XVII Emerald Ash Borer

(*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae)

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DESCRIPTION OF PEST

Taxonomy

Agrilus planipennis Fairmaire, 1888 (type locality: China) is considered the senior synonym to *A. marcopoli* Obenberger, 1930 (type locality: China), *A. marcopoli ulmi* Kurosawa, 1956 (type locality: Japan), and *A. feretrius* Obenberger, 1936 (type locality: Taiwan) by Jendek (1994) in a revision of Eastern Palearctic *Agrilus* species.

Agrilus is the largest genus in the family Buprestidae with ~2,800 described species worldwide (Bellamy, 2008). Adults of this genus are flashy, metallic-colored beetles, frequently collected using nets or traps (Fig. 1). However, there is little interest in their immature stages, which must be collected from inside tree trunks, branches, or woody stems. Consequently, critical information on the biology, population dynamics, and host ranges of most *Agrilus* species is lacking.

Figure 1 Adult of emerald ash borer (*Agrilus planipennis*) on ash leaf. Leah Bauer, USDA Forest Service, Northern Research Station, East Lansing, Michigan.

In the Palearctic region, species in this genus are grouped into 36 subgenera and 34 informal species-groups based on morphological characters of adults (Chamorro et al., 2012). On this basis, *A. planipennis* was placed in the subgenus *Uragrilus* Semenov (Alexeev, 1998). However, more recent analyses using adult and larval characters suggest *A. planipennis* be moved to the *Agrilus cyaneoniger* species-group (Jendek and Grebennikov, 2011; Volkovitsh and Hawkeswood, 1990).

Distribution

Countries in Asia where *A. planipennis* is reported include China, Korea, Russian Far East, Japan, Taiwan, Laos, and Mongolia (Ko, 1969; Kurosawa et al., 1956, 1985; Chinese Academy of Science, 1986; Yu, 1992; Akiyama and Ohmomo, 1997; Mühle, 2003; Wei et al., 2004; Fukutomi and Hori, 2004; Jendek and Grebennikov, 2011). In areas of northeast China, Korea, and the Russian Far East, the distribution of *A. planipennis* generally coincides with that of ash trees (*Fraxinus* spp.) including *F. chinensis* Roxb., *F. chinensis* var. *rhynchophylla, F. chinensis* var. *japonica, F. mandshurica* Rupr., *F. lanuginosa* Koidz., and the introduced Nearctic species *F. americana* L., *F. pennsylvanica* Marsh., and *F. velutina* Torr. (Liu, 1966; Hou, 1993; Chinese Academy of Science, 1986; Yu, 1992; Zhang et al., 1995; Liu et al., 1996; Liu et al., 2003; Duan et al., 2012a). However, in Japan, Taiwan, and Laos, confirmation that *A. planipennis* is native will require more information on species of *Agrilus* that feed exclusively on *Fraxinus* spp. (Mühle, 2003; Bray et al., 2011). In Mongolia, the genus *Fraxinus* is unknown (Grubov, 1982), thus an early, unconfirmed report of *A. planipennis* there is suspect (Alexeev, 1979).

In 2002, *A. planipennis* was discovered in North America after being reared from dead and dying ash trees from southeastern Michigan and nearby Ontario, Canada, (Haack et al., 2002). Due to the bright green coloration of *A. planipennis* adults, this species was given the common name of emerald ash borer (EAB) (Entsoc.org, 2012). In areas of North America currently infested with EAB, its host range and distribution (Fig. 2) coincides with that of *Fraxinus*).

America and Europe, respectively (Baranchikov, 2008; Izhevskii et al., 2010). The expansion of EAB's range to the Western Palearctic region threatens European ash species, including *F. angustifolia* Vahl., *F. excelsior*, and *F. ornus* L. (Wessels-Berk and Scholte, 2008). The invasive population of EAB in North America only attacks *Fraxinus* spp. (Anulewicz et al., 2008), and several studies report that species of Nearctic and European ash are more attractive and susceptible to EAB attack than are species of Asian ash, which coevolved with EAB (Liu et al., 2003; Rebek et al., 2008; Duan et al., 2012b).

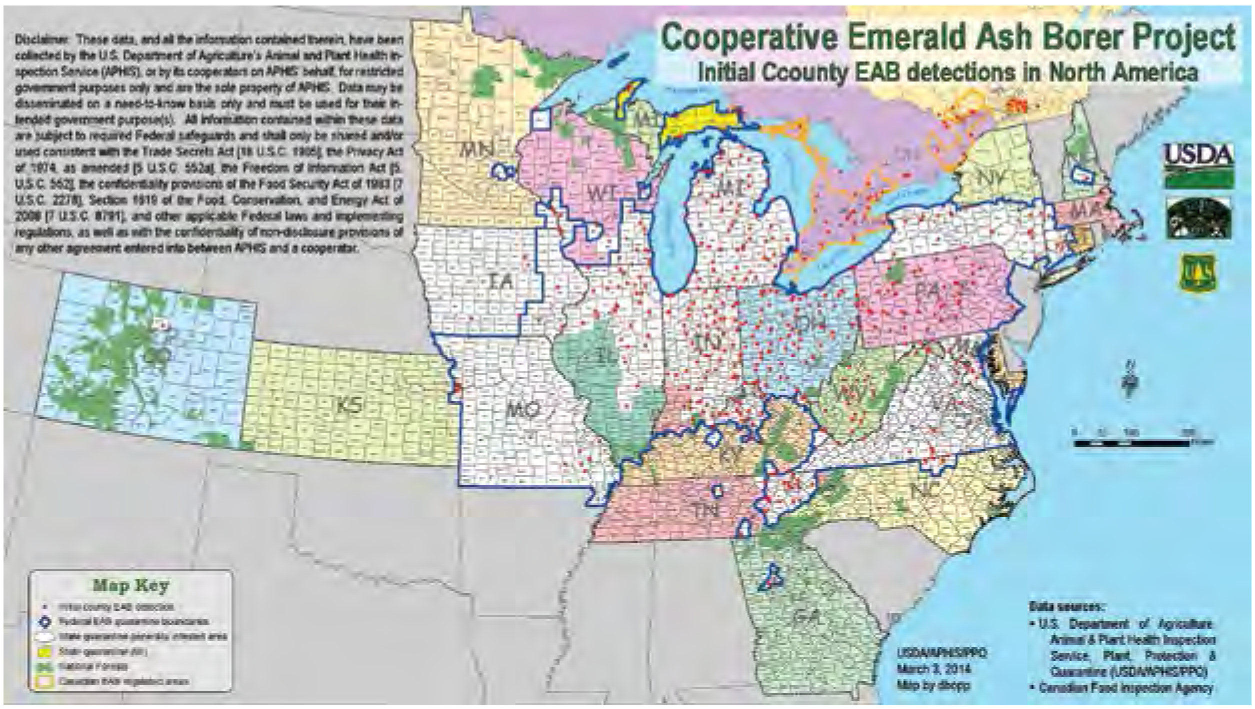

Figure 2 The known distribution and quarantines of emerald ash borer in North America as of June 1, 2012.

Genetic studies of EAB from North America and Asia, and tree-ring analyses of ash trees in southeast Michigan, indicate that this beetle was introduced from China during the 1990s (Siegert et al., 2009; Bray et al., 2011). The most likely route of entry was EAB-infested ash lumber used for the manufacture of crates, palettes, and dunnage used in international shipping. Within a few years of its detection, EAB was determined to be the cause of ash mortality in other nearby states and provinces (Fig. 2).

In 2006, EAB was found in Moscow, Russia, where it caused extensive mortality in urban plantings of *F. pennsylvanica* and *F. excelsior* L., ash species native to North

Upon arrival in North America, EAB became established and spread throughout the Great Lakes Region, due in part to the abundance of ash trees in the urban and forested landscapes (MacFarlane and Meyer, 2005; Poland and McCullough, 2006; Pugh et al., 2011), limited EAB resistance to attack among native ash (Rebek et al., 2008), and release from its native natural enemies (Bauer et al., 2004, 2005; Duan et al., 2009). Although EAB adults are capable of long-distance flight (Taylor et al., 2010), much of the spread of EAB in North America is facilitated by human-assisted movement of infested ash firewood, nursery stock, and lumber (Cappaert et al., 2005; Poland and McCullough, 2006). In an effort to reduce the loss of North American ash trees, regulatory agencies in both the United States and Canada imposed quarantines on the movement of ash materials and attempted eradication of EAB by removal of the ash trees around known infestations. The eradication efforts ended when it was found that EAB was distributed across much of central and northeastern areas of North America. Infestations of EAB are now known in 22 states (Colorado, Connecticut, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin) and Ontario and Quebec, Canada (Fig. 2).

Figure 3 Emerald ash borer eggs are white (left) when freshly laid, but turn tan as they age (right). David Cappaert, Michigan State University, Bugwood.org.

Figure 4 Feeding stage larvae of emerald ash borer: above, second, third and 4th instars; below, full-grown 4th instar. David Cappaert, Michigan State University, Bugwood.org.

Damage

Type Emerald ash borer females lay their eggs (Fig. 3) singly or in small clusters between the layers of bark or in bark crevices of ash trees. Upon egg hatch, the neonates bore directly through the bark and into the tree until reaching the phloem and cambial region, where they feed (Cappaert et al., 2005). As larvae grow through four larval stages (Fig. 4), they leave behind increasingly large, frass-filled, serpentine galleries (Fig. 5). Larval feeding disrupts the transport of nutrients and water in the phloem and outer sapwood. At low EAB-larval densities, ash trees exhibit some immune response, notably the formation of callous around EAB galleries (Duan et al., 2012b). However, as larval densities increase over a period of two to five years, the phloem is consumed or sufficiently damaged to cause tree death (Figs. 6, 7) (Smith, 2006).

Extent The establishment and spread of EAB in North America has resulted in the death of tens of millions of ash trees in urban and forested ecosystems. In forested ecosystem of the eastern United States, there are an estimated 8 billion ash trees valued at $US 282.25 billion (Federal Register, 2003; Nowak et al., 2003). Until recently, ash trees were one of the most commonly planted landscape trees in the urban environment because they grow rapidly, tolerate adverse growing conditions, are easy to propagate, and were considered resistant to most pests. The costs for removal and replacement of ash trees killed by EAB to communities and smaller landholders are high; e.g., the expense for ash removal and replacement in six infested southeastern Michigan counties was estimated at $US 11.7 billion (Federal Register, 2003; Kovacs et al., 2010). The long-term ecological effects of EAB in forested and riparian ecosystems are more difficult to quantify (Federal Register, 2007). According to a recent study, EAB has killed virtually the entire ash canopy of southeast Michigan, and despite ash seedlings and saplings in gaps, recovery of an ash overstory is unlikely due to the continued EAB infestation across the landscape (Kashian and Witter, 2011). Models of EAB spread predict a rapid

Figure 5 Galleries caused by feeding emerald ash borer larvae. Left, Michigan Department of Agriculture, Bugwood.org. RIght, Edward Czerwinski, Ontario Ministry of Natural Resources, Bugwood.org.

Figure 6 Dead and dying ash in forest area due to emerald ash borer. Troy Kimoto, Canadian Food Inspection Agency, Bugwood.org.

Figure 7 Small trees with epicomic shoots due to the emerald ash borer. David Cappaert, Michigan State University, Bugwood.org.

expansion of the infestation throughout North America (BenDor et al., 2006; Muirhead et al., 2006; Prasad et al., 2010; Mercader et al., 2011), and researchers are concerned that EAB threatens all native ash tree species (Gandhi and Herms, 2010).

Biology of Pest

EAB requires one or two years to complete its development, depending on the climate and condition of the host tree (Cappaert et al., 2005; Wang et al., 2010; Tluczek et al., 2011). For EAB populations that complete development in a single year, adult emergence starts in the spring at 200 to 260 growing degree-days base 10°C (DD10), with peak emergence around 540 DD10 (Brown-Rytlewski, 2004, McCullough and Siegert, 2007a). EAB adults emerge from D-shaped exit holes and fly into the canopy where they feed on ash leaves. Mating begins about a week later, and females start laying eggs two to three weeks later, preferring to oviposit on ash trees under stress (McCullough et al., 2009a,b; Mercader et al., 2011). EAB females place eggs in concealed areas such as between layers of loose bark and in bark crevices. The eggs of EAB are ca. 1.0 mm in diameter and amber in color when mature. Neonate larvae hatch in about two weeks and bore through the bark until reaching the phloem, where they make galleries in the outer sapwood and inner bark as they feed. In late summer and fall, mature fourth-instar larvae excavate pupal chambers in the outer sapwood or outer bark, where they spend the winter folded into a J shape, also referred to as J-larvae (Duan et al., 2010). In early spring, the J-larvae shorten into prepupae before pupation. The pupae gradually darken as they mature and after about four weeks mature into pharate adults. For EAB with a two-year life cycle, larvae that are immature when cold weather arrives in the fall simply overwinter in their feeding gallery, complete development the following summer, spend their second winter as J-larvae, and emerge as adults in the following spring.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Nontarget Insect Species Related to the Pest

In North America, the family Buprestidae has 53 genera, of which *Agrilus* is the largest with 174 described species (Fisher, 1928; Poole, 1997; Bellamy, 2008). Species of *Agrilus* feed exclusively on woody angiosperms and are generally restricted to host species within a single genus or family. The only native species in the genus known to feed on ash trees in North America is *Agrilus subcinctus* Gory, a small beetle that feeds on the phloem of dead or dying ash twigs (Petrice et al., 2009). Other native wood-boring coleopterans that feed on ash include species of *Chrysobothris*, *Dicerca*, *Polycesta*, and *Spectralia* (Buprestidae), *Neoclytus* (Cerambycidae), and *Hylesinus* (Curculionidae) (Solomon, 1995).

Since the parasitoid guilds of *Agrilus* spp. are less specific to host tree than to host niche (e.g., host size, and location of feeding larvae) (Taylor et al., 2012), some native *Agrilus* are potentially susceptible to attack by parasitoids introduced for biological control of EAB. Although most *Agrilus* are considerably smaller than EAB (>8.5-mm long adults), some overlap in parasitoid-host ranges is possible between EAB and the larger species of *Agrilus*. *Agrilus* species that fall in this category in eastern North America are *A. acutipennis* Mannerheim, *A. anxius* Gory, *A. arcuatus* LeConte, *A. bilineatus* (Weber), *A. burkei* Fisher, *A. difficilis* Gory, *A. horni* Kerremans, *A. granulatus* (Say), *A. liragus* Barter & Brown, *A. macer* LeConte, *A. nigricans* Gory, *A. politus* (Say), and *A. vittaticollis* (Randall) (Solomon, 1995; Parsons, 2008). These species may be at some risk of attack by introduced parasitoids targeted at EAB.

Native Natural Enemies Affecting the Pest

From *Agrilus* species of similar size and habits as EAB, there are parasitoid species that also attack EAB, as has been demonstrated by field studies of EAB in North America (see references below). However, research on the population dynamics of native *Agrilus* is generally limited to pest species, which periodically experience outbreaks damaging to their host trees (Vansteenkiste et al., 2005). Consequently, the literature on natural enemies of *Agrilus* species is largely drawn from a few pests, of which a diverse group of hymenopteran parasitoids is known.

Perhaps the most studied species is *A. anxius* due to periodic and damaging outbreaks in birch stands (*Betula*) across much of North America (Nash et al., 1951; Barter, 1957; Loerch and Cameron, 1983). These authors report a variety of parasitoids from *A. anxius*, including five egg parasitoids from two families (*Ablerus* sp. [Aphelinidae]; *Avetienella* sp., *Ooencyrtus* sp., *Thysanus* sp., [Encyrtidae]), and over 15 species of larval parasitoids from four families (*Atanycolus* spp., *Doryctes* spp., *Spathius floridanus* Ashmead [= *S. simillimus* Ashmead], *Wroughtonia ligator* (Say) [all Braconidae]; *Phasgonophora sulcata* Westwood [Chalcididae]; *Tetrastichus* nr. *rugglesi* Rohwer [Eulophidae]; *Bephratoides agrili* (Ashmead), *Eurytoma* sp. [both Erytomidae]; and species of *Ephialtes*, *Dolichomitus, Glypta*, *Ichneumon*, *Olesicampe*, *Orthizema*, *Pimploterus* [all Ichneumonidae]). Egg parasitism averaged 55% in a New Brunswick study and 7% in a similar study in Pennsylvania, whereas larval parasitism averaged 20% in both studies (Barter, 1957; Loerch and Cameron, 1983).

Agrilus bilineatus, the two-lined chestnut borer, is another well-studied species prone to damaging outbreaks in drought-stressed oaks (*Quercus* spp.) and sometimes American beech (*Fagus grandifolia* Ehrh.). This species was originally a pest of the American chestnut (*Castanea dentata* (Marsh.) Borkh.). Several authors have documented a guild of larval parasitoids attacking *A. bilineatus* larvae that are similar to those attacking *A. anxius*, including *P. sulcata* (Chalcididae), *Atanycolus* spp., *Doryctes* spp., *S. floridanus*, and *W. ligator* (Braconidae) (Chittenden, 1897; Chapman, 1915; Dunbar and Stephens, 1976; Côté and Allen, 1980; Haack and Benjamin, 1982; Cappaert and McCullough, 2009). Of these, *P. sulcata* was the most abundant, averaging 10.5% parasitism in *A. bilineatus*. No egg parasitoids are known.

The population dynamics of *Agrilus liragus*, a periodic pest of poplars (*Populus* spp.), was studied in New Brunswick (Barter, 1965). Several parasitoids in the same genera were reported, including unknown species of egg parasitoids in the genera *Thysanus* and *Avetienella* (Encyrtidae) and the larval parasitoids *P. sulcata* (Chalcididae) and *S. floridanus*, *Atanycolus* spp., *W. ligator*, *Doryctes* spp.*, T.* nr. *rugglesi*, and *Ephialtes* sp. (Braconidae). Of these, *P. sulcata* was the most prevalent, with parasitism ranging from 2 to 20%.

Interestingly, the guilds of egg and larval parasitoid from species of *Agrilus* are similar throughout the world (Taylor et al., 2012). In North America, *Agrilus* egg parasitoids are mainly from the family Encyrtidae (4 genera/5 species), and the larval parasitoids are from the Braconidae (7 genera/19 species), Ichneumonidae (10 genera/11 species), a few species from Eulophidae (2 genera), Eupelmidae (4 genera), Eurytomidae (2 genera), Pteromalidae (2 genera), and a single species of Chalcididae (Taylor et al., 2012). This indicates that the parasitoids of *Agrilus* are more specific to host niches than to host tree species.

From field studies since EAB's invasion in North America, a diverse guild of *Agrilus* parasitoids has been observed attacking EAB larvae. However, parasitoid prevalence is generally low and no native egg parasitoids are known (Taylor et al., 2012). In Michigan, the two most abundant native larval parasitoids are the solitary ectoparasitoids in the genus *Atanycolus* (Braconidae) (several species) and the solitary endoparasitoid *P. sulcata* (Chalcididae) (Cappaert and McCullough, 2009; Duan et al., 2012b). Other less less-common species reported from studies done in Michigan, Ohio, and Pennsylvania include *Atanycolus hicoriae* Shenefelt, *A. simplex* Cresson, *A. nigropopyga* Shenefelt, *A. disputabilis* (Cresson), *S. floridanus*, *S. laflammei, Spathius n. sp.*, *Leluthia astigmata* (all Braconidae); species of *Dolichomitus, Orthizema, Cubocephalus* (Ichneumonidae); *Eulmus* sp.; and *Balcha indica* (Mani & Kaul) (Eupelmidae) (Bauer et al., 2005, 2008; Duan et al., 2009; Kula et al., 2010; Duan et al., 2012b). These parasitic hymenopterans are presumed to be native except *B. indica*, which is an exotic parasitoid of wood-boring beetle larvae in the eastern United States from Southeast Asia (Gibson, 2005).

Although several native or self-introduced hymenopteran species parasitize EAB larvae in Michigan, the overall level of parasitism is low (<4% combined parasitism) (Bauer et al., 2008; Duan et al., 2009). However, even though such parasitoids are generally scarce, *Atanycolus cappaerti* Marsh and Strazanac was recently discovered at several Michigan field sites with parasitism of EAB larvae ranging from 9% to 71% (Cappaert and McCullough, 2009). In another Michigan study, the prevalence of *Atanycolus* spp. increased from <1% to 19%, and that of *P. sulcata* from <1% to 13%, in one year (Duan et al., 2012b). The long-term impact that these native parasitoids will have on EAB population density and ash health is still unknown and must be determined by further monitoring.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Pest

The emerald ash borer is native to Asia, including northeast China (Jilin, Liaoning, Heilongjiang, Hebei, and Shandong provinces), Korea, the Russian Far East, Taiwan, and Japan (Chinese Academy of Science, 1986; Jendek, 1994; Jendek and Grebennikov, 2011).

Areas Surveyed for Natural Enemies

China In 2003, exploration for EAB natural enemies began in China with the sampling of Asian (*F. chinensis*, *F. mandshurica*) and North American (*F. pennsylvanica*, *F. velutina*) ash species for EAB in the cities of Beijing and Tianjin and the provinces of Hebei, Heilongjiang, Jilin, Liaoning, and Shandong (Liu et al., 2003; Liu et al., 2007). Evidence of past EAB infestations or active infestations was found in each city and province except Shandong. The authors also found that ash species native to North America and ash trees (of any species) planted in urban areas were more susceptible to EAB attack than ash species native to China and those growing in forested natural areas (Liu et al., 2003).

Russian Far East From 2007–2011, surveys for EAB were conducted in and around the cities of Vladivostok, Khabarovsk, and on Sakhalin Island (Yurchenko et al., 2007; Williams et al., 2010; Duan et al., 2012a). Researchers found that EAB in ash trees planted along city streets in Vladivostok, including green ash (*F. pennsylvanica*) from North America, *F. excelsior* from Europe, and the endemic ash species *F. mandshurica* and *F. chinensis* var. *rhynhophylla*. A report of EAB near the Korean border (Alexeev, 1979) was not confirmed during a survey for EAB in 2004, nor was EAB among the 36 species of *Agrilus* listed in collections at the Siberian Zoological Museum, Novosibirsk (Schaefer, 2005).

South Korea In north and central South Korea in 2004 and 2005, researchers searched for EAB in forested areas containing *F. chinensis* var. *rhynchophylla* and *F. mandshurica* (Williams et al., 2005, 2006). EAB is apparently rare in South Korea as these surveys failed to find EAB until a small EAB population was discovered attacking water-stressed *F. chinensis* planted along a road near the city of Daejeon in central South Korea in 2005. Another EAB population attacking *F. chinensis* trees damaged by construction was found in 2007 in the Yangsuri, which is about 50 km east of Seoul (Williams et al., 2010).

Japan EAB populations are extremely low and difficult to find in Japan, and EAB natural enemies were not found during foreign explorations in 2003 and 2004 (Schaefer, 2004, 2005).

Natural Enemies Found

Historically, emerald ash borer was considered only a minor, sporadic pest of native ash tree species in Asia. Thus, only limited literature was found in 2002, when it was discovered in North America. However, in areas of China and Russia, plantings of North American ash species, which are less resistant to EAB than are Asian ash species, have caused an increase in EAB density since the 1960s (Yu, 1992; Zhang et al., 1995; Liu et al., 1996, 2003, 2007; Zhao et al., 2005; Duan et al., 2012a). In rural parks, nurseries, and urban areas, where many of these non-native ash trees are planted, researchers have discovered several hymenopteran parasitoid species attacking EAB larvae and eggs. Three species from northeast China are being introduced in the United States for biological control of EAB. A fourth species from Russia is being evaluated for future release.

China The first report of a parasitoid attacking EAB came from the provincial port city of Tianjin, southeast of Beijing, whre EAB had become a major pest of *F. velutina*, a North American ash species that was planted extensively in the region. A gregarious ectoparasitoid, later described as *Spathius agrili* Yang (Braconidae) (Fig. 8), was found parasitizing EAB larvae in these ash plantings (Xu, 2003; Liu et al., 2003; Yang et al., 2005). It was also collected from EAB larvae infesting *F. pennsylvanica* and *F. mandshurica* trees in Jilin province (Liu et al., 2003) and in Beijing (LSB, unpublished). *Spathius agrili* is the dominant parasitoid of EAB in Tianjin (Wang et al. 2010); however, it is rare further north (JJD and JG, unpublished).

A second larval parasitoid, later described as *Tetrastichus planipennisi* Yang (Fig. 9) (Yang et al., 2006), was found attacking EAB larvae from *F. pennsylvanica* and *F. mandshurica* trees planted in Jilin province (Liu et al., 2006). This gregarious larval endoparasitoid is also found in Liaoning and Heilongjiang provinces (LSB and JJD, unpublished) and is the dominant parasitoid of EAB larvae in northeast China (Liu et al., 2007).

A third parasitoid of immature EAB, later described as *Sclerodermus pupariae* Yang and Yao (Wu et al., 2008; Wang et al., 2010; Yang et al., 2012), was discovered attacking EAB larvae and pupae in Tianjin. Due to its broad host range among woodborers (Tang et al., 2012), low prevalence in China, and propensity of some species in this genus to sting humans, *S. pupariae* was not considered further for use in biological control of EAB in the United States.

A solitary, parthenogenic egg parasitoid in the genus *Oobius* (Encyrtidae) was reared from EAB eggs collected from *F. mandshurica* and *F. pennsylvanica* trees in Jilin province in 2004. It was later described as *Oobius agrili* Zhang & Huang (Fig. 10) (Zhang et al., 2005). Another population of *O. agrili* was recently found in Liaoning province (JRG and JJD, unpublished). In 2010, an undescribed species of *Oenycyrtus* (Encyrtidae) was reared from EAB eggs

Figure 8 Adult *Spathius agrili*. Jennifer Ayer, Bugwood.org.

Figure 9 Adult *Tetrastichus planipennisi*. David Cappaert, Michigan State University, Bugwood.org.

Figure 10 Adult *Oobius agrili* ovipositing in an emerald ash borer egg. Debbie Miller, USDA Forest Service, Bugwood.org.

sampled the previous fall at the same site in Jilin province (LSB, unpublished).

Russian Far East From 2009–2011, surveys for EAB and its natural enemies in the Russian Far East led to the recovery of three larval parasitoids: *T. planipennisi, Atanycolus nigriventris* Vojnovskaja-Krieger, and the recently described *Spathius galinae* Belokobylskij (Williams et al., 2010; Belokobylskij et al., 2012*)*. Among these, *S. galinae* is the dominant parasitoid of EAB in this part of Russia, parasitizing up to 63% of larvae collected from *F. pennsylvanica* planted in and around Vladivostok (Duan et al., 2012a). In addition, an unidentified species of egg parasitoid (Hymenopteran: Encyrtidae) was collected from EAB-infested ash trees (*F. pennsylvanica*) trees in Vladivostok (Duan et al., 2012c).

South Korea *Spathius galinae*, a species of *Tetrastichus*, tentatively identified as *Tetrastichus telon* (Graham), and *Teneroides maculicollis* Lewis (Coleoptera: Cleridae) were found attacking EAB larvae in girdled ash trees in Daejeon in 2008 (Williams et al., 2010). Attempts to culture these species in quarantine in the United States were unsuccessful.

Host Range Test Results

Spathius agrili The host specificity of *S. agrili* was evaluated by comparing parasitism of EAB larvae to that in other insect species using no-choice-laboratory assays performed in both the United States and China (Gould et al., 2007; Yang et al., 2008). In these assays, groups of female and male *S. agrili* were exposed to either larvae of EAB or the following nontarget species (1) nine species of *Agrilus*, including three from the United States (*A. anxius*, *A. bilineatus*, and *A. ruficollis* [Fabricius]) and six from China (*A. auriventris* Saunders, *A. inamoenus* Kerremans, *A. lewisiellus* Kerremans*, A. mali* Matsumura*, A. sorocinus* Kurosawus, *A. zanthoxylumi* Li), (2) one other Chinese buprestid (*Sphenoptera*), (3) one cerambycid from China (*Thyestilla gebleri* Fann); (4) one curculionid from China (*Eucryptorrhynchus chinensis*); and (5) six lepidopterans from three families from China: Pyralidae (*Ostrinia orientalis* [Mutuura and Munroe], *Chilo luteellus* Motschulsky, *Sylepta derogate* F., unknown pyralid larvae), Cossidae (*Holcocerus insularis* Staudinger), and Carposinidae (*Carposina niponensis* Walsingham).

Larvae of each species were implanted into their respective natural host plants before exposure to *S. agrili* adults. The results of these no-choice assays showed that *S. agrili* parasitized and developed only in the larvae of the following *Agrilus* species: *A. anxius, A. bilineatus, A. inamoenus, A. mali,* and *A. zanthoxylumi*. Parasitism by *S. agrili* was significantly lower in these nontarget species than in EAB larvae (Yang et al., 2008).

Using a Y-tube olfactometer, the behavioral responses of adult *S. agrili* were assessed to leaf volatiles from 14 woody plant species growing in China from the following families: Oleaceae (2 spp.), Rutaceae (2 spp.), Rosaceae (3 spp.), Salicaceae (2 spp.), and one each in Celastraceae, Juglandaceae, Leguminosae, and Simaroubaceae. Only the leaves of *F. velutina*, *F. pennsylvanica* (Oleaceae), *Prunus persica* L., and *Ailanthus altissima* (Mill.) Swingle were attractive to *S. agrili* females, supporting the view that EAB is its primary host in China (Yang et al., 2008).

The above cited authors also sampled other insects from *F. velutina* and other tree species at field sites in China, recovering 17 species of wood-boring larvae, nine of which were buprestids and of those, six were *Agrilus* spp. (others were Cerambycidae and several were families of Lepidoptera). These wood-boring larvae were returned to the laboratory and reared for emergence of parasitoids, but neither *S. agrili* nor *T. planipennisi* emerged. However, other hymenopteran parasitoid species reared from the larvae of other species of *Agrilus* larvae included an unknown *Tetrastichus* sp. from *A. sorocinus* in Tianjin; *Tetrastichus* sp. and *Doryctes* sp. from *A. mali*, *Tetrastichus* sp. from *A. lewisiellus, Tetraichus* sp., and an unknown braconid from *A. zanthoxylumi* from Shaanxi; *Atanycolus* sp. and *Eupelmus* sp.

from *A. mali* in Xinjiang; and *Spathius* sp. from *A. auriventris* in Zhejiang (Yang et al., 2008). These findings support the host-specificity of *S. agrili* in China.

Tetrastichus planipennisi The host specificity of *T. planipennisi* was evaluated by comparing EAB-larval parasitism to that of other insect species in the United States using paired, no-choice laboratory assays with EAB larvae as positive controls (methods as per Badendreier, et al. [2005]). In these assays, groups of female and male *T. planipennisi* were exposed to larvae of EAB or other species that were similar in stage or size. Nontarget test species included eight buprestids (*A. anxius*, *A. bilineatus*, *A. ruficollis*, *A. subcinctus, Agrilus sulcicollis* Lacordaire, *Chrysobothris femorata (Olivier)*, *C. floricola* Gory, *C. sexsignata* Say), five cerambycids (*Neoclytus acuminatus* F.*, Megacyllene robiniae* Forster, *Astylopsis sexguttata* [Say], *Monochamus scutellatus* [Say], unknown sp. from apple), and one species of tenthredinid in the Hymenoptera (*Janus abbreviates* [Say]). The larvae of each species were implanted into their respective natural host plants. We also assayed the following non-wood-boring insect larvae by insertion into ash: Coleoptera: Tenebrionidae (*Tenebrio molitor* L.)*,* Lepidoptera: Pyralidae (*Galleria mellonella* L.), and Lepidoptera: Sphinghidae (*Manduca sexta* L.). The latter was tested as a surrogate for sphinx moths (Sphingidae) that pollinate the eastern prairie fringed orchid (*Platanthera leucophaea* [Nuttall] Lindley), a federally listed threatened orchid found in Michigan. Larvae of *M. sexta* were also exposed to *T. planipennisi* as they fed on tomato leaves (Federal Register, 2007). *Tetrastichus planipennisi* rejected the larvae of all species except EAB, indicating a narrow host range for this species (Liu and Bauer, 2007; Federal Register, 2007).

Oobius agrili The host specificity of *O. agrili* was evaluated by comparing *O. agrili* parasitism in EAB eggs laid on ash branches to those of other insect species in the United States using both no-choice and choice assays with EAB eggs as positive controls (Bauer and Liu, 2007; Federal Register, 2007). Female *O. agrili* females were exposed to eggs of EAB or those of six wood-boring buprestids (*A. anxius*, *A. bilineatus*, *A. egenus* Gory, *A. ruficollis, A. subcinctus, A. sulcicollis,*) and two cerambycids (*M. robiniae, N. acuminatus*) on their respective natural host trees. Also tested were eggs of several lepidopteran species (*Bombyx mori* L.*, Choristoneura rosaceana* (Harris)*, M. sexta, Pieris rapae* [L.]) laid on ash branches. In the no-choice assays, *O. agrili* did not parasitize eggs of the cerambycids, lepidopterans, or those of the smaller *Agrilus* spp. (*A. sucinctus, A. sulcicollis, A. egenus)*, although it did parasitize eggs of the larger *Agrilus* spp. (*A. anxius*, *A. bilineatus*, *A. ruficollis).* It was determined that *Agrilus* eggs laid by small *Agrilus* spp. were about half the size of those *Agrilus* eggs accepted by *O. agrili*, suggesting that egg size may limit acceptance. As a result, choice-laboratory assays were conducted by exposing *O. agrili* females to eggs of EAB and eggs from each of the three larger *Agrilus* species on their respective hosts: *A. anxius* on birch (*Betula*), *A. bilineatus* on oak (*Quercus*)*,* and *A. ruficollis* on raspberry (*Rubus*). When given a choice, *O. agrili* preferred the EAB eggs on ash vs. eggs of the other three species on their respective host plants. These results show that *O. agrili* prefers eggs of EAB on *Fraxinus*, but will parasitize eggs of larger *Agrilus* spp. and can physiologically develop inside them.

Releases Made

After research on *O. agrili*, *T. planipennisi,* and *S. agrili* biology, laboratory rearing, and host specificity was completed in 2007, researchers submitted petitions to the North American Plant Protection Organization (NAPPO) and permit requests to USDA Animal, Plant Health Inspection Service (APHIS) for field release of these parasitoid species for the biological control of EAB in the United States (NAPPO, 2012; USDA APHIS, 2012a). From the NAPPO petitions, APHIS compiled an Environmental Assessment, which was posted on the *Federal Register* for public comment (Federal Register, 2007). Meanwhile, federal and state researchers and regulatory agencies, university faculty, tribal councils, and land managers evaluated the pros and cons of releasing these parasitoids in the United States for management of EAB. After the public comment period ended and a risk analysis was completed, APHIS posted a "finding of no significant impact" on the *Federal Register* (Federal Register, 2007). Following final approval by Michigan, APHIS issued release permits on July 23, 2007 to L. Bauer for release of *O. agrili* and *T. planipennisi* and to J. Gould for release of *S. agrili* (Bauer et al., 2008).

In the summer and fall of 2007, a combined total of ~2,900 *O. agrili*, *T. planipennisi,* and *S. agrili* females (count includes females only) were released at seven field sites in

Michigan (Bauer et al., 2008). The following year, similar numbers were released at 12 sites in Michigan, Ohio, and Indiana (Bauer et al., 2010). At this time, USDA APHIS determined there were no cost effective control methods to eradicate or prevent dispersal of EAB, and; therefore, they recommended that "authorities plan and prepare for an infestation of EAB" (USDA APHIS, 2012b). According to principal researchers, demand for EAB parasitoids far exceeded supply, based on rearing in research laboratories. To increase supply, Forest Service and APHIS scientists and managers initiated the EAB Biological Control Program (USDA APHIS, 2012c), which included the construction and staffing of the EAB Biocontrol Facility, an EAB parasitoid mass-rearing laboratory in Brighton, Michigan, which became operational in 2009 after researchers successfully transferred rearing technology and parasitoid colonies (Bauer et al., 2010; Emeraldashborer, 2012). More than 34,000 female parasitoids (all species combined) were produced in 2009, allowing for expanded releases in Michigan, Ohio, and Indiana, and the establishment of new research sites in Maryland and Illinois.

In 2010, USDA researchers wrote and posted the online manual, *Emerald Ash Borer Biological Control Release Guidelines*, which provides information on EAB and parasitoid biology, data collection, release-site selection, permits, and parasitoid-release methods. In 2012, the online manual was updated and expanded to include methods for determining parasitoid establishment or recovery from release sites and designated the "Emerald Ash Borer Biological Control Release and Recovery Guidelines" (USDA FS APHIS/ARS/FS, 2012).During this time, researchers continued to improve rearing methods and to transfer that technology to the EAB Biocontrol Facility, which led to improved parasitoid production (Ulyshen et al., 2010; Gould et al., 2011a; Duan et al., 2011a). In 2010, more than 100,000 female parasitoids (all species combined) were released in Michigan, Maryland, Illinois, Indiana West Virginia, Kentucky, and Minnesota. In 2011, more than 200,000 parasitoids were reared and released in states already involved in EAB biological control research and program releases, and new sites were started in New York, Pennsylvania, Virginia, and Wisconsin. To keep track of parasitoid releases and recoveries, APHIS and FS collaborated with Michigan State University to develop an online database (Mapbiocontrol, 2012).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

EAB parasitoids are considered established in the field if they are detected by trapping or recovery from EAB eggs or larvae at least one year after a parasitoid species was last released (Bauer et al., 2011; USDA FS AUSDA/F/NRS, 2012). Depending on the species and the recovery method used, sampling for field recovery of EAB parasitoids is done in late summer or early fall when parasitoid densities are highest, or during late winter or early spring after parasitoids have broken diapause. The simplest parasitoid-recovery method involves felling EAB-infested ash trees, placing logs in large cardboard-rearing tubes in a brightly lit room, and collecting the parasitoid adults as they emerge and enter clear collection cups attached to the ends of rearing tubes. This method works for emergence of the EAB parasitoids and other insects living in and on ash logs. Alternatively, the logs can be debarked and EAB larvae and associated larval parasitoids collected from galleries. Parasitoids are then reared to the adult stage for identification (Bauer et al., 2011).

Less-destructive sampling methods for recovery of *O. agrili* developing or diapausing inside EAB eggs (laid on the outer bark of ash trees) include either collecting EAB eggs from the bark or placing egg-bearing bark samples in cardboard rearing tubes for emergence of *O. agrili* adults. After the bark samples are dry, eggs are recovered from sifted debris and evaluated for parasitism by *O. agrili*. Alternatively, a trap to detect parasitoids can be made by hanging logs, on which EAB eggs were laid in the laboratory, on ash trees in the field. These "egg sentinel logs" are then retrieved from the field after ten to 14 days of exposure, and each egg is then examined for an *O. agrili* exit hole, dissected, or reared in the laboratory to determine if the egg is parasitized (Bauer et al., 2013; USDA FS APHIS/ARS/FS, 2012).

A similar, non-destructive method for recovery of the larval parasitoids uses small ash logs, in which last-instar EAB larvae have been inserted under the bark. These "larval sentinel logs" are hung on ash trees in the field for a seven-day exposure period. The sentinel logs are then returned to the laboratory, and each larva is examined for parasitoids or reared for identification of adult parasitoids. Finally, yellow pan traps can also be used to recover EAB parasitoid species (Bauer et al., 2013; USDA FS APHIS/ARS/FS, 2012).

Since 2008, establishment of *O. agrili*, *T. planipennisi*, or *S. agrili* has been confirmed using a variety of methods at many study sites in Michigan. More recently, one or more of the parasitoid species were recovered at release sites in Ohio, Maryland, Indiana, Illinois, and Pennsylvania (Bauer et al., 2009, 2010, 2011, 2013; Gould et al. 2011b). More detailed studies are ongoing at six long-term study sites (each comprised of release and control plots) in southern Michigan, where *O. agrili*, *T. planipennisi*, and *S. agrili* were released between 2007 and 2010. Since the last release of *O. agrili* at these long-term study sites in 2009, EAB-egg parasitism has been monitored annually, and the establishment of *O. agrili* has been confirmed. From samples of EAB eggs and placement of egg sentinel logs at sites, parasitism of EAB eggs was approximately 5% in 2010 and 20% in 2011 (Duan et al., 2011b, 2012d; Abell et al., 2011). In 2011, EAB-egg parasitism was found from 73% of the sampled trees in parasitoid-release plots and 25% of trees in control plots, a dispersal of ~800 m (LSB, unpublished). These results confirm that established populations of *O. agrili* are expanding and gradually dispersing from the original release epicenters.

Changes in EAB larval parasitism are also being monitored each year at these study sites by destructively sampling EAB-infested ash trees (Duan et al., 2013). In 2012, three to four years after *T. planipennisi* releases, the proportion of sampled ash trees with at least one brood of *T. planipennisi* increased steadily from 33% to 92% in the parasitoid-release plots and from 4% to 83% in the control plots. Over the same period, EAB larval parasitism by *T. planipennisi* increased from 1.2% to 21.2% in the release plots and from 0.2% to 12.8% for the control plots. The results of this five-year study demonstrate that *T. planipennisi* is established and spreading throughout EAB populations of southern Michigan (Duan et al., 2013, 2014).

However, *S. agrili* has not been recovered from EAB larvae sampled in southern Michigan one or two years after release, although adults are occasionally recovered in yellow pan traps (Bauer et al., 2011; Gould et al., 2011b). Gould et al. (in press) suggested poor recovery of *S. agrili*, which was originally collected in Tianjin, China (39th parallel north), resulted from incompatible climate matching Tianjin and with northern regions of the United States. Although poor synchrony with required host life stages may be a factor, the establishment of *S. agrili* remains unknown in more southerly states, such as Maryland, West Virginia, and Kentucky because releases were done relatively recently. Until more information becomes available, APHIS plans to continue to release this parasitoid in areas below 40 NL north (USDA–APHIS/ARS/FS, 2013).

Nontarget Effects

Potential attack on nontarget *Agrilus* species. by the introduced larval ectoparasitoid *S. agrili* was examined at three sites in 2007, 2008, and 2009. Potted trees (large nursery stock) of European paper birch (*Betula pendula* Roth) and pin oak (*Quercus palustris* Münch) were planted at each site. To ensure these trees contained nontarget *Agrilus* larvae, adult bronze birch borers (*A. anxius*) were caged on the birch trees and adults of the two-lined chestnut borer (*A. bilineatus*) were caged on the oak trees. Ash, birch, and oak trees were felled at each site during the following winter after sufficient chill to break insect diapause. The logs were placed in cardboard-rearing tubes in a warm environment to stimulate insect emergence. All logs produced adult *Agrilus,* indicating that EAB and the nontarget hosts were available for attack by *S. agrili*. The native *S. floridanus* was found attacking all three *Agrilus* species at all sites. In 2009, five *S. agrili* emerged from a birch log, showing parasitism of *A. anxius*, but no parasitism by *S. agrili* from ash or oak logs was confirmed in 2008 or 2009. Although more *S.* a*grili* were released in 2010 and recovered from ash at all three sites, *S. agrili* was not reared from the test birch or oak logs that year. These results support the results of laboratory host-range testing that some parasitism of nontarget *Agrilus* species may occur in the field.

Recovery of Affected Tree Species or Ecosystems

The population density of EAB is difficult to determine in an absolute sense (number per unit area) and requires destructive sampling and considerable labor (McCullough and Siegert, 2007b). Therefore, trends in EAB population densities are based on indirect estimates using ash decline and mortality over time (Smith, 2006). Parasitoids were introduced at seven EAB biological control research sites in Michigan and two sites in Ohio in 2008 and 2009. At each research site, a release plot was paired with a non-release control plot, and 50 ash trees >4-cm DBH were selected and tagged in each plot. From 2008 to 2010, the following data were collected annually: GPS coordinates, crown class, epicormic shoots, EAB exit holes, DBH, and woodpecker feeding (Gould et al., 2011b). No significant differences were found between ash health at the release and control plots, with most of the larger trees dying from EAB attack before the exotic parasitoids were detectable at most sites. Future plans to assess the impact of EAB biological control at these and other sites include documenting growth and survival of young ash trees at the sites (the regrowth) and estimating the recruitment, growth, and survival of these new trees as they become large enough to be susceptible to EAB attack.

Broad Assessment of Factors Affecting Success or Failure of Project

At a limited number of study sites in Michigan, where the EAB parasitoids from China were first introduced, they are established and spreading, and their population densities are increasing. The long-term impact these parasitoids will have on ash health and recovery is not yet known; however, the longevity and condition of North American ash species planted in northeast China and the Russian Far East provide a basis for some optimism. Life-table studies in China and Russia indicate that the main mortality factors affecting EAB attacking North American ash in Asia are egg and/or larval parasitoids. To assess the effects of biological control in different ash species and genotypes across geographical regions, detailed data on ash density and health must be collected over time and analyzed.

Biological control is a long-term but sustainable management strategy, and EAB natural enemy complexes may eventually stabilize eventually and suppress host population densities below a tolerance threshold allowing the survival and reproduction of native ash species. As the EAB invasion spreads across North America, most ash trees die due the high EAB populations that develop in this abundant and susceptible resource. This tree mortality then results in collapse of EAB population, and provides an intense selection event that may favor the proliferation of EAB-resistant ash genotypes. In fact, several researchers are now screening the surviving ash trees in Michigan for EAB resistance. The parasitoids, both introduced and native species, are likely to be crucial in supporting the survival of ash seedlings and saplings that grow up in the aftermath of EAB. In the decades to come, researchers will need to continue to monitor the relative importance of the various interactions affecting ash survival and EAB population dynamics in North America.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Natural Enemies in the United States

***Antanyolus* spp.** In North America, eleven native species of *Atanycolus* are listed as parasitoids of *Agrilus* spp. (Marsh et al., 2009). These *Atanycolus* are solitary, ectoparasitic idiobionts of late-instar larvae, and several species parasitize EAB. Surveys of natural enemies in southeastern Michigan from 2003 to 2004 detected larval parasitism of EAB by *A. hicoriae* and *A. simplex*; however, total larval parasitism was <1% (Bauer et al., 2005). In 2007 and 2008, Cappaert and McCullough (2009) found that EAB larval parasitism ranged from 9 to 71% by a new species of *Atanycolus*, later described as *A. cappaerti* (Marsh et al., 2009). The following year, EAB populations collapsed in that area, and the prevalence of *A. cappaerti* fell to <1% (Tluczek et al., 2010). In a different Michigan study, at sites where EAB populations were building, EAB larval parasitism by *Atanycolus* spp. increased from <1% in 2009 to 19% in 2010 (Duan e al., 2012b). Of individuals reared to the adult stage and identified (n=383) in that study, 93% were *A. cappaerti,* 5% were *A. hicoriae*, ~1% were *A. tranquebaricae* Shenefelt, and <1% were *A. disputabilis*. *Atanycolus cappaerti* is known to parasitize other species of *Agrilus* in Michigan, indicating a broader host range for *A. cappaerti* than for other *Atanycolus* species (Cappaert and McCullough 2009). Long-term studies are needed to monitor successional changes occurring in parasitoid guilds associated with EAB populations, as EAB density declines due to ash mortality and as the introduced parasitoids increase in density.

Oobius agrili This species is a solitary and parthenogenic egg parasitoid discovered parasitizing EAB eggs sampled from ash trees in Jilin province, China, in 2004 (Zhang et al., 2005) and later in Liaoning province (JJD, unpublished) that has been released and established in the United States. Mature *O. agrili* larvae diapause during the winter inside EAB eggs and typically complete two generations each year (Bauer and Liu, 2007). Adult emergence is synchronized with the oviposition period of EAB, starting in late June and continuing into September in China (Liu et al., 2007). Similar emergence phenology for *O. agrili* was detected in Michigan, with adults starting to emerge in late June and peak parasitism in August (Abell et al., 2011). When reared in the laboratory at 24ºC, *O. agrili* completes one generation every three days with a realized fecundity of ~80 female progeny (LSB unpublished).

Phasgonophora sulcata *Phasgonophora sulcata* is a solitary endoparasitic koinobiont of larvae of native North American *Agrilus* species (Barter, 1957, 1965; Côté and Allen, 1980). In eastern North America, *P. sulcata* also parasitizes EAB larvae (Bauer et al., 2004, 2005; Duan et al., 2012b). Adults of this large chalcidid can be readily observed ovipositing through the bark of EAB-infested ash trees between June and August. Eggs and larvae of *P. sulcata* slowly develop in the hemocoel of EAB larvae, with maturation and pupation occurring the next year, often as their host larva enters the prepupal stage (LSB and JJD, unpublished). Laboratory studies are continuing on the biology of *P. sulcata* and to evaluate its impact on EAB populations in the field.

Spathius agrili A gregarious, ectoparasitic idiobiont of late-instar EAB larvae, this parasitoid was first reported in Tianjin province, China (Xu, 2003) and later in Jilin province (Liu et al., 2003; Yang et al., 2005) and has been released and recovered in the United States. *Spathius agrili* overwinter as mature larvae, and adults emerge in July and August (Wang et al., 2006). In Michigan, adults began to emerge in mid-July and continued into mid-September (LSB, unpublished). When reared in the laboratory at a day: night temperature cycle of 25: 20ºC, has a 4:1 female: male sex ratio and an estimated realized fecundity of ~40 female progeny during the female lifespan (average 61 days) (Wang et al., 2008; Gould et al. 2011a).

Spathius galinae A gregarious, ectoparasitic idiobiont parasitoid, this species was recently discovered in Primorskiy Krai of the Russian Far East, but was initially identified as a similar, closely related species (Yurchenko et al., 2007). This species is being held (as of 2014) in USDA quarantine facility for study. This parasitoid was repeatedly collected from EAB larvae in and around Vladivostok and in Daejeon, South Korea (Baranchikov, 2008; Williams et al., 2010; Duan al., 2012a). It was recently described as *S. galinae*, a new species (Belokobylskij et al., 2012). From EAB natural enemy surveys of infested green ash trees (*F. pennsylvanica*) planted up to 40 years ago in Vladivostok, parasitism by *S. galinae* ranged from 27.5 to 75.5% (Duan al. 2012a). *Spathius galinae* overwinters as mature larvae or prepupae, and adults emerge from EAB galleries in early spring. In the Vladivostok region, *S. galinae* completes two to three generations each year producing six to 15 larvae per EAB larva (Belokobylskij et al., 2012; Duan et al. 2012a). It is being evaluated for possible release in the United States for biological control of EAB, particularly in northern areas because of its greater cold-hardiness (Duan et al., 2012a).

Tetrastichus planipennisi This parasite, a gregarious endoparasitic koinobiont of EAB larvae, was discovered while surveying EAB-infested ash trees in Jilin and Liaoning provinces in 2003 (Liu et al., 2003) and later in Heilongjiang province (Yang et al., 2006), and has been released and established in the United States. *Tetrastichus planipennisi* parasitizes all larval stages of EAB, overwinters as a larva, and completes up four generations each year in Jilin province (Liu et al., 2007). Adult emergence begins in April or May, and females begin parasitizing overwintering *A. planipennis* larvae soon thereafter, with parasitism increasing up to 40% by August (Liu et al., 2007). Similar emergence phenology was found for *T. planipennisi* in Michigan, with adults starting to emerge in late April or early May (LSB, unpublished). The results of a recent study suggest that *T. planipennisi* may be more effective at parasitizing EAB larvae in thin-barked, small diameter ash trees (<12-cm DBH) due to its relatively short ovipositor (2.0 to 2.5 mm long) (Abell et al., 2012). When reared in the laboratory at 25ºC, *T. planipennisi* completes one generation every 27 days, has a 4:1 female:male sex ratio, and an average realized fecundity of ~45 female progeny during the female lifespan (average 42 days) (Liu and Bauer, 2007; Ulyshen et al., 2010; Duan et al., 2011a).

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