provinces (Xu, 2003; Liu, H-P. et al., 2003; Yang et al., 2005; Wang et al., 2010). In the vicinity of Vladivostok in the Russian Far East, both *Spathius galinae* Belokobylskij and *Atanycolus nigriventris* Vojnovskaja-Krieger parasitize EAB larvae (Williams et al., 2010; Belokobylskij et al., 2012; Duan et al., 2012b). *Spathius galinae* was also reported attacking EAB in South Korea. More recently, *Spathius polonicus* Niezabitowski, a braconid native to Europe, was discovered attacking EAB larvae in Moscow (Orlova-bienkowskaja and Belokobylskij, 2014). Another hymenopteran parasitoid, *Sclerodermus pupariae* Yang and Yao (Bethylidae) attacks EAB larvae and pupae in the region of Tianjin, China (Wu et al., 2008; Wang et al., 2010; Tang et al., 2012; Yang et al., 2012). Due to a broad host range and tendency to sting humans, this species was not considered for EAB biological control in North America.

Few egg parasitoids are known to attack EAB in Asia (Table 1). *Oobius agrili* (Hymenop.: Encyrtidae) is the most widespread parasitoid of EAB eggs and was first discovered in 2004 in Jilin province, China (Zhang et al., 2005). It is now known from other provinces in northeast China (LSB & JJD, unpublished data). More recently, a closely related species of *Oobius* was discovered in the Russian Far East (JJD, unpublished data) and an undescribed species of *Oenycyrtus* (Hymenop.: Encyrtidae) was reared from EAB eggs collected in Jilin province, China (LSB, unpublished data).

Oobius agrili (Encyrtidae)

Discovered in northeast China, *O. agrili* is a solitary parthenogenic parasitoid of EAB eggs. Due to its importance as a natural enemy of EAB in northeast China, where egg parasitism averaged 44% (Liu, H-P. et al., 2007), *O. agrili* was approved for use as a biological control agent of EAB in the United States in 2007 (Federal Register, 2003). Establishment and spread is confirmed in Michigan and other states (Duan et al., 2011b, 2012c; Bauer et al., 2013, 2014, in press). At six EAB biological control study sites in Michigan where researchers began monitoring EAB mortality following the first parasitoid releases in 2007, the level of egg parasitism by *O. agrili* increased from 0.7% to 22% from 2008 to 2012 (Abell et al., 2014).

Oobius agrili (Fig. 5a-d) overwinter as diapausing prepupae inside EAB eggs, and adult eclosion is well synchronized with the oviposition period of EAB, starting in late June and continuing into September in China and Michigan (Liu, H-P. et al., 2007; Bauer and Liu, 2007; Abell et al., 2011). When *O. agrili* completes two generations per year, ~80% of the first generation progeny emerge and parasitize newly laid EAB eggs, whereas ~80% of the second generation enter obligate diapause for the winter. Moreover, the number of progeny entering diapause also increases as the female ages, and diapause may also be induced by exposure of adults to short day length (LSB, unpublished data). Consequently, *O. agrili* completes one or two generations per year (Liu, H-P. et al., 2007). Because this species is parthenogenic, only females are reared and released in the United States for EAB biological control. Males were recovered from parasitized EAB eggs collected in 2005 Jilin province, China; the sex ratio of adults reared from that sample was 15:1 (female: male). In the laboratory when reared at 24°C, non-diapausing *O. agrili* complete one generation every 28 to 34 days, with an average fecundity of 80 progeny per wasp. The average longevity of females exposed to eggs in the laboratory is 34 days (LSB, unpublished data).

Tetrastichus planipennisi (Eulophidae)

Native to regions of China and the Russian Far East, *T. planipennisi* is a gregarious endoparasitic koinobiont of EAB larvae. Due to its importance as a natural enemy of EAB in regions of Asia where larval parasitism averaged 22% (Liu, H-P. et al., 2007), *T. planipennisi* was approved for biological control of EAB in the United States in 2007 (Federal Register, 2007) and Canada in 2013 (CFIA, 2013). Its establishment and spread was confirmed in Michigan and other states (Bauer et al., 2014, in press; Gould et al. 2011a, 2013; Duan et al. 2013b, 2014a). At the six Michigan EAB-biological control study sites where releases began in 2007, researchers found EAB larval parasitism by *T. planipennisi* increased from 1.2% to 21% from 2008 to

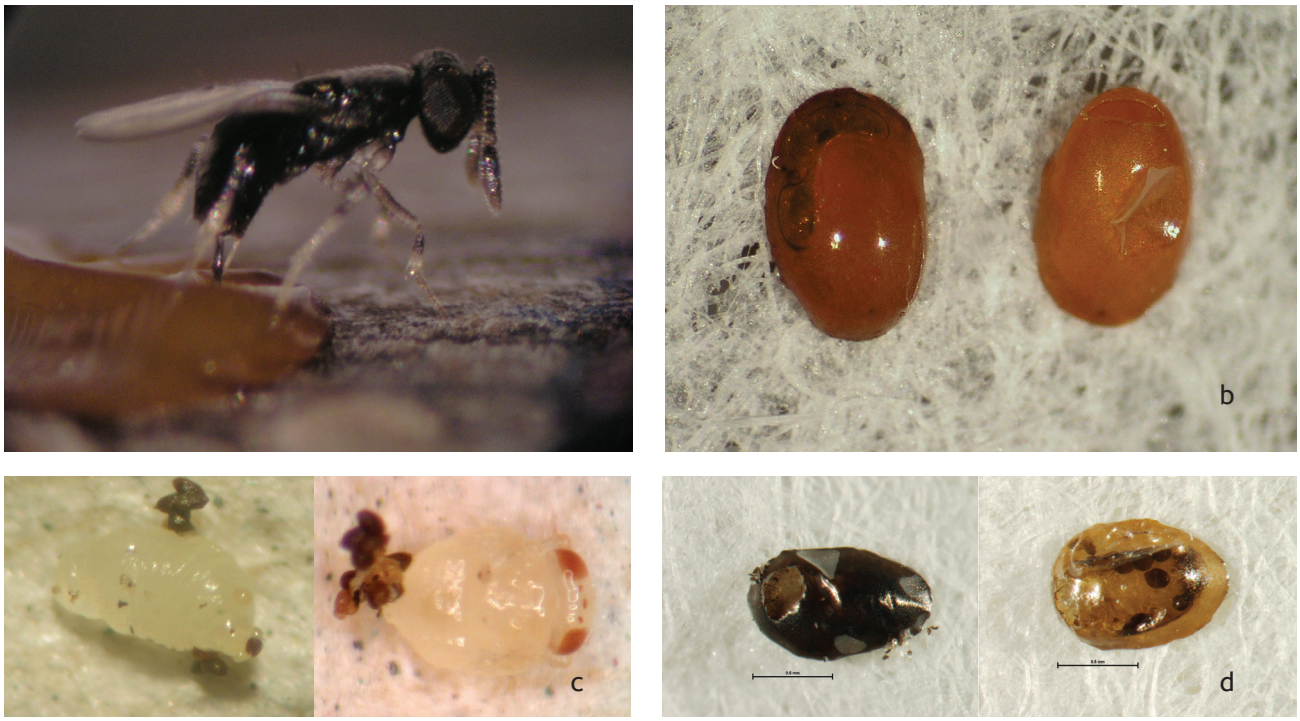

Figure 5. *Oobius agrili* life stages. (a) *O. agrili* adult ovipositing in an EAB egg, as observed through a dissecting microscope. (Photo credit: Deborah Miller); (b) *O. agrili*-parasitized EAB egg (left) with early symptoms of *O. agrili* development, characterized by darkening coloration of egg, breathing tube and air bubble; a healthy, unparasitized EAB egg (right). (Photo credit: Deborah Miller); (c) *O. agrili* prepupa (left) and young, developing pupa (right) dissected from a field-collected parasitized EAB egg. (Photo credit: Houping Liu); (d) *O. agrili*-parasitized EAB eggs range in color from black (left) to tan (right, for comparison). Adult *O. agrili* chew a round exit hole on the dorsal surface of the egg to emerge. *O. agrili* meconium pellets are excreted prior to pupation and remain visible as dark beads inside a lighter colored parasitized egg (right). (Photo credit: Deborah Miller)

Tetrastichus planipennisi (Fig. 6a-f) lacks obligate diapause and overwinters as prepupae inside host galleries or as young larvae inside host larvae. In northeast China and Michigan, adult emergence begins in April or May when females begin parasitizing overwintered EAB larvae ranging in age from second through fourth instar (Liu, H-P. et al., 2007; Duan et al., 2013a). After maturation, pupation, and eclosion, which all occur in the host gallery the following spring, adults chew small, round exit holes in the tree bark, emerge, and disperse. From field collections in Jilin province, China, *T. planipennisi* completed about four generations per year (Liu, H-P. et al., 2007). An average of 35 individual wasps (range 5 to 122) developed within a single host larva, with a sex ratio of 2.5:1 (female: male) (Liu and Bauer, 2007; Liu, H-P. et al., 2007).

Tetrastichus planipennisi is a relatively small parasitoid (3 to 4 mm long) and may be more effective at parasitizing EAB larvae in small ash trees (<12 cm DBH) with thin bark, due to its short ovipositor (2.0 to 2.5 mm long), than in large ash trees (Yang et al., 2006; Abell et al., 2012). The rate of spread of *T. planipennisi* in Michigan was estimated at >5 km per year between 2007 and 2010 (LB and JL, unpublished data). In the laboratory, *T. planipennisi* completes one generation every 27 days at 25 °C, has a sex ratio of 4:1 (female: male), has an average realized fecundity of ~45 female progeny per female; and has an average female longevity of 42 days (Ulyshen et al., 2010; Duan et al., 2011b; Duan and Oppel, 2012).

Spathius agrili (Braconidae)

Known mainly from China southeast of Beijing, *S. agrili* is a gregarious ectoparasitic idiobiont of late-instar EAB larvae (Xu, 2003; Liu, H-P. et al., 2003; Yang et al., 2005, 2010). *Spathius agrili* was approved for biological control of EAB in the United States in 2007 (Federal Register, 2007); however, in 2013 APHIS restricted its release to regions below the 40th parallel because of a failure to establish further north

Figure 6. *Tetrastichus planipennisi* life stages (a) adult female (Photo credit: David Cappaert; (b) Young *T. planipennisi* larvae are visible inside an emerald ash borer larva. (Photo credit: Deborah Miller); (c) Mature *T. planipennisi* larvae completing development inside an emerald ash borer larva. (Photo credit: Houping Liu); (d) Fully mature *T. planipennisi* larvae break free of emerald ash borer larval skin and pupate in the larval gallery under the tree bark. (Photo credit: Clifford Sadof). (e) *T. planipennisi* pupae in emerald ash borer larval gallery. (Photo credit: Houping Liu). (f) After eclosion to the adult stage in emerald ash borer galleries, adult *T. planipennisi* chew an exit hole to emerge from the ash trees (with tip of pen for scale). (Photo credit: Leah Bauer)

(Bauer et al., 2014, in press; Gould et al., 2011a,b; 2013;USDA APHIS/FS/ARS, 2013).

Spathius agrili (Fig. 7a-d) overwinter as mature larvae or prepupae in silken cocoons, emerge as adults in July and August and complete one or two generations per year, with a clutch size of 5 to 6 individuals per EAB larva (Wang et al., 2006, 2008; Gould et al., 2011a). In the laboratory when reared at 25:20 ºC (day:night temperature cycles) and 16:8 (light:dark photoperiod), the sex ratio of *S. agrili* averaged 4:1 (female: male), and an average fecundity of ~40 female progeny per female. The average longevity of females is 61 days (Gould et al., 2011a).

Spathius galinae (Braconidae)

Spathius galinae (Fig. 8), recently discovered in the Russian Far East and reported in South Korea, is a gregarious, ectoparasitic idiobiont of EAB larvae (Williams et al., 2010; Belokobylskij et al., 2012; Duan et al., 2012b). When reared in the laboratory at 25 °C and 16:8 (light:dark photoperiod), *S. galinae* develops from egg to adult in about a month and completes with one generation per year; female longevity averages 49 days and produce an average of 31 progeny in clutches ranges in size from 5 to 12 individuals per EAB larva (Duan et al. 2014b). Due to better climate matching of the Russian Far East with northern regions of the

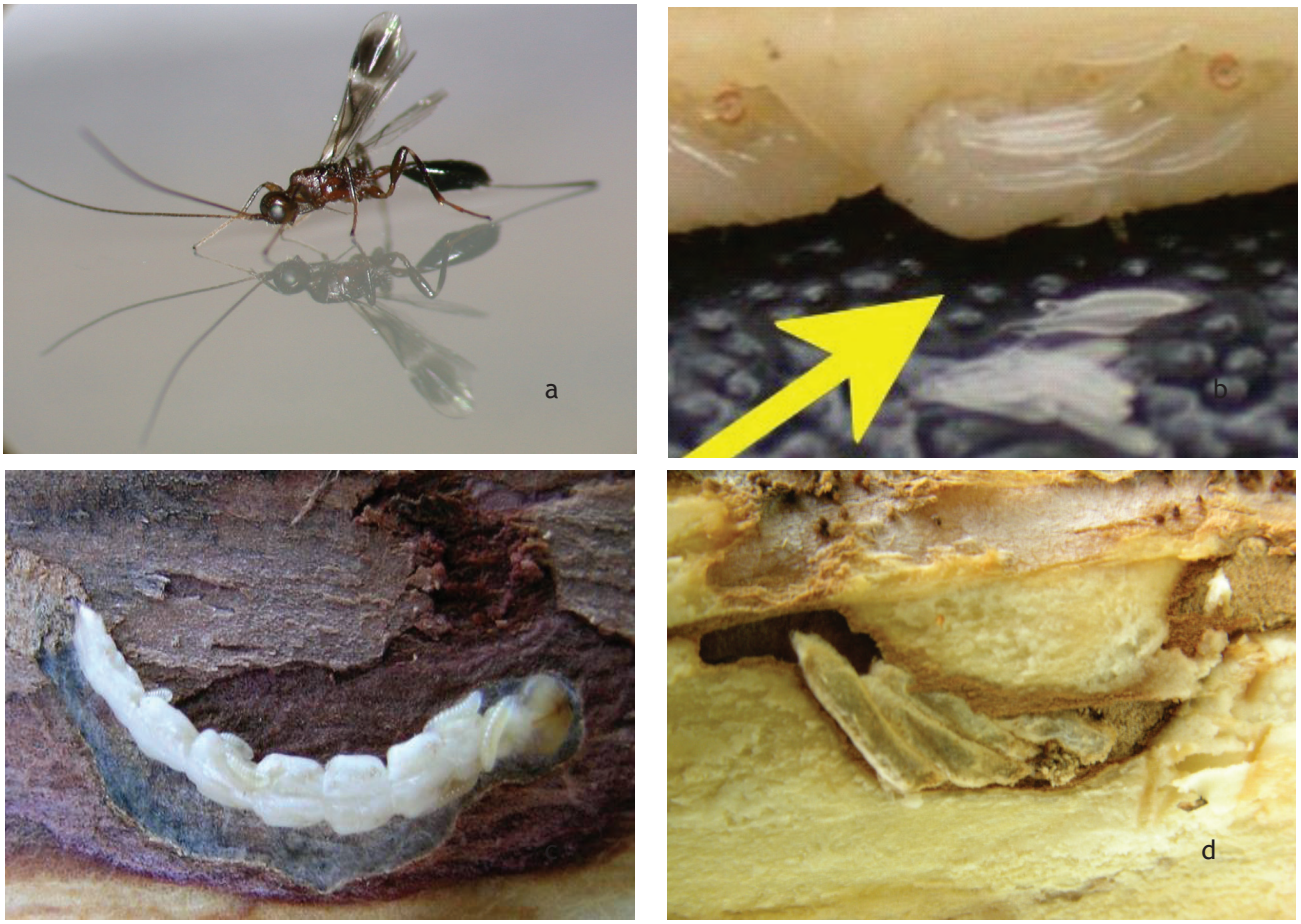

Figure 7. *Spathius agrili* life stages: (a) *S. agrili* adult female. (Photo credit: Tracy Ayers); (b) *S. agrili* eggs on an emerald ash borer larva. (Photo credit: Zhong-qi Yang); (c) *S. agrili* larvae feeding externally on an emerald ash borer larva. (Photo credit: Houping Liu); (d) *S. agrili* cocoons in emerald ash borer larval gallery. (Photo credit: Houping Liu)

Figure 8. *Spathius galinae* adult female ovipositing in an ash log. (Photo credit: Jian Duan)

United States and narrow host specificity, researchers requested permission to release *S. galinae* as an EAB biological control agent in the United States in 2014.

CONCLUSIONS

Although EAB is attacked by a diversity of native parasitoids of wood-boring beetles in North America, their prevalence is relatively low compared to that of the EAB-parasitoid complex in northeast Asia, where this buprestid originated. Consequently, classical biological control of EAB, with the introduction of three parasitoid species from China, was initiated in Michigan in 2007. By 2012, the establishment and increasing prevalence of two introduced parasitoids, *T. planipennisi* and *O. agrili*, was confirmed in Michigan and several other states. Besides increasing parasitism by the introduced and native parasitoid species, other important mortality factors are now known to suppress EAB population densities including host resistance in healthy ash trees, woodpecker predation, and entomopathogens. With the continued persistence of EAB and ash in the environment, we expect a cumulative effect of biotic and abiotic mortality factors to suppress EAB population densities below a tolerance threshold, ensuring the survival and reproduction of some native ash. The continuation and expansion of long-term field studies in EAB-infested forest ecosystems, where EAB biological control agents are released, is essential for further development of an integrated pest management approach to EAB in North America.

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