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Source: Florida Entomologist, 104(3) : 213-217

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.104.0310>

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# Overwintering developmental stages of emerald ash borer in North Carolina

Christine A. Nalepa<sup>1,\*</sup>, Kelly L. F. Oten<sup>2,3</sup>, and Matthew A. Bertone<sup>4</sup>

## Abstract

The invasive woodboring beetle emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) first was detected in the US in 2002 near Detroit, Michigan, USA. Since then it has continued to expand its range into the southern and midwestern sections of the country. Emerald ash borer was discovered in North Carolina, USA, in 2013, and is currently reported from more than 60 counties in the state. The present study was undertaken to begin determining the phenology of emerald ash borer in its newly expanded range below 40 °N latitude in North America. Here we report 4 yr of data on the overwintering stages of emerald ash borer in north-central North Carolina, obtained by debarking infested trees harvested from a single site near the northern border with Virginia, USA, with 1-yr additional data from a site about 39 km away. Results indicated that most emerald ash borers overwinter as fourth instars, with a small proportion advancing to the J-larva stage. Parasitoids that emerged from cocoons collected from emerald ash borer galleries and from logs held in emergence cages also were identified. These Hymenoptera include specimens of *Xorides* (*Exomus*) *humeralis* (Say) (Ichneumonidae), *Atanycolus* cf. *cappaerti* Marsh and Strazanac (Braconidae), *Balcha indica* (Mani & Kau) (Eupelmidae), *Spathius* sp. Nees (Braconidae), and *Wroughtonia* sp. Cameron (Braconidae).

Key Words: *Agrilus planipennis*; life history; parasitoids

## Resumo

El invasor coleoptero conocido como barrenador esmeralda del fresno *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) se detectó por primera vez en los EE. UU. en el 2002 cerca de Detroit, Michigan, EE. UU. Desde entonces, ha seguido ampliando su área de distribución en las áreas del sur y de medio oeste del país. El barrenador esmeralda del fresno se detectó por primera vez en Carolina del Norte, EE. UU., en el 2013, y actualmente se informa en más de 60 condados de ese Estado. Se realizó el presente estudio para comenzar a determinar la fenología del barrenador esmeralda del fresno en su rango recientemente ampliado por debajo de los 40 °N de latitud en América del Norte. Aquí presentamos 4 años de datos sobre los estadios de hibernación del barrenador esmeralda del fresno en el centro-norte de Carolina del Norte, obtenidos al descortezar árboles infestados cosechados en un solo sitio cerca de la frontera norte con Virginia, EE. UU., con datos adicionales de 1 año de un sitio a unos 39 km de distancia. Los resultados indicaron que la mayoría de los barrenadores esmeralda del fresno invernan como en el cuarto estadio, y una pequeña proporción avanza al estadio de J-larva. También, se identificaron parasitoides que emergieron de pupas recolectadas de galerías de barrenadores de fresno esmeralda y de troncos mantenidos en jaulas de emergencia. Estos himenópteros incluyen especímenes de *Xorides* (*Exomus*) *humeralis* (Say) (Ichneumonidae), *Atanycolus* cf. *cappaerti* Marsh & Strazanac (Braconidae), *Balcha indica* (Mani & Kau) (Eupelmidae), *Spathius* sp. Nees (Braconidae) y una especie del género *Wroughtonia* Cameron (Braconidae).

Palabras Clave: *Agrilus planipennis*; historia de vida; parasitoides

Emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a highly destructive pest of ash trees (*Fraxinus* L.; Oleaceae), is native to East Asia and first was detected in North America (Michigan, USA) in 2002 (Haack et al. 2002). Since then it has spread progressively into the northeastern and southern US and is considered the most destructive and costly wood boring pest to invade the country (Aukema et al. 2011). The leading long-term strategy for managing emerald ash borer in forest settings is classical biological control, using natural enemies collected from its native range in Asia (Herms & McCullough 2014; Gaudon & Smith 2020).

Four hymenopteran parasitoid species from the natural range of this pest in China (*Oobius agrili* Zhang & Huang [Hymenoptera: En-

cyrtidae], *Tetrastichus planipennisi* Yang [Hymenoptera: Eulophidae], *Spathius agrili* Yang [Hymenoptera: Braconidae]) and Russia (*Spathius galinae* Belokobylskij [Hymenoptera: Braconidae]) have been released by the United States Department of Agriculture (USDA) and its partners for control of emerald ash borer in the US (Duan et al. 2018). However, only the egg parasitoid *O. agrili* and the larval parasitoid *T. planipennisi* have been recovered consistently more than a yr after release in the northern half of the US (USDA-APHIS 2015). Furthermore, it is too soon to assess establishment by the larval parasitoid *S. galinae*, thought to be adapted to higher latitudes and first released in 2015, 8 yr after the initial releases of the other 3. *Tetrastichus planipennisi* and *O. agrili* have failed to establish in the southern US (Duan et al. 2018).

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*Spathius agrili* is a parasitoid of particular interest to the southern US, because individuals of *S. agrili* that were released in the US originated from the southern limit of the emerald ash borer range in China (about 39°N) where it is a significant source of emerald ash borer parasitism (Liu et al. 2003; Yang et al. 2005). In this part of its range in China, emerald ash borer is primarily univoltine (Wei et al. 2007) and *S. agrili* emerges over a mo later than adult emerald ash borer, when parasitoid susceptible emerald ash borer larvae are available as hosts (Wang et al. 2010). Thus, this wasp may be best suited to the warmer climates of the US, particularly in states located below 40°N latitude (Bauer et al. 2015). *Spathius agrili* failed to establish in the northeastern US (Jones et al. 2020), but establishment has been confirmed at 1 site in Maryland, USA (Duan et al. 2018), and at a release site in eastern Tennessee, USA. Although the latter finding indicates that *S. agrili* may overwinter below 40°N latitude, it may be too soon to indicate that it is established (Hooie et al. 2015). The limited success of *S. agrili* is thought to be a result of failure to release the parasitoids when a suitable stage of the host is available (Bauer et al. 2015; USDA-APHIS 2015). Larval parasitoids imported for release in the US are host stage specific, typically using the third or fourth instar emerald ash borer (Duan et al. 2018). It is therefore critical to determine the life cycle of emerald ash borer in all parts of its range so that parasitoids are released when they temporally coincide with the host stages susceptible to parasitism, thus giving them the optimal chance for establishment. In the northern US, the life cycle of emerald ash borer is well characterized; the insect completes its life cycle in 1 or 2 yr. Not every member of each generation reaches the pupation stage in a given yr, resulting in an asynchronous pattern of development and overlapping life stages. Therefore, larval parasitoids presumably have a higher probability of finding a host in the appropriate stage (late larval instars) throughout the year (Cappaert et al. 2005; Duan et al. 2010). The life cycle of emerald ash borer in the southern half of its recently expanded range is less well-defined, with a single study in Maryland, USA, finding it to be completed in 1 yr, i.e., the insect is univoltine in that location (Abell et al. 2019).

The present study was conducted as a first step in determining the phenology of emerald ash borer in North Carolina, USA. We collected 4 yr of data on the overwintering stages of this destructive pest in Granville County, North Carolina, USA, located near where emerald ash borer first was detected in North Carolina in 2013. We also collected parasitoids associated with emerald ash borer, either as cocoons collected from emerald ash borer galleries and reared to emergence, or from emerald ash borer-infested ash logs held in emergence cages. The goal was to determine native parasitoids that may be using emerald ash borer as a host in this state, because North America has a rich complex of native natural enemies of *Agilus* beetles, many with the potential to use emerald ash borer for development (Duan et al. 2018; Gaudon & Smith 2020).

## Materials and Methods

### STUDY AREA AND SAMPLING

Green ash trees (*Fraxinus pennsylvanica* Marshall; Oleaceae) infested with emerald ash borer were selected and felled to quantify emerald ash borer overwintering stages in North Carolina. Live trees with signs of decline, such as bark splits, epicormic shoots, or emerald ash borer exit holes were chosen from a 3-ha area of bottomland hardwood forest; selected trees were at least 3 m apart. Each tree was cut near the soil line and the bole sawed into manageable sections labelled sequentially from the base to the top; log sections ranged from 7 to

28 cm in diameter. These were transported to a North Carolina Department of Agriculture & Consumer Services property, Raleigh, North Carolina, USA, where the logs were debarked and inspected for life stages of emerald ash borer.

In 2017, we worked in 2 sites in Granville County, near the northern border of North Carolina with Virginia: a residential property north of Stovall (36.463046°N, 78.566499°W), and a state-owned forestland in Butner (36.15290°N, 78.767530°W). The 2 sites are approximately 39 km apart. Two ash trees were felled in Stovall and 3 in Butner on 28 Feb 2017; 4 trees were felled in Butner on 9 Feb 2018 and 5 Feb 2019. Because our 2017 results indicated that the emerald ash borer infestation in Stovall had already progressed to near total mortality of the trees, our studies in 2018 to 2020 were conducted exclusively at the site in Butner.

Debarking took place 1 to 14 Mar 2017, 12 to 21 Feb 2018, and 6 to 13 Feb 2019. In 2017, the results from the Stovall and Butner sites were combined; just 15% (9 of 59) of the insects collected were from Stovall. On 4 Feb 2020, we travelled to the Butner site with the intention of again felling trees for debarking in the laboratory, but the ash had reached near complete mortality. Instead, trees were debarked in the field until we located emerald ash borer life stages. Eventually these were found in 3 trees, where  $n = 13$ , 1, and 1 live emerald ash borer life stages were found, respectively.

The number of cumulative developmental degree d on the date of tree harvest were taken from the Duarte 2013 OSU IPPC model, base 50 (<http://uspest.org/cgi-bin/ddmodel.us>; last accessed 8 Apr 2021). The weather station used was at Creedmoor, located 8 km southeast of the Butner collection site.

### DETERMINING DEVELOPMENTAL STAGES

The developmental stage of each emerald ash borer (larva, J-larva, pupa) was recorded, and those that were undamaged during collection were preserved in alcohol. The instar of each alcohol-preserved larva was determined by measuring, from the dorsal aspect, the length of sclerotized terminal processes on the abdomen using an ocular micrometer (0.05 mm) on a dissecting microscope (Nikon SMZ1500, Melville, New York, USA). The length of these terminal processes, also called urogomphi (see Chamorro et al. 2012), are a consistent character for separating larval instars of emerald ash borer (Wang et al. 2005; Orlova-Bienkowskaja & Bienkowski 2016). The formula we used for categorizing instars was a combination of the ranges published in Wang et al. (2005) and Orlova-Bienkowskaja & Bienkowski (2016) as follows: < 0.2 mm (first instar), 0.21 to 0.37 mm (second instar), 0.38 to 0.72 mm (third instar), and > 0.73 (fourth instar).

### COLLECTION AND IDENTIFICATION OF POSSIBLE PARASITOIDS

From 2017 to 2020, cocoons of possible parasitoids encountered during debarking were collected from emerald ash borer overwintering chambers and reared to maturity. Adult wasps that successfully emerged were identified and photographed by M. Bertone. We note that our technique did not allow for identification of larval endoparasitoids and those failing to emerge, disallowing estimates of parasitism rates. Three emerald ash borer-infested trees additional to the ones used for debarking were harvested at the Butner site on 13 Mar 2019 to better screen for emergence of overwintering parasitoids. These trees were sectioned into logs of a length that would fit into 61 cm L × 61 cm W × 49 cm H laboratory built Plexiglas emergence cages ( $n = 42$  logs in 30 cages), held at 24 to 25 °C, and checked every 1 to 3 d for emerged Hymenoptera. The insects have been deposited in the North Carolina State University Insect Museum, Raleigh, North Carolina, USA.

Results

EMERALD ASH BORER DEVELOPMENT

In 2017, 252 degree d already had accumulated near the field sites by 28 Feb; the majority (85%) of emerald ash borer collected ( $n = 59$ ) had developed to the pupal stage. In 2018 and 2019, a combination of earlier log harvesting and a winter season more typical for the area led to a better reflection of emerald ash borer development prior to the onset of spring warming (harvested at 78.3 and 76.6 degree d, respectively). In both yr, more than 92% of emerald ash borer overwintered as larvae, with just a small percentage classified as J-larvae (Table 1).

Urogomphi length indicated that all collected emerald ash borer larvae fell into the range reported for the fourth instar in 2018; in 2019 all but 1 larva ( $n = 466$ ) measured as fourth instar (Fig. 1). The lone exception measured 0.70 mm; however, 2 additional larvae measured at 0.75 mm, which might be interpreted as third instar according to the criteria presented by Wang et al. (2005).

PARASITOIDS ASSOCIATED WITH EMERALD ASH BORER GALLERIES

Three specimens identified as *Xorides (Exomus) humeralis* (Say) (Hymenoptera: Ichneumonidae) (Fig. 2E) were dissected from cocoons collected from emerald ash borer galleries in 2017 (reported in Bertone et al. 2017). In 2018, 7 adult specimens of *Atanycolus* cf. *cappaerti* Marsh and Strazanac (Hymenoptera: Braconidae) (Fig. 2D) were reared from cocoons. One specimen of *Eurytoma* sp. (Hymenoptera: Eurytomidae) also emerged from the collected material (Fig. 2B), but because *Eury-*

*toma* is a known hyperparasitoid of *Atanycolus* (Cappaert & McCullough 2008), it is uncertain whether this wasp was parasitizing emerald ash borer or *Atanycolus*. In 2019, 6 adult specimens of *Atanycolus* cf. *cappaerti* and 1 *Spathius* sp. (Fig. 2C) were reared from cocoons collected from the emerald ash borer galleries. The single *Spathius* specimen did not match any species known (in litt. Robert Kula, USDA-SEL), including species introduced for control of emerald ash borer (*S. agrilli* and *S. galinae*). Currently, it appears to be an undescribed species, though more specimens are needed to assess that hypothesis and formally describe the species. Three possible parasitoids of emerald ash borer collected from emergence cages await further study: a species of *Atanycolus*, a species of *Wroughtonia*, and the species of *Spathius* mentioned above. Morphologically, the *Atanycolus* identifies as *Atanycolus* cf. *cappaerti*, but a BLAST analysis (Basic Local Alignment Search Tool) places it closer to *Atanycolus hicoloriae* Shenefelt (Hymenoptera: Braconidae); these 2 species are difficult to distinguish (Marsh et al. 2009).

Discussion

EMERALD ASH BORER DEVELOPMENT IN NORTH CAROLINA

Overall, our results indicate that emerald ash borer development is synchronous in north-central North Carolina, with the majority overwintering as fourth instar larvae that advance to the J-larva stage as degree d accumulate in the new yr. Although 15% of collected emerald ash borer in 2017 were classified as fourth instar larvae by measuring their urogomphi, these likely were prepupae, but not noted as such at the time of collection. Prepupae are the stage between J-larva and pupa, when the larva contracts prior to pupation; urogomphi length, however, remains the same in fourth instars, J-larvae, and prepupae. The distinction between fourth instars and prepupae is not crucial, because both are likely to develop to the emergent adult stage in early spring. On the other hand, a recent laboratory study (Jian et al. 2021) suggests that only those emerald ash borers overwintering as J-larvae emerge as adults when the growing season begins, because it is the only stage that undergoes an obligatory diapause. All other larval stages seem to require another growing season to reach adulthood. Only field sampling that continues throughout the yr will determine if this is the case in North Carolina.

A key result is that no early instars overwintered, thus supporting the idea that the different life cycle in the South may influence the timing of release of parasitoids for classical biological control and the subsequent establishment of these wasps in the southern US. It has been noted that as one moves from north to south in the US, the proportion of emerald ash borer overwintering as fourth instar larvae versus prepupae decreases until in the Deep South it reaches 0% (Jones et al. 2020). Although we acknowledge the limitations of primarily using a single sampling site in our study, proportions of the different developmental stages overwintering would depend not only on the location but the yr, because winter temperatures can vary widely in North

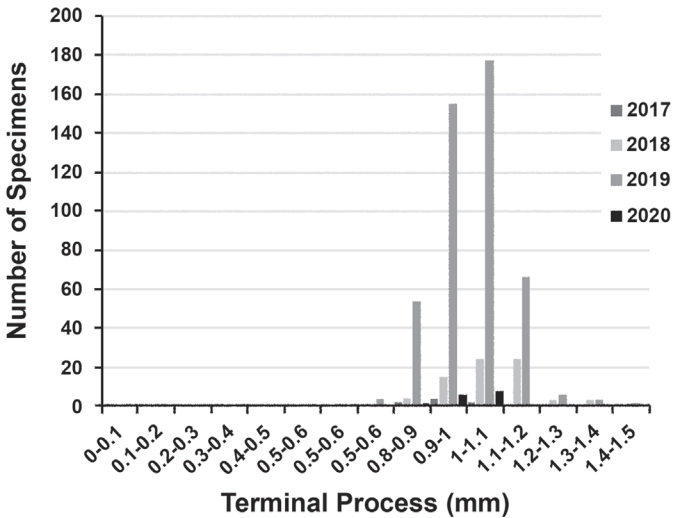


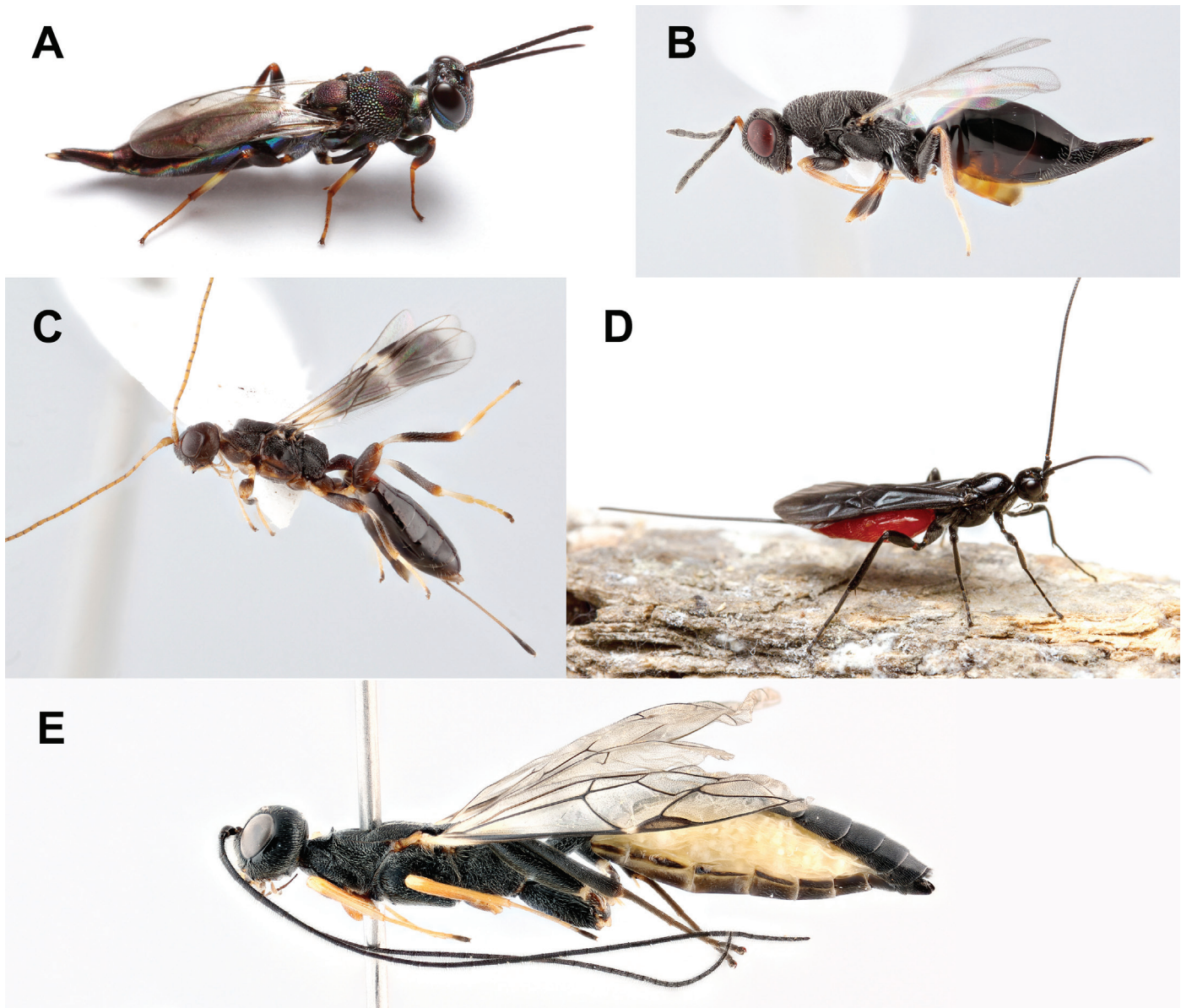
Fig. 1. Length of the terminal process of emerald ash borer (*Agrilus planipennis*) larvae collected under bark in the winters of 2017 to 2020 ( $n = 547$  total).

Table 1. Developmental stages of overwintering emerald ash borer (*Agrilus planipennis*) during winter in Granville County, North Carolina, ranked in order of increasing accumulated degree d on the date of tree harvest. Degree d were based on model of Duarte 2013 OSU IPCC, base 50, Version 5.52.

Year	Date	Degree d	Emerald ash borer total	% Emerald ash borer larvae	% Emerald ash borer J-larvae	% Emerald ash borer pupae
2019	5 Feb	77.5	783	92.3	7.7	0
2018	9 Feb	78.1	84	95.2	4.8	0
2020	4 Feb	131.7	15	46.7	53.3	0
2017	28 Feb	252.0	59	15.3 <sup>a</sup>	0	84.7

<sup>a</sup>These likely were prepupae (the stage after J-larvae, prior to pupation)





**Fig. 2.** (A) *Balcha indica* (Eupelmidae); (B) *Eurytoma* sp. (Eurytomidae); (C) *Spathius* sp. (Braconidae: Doryctinae); (D) *Atanycolus* cf. *cappaerti* (Braconidae: Bracninae); (E) *Xorides humeralis* (Ichneumonidae: Xoridae). Not to scale. Photographs by Matt Bertone.

Carolina. In 2019, for example, there were 77.5 accumulated degree d on 5 Feb at our experimental site, but 131.7 degree d on 4 Feb in 2020 (Table 1).

#### EMERGED PARASITOIDS

Recorded hosts of *X. humeralis* in the US include *Dicerca* Eschscholtz (Coleoptera: Buprestidae) (Porter 2005), but other species of *Xorides* are reported to parasitize *Agrilus* in Michigan and Europe (Kenis & Hilszczanski 2007; Petrice & Haack 2014). Related species in the genus use emerald ash borer as hosts in China (Wei et al. 2004; Wang et al. 2016). *Wroughtonia* species are known parasitoids of Coleoptera, but may attack both Cerambycidae and Buprestidae (Taylor et al. 2012). We collected several adults of the cerambycid *Obrium rufulum* Gahan (Coleoptera: Cerambycidae) from our emergence cages, and therefore cannot be certain if *Wroughtonia* was attacking *O. rufulum*, emerald ash borer, or possibly both.

*Atanycolus* is a cosmopolitan genus of solitary ectoparasitoids that attack the larvae of various wood-boring beetles (Wang et al 2009). There are at least 7 species throughout the Holarctic that use emerald ash borer as host (Taylor et al. 2012), but exact determination of *Atanycolus* species is extremely difficult (Abell et al. 2012), and individual *Atanycolus* species often attack both buprestid and cerambycid larvae (P. Marsh, personal communication). *Atanycolus cappaerti* is native to North America and appears to be the native species with most potential to have a role in managing emerald ash borer (Cappaert & McCullough 2008). It has been considered a candidate for potential mass rearing for augmentative biocontrol (Taylor et al. 2012; Duan & Schmude 2016).

In Michigan, *A. cappaerti* emerges from overwintering cocoons and attacks emerald ash borer larvae that overwinter as early instars (Cappaert & McCullough 2008). It is thought that in a univoltine host, emerging wasps have a minimal window of opportunity and may not encounter suitable hosts (second, third, and fourth instar larvae) for

most of their life span (Cappaert & McCullough 2008). It will be interesting then to see how host usage or the life history of this native parasitoid may have shifted to accommodate emerald ash borer in North Carolina, where emerald ash borer in the site we studied overwinters as late stage fourth instars, pupates in late winter or early spring, and emerges as adults shortly after. This and ongoing work will inform release decisions on future biocontrol efforts in the southern US.

## Acknowledgments

We thank all cooperators who participated in felling trees, transporting logs, debarking, supplying space and equipment, or determining emerald ash borer larval instars: John Banask, Kevin Carpenter, Jessica Grant, Wayne Langston, Sam Larsen, Nathan LaSala, Rob Montague, James Slye, Rob Trickel, and Steve Turner. The need for an overwintering study in North Carolina was suggested by Julie Gould (USDA-APHIS).

## References Cited

- Abell K, Duan JJ, Bauer L, Lelito JP, Van Driesche RG. 2012. The effect of bark thickness on host partitioning between *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) and *Atanycolus* spp. (Hymenoptera: Braconidae), two parasitoids of emerald ash borer (Coleoptera: Buprestidae). *Biological Control* 63: 320–325.
- Abell K, Duan JJ, Shrewsbury PM. 2019. Determining optimal parasitoid release timing for the biological control of emerald ash borer (Coleoptera: Buprestidae). *Florida Entomologist* 102: 691–694.
- Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B. 2011. Economic impacts of non-native forest insects in the United States. *PLoS One* 6: e24587. <https://doi.org/10.1371/journal.pone.0024587>
- Bauer LS, Duan JJ, Lelito JP, Liu H, Gould JR. 2015. Biology of emerald ash borer parasitoids, pp. 97–112 *In* Van Driesche RG, Reardon RC [eds.], *Biology and Control of Emerald Ash Borer*, Publication #FHTET-2014-09. US Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, West Virginia, USA.
- Bertone MA, Nalepa CA, Oten KL, Turner SP. 2017. Record of the hymenopteran parasitoid *Xorides (Exomus) humeralis* (Ichneumonidae: Xoridinae) from emerald ash borer galleries (Coleoptera: Buprestidae) in North Carolina. *Proceedings of the Entomological Society of Washington* 119: 514–517.
- Cappaert D, McCullough DG. 2008. Occurrence and seasonal abundance of *Atanycolus cappaerti* (Hymenoptera: Braconidae) a native parasitoid of emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae). *Great Lakes Entomologist* 42: 16–29.
- Cappaert D, McCullough DG, Poland TM, Siegert NW. 2005. Emerald ash borer in North America: a research and regulatory challenge. *American Entomologist* 51: 152–165.
- Chamorro ML, Volkovitch MG, Poland TM, Haack RA, Lingafelter SW. 2012. Preimaginal stages of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae): an invasive pest on ash trees (*Fraxinus*). *PLoS One* 7: 12. doi:10.1371/journal.pone.0033185
- Duan JJ, Bauer L, van Driesche R, Gould J. 2018. Progress and challenges of protecting North American ash trees from the emerald ash borer using biological control. *Forests* 9, 142. doi.org/10.3390/f9030142
- Duan JJ, Schmude J. 2016. Biology and life history of *Atanycolus cappaerti* (Hymenoptera: Braconidae), a North American larval parasitoid attacking the invasive emerald ash borer (Coleoptera: Buprestidae). *Florida Entomologist* 99: 722–728.
- Duan JJ, Ulyshen MD, Bauer LS, Gould J, Van Driesche R. 2010. Measuring the impact of biotic factors on populations of immature emerald ash borer (Coleoptera: Buprestidae). *Environmental Entomology* 39: 1513–1522.
- Gaudon JM, Smith SM. 2020. Augmentation of native North American natural enemies for the biological control of the introduced emerald ash borer in central Canada. *BioControl* 65: 71–79.
- Haack RA, Liu EJ, Marchant KR, Petrice TR, Poland TM, He H. 2002. The emerald ash borer: a new exotic pest in North America. *Newsletter of the Michigan Entomological Society* 47: 1–5.
- Herms DA, McCullough DG. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology* 59: 13–30.
- Hooie NA, Wiggins GJ, Lambdin PL, Grant JF, Powell SD, Lelito JP. 2015. Native parasitoids and recovery of *Spathius agrili* from areas of release against emerald ash borer in eastern Tennessee, USA. *Biocontrol Science and Technology* 25: 345–351.
- Jian JJ, Schmude JM, Larson KM. 2021. Effects of low temperature exposure on diapause, development, and reproductive fitness of the emerald ash borer (Coleoptera: Buprestidae): implications for voltinism and laboratory rearing. *Journal of Economic Entomology* 114: 201–208.
- Jones MI, Gould JR, Mahon HJ, Fierke MK. 2020. Phenology of emerald ash borer (Coleoptera: Buprestidae) and its introduced larval parasitoids in the northeastern United States. *Journal of Economic Entomology* 113: 622–632.
- Kenis M, Hilszczanski J. 2007. Natural enemies of Cerambycidae and Buprestidae infesting living trees, pp. 475–498 *In* Lieutier F, Day KR, Battisti A, Grégoire JC, Evans HF [eds.], *Bark and Wood Boring Insects in Living Trees in Europe*, a Synthesis. Springer, Dordrecht, The Netherlands.
- Liu H, Bauer LS, Gao R, Zhao T, Petrice TR, Haack RA. 2003. Exploratory survey for the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), and its natural enemies in China. *The Great Lakes Entomologist* 36: 191–204.
- Marsh PM, Strazanac JS, Laurusonis SY. 2009. Description of a new species of *Atanycolus* (Hymenoptera: Braconidae) from Michigan reared from the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae: Agrilinae). *The Great Lakes Entomologist* 42: 9. <https://scholar.valpo.edu/tgle/vol42/iss1/9>
- Orlova-Bienkowskaja M, Bienkowski A. 2016. The life cycle of the emerald ash borer *Agrilus planipennis* in European Russia and comparison with its life cycle in Asia and North America. *Agricultural and Forest Entomology* 18: 182–188.
- Petrice TR, Haack RA. 2014. Biology of the European oak borer in Michigan, United States of America, with comparisons to the native twolined chestnut borer. *The Canadian Entomologist* 146: 36–51.
- Porter CC. 2005. New records of *Xorides* (Hymenoptera: Ichneumonidae: Xoridinae) from Florida. *Insecta Mundi* 19: 187–190.
- Taylor PB, Duan JJ, Fuester RW, Hoddle M, Van Driesche R. 2012. Parasitoid guilds of *Agrilus* woodborers (Coleoptera: Buprestidae): their diversity and potential for use in biological control. *Psyche: A Journal of Entomology* 2012: 813929. doi.org/10.1155/2012/813929
- USDA-APHIS. 2015. Field release of the parasitoid *Spathius galinae* for the biological control of the emerald ash borer (*Agrilus planipennis*) in the contiguous United States. *Environmental Assessment*, March 2015. [https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=3&cad=rja&uact=8&ved=2ahUKEwiU9NGn0LThAhVFUK0KHdJ0BhwQFjACegQIBxAc&url=https%3A%2F%2Fwww.aphis.usda.gov%2Fplant\\_health%2Fdownloads%2F2015%2Fspathius-galinae-eab-biocontrol.pdf&usq=AOvVaw14YJ-L2tb46R7ploFejROU](https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=3&cad=rja&uact=8&ved=2ahUKEwiU9NGn0LThAhVFUK0KHdJ0BhwQFjACegQIBxAc&url=https%3A%2F%2Fwww.aphis.usda.gov%2Fplant_health%2Fdownloads%2F2015%2Fspathius-galinae-eab-biocontrol.pdf&usq=AOvVaw14YJ-L2tb46R7ploFejROU) (last accessed 8 Apr 2021).
- Wang X-Y, Cao L-M, Yang Z-Q, Duan JJ, Gould JR, Bauer LS. 2016. Natural enemies of emerald ash borer (Coleoptera: Buprestidae) in northeast China, with notes on two species of parasitic Coleoptera. *The Canadian Entomologist* 148: 329–342.
- Wang X-Y, Yang, Z-Q, Gould JR, Zhang Y-N, Liu G-J, Liu E. 2010. The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. *Journal of Insect Science* 10: 1–23.
- Wang X, Yang Z, Liu G, Liu E. 2005. Larval instars and stadia of *Agrilus planipennis* (Coleoptera: Buprestidae). *Scientia Silvae Sinicae* 41: 97–102.
- Wang Y-P, Shi M, Chen X-X, He J-H. 2009. The genus *Atanycolus* Foerster (Hymenoptera, Braconidae, Braconinae) in China, with description of one new species. *ZooKeys* 27: 31–41.
- Wei X, Reardon D, Wu Y, Sun J-H. 2004. Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), in China: a review and distribution survey. *Acta Entomologica Sinica* 47: 679–685.
- Wei X, Wu Y, Reardon R, Sun TH, Lu M, Sun JH. 2007. Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. *Insect Science* 14: 367–373.
- Yang Z-Q, Strazanac JS, Marsh PM, Van Achterberg C, Choi W-Y. 2005. First recorded parasitoid from China of *Agrilus planipennis*: a new species of *Spathius* (Hymenoptera: Braconidae: Doryctinae). *Annals of the Entomological Society of America* 98: 636–642.