

**ACTUAL AND INFERRED CHECKLIST OF THE APHIDS (HEMIPTERA:  
APHIDIDAE) OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK,  
WITH ATTENDANT ANT AND HOST PLANT ASSOCIATIONS**

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*Abstract.*—During 2003–2006, a general aphid survey was conducted in the Great Smoky Mountains National Park in the American states of Tennessee and North Carolina. The project was undertaken within the context of the All Taxa Biodiversity Inventory and funded by Discover Life in America. In all, 121 aphid species were documented. When present, attendant ants were also collected and identified, as were the aphid host plants. The aphids, their attendant ants, and host plants are listed here. In addition, a checklist of the plants of the park and a catalog of the aphids of North America were cross-referenced to create a list of aphids not actually found but likely present in the Great Smoky Mountains National Park, increasing the number to 206. Finally, we used Chao1 statistical techniques to estimate the total number of aphid species based on our sampling to date. These produced estimates of 201–214 species.

*Key Words:* biodiversity, plant lice, survey, Formicidae

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The All Taxa Biodiversity Inventory (ATBI) of the Great Smoky Mountains National Park (GRSM) was initiated in 1997 with the aim of cataloging the diversity of all life within the park (Nichols and Langdon 2007). Insects and other arthropods have constituted a significant portion of the ATBI (Sanders et al. 2010) due to their tremendous species diversity. To date, however, no

studies have reported on aphids (Hemiptera: Aphididae).

Aphids are phloem-sucking insects with over 4,500 species worldwide (Remaudière and Remaudière 1997). Most species are strongly host-specific (Dixon 1987) and many are tended by ants: the aphids provide nutrient-rich honeydew in return for protection from predators and parasitoids (Way 1963). Given the high plant diversity in GRSM (over 1,300 species; Jenkins 2007) and the otherwise biologically rich nature of

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the park (Nichols and Langdon 2007), a large number of aphid species are likely present. Historically, few aphid collections have been made in the park, and these were restricted to a few localities. The study presented here is the first systematic survey of the aphids of GRSM.

#### MATERIALS AND METHODS

A general survey of the aphids of the park was initiated in late spring 2003 and continued with sampling in the spring and summer of 2004, fall of 2005, and spring 2006. A cumulative total of 46 days were spent collecting at 115 sites. Because host identity is important in identifying aphids, sampling was mostly done by visual inspection of plants, and the aphids were removed by hand. In order to collect grass-feeding aphids, which may be hidden within the thatch of a field, a modified leaf-blower was used to aspirate insects into a net. In some cases, the aphids were then allowed to self-sort onto their preferred host in a cage containing multiple potential hosts, but in other cases, no clear host association was made. A beating sheet was used occasionally to sample aphids on trees and shrubs, especially conifers.

The aphids, and when tended, their attendant ants, were collected into 95% ethanol. A cutting of the host plant was pressed and dried. Geoposition coordinates were recorded with a hand-held GPS unit. Aphids, ants, and plants were brought back to the laboratory for processing and identification. Approximately 1,100 aphids were mounted to microscope slides and 144 ants were pinned.

Aphids were identified by CF using a large volume of literature sources. Most helpful were the host-based keys by Blackman and Eastop (1994 and 2006). Other important resources were those by: Boudreaux and Tissot (1962),

Corpuz-Raros and Cook (1974), Eastop (1971), Heie (1979), MacGillivray (1958), Pepper and Tissot (1973), Richards (1968a, b, 1972), Robinson (1985, 1986, 1987), and Quednau (1999, 2003). Ants were identified by NJS using standard resources (e.g., Creighton 1950, Fisher and Cover 2007, MacGown et al. 2007).

A complete set of aphid specimens from every collection were deposited in the insect collection of the Illinois Natural History Survey, Champaign, IL (INHS). Some duplicates were selected to form synoptic collections deposited in the insect collection of the Great Smoky Mountains National Park, Gatlinburg, TN and the Aphid Collection of the National Museum of Natural History, Beltsville, MD. The ants and some of the plants were deposited at the INHS. The insects were databased and their data made available on the Discover Life in America (DLIA) ATBI and INHS insect databases ([www.dlia.org](http://www.dlia.org), [www.inhs.uiuc.edu](http://www.inhs.uiuc.edu)).

During the course of the project, it became clear that many species actually present within GRSM would not be found. In order to form an estimate of the number of likely but unconfirmed species, we cross-referenced a list of North American aphids (Smith and Parron 1978) with a checklist of the plants of GRSM (Great Smoky Mountains Natural History Association 2004). If the typical host of an aphid species, listed by Smith and Parron (1978) as occurring in either North Carolina or Tennessee, was known to be present in GRSM, that species was added to the inferred checklist of the aphids of GRSM. Aphid names occurring in the literature were updated with reference to Aphid Species File (Favret 2009), ant names were checked with Antbase (Agosti and Johnson 2005), and host names were checked with the

USDA Plants database (USDA, NRCS 2009).

We estimated the asymptotic number of aphid species (the total number had sampling gone to completion) in GRSM by calculating the Chao1 estimate of species richness (Chao 1984) as  $S_{Chao1} = S_{Obs} + F_1^2/2F_2$ , where  $S_{Obs}$  is the number of species observed,  $F_1$  is the number of singletons, and  $F_2$  is the number of doubletons. We calculated the Chao1 estimate in two ways. First, we used the number of sites as samples. So a singleton would be a species that occurred at only one site, and a doubleton a species that occurred at two sites. Second, we used the number of days as samples. In this case, a singleton would be a species that was collected on only one day, and a doubleton would be a species that was collected on only two days. Finally, we estimated the number of sites or days that would be required to fully sample aphid diversity in GRSM following the procedure outlined in Chao et al. (2009).

#### RESULTS AND DISCUSSION

Over the course of four field seasons, 121 aphid species were documented in GRSM (Table 1). The full complement of collection data, including geolocation coordinates, locality and date of collection, collector and host, are available on the searchable databases ([www.dlia.org](http://www.dlia.org), [www.inhs.illinois.edu](http://www.inhs.illinois.edu)). All but two species are represented by specimens deposited in museums. The remaining species, *Grylloprociphilus imbricator* (Fitch) and *Prociphilus tessellatus* (Fitch), were sighted and photographed by Jason Love of the Great Smoky Mountains Institute at Tremont. These two species are distinct and accurate identifications were straightforward. The observed aphid data are comparable to other surveys of homopterous insects in GRSM. Fifty-three

species of treehopper and 97 species of planthopper were observed and recorded (Wallace et al. 2003, Gonzon et al. 2006, respectively).

The list of 121 species includes one *Capitophorus*, two *Drepanaphis*, and one *Tuberculaphis* species that were not identifiable. Listed in Table 1, they represent species clearly not listed by name, and are possibly new to science. Not listed in Table 1 are specimens from one collection of *Hyperomyzus*, nine of *Macrosiphum*, one of *Monelliopsis*, one of *Myzus*, one of *Nasonovia*, five of *Rhopalosiphum*, and three of *Uroleucon*. Specimens of these latter seven genera remain unidentified for a variety of reasons: a lack of host plant data, specimen damage, or an inadequate resolution of their taxonomy and cryptic morphology. Furthermore, it was not possible to confirm that these latter species were not otherwise already recorded in the list.

Beyond the 121 listed and confirmed species, an additional 85 are likely present in the park, as inferred by cross-referencing aphid and plant lists (Table 1). However, well over half of the observed aphid species were not on the inferred list, suggesting that the estimate of 206 species is conservative. The Chao1 estimate of species richness based on the number of sites visited suggests that the total number of aphid species in GRSM might be 214. To comprehensively sample GRSM aphid species would require sampling at an additional 1,123 sites. The Chao1 estimate of species richness based on the number of sample days suggest that there might be 201 aphid species in GRSM, and sampling all of the species would require an additional 470 days. The three methods of estimating the total number of species in GRSM produced remarkably similar estimates (201, 206, and 214), and both estimates of required additional sampling are

Table 1. Actual (in parentheses) and inferred list of aphid species, host plants, and attendant ants for GRSM.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
1	<i>Abstrusomyzus reticulatus</i> (Heie)	<i>Oxalis</i>		
2	<i>Acuticauda solidaginifoliae</i> (Williams)	<i>Solidago canadensis</i> L.		
3 (1)	<i>Acyrthosiphon pisum</i> (Harris)		<i>Trifolium pratense</i> L.	
4	<i>Amphorophora ampullata</i> Buckton	<i>Oenoclea sensibilis</i> L.		
5 (2)	<i>Amphorophora sensoriata</i> Mason	<i>Rubus</i>	<i>Rubus occidentalis</i> L.	
6 (3)	<i>Anoecia corni</i> (Fabricius)		unknown host	
7	<i>Anoecia oenotherae</i> Wilson	<i>Oenothera</i>		
8	<i>Aphis caliginosa</i> Hottes and Frison	<i>Cornus</i>		
9 (4)	<i>Aphis carduella</i> Walsh	<i>Helianthus</i>	<i>Cryptotaenia canadensis</i> (L.) DC., <i>Taenidia integerrima</i> (L.) Drude	
10	<i>Aphis clydesmithi</i> Stroyan	<i>Sanicula canadensis</i> L.		
11 (5)	<i>Aphis coreopsidis</i> (Thomas)		<i>Carex brunnescens</i> Thunb., <i>Eupatorium rugosum</i> Houtt., <i>Nyssa sylvatica</i> Marsh., <i>Platanus occidentalis</i> L., <i>Prenanthes</i>	<i>Crematogaster lineolata</i> (Say), <i>Formica subsericea</i> Say, <i>Paratrechina longicornis</i> (Latreille), <i>Paratrechina parvula</i> (Mayr)
12 (6)	<i>Aphis cornifoliae</i> Fitch	<i>Cornus florida</i> L.		<i>Prenolepis imparis</i> (Say)
13 (7)	<i>Aphis craccivora</i> Koch	unknown host		
14 (8)	<i>Aphis fabae</i> Scopoli	<i>Carduus nutans</i> L., Hill	<i>Cirsium altissimum</i> (L.) Hill	<i>Crematogaster lineolata</i> (Say), <i>Prenolepis imparis</i> (Say)
15 (9)	<i>Aphis gossypii</i> Glover	<i>Pycnanthemum</i>		<i>Crematogaster lineolata</i> (Say)

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
16 (10)	<i>Aphis illinoensis</i> Shimer		<i>Aureolaria laevigata</i> (Raf.) Raf., <i>Vitis aestivalis</i> Michx.	<i>Myrmica punctiventris</i> Roger
17 (11)	<i>Aphis lugentis</i> Williams		unknown host	<i>Myrmica punctiventris</i> Roger, <i>Tapinoma sessile</i> (Say)
18 (12)	<i>Aphis middletonii</i> Thomas		unknown host	
19	<i>Aphis nasturtii</i> Kaltenbach	<i>Capsella bursa-pastoris</i> (L.) Medik.		
20	<i>Aphis oestlundii</i> Gillette	<i>Oenothera biennis</i> L.		
21 (13)	<i>Aphis pulchella</i> Hottes and Frison	<i>Euphorbia</i>	unknown host	
22	<i>Aphis rubicola</i>	<i>Rubus idaeus</i> L. <i>strigosus</i>		
23 (14)	Oestlund <i>Aphis rubifolii</i> (Thomas)	(Michx.) Focke	<i>Rubus occidentalis</i> L.	
24 (15)	<i>Aphis rumicis</i> Linnaeus			
25 (16)	<i>Aphis spiraeicola</i> Patch	<i>Rumex</i>	<i>Rumex obtusifolius</i> L. <i>Crataegus macrosperma</i> Ashe, <i>Prunus serotinus</i> Ehrh., <i>Pseudognaphalium obtusifolium</i> (L.) Hilliard & B.L. Burtt, <i>Pyrus</i> , <i>Ranunculus bulbosus</i> L., <i>Tilia americana</i> L. var. <i>heterophylla</i> (Vent.) Louden	
26	<i>Aphis viburniphila</i> Patch	<i>Viburnum</i>		
27 (17)	<i>Aulacorthum solani</i> (Kaltenbach)		<i>Aconitum uncinatum</i> L., <i>Ambrosia trifida</i> L., <i>Amelanchier laevis</i> Wiegand, <i>Aralia racemosa</i> L., <i>Aster puniceus</i> L., <i>Conopholis americana</i> (L.) Wallr., <i>Coreopsis major</i> Walter, <i>Cryptotaenia canadensis</i> (L.) DC., <i>Erigeron philadelphicus</i> L., <i>Eupatorium</i> ,	<i>Formica subsericea</i> Say

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
28	<i>Brachycaudus cardui</i> (Linnaeus)	<i>Carduus</i>	<i>Hieracium caespitosum</i> Dumort., <i>Lilium superbum</i> L., <i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke, <i>Oxydendrum arboreum</i> (L.) DC., <i>Pedicularis canadensis</i> L., <i>Platanus occidentalis</i> L., <i>Prunus</i> , <i>Pyralaria pubera</i> Michx., <i>Quercus rubra</i> L., <i>Ranunculus bulbosus</i> L., <i>Rhododendron maximum</i> L., <i>Rubus allegheniensis</i> Porter, <i>Rubus canadensis</i> L., <i>Rugelia nudicaulis</i> Shuttlw. ex Chapm., <i>Rumex crispus</i> L., <i>Rumex obtusifolius</i> L., <i>Salvia lyrata</i> L., <i>Sambucus racemosa</i> L., <i>Saxifraga careyana</i> A. Gray, <i>Tiarella cordifolia</i> L., <i>Tilia americana</i> L., <i>Veratrum viride</i> Aiton	
29 (18)	<i>Brachycaudus helichrysi</i> (Kaltenbach)	<i>Brassica</i>	<i>Erechtites hieracifolia</i> (L.) Raf. ex DC., <i>Erigeron</i> , <i>Eupatorium</i>	
30	<i>Brevicoryne brassicae</i> (Linnaeus)	<i>Solidago canadensis</i> L.		
31	<i>Cachryphora canadensis</i> Hille Ris Lambers			
32 (19)	<i>Calaphis betulaecolens</i> (Fitch)		<i>Amelanchier arborea</i> (Michx. f.) Fernald	
33	<i>Calaphis betulella</i> Walsh	<i>Betula nigra</i> L.		

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
34 (20)	<i>Capitophorus elaeagni</i> (Del Guercio)	<i>Elaeagnus</i>	<i>Cirsium altissimum</i> (L.) Hill, <i>Cirsium discolor</i> (Muhl ex Wild.) Spreng.	<i>Crematogaster lineolata</i> (Say), <i>Prenolepis imparis</i> (Say)
35	<i>Capitophorus jopepperi</i> Corpuz-Raros and Cook	<i>Ambrosia artemisiifolia</i> L.	unknown host	
36 (21)	<i>Capitophorus</i> sp.		unknown host	
37 (22)	<i>Carolinaia caricis</i> Wilson	<i>Carex</i>		
38 (23)	<i>Carolinaia rhois</i> (Monell)		<i>Amelanchier arborea</i> (Michx. f.) Fernald, <i>Elymus hystrix</i> L., <i>Festuca pratensis</i> Huds., <i>Phleum pratense</i> L., <i>Sphenopholis nitida</i> (Biehler) Scribn.	
39	<i>Catamergus kickapoo</i> (Hottes and Frison)	<i>Polygonatum</i>		
40 (24)	<i>Cavariella aegopodii</i> (Scopoli)		<i>Aralia racemosa</i> L., <i>Osmorhizae claytonii</i> (Michx.) C.B. Clarke, <i>Verbesina occidentalis</i> (L.) Walter	
41	<i>Cavariella hendersoni</i> (Knowlton and Smith)	<i>Salix</i>		
42	<i>Chaitophorus nigrae</i> Oestlund	<i>Salix nigra</i> Marsh.		
43	<i>Chaitophorus populifolii</i> (Essig)	<i>Populus</i>		
44	<i>Chaitophorus viminalis</i> Monell	<i>Salix</i>		
45 (25)	<i>Chaitophorus viminicola</i> Hille Ris Lambers	<i>Salix</i>	<i>Salix sericea</i> Marsh.	<i>Crematogaster lineolata</i> (Say)

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)		Attendant ants
		Aphid species	Observed host	
46 (26)	<i>Cinara atlantica</i> (Wilson)	<i>Pinus</i>	<i>Pinus rigida</i> Mill., <i>Pinus strobus</i> L., <i>Pinus virginiana</i> Mill.	<i>Formica subsericea</i> Say, <i>Lasius alienus</i> (Förster), <i>Tapinoma sessile</i> (Say)
47 (27)	<i>Cinara braggii</i> (Gillette)		<i>Picea rubens</i> Sarg.	
48 (28)	<i>Cinara confinis</i> (Koch)		<i>Abies fraseri</i> (Pursh) Poir., <i>Picea rubens</i> Sarg.	
49 (29)	<i>Cinara cupressi</i> (Buckton)		<i>Juniperus virginiana</i> L.	
50 (30)	<i>Cinara engelmanniensis</i> (Gillette and Palmer)		<i>Picea rubens</i> Sarg.	
51 (31)	<i>Cinara gracilis</i> (Wilson)		<i>Pinus virginiana</i> Mill.	
52 (32)	<i>Cinara melaina</i> Boudreaux		<i>Pinus rigida</i> Mill.	
53	<i>Cinara newelli</i> Tissot	<i>Pinus palustris</i> Mill.		
54 (33)	<i>Cinara pergandei</i> (Wilson)		<i>Pinus strobus</i> L., <i>Pinus virginiana</i> Mill.	
55 (34)	<i>Cinara pinivora</i> (Wilson)	<i>Pinus</i>	<i>Pinus rigida</i> Mill., <i>Pinus virginiana</i> Mill.	<i>Formica subsericea</i> Say
56 (35)	<i>Cinara strobi</i> (Fitch)		<i>Pinus strobus</i> L.	<i>Camponotus pennsylvanicus</i> (DeGeer)
57	<i>Cinara taedae</i> (Tissot)	<i>Pinus taeda</i> L.		
58 (36)	<i>Cinara vandykei</i> (Wilson)		<i>Abies fraseri</i> (Pursh) Poir., <i>Picea rubens</i> Sarg.	
59 (37)	<i>Cinara watsoni</i> (Tissot)	<i>Pinus taeda</i> L.	<i>Pinus rigida</i> Mill., <i>Pinus virginiana</i> Mill.	
60	<i>Diphylaphis microtrema</i> Quednau	<i>Quercus rubra</i> L.		
61 (38)	<i>Drepanaphis acerifoliae</i> (Thomas)		<i>Acer rubrum</i> L.	



Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
62	<i>Drepanaphis carolinensis</i> Smith	<i>Acer saccharum</i> Marsh.	<i>Acer saccharum</i> Marsh.	
63 (39)	<i>Drepanaphis choanotricha</i> Smith and Dillery	<i>Acer saccharum</i> Marsh.	<i>Acer saccharum</i> Marsh.	
64 (40)	<i>Drepanaphis knowltoni</i> Smith and Dillery	<i>Acer rubrum</i> L.	<i>Acer rubrum</i> L.	
65 (41)	<i>Drepanaphis nigricans</i> Smith	<i>Acer rubrum</i> L.	<i>Acer rubrum</i> L.	<i>Camponotus subbarbatus</i> Emery, <i>Myrmica punctiventris</i> Roger
66 (42)	<i>Drepanaphis parva</i> Smith	<i>Acer rubrum</i> L.	<i>Amelanchier arborea</i> (Michx. f.) Fernald	
67	<i>Drepanaphis sabrinae</i> Miller	<i>Acer saccharinum</i> L.	<i>Acer saccharinum</i> L.	
68	<i>Drepanaphis simpsoni</i> Smith	<i>Acer saccharum</i> Marsh.	<i>Acer saccharum</i> Marsh.	
69 (43)	<i>Drepanaphis</i> sp. 1	unknown host	unknown host	
70 (44)	<i>Drepanaphis</i> sp. 2	<i>Rubus allegheniensis</i> L.	<i>Rubus allegheniensis</i> Porter	
71 (45)	<i>Ericaphis wakibae</i> (Hottes) (Riley)	<i>Pedicularis canadensis</i> L.	<i>Rubus allegheniensis</i> Porter	
72 (46)	<i>Eriosoma americanum</i> (Riley)	<i>Ulmus americana</i> L.	unknown host	
73	<i>Eriosoma crataegi</i> (Oestlund)	<i>Crataegus punctata</i> Jacq.	unknown host	
74 (47)	<i>Essigella pini</i> Wilson	<i>Crataegus punctata</i> Jacq.	<i>Picea rubens</i> Sarg., <i>Pinus rigida</i> Mill., <i>Pinus virginiana</i> Mill.	<i>Tilia americana</i> L.
75 (48)	<i>Eucallipterus tiliae</i> (Linnaeus)	<i>Crataegus punctata</i> Jacq.	<i>Picea rubens</i> Sarg., <i>Pinus rigida</i> Mill., <i>Pinus virginiana</i> Mill.	<i>Tilia americana</i> L.
76 (49)	<i>Eucерaphis mucida</i> (Fitch)	<i>Crataegus punctata</i> Jacq.	<i>Amelanchier arborea</i> (Michx. f.) Fernald, <i>Betula lenta</i> L.	

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
77	<i>Euceraphis punctipennis</i> (Zetterstedt)	<i>Betula</i>		
78 (50)	<i>Grylloprocaptilus imbricator</i> (Fitch)*	<i>Fagus</i>	<i>Fagus grandifolia</i> Ehrh.	
79	<i>Hamamelistes spinosus</i> Shimer	<i>Hamamelis virginiana</i> L.		
80	<i>Hyalomyzus collinsoniae</i> (Pepper)	<i>Collinsonia canadensis</i> L.		
81 (51)	<i>Hyalopteroides humilis</i> (Walker)		unknown host	
82	<i>Hyperomyzus inflatus</i> (Richards)	<i>Solidago</i>		
83 (52)	<i>Hyperomyzus nabali</i> (Oestlund)		<i>Prenanthes altissima</i> L.	<i>Formica subsericea</i> Say
84 (53)	<i>Hyperomyzus picridis</i> (Börner)		unknown host	
85 (54)	<i>Hysteroneura setariae</i> (Thomas)		<i>Tridens flavus</i> (L.) Hitchc.	
86 (55)	<i>Illinoia goldmaryae</i> (Knowlton)		<i>Erigeron philadelphicus</i> L.	
87 (56)	<i>Illinoia liriiodendri</i> (Moneil)	<i>Liriodendron tulipifera</i> L.	<i>Liriodendron tulipifera</i> L., <i>Magnolia tripetala</i> (L.) L.	
88	<i>Illinoia pepperi</i> (MacGillivray)	<i>Vaccinium</i>		
89 (57)	<i>Illinoia rhokalaza</i> (Tissot and Pepper)	<i>Rhododendron maximum</i> L.	<i>Rhododendron maximum</i> L.	
90 (58)	<i>Illinoia spiraeicola</i> (Patch)		<i>Magnolia fraseri</i> Walter, <i>Polystichum acrostichoides</i> (Michx.) Schott., <i>Prenanthes</i> , <i>Tilia americana</i> L.	

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
91 (59)	<i>Iziphya flabellata</i> (Sanborn)		<i>Carex bromoides</i> Schkuhr ex Wild., <i>Carex pensylvanica</i> Lam, unknown host	
92 (60)	<i>Macrosiphoniella millefolii</i> (De Geer)			
93	<i>Macrosiphoniella pennsylvanica</i> (Pepper)	<i>Achillea millefolium</i> L.		
94 (61)	<i>Macrosiphoniella tapuskae</i> (Hottes and Frison)	<i>Achillea millefolium</i> L.	unknown host	
95	<i>Macrosiphum</i>	<i>Carpinus caroliniana</i>		
96	<i>carpinicolens</i> Patch <i>Macrosiphum coryli</i> Davis	Walter <i>Corylus americana</i> Walter		
97	<i>Macrosiphum geranii</i> (Oestlund)	<i>Geranium maculatum</i> L.		
98	<i>Macrosiphum</i>	<i>Ostrya virginiana</i> (Mill.)		
99 (62)	<i>pseudocoryli</i> Patch <i>Macrosiphum rosae</i> (Linnaeus)	K. Koch	<i>Rosa carolina</i> L.	
100	<i>Microparus desmodiorum</i> Smith and Tuatay	<i>Desmodium paniculatum</i> (L.) DC.		
101 (63)	<i>Microparus singularis</i> (Hottes and Frison)		unknown host	
102	<i>Microparus tephrosiae</i> (Smith)	<i>Tephrosia virginiana</i> (L.) Pers.		
103 (64)	<i>Mindarus pinicola</i> (Thomas)		<i>Abies fraseri</i> (Pursh) Poir.	

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
104	<i>Monellia hispida</i>	<i>Carya glabra</i> (Mill.) Sweet.		
105	<i>Monellia microsetosa</i> Richards	<i>Carya</i>		
106 (65)	<i>Monelliopsis bisselli</i>		unknown host	
107 (66)	Quednau <i>Monelliopsis caryae</i> (Monell)		<i>Carya glabra</i> (Mill.) Sweet	
108 (67)	<i>Monelliopsis nigropunctata</i> (Granovsky)	<i>Juglans</i>	<i>Carya glabra</i> (Mill.) Sweet, <i>Carya pallida</i> (Ashe) Engl. & Graebn.	
109 (68)	<i>Monelliopsis pecanis</i> Bissell		<i>Juglans cinerea</i> L.	
110 (69)	<i>Myzocallis castaneae</i> (Fitch)		<i>Castanea dentata</i> (Marsh.) Borkh.	
111	<i>Myzocallis castaneoides</i> (Baker)	<i>Castanea</i>		
112 (70)	<i>Myzocallis discolor</i> (Monell)		<i>Quercus alba</i> L.	
113	<i>Myzocallis frisoni</i> Boudreaux and Tissot	<i>Quercus</i>		
114 (71)	<i>Myzocallis granovskyi</i> Boudreaux and Tissot		<i>Kalmia latifolia</i> L.	
115 (72)	<i>Myzocallis longirostris</i> Richards	<i>Quercus</i>	<i>Quercus</i>	
116	<i>Myzocallis longiunguis</i> Boudreaux and Tissot	<i>Quercus</i>		
117	<i>Myzocallis melanocera</i> Boudreaux and Tissot	<i>Quercus</i>		
118	<i>Myzocallis multisetis</i> Boudreaux and Tissot	<i>Quercus</i>		

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
119 (73)	<i>Myzocallis punctatus</i> (Monell)	<i>Quercus</i>	<i>Quercus montana</i> Wild.	
120	<i>Myzocallis spinosus</i> Boudreaux and Tissot			
121 (74)	<i>Myzocallis tuberculatus</i> Richards		unknown host	
122 (75)	<i>Myzocallis walshii</i> (Monell)	<i>Quercus rubra</i> L.	<i>Quercus rubra</i> L.	
123	<i>Myzus cerasi</i> (Fabricius)	<i>Prunus cerasus</i> L.		
124	<i>Myzus hemerocallis</i> Takahashi	<i>Hemerocallis fulva</i> (L.) L.		
125	<i>Myzus ornatus</i> Laing	<i>Viola</i>		
126 (76)	<i>Nasonovia carolinensis</i> Heie		<i>Saxifraga careyana</i> A. Gray	
127 (77)	<i>Nasonovia heucherae</i> (Thomas)		<i>Heuchera longiflora</i> Rydb.	
128 (78)	<i>Nasonovia purpurascens</i> (Oeslund)		<i>Thalictrum coriaceum</i> (Britton) Small, <i>Thalictrum pubescens</i> Pursh	
129 (79)	<i>Nasonovia ribisnigri</i> (Mosley)		<i>Hieracium caespitosum</i> Dumort.	
130 (80)	<i>Nasonovia tiarella</i> Heie		<i>Tiarella cordifolia</i> L.	
131 (81)	<i>Nearctaphis bakeri</i> (Cowen)	<i>Trifolium pratense</i> L.	<i>Hieracium venosum</i> L., <i>Trifolium pratense</i> L.	<i>Prenolepis imparis</i> (Say)
132	<i>Nearctaphis clydesmithi</i> Hille Ris Lambers	<i>Crataegus</i>		
133	<i>Nearctaphis crataegifoliae</i> (Fitch)	<i>Crataegus punctata</i> Jacq.		

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
134 (82)	<i>Neomyzus circumflexum</i> (Buckton)		<i>Cacalia atriplicifolia</i> L.	<i>Formica subsericea</i> Say
135	<i>Papulaphis sleesmani</i> (Pepper)	<i>Adiantum pedatum</i> L.		
136	<i>Pemphigus bursarius</i> (Linnaeus)	<i>Populus nigra</i> L.		
137	<i>Pemphigus ephemeratus</i> Hottes and Frison	<i>Betula nigra</i> L.		
138	<i>Pemphigus monophagus</i> Maxson	<i>Populus balsamifera</i> L.		
139	<i>Pemphigus nortonii</i> Maxson	<i>Populus deltoides</i> Bartram ex Marsh.		
140	<i>Pemphigus tartareus</i> Hottes and Frison	<i>Populus deltoides</i> Bartram ex Marsh.		
141 (83)	<i>Pleotrichophorus asterifoliae</i> (Strom)		unknown host	
142	<i>Pleotrichophorus glandulosus</i> (Kaltenbach)	<i>Artemisia vulgaris</i> L.		
143	<i>Pleotrichophorus hottesi</i> Hille Ris Lambers	<i>Achillea</i>		
144	<i>Pleotrichophorus patonkus</i> (Hottes and Frison)	<i>Achillea millefolium</i> L.		
145	<i>Pleotrichophorus pseudopatonkus</i> Corpuz-Raros and Cook	<i>Achillea millefolium</i> L.		
146	<i>Prociphilus fraxinifolii</i> (Riley)	<i>Fraxinus americana</i> L.		

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
147	<i>Prociphilus</i> <i>picearubensis</i> (Smith)	<i>Picea rubens</i> Sarg.		
148 (84)	<i>Prociphilus tessallatus</i> (Fitch)*		<i>Alnus serrulata</i> (Aiton) Wild.	
149	<i>Pterocomma smithiae</i> (Monell)	<i>Salix alba</i> L.		
150 (85)	<i>Rhodobium porosum</i> (Sanderson)		unknown host	
151 (86)	<i>Rhopalomyzus</i> <i>loniceræ</i> (Siebold)		unknown host	
152	<i>Rhopalomyzus poae</i> (Gillette)	<i>Poa pratensis</i> L.		
153 (87)	<i>Rhopalosiphum</i> <i>cerasifoliae</i> (Fitch)		<i>Carex plantaginea</i> Lam.	<i>Lasius alienus</i> (Förster)
154 (88)	<i>Rhopalosiphum maidis</i> Fitch		<i>Platanus occidentalis</i> L.	
155 (89)	<i>Rhopalosiphum</i> <i>oxyacanthæ</i> (Schrank)		unknown host	
156 (90)	<i>Rhopalosiphum padi</i> (Linnaeus)		<i>Carex brunnescens</i> (Pers.) Poir., <i>Carex</i> <i>lurida</i> Wahlenb., <i>Holcus lanatus</i> L.	
157 (91)	<i>Rhopalosiphum</i> <i>ruffabdominalis</i> (Sasaki)		unknown host	
158 (92)	<i>Schizaphis graminum</i> (Rondani)		<i>Carex lurida</i> Wahlenb.	
159 (93)	<i>Schizolachnus</i> <i>flocculosus</i> (Williams)		<i>Pinus rigida</i> Mill., <i>Pinus virginiana</i> Mill.	

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
160	<i>Schizolachnus parvus</i> (Wilson)	<i>Pinus virginiana</i> Mill.		
161	<i>Shenahweum minutum</i> (Davis)	<i>Acer saccharum</i> Marsh.		
162 (94)	<i>Sipha flava</i> (Forbes)		<i>Carex</i>	
163 (95)	<i>Sitobion avenae</i> (Fabricius)		<i>Anthoxanthum odoratum</i> L., <i>Carex prasina</i> Wahlenb., <i>Dactylis glomerata</i> L., <i>Festuca pratensis</i> Huds., <i>Holcus lanatus</i> L., <i>Juncus</i> , <i>Phleum pratense</i> L., <i>Plantago</i> , <i>Poa alsodes</i> A. Gray, <i>Salvia lyrata</i> L.	
164	<i>Sitobion pterinigrum</i> (Richards)			
165	<i>Subsaltusaphis virginica</i> (Baker)	<i>Carex</i>		
166	<i>Takecallis arundinariae</i> (Essig)	<i>Arundo</i> , <i>Arundinaria</i>		
167 (96)	<i>Takecallis taiwanus</i> (Takahashi)		<i>Aundinaria gigantea</i> (Walter) Muhl.	
168 (97)	<i>Tetraneura ulmi</i> (Linnaeus)		unknown host	
169	<i>Thecabius affinis</i> (Kaltenbach)	<i>Populus nigra</i> L.		
170 (98)	<i>Thecabius gravicornis</i> (Patch)		unknown host	
171 (99)	<i>Therioaphis trifolii</i> (Monell)		unknown host	
172	<i>Tiliphagus lycoposugus</i> Smith	<i>Tilia americana</i> L.		
173	<i>Tinocallis ulmifolii</i> (Monell)	<i>Ulmus americana</i> L.		



Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
174 (100)	<i>Tuberculatus</i> sp.		unknown host	
175	<i>Tuberolachnus salignus</i> (Gmelin)	<i>Salix</i>		
176	<i>Uroleucon anomalae</i> (Hottes and Frison)	<i>Aster novae-angliae</i> L.		
177	<i>Uroleucon brachychaetum</i> (Olive)	<i>Krigia montana</i> (Michx.) Nutt.		
178	<i>Uroleucon bradburyi</i> (Olive)	<i>Aster</i>		
179 (101)	<i>Uroleucon chrysanthemii</i> (Oestlund)		<i>Leucanthemum vulgare</i> Lam.	
180	<i>Uroleucon chrysopticola</i> (Olive)	<i>Chrysoopsis mariana</i> (L.) Elliot		
181	<i>Uroleucon ciefi</i> (Olive)	<i>Eupatorium capillifolium</i> (Lam.) Small		
182 (102)	<i>Uroleucon crepusisiphon</i> (Olive)	<i>Aster</i>	<i>Aster cordifolius</i> L., <i>Aster patens</i> Aiton, <i>Symphotrichum dumosum</i> (L.) G.L. Nesom, <i>Symphotrichum lateriflorum</i> (L.) A. Löve & D. Löve	
183 (103)	<i>Uroleucon eupatoricolens</i> (Patch)		<i>Eupatorium venosum</i> L., <i>Senecio aurea</i> (L.) A. Löve & D. Löve, <i>Verbesina alternifolia</i> (L.) Britton ex Kearney	
184 (104)	<i>Uroleucon eupatorifoliae</i> (Tissot)		<i>Ageratina altissima</i> (L.) King & H. Rob.	

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Parron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
185 (105)	<i>Uroleucon gravicornae</i> (Patch)	<i>Solidago</i>	<i>Erigeron annuus</i> (L.) Pers., <i>Erigeron pulchellus</i> Michx., <i>Lysimachia quadrifolia</i> L.	
186 (106)	<i>Uroleucon helianthicola</i> (Olive)	<i>Helianthus microcephalus</i> Torr. & A. Gray	<i>Helianthus atrorubens</i>	
187 (107)	<i>Uroleucon hieracicola</i> (Hille Ris Lambers)		unknown host	
188	<i>Uroleucon illini</i> (Hottes and Frison)	<i>Helianthus</i>		
189 (108)	<i>Uroleucon impatiensicolens</i> (Patch)		unknown host	
190	<i>Uroleucon leonardi</i> (Olive)		<i>Rudbeckia laciniata</i> L.	
191 (110)	<i>Uroleucon luteolum</i> (Williams)		<i>Solidago gigantea</i> Aiton	
192	<i>Uroleucon nigrotibium</i> (Olive)	<i>Solidago</i>		
193 (111)	<i>Uroleucon nigrotuberculatum</i> (Olive)	<i>Solidago</i>	<i>Solidago canadensis</i> L.	
194 (112)	<i>Uroleucon parvotuberculatum</i> (Olive)	<i>Helianthus atrorubens</i> L.	<i>Erechtites hieracifolia</i> (L.) Raf. ex DC., <i>Nyssa sylvatica</i> Marsh., <i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke, <i>Verbesina occidentalis</i> (L.) Walter	
195	<i>Uroleucon paucosensoriatum</i> (Hille Ris Lambers)	<i>Aster</i>		
196	<i>Uroleucon pepperi</i> (Olive)	<i>Cirsium</i>		

Table 1. Continued.

Number (observed)	Aphid species	Typical host of aphid recorded from NC or TN (Smith and Patron 1976) found in park (Great Smoky Mountains Natural History Association 2004)	Observed host	Attendant ants
197	<i>Uroleucon pielouii</i> (Richards)		<i>Solidago canadensis</i> L.	<i>Formica subsericea</i> Say
198	<i>Uroleucon pseudambrosiae</i> (Olive)	<i>Lactuca</i>	<i>Erechtites hieracifolia</i> (L.) Raf. ex DC., <i>Lactuca canadensis</i> L., <i>Packera aurea</i> (L.) A. Löve & D. Löve, <i>Verbesina occidentalis</i> (L.) Walter	
199	<i>Uroleucon reynoldense</i> (Olive)	<i>Coreopsis major</i> Walter	<i>Coreopsisidis major</i> Walter	
200	<i>Uroleucon rudbeckiae</i> (Fitch)	<i>Rudbeckia, Solidago</i>	<i>Rudbeckia laciniata</i> L.	
201	<i>Uroleucon rurale</i> (Hottes and Frison)		<i>Verbesina alternifolia</i> (L.) Britton ex Kearney	
202	<i>Uroleucon sonchellum</i> (Monell)		<i>Lactuca floridana</i> (L.) Gaertn.	<i>Prenolepis imparis</i> (Say)
203	<i>Uroleucon tardae</i> (Hottes and Frison)	<i>Helenium autumnale</i> L.	unknown host	
204	<i>Uroleucon tuataiae</i> (Olive)	<i>Ambrosia artemisiifolia</i> L.	<i>Ambrosia artemisiifolia</i> L.	
205	<i>Uroleucon verbesinae</i> (Boudreaux)		<i>Verbesina occidentalis</i> (L.) Walter	
206	<i>Vesiculaphis caricis</i> (Fullaway)	<i>Carex</i>		

\* Sight record by Jason Love.

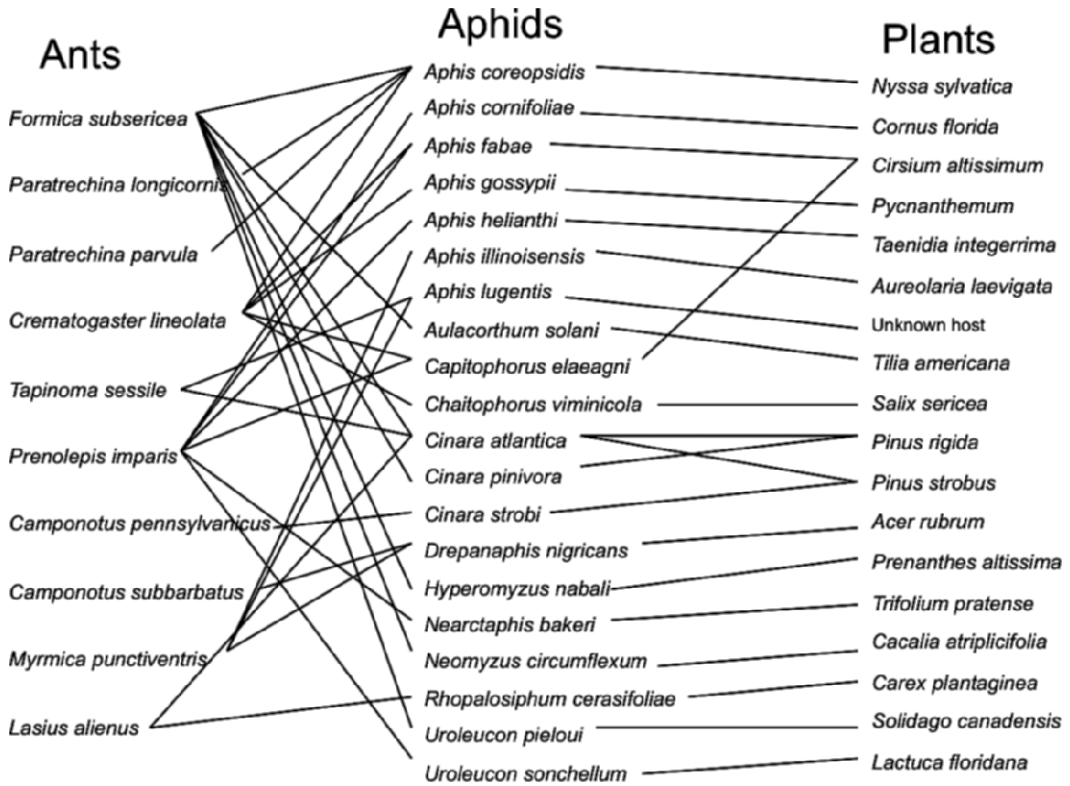


Fig. 1. Diagram of trilateral associations between aphids, their attendant ants, and their host plants.

roughly ten times the actual sampling (115 actual versus 1,123 estimated sites; 46 actual versus 470 estimated days).

A side-by-side comparison of the inferred and observed checklists suggests future study of particular taxa. *Chaitophorus*, *Myzocallis*, *Pemphigus*, and *Pleotrichophorus* are four genera of relatively host-specific aphid species. Only a small number of species of these genera were actually collected, but they contain a large number of species whose hosts are known to occur in the park. Future targeted collecting of species of these four genera should focus on all the GRSM species of *Salix*, *Populus*, *Quercus*, and *Achillea* (wil- lows, poplars, oaks, and yarrow, respectively). The genus *Uroleucon* needs a

significant amount of revisionary taxonomic work. The inferred and observed lists each contain 20 species, and when combined indicate 30 species at GRSM, making it the most speciose aphid genus in the park. This diversity may simply be a result of historical reliance on host plant data to describe species. Host based keys (e.g., Blackman and Eastop 2006) permitted the identification of 20 observed species, but continued preliminary study suggests that a number of these are synonyms. In contrast, the observed list for species of *Cinara* is over twice as long as the inferred list, reflecting the first author's taxonomic expertise.

Aphid species exhibit the full range of ant tending, with some species obligately tended, some never tended,

and some facultatively tended (Stadler and Dixon 2005). Ten species of ants were found tending 20 species of aphids (Figure 1). Unfortunately, ants were not always systematically collected during the project, so the recorded associations are an undercount. *Aphis coreopsidis* (Thomas) had the greatest variety of ants tending it, despite it being recorded with ants on only one host plant species. Of the four ant species found tending *A. coreopsidis*, two of them were exclusive to it, not being found tending any other aphid species. In contrast, *Formica subsericea* Say was found tending seven aphid species, *Prenolepis imparis* (Say) tended six, and *Crematogaster lineolata* (Say) tended five.

Several aphid-host associations bear mentioning because of their uniqueness. *Aphis illinoisensis* Shimer was found feeding on *Aureolaria laevigata* (Raf.) Raf., a member of the Scrophulariaceae (figwort family). This host, a perennial herb, is a new host record for *A. illinoisensis* and is a far departure from its typical use of *Vitis* spp. as host, a perennial vine in the Vitaceae (grape family). *Aulacorthum solani* (Kaltenbach), a polyphagous aphid, was found on 32 different host plants representing 16 families. Of particular note was a colony of *A. solani* feeding on *Conopholis americana* (L.) Wallr., a parasitic perennial herb found on the roots of several kinds of oaks and a member of the Orobanchaceae (broomrape family).

Finally, five aphid species found in GRSM were previously known only from western North America or Canada (Blackman and Eastop 1994, 2006): *Cinara engelmanniensis* (Gillette and Palmer), *C. vandykei* (Wilson), *Schizolachnus flocculosus* (Williams), *Sitobion pterinigrum* (Richards), and *Uroleucon hieracicola* (Hille Ris Lambers). These Smoky Mountain records may represent relict populations, or perhaps

sibling species of their western and northern counterparts.

Taken together, our work on aphid diversity in GRSM, and the aphid associations with both their host plants and their attendant ants, provides an important baseline for studying changes in the distribution and abundance of these important species as a result of habitat modification and climatic change. Importantly, we have also suggested several important lines of future research.

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