

The Natural History of Caterpillar-Ant Associations



Naomi E. Pierce and Even Dankowicz



A larva of *Nudina artaxidia* (Erebidae) steals honeydew from a monophlebid scale insect attended by *Lasius nipponensis*, as described in Komatsu and Itino (2014). (Photo by Takashi Komatsu)

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N. E. Pierce (✉) · E. Dankowicz
Harvard University, Museum of Comparative Zoology, Cambridge, MA, USA
e-mail: npierce@oeb.harvard.edu; danko@brandeis.edu

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Introduction

Caterpillars have a fantastic array of chemical, physical, and behavioral defenses to protect themselves against ants (Borges et al. 2014; Darling et al. 2001; DeVries 1991a; Dyer 1995; Freitas 1999; Honda 1983; Peterson et al. 1987; Rostás 1657; Roux et al. 2011; Uemura et al. 2017). Larvae of diverse Lepidoptera are ignored by marauding ants foraging on their host plants, either due to chemical manipulation and camouflage (Akino et al. 2004; Eubanks et al. 1997; Portugal and Trigo 2005) or physical concealment (Bächtold and Alves-Silva 2013; Farquharson et al. 1922; Ito and Higashi 1991; Jones et al. 2002; Loeffler 1996; Sendoya and Oliveira 2017). Unharmful larvae of various butterfly and moth species are also occasionally known to live close to or within ant nests (Fiedler 1991; Kistner 1982; Lamborn et al. 1914, iNaturalist #65727498). Larvae that can survive encounters with ants and colonize ant territories, whether on host plants or inside structures built by ants, may enjoy a range of benefits including reduced competition, enemy-free space, and favorable microclimates (Atsatt 1981a; Hinton 1951; Koptur 1985; Saarinen and Daniels 2006). Passive coexistence of larvae and ants, through physical/chemical protection or signaling by larvae, may be an important prerequisite to the appearance of stable ant associations in caterpillars (DeVries 1991b; Fiedler 1991) much as in other arthropod groups (Cushing 1997; Cushing 2012; Hölldobler and Wilson 1990; Parker 2016; Stadler and Dixon 2005; Vantaux et al. 2012). Particularly in tropical tree canopies, mosaics of competing ant colonies and ant species play a major role in diversifying available host plant niches, structuring caterpillar communities and creating specialized niches for those able to coexist with them (Agassiz and Kallies 2018; Baker et al. 2016; Blüthgen and Stork 2007; Camarota et al. 2020; Dejean et al. 2017; Floren et al. 2002; Sendoya and Oliveira 2014; Seufert and Fiedler 1996; Wiens et al. 1993).

In this chapter, we provide an overview of caterpillar-ant associations. A number of recent reviews focus on ant associations in Lycaenidae and Riodinidae, including Pierce et al. (2002) and Casacci et al. (2019b). Other treatments such as Kistner (1982), Hölldobler and Wilson (1990) and Pierce (1995) have reviewed the caterpillars found in nests of social insects. However, ant associations have not been summarized and critically examined across all Lepidoptera since Hinton (1951). Many novel relationships have been uncovered in the intervening 70 years, and we discuss factors that may contribute to the phylogenetic distribution and biogeography of these unusual life histories at the end of the chapter. We have not used comparative methods to analyze potential correlates of different forms of ant association, although we plan to do so in a subsequent publication that will include additional phylogenetic and quantitative life history measurements. Our goal here is to describe the full range of natural histories exhibited by these taxa and to identify questions that require further study.

Over 70% of species in the large butterfly family Lycaenidae appear to be ant-associated, making them the largest single group of lepidopteran myrmecophiles (Tables 1 and 2). Two additional radiations of ant associates make up 20% of

Table 1 Based on life history records and recent phylogenies, myrmecophily appears to have arisen at least 30 times across the Lepidoptera as a whole in at least 17 families (Espeland et al. 2018; Kawahara et al. 2019; Léger et al. 2021; Mitter et al. 2017; Regier et al. 2015)

Family	Ant-associated group	Degree of association and type of relationship with ants	Number of ant-associated species	Distribution	References
Psychidae	<i>Iphiherga</i> , <i>Ardiosteres</i> (may constitute more than one distinct group of ant associates)	Obligate. Larvae feed on debris or ants in <i>Iridomyrmex</i> or other nests	3 species	Australia	Hinton (1951), Kistner (1982)
Tineidae	Myrmecozelinae (in part may constitute more than one distinct group of ant associates)	Obligate. <i>Myrmecozela ochraceella</i> feed on <i>Formica</i> nest material and possibly also ants. <i>Ippa</i> are carnivorous and along with others occur with diverse ant groups	>8 species in >3 genera	Europe to New Guinea	Ahn et al. (2014), Gray (1974), Hinton (1951), Hölldobler and Kwapich (in review), Kistner (1982), Parmentier et al. (2014)
	<i>Setomorpha melichrosta</i>	Obligate (?). Larvae feed on plant materials in fungus gardens of <i>Atta</i> and <i>Acromyrmex</i> leaf-cutter ants	1 species	New World tropics/ subtropics	Kistner (1982), Robinson and Nielsen (1993)
	<i>Amydria anceps</i>	Obligate. Feed on fungal substrate accumulations outside of <i>Atta</i> nests	1 species	Mexico	Sanchez-Pena et al. (2003)
Tortricidae	<i>Hystrichophora</i> spp.	Obligate (?). Larvae feed within <i>Vachellia</i> ant-plant domatia	3 species	East Africa	Agassiz (2011), Baker et al. (2016)
	<i>Semutophila saccharopa</i>	Facultative (?). Trophobiotic relationship	1 species	Malaysian peninsula	Maschwitz et al. (1986)

(continued)

Table 1 (continued)

Family	Ant-associated group	Degree of association and type of relationship with ants	Number of ant-associated species	Distribution	References
Sesiidae	<i>Osmanthodon domaticola</i>	Facultative (?). Larvae feed on <i>Vachellia</i> ant-plant domatia within silk shelters	1 species	East Africa	Agassiz and Kallies (2018)
Cyclotornidae	<i>Cyclotorna</i> spp.	Obligate. Ant-attended and parasitic within ant nests	12 species	Australia	Dodd (1902), Dodd (1912), Pierce (1995)
Coleophoridae	<i>Batrachedra myrmecophila</i>	Obligate. Preys on ant brood	1 species	Java	Hinton (1951), Pierce (1995)
Oecophoridae	<i>Stathmopoda</i> sp.	Obligate (?). Known from <i>Oecophylla</i> nests	1 species	Australia	Downes and Edwards (2016)
Pyralidae	<i>Pachypodistes goeldii</i>	Obligate. Larvae feed on <i>Dolichoderus</i> ant nest cartons	1 species	Brazil	Hinton (1951), Pierce (1995)
	<i>Stenachroia myrmecophila</i>	Obligate. Larvae may feed on <i>Crematogaster</i> brood	1 species	Australia	Hinton (1951), Pierce (1995)
	Gen. sp.	Obligate (?). Found in <i>Dinomyrmex</i> nest	1 species	Borneo	Orr et al. (1996)
	Gen. sp.	Obligate (?). Found in <i>Oecophylla</i> nest	1 species	Cameroon	Dejean et al. (2017)
	Gen. sp.	Facultative (?). Found only on plants with <i>Crematogaster</i>	1 species	Cameroon	Dejean et al. (2017)
	Gen. sp.	Facultative (?). Found only on plants with <i>Oecophylla</i>	1 species	Cameroon	Dejean et al. (2017)
Crambidae	<i>Niphopyralis</i> and allies	Obligate. Feed on <i>Oecophylla</i> eggs and brood	4 species	Australia, Java, and Cameroon	Dejean et al. (2017), Hinton (1951), Pierce (1995)

(continued)

Table 1 (continued)

Family	Ant-associated group	Degree of association and type of relationship with ants	Number of ant-associated species	Distribution	References
Noctuidae	<i>Dyops</i> spp.	Facultative. Larvae feed on <i>Cecropia</i> ant-plants defended by <i>Azteca</i> ants	>10 species	Central and South America	Janzen and Hallwachs (2021, Ramos et al. 2018)
Erebidae	<i>Coxina</i> spp.	Facultative (?). Larvae feed on <i>Acacia</i> ant-plants	1 species	Central America	Janzen (1967), Janzen and Hallwachs (2021)
	<i>Eublemma albifascia</i>	Obligate (?). Larvae feed on <i>Oecophylla</i> regurgitations	1 species	Cameroon	Dejean et al. (2016, (2017)
	<i>Homodes</i> spp.	Obligate (?). Larvae feed on foliage around <i>Oecophylla</i> ants	>6 species	Tropical Asia and Australia	Entomological Network of Singapore (2017), Fiedler (1991), Holloway (2005), Leong and D’Rozario (2012), and additional references in text
	<i>Nudina artaxidia</i>	Obligate (?). Larvae feed from ant-attended scale insects	1 species	Japan	Komatsu and Itino (2014)
Notodontidae	<i>Rosema dentifera</i>	Facultative (?). Larvae feed only on <i>Acacia</i> ant-plants	1 species	Central America	Janzen (1967), Janzen and Hallwachs (2021)
	Gen. sp. (near <i>Stauropus</i>)	Obligate (?). May solicit trophallaxis from <i>Oecophylla</i>	1 species	Cameroon	Dejean et al. (2017)

(continued)

Table 1 (continued)

Family	Ant-associated group	Degree of association and type of relationship with ants	Number of ant-associated species	Distribution	References
Saturniidae	<i>Syssphinx mexicana</i>	Facultative (?). Larvae feed only on <i>Acacia</i> ant-plants	1 species	Central America	Janzen (1967), Janzen (1984), Janzen and Hallwachs (2021)
Hesperiidae	<i>Lotongus calathus</i>	Obligate (?). Larvae build nests always shared with ants	1 species	Malaysia	Igarashi and Fukuda (1997)
Pieridae	<i>Catopsilia</i> spp.	Facultative. Larvae regularly attract ants to excretions and leaf exudates	>3 species	Africa and tropical Asia	Williams (1995-2020) and additional references in text
Lycaenidae	Lycaenidae	See Table 2. Most form trophobiotic relationships with ants	>3830 species estimated	Widespread globally	See Table 2
Riodinidae	Eurybiina (Riodiniinae: Eurybiini)	See Table 2. All appear to form trophobiotic relationships with ants	>35 species estimated	Central and South America	See Table 2
	Nymphiidini (Riodiniinae)	See Table 2. Most form trophobiotic relationships with ants	> 273 species estimated	Central and South America	See Table 2

In the absence of detailed phylogenies, we base this estimate on the assumption that a myrmecophilous species observed in a clade of taxa whose larvae are not otherwise known to be ant-associated is likely to have independently evolved ant association, and for those families that show multiple cases of myrmecophily, each also appears embedded in a lineage with other species whose caterpillars are not ant-associated. Ant associations in which trophobiotic caterpillars consistently provide ants with food rewards are not as common and to date have only been well-documented in Tortricidae, Cyclotornidae, Pieridae, Lycaenidae, and twice in Riodinidae. Additional small radiations of caterpillars that appear obligately ant-associated are known from Psychidae; at least three groups of Tineidae, Tortricidae, Coleophoridae, Oecophoridae, Crambidae; at least four groups of Pyralidae; and three groups of Erebidae, Notodontidae, and Hesperidae. Caterpillars specializing on ant-plants are often poorly described but include numerous additional ant-associated taxa as discussed in the text. Please refer to the text for explanation regarding criteria for inclusion as a myrmecophilous species

Table 2 Ant associations in Lycaenidae and Riodinidae

	Number of described species	Distribution	Ant association		Degree of association, if associated			Trophobiosis	
			Non-ant-associated	Ant-associated	Facultative	Obligate	Non-trophobiotic	Trophobiotic	
LYCAENIDAE	5390	Global	16 (96)	881 (3830)	354 (1761)	344 (1281)	217 (1116)	687 (2096)	
CURETINAE	18	AU, OR, PA	0 (0)	5 (18)	3 (18)	0 (0)	6 (18)	0 (0)	
THECLINAE + POLYOMMATINAE	4019	Global	9 (62)	622 (2878)	341 (1654)	134 (442)	95 (339)	591 (1833)	
LYCAENINAE	114	Global	1 (1)	10 (79)	6 (79)	0 (0)	25 (106)	0 (0)	
MILETINAE	208	AT, AU, NA, OR, PA	0 (0)	51 (207)	4 (10)	32 (197)	42 (207)	0 (0)	
APHNAEINAE	302	AT, OR, PA	0 (0)	122 (264)	0 (0)	115 (264)	0 (0)	96 (263)	
PORITINAE	729	AT, AU, OR	6 (33)	71 (384)	0 (0)	63 (378)	49 (446)	0 (0)	
RIODINIDAE	1562	Global	0 (0)	68 (308)	3 (40)	22 (163)	145 (982)	62 (257)	
NEMEOBIINAE	301	Global	0 (0)	0 (0)	0 (0)	0 (0)	32 (252)	0 (0)	
RIODININAE	1261	NA, NT	0 (0)	68 (308)	3 (40)	22 (163)	113 (730)	62 (257)	
Eurybini	247	NT	0 (0)	7 (35)	0 (0)	3 (35)	37 (199)	7 (35)	
Dianesiini	1	NT	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
Calydnini	27	NT	0 (0)	0 (0)	0 (0)	0 (0)	1 (21)	0 (0)	
Nymphidiini	367	NT	0 (0)	61 (273)	3 (40)	19 (128)	3 (26)	55 (222)	
Symmachiini, Emesidini, Riodimini, and Helicopini	615	NA, NT	0 (0)	0 (0)	0 (0)	0 (0)	72 (484)	0 (0)	

Based on available life history information, **all described species** were classified as **ant-associated**, **non-ant-associated**, or data deficient. The number of species in this latter category is not listed. **Ant association** indicates whether larvae occur with ants, either based on direct observation or inferred from adult behavior—associations may range from mutualism to parasitism. We were unable to locate detailed descriptions that confirm the lack of ant associations in any non-trophobiotic riodinid caterpillars. Caution is definitely necessary: regular associates, such as *Stalactis* (Riodinidae: Nymphidiini) and *Deloneura*

Table 2 (continued)

(Lycæniidae: Portitiinae), have been overlooked and scored as non-ant-associated in previous reports. Ant-associated species were further classified as **obligate** myrmecophiles, **facultative** myrmecophiles, or myrmecophiles whose degree of association could not be determined due to low sample size. Finally, we classified each species with available observations as **trophobiotic** or **non-trophobiotic**. Where field observations are lacking, a functional dorsal nectary organ is a good indicator that larvae are ant-attended, while long bristles on the thorax and abdomen reliably signal the absence of ant attendance (e.g., DeVries 1991c). Each cell in the table first reports the number of documented species records. For characters not known to vary among known species of a genus, the same character state was assigned to all other congeners. The number of these inferred species counts is given in **parentheses** within each cell. Species lists were modified from G. Lamas (personal communication). For species whose life histories we could not document from published literature, we searched for relevant reports on Google Scholar, iNaturalist, and BugGuide. Altogether, ant association data of any kind remain unavailable for more than 75% of lycænid and rioidiid species. *AT* Afrotropical, *AU* Australasian, *NA* Nearctic, *NT* Neotropical, *OR* Oriental, *PA* Palearctic

References compiled for table: (Albar-Abregú 2014; Albanese et al. 2007; Alves-Silva et al. 2018; Austin et al. 2008; Bálint and Benyamini 2001; Ballmer 2008; Ballmer and Pratt 1991; Ballmer and Wright 2008; Bascombe et al. 1999; Basu et al. 2019; Basu and Kunte 2020; Benyamini 1995; Benyamini 2013; Benyamini and Bálint 1995; Benyamini et al. 2018; Benyamini et al. 2019; Braby 2011; Braby 2012; Braby 2013; Braby and Douglas 2004; Bury and Savchuk 2015; Callaghan 1985; Callaghan 1986; Callaghan 1992a; Callaghan 1997; Callaghan 2008; Casagrande et al. 2009; Castillo Guevara and Rico Gray 2002; Claassens 1996; Cock 2010; Comstock and Dammers 1932; Cottrell 1984; Dantchenko 1997; Dejean et al. 2017; DeVries 1984; DeVries 1988a; DeVries 1991c; DeVries 1991d; DeVries 1997; DeVries and Penz 2000; DeVries et al. 2004; DeVries et al. 1986; Duarte and Robbins 2008; Duarte and Robbins 2010; Eastwood et al. 2005; Eastwood et al. 2008b; Faynel and González-Mercado 2019; Fiedler 1989a), supplemental table from (Fiedler 2001; Fiedler et al. 1995; Fukuda et al. 1984; Gibbs 1980; Hall 1998; Hall 2018; Hall et al. 2004; Harvey and Longino 1989; Harvey and Webb 1980; Hawkeswood et al. 2016; Heath 1997; Heath and Claassens 2003; Heredia and Robbins 2016; Hinton 1951; Hsu and Johnson 1998; Hsu et al. 2004; Igarashi and Fukuda 1997; Igarashi and Fukuda 2000; Itoaka et al. 2009; Jackson 1937; Jackson 1957; Janzen and Hallwachs 2021; Jeratthitikul et al. 2011; Johnson and Valentine 2001; Kaminski 2008a; Kaminski 2008b; Kaminski 2017; Kaminski and Carvalho-Filho 2012; Kaminski et al. 2016; Kaminski et al. 2012a; Kaminski et al. 2014; Kaminski et al. 2013; Kaminski et al. 2015; Kaminski et al. 2020a; Kaminski et al. 2010b; Kaminski et al. 2020b; Kim and Ho 2012; Kitching and Luke 1985; Kubik and Schorr 2018; Kumar et al. 2017; Lafranchis 2019; Lafranchis et al. 2007; Larsen 2005; Lo et al. 2017; Lohman and Samarita 2009; Marrins et al. 2013; Maschwitz et al. 1988; Megens et al. 2005; Mota et al. 2014; Mota et al. 2020; Neild and Bálint 2014; New 1993; Nielsen and Kaminski 2018; Nishida 2010; Obregón et al. 2015; Okubo et al. 2009; Opler 1999; Pan and Morishita 1990; Parsons 1984; Parsons 1999; van der Poorten and van der Poorten 2016; Riva et al. 2017; Robbins and Aiello 1982; Robbins et al. 1996; Ross 1964; Saarinen 2005; Saarinen and Daniels 2006; Safian 2012; Sáfián 2015a; Sáfián 2015b; Sáfián and Collins 2014; Safian and Collins 2015; Sáfián and Larsen 2009; Sands 1986; Santos et al. 2014; Sartot and Ginés 2011), supplemental table from (Schär et al. 2018; Schmid et al. 2010; Schmidt et al. 2014; Schurian and Eckweiler 2002; Schurian and Fiedler 1994; Schurian and Reif 1992; Schurian et al. 2005; Seuffert and Fiedler 1996; Shapiro 2007; Shimizu-Kaya et al. 2015; Silva et al. 2014; Singh 2003; Stradomsky and Fomina 2009; Talavera et al. 2016; Tenmet 1996; Torres and Pomerantz 2016; Tshikolovets 2011; Vargas and Duarte 2016; Williams 1995-2020; Yago et al. 2010; Youngsteadt and Devries 2005; Zanuncio et al. 2009; Zanuncio et al. 2013; Zhou and Zhuang 2018), BugGuide #1133247, BugGuide #1503993, BugGuide #1745213, BugGuide #1824230, BugGuide #329907, BugGuide #393584, BugGuide #405974, BugGuide #731179, BugGuide #803004, BugGuide #866019, iNaturalist #19541629, iNaturalist #19626729, iNaturalist #21747729, iNaturalist #280592, iNaturalist #3270216, iNaturalist #36569419, iNaturalist #40848069, iNaturalist #4312429, iNaturalist #5888085, iNaturalist #9351793, iNaturalist #67275324, <https://entomologytoday.org/2015/12/07/caterpillar-depends-on-parasitic-plants-and-nectar-drinking-ants>, <https://butterflycircle.blogspot.com/2010/06/life-history-of-branded-imperial.html>, <https://butterflycircle.blogspot.com/2011/1/life-history-of-singapore-four-line.html>, <https://www.flickr.com/photos/142712970@N03/3322969114>

species in the closely related butterfly family Riodinidae (Table 2). While caterpillars in these two families are generally characterized as ant mutualists, we discuss evidence suggesting that interactions with negative consequences for ants are far more common than previously recognized, and that despite appearances, these associations might be better characterized as parasitic on the part of the lycaenids or, at best, reciprocally parasitic by both parties. Most other ant-associated groups, like the Australian moth family Cyclotornidae, are individually species-poor and rarely encountered but collectively span almost the entire lepidopteran tree of life and display great diversity, particularly in the tropics (Table 1). We show that myrmecophilous caterpillars that passively coexist with ants are far more diverse than previously recognized and suggest that many such caterpillar groups remain undiscovered.

Terminology and Overview

Myrmecophiles are “ant loving” organisms with adaptations that enable them to benefit from ant association, and we will refer to them interchangeably as **ant associates** (narrower definitions are also sometimes used: (Hölldobler and Wilson 1990; Kronauer and Pierce 2011; Nichols 1989). Specializations that help these species find or attract and subsequently stay in contact with ants are important and could be considered part of a basic signature of myrmecophily. Ants themselves, their pheromones, and even volatiles released by other organisms disturbed by ants are used as cues by adults or larvae to find ants, as discussed below. Within Lepidoptera, we consider caterpillars ant-associated if we can directly observe or infer from available evidence that caterpillars or ovipositing females use these cues to locate ants or that caterpillars themselves produce secretions or vibratory signals specialized to attract ants. Caterpillars may also qualify as ant-associated if they appear specialized to live in close proximity to ants on myrmecophytes, plants with a strong mutualistic relationship with ants and that typically provide ants with cavities for shelter.

Obligate ant associates are species that cannot complete their life cycle without ants. In cases where full life histories have been well documented, these species are easily identified. However, for cases where relationships must be inferred, a species is likely to be an obligate ant associate if the caterpillars are never found without ants nearby; if caterpillars rely on ants as a food source; if females hesitate or refuse to oviposit, even in captivity, without ants present; or if adults are typically only observed near the openings of ant nests. In contrast, **facultative** ant associates are sometimes found without ants. Facultative association of caterpillars with ants has only been well documented in Lycaenidae and Riodinidae, although it seems likely to occur in other groups that have not been so well characterized. Obligate ant associates usually associate with ants from only one genus or species, while most facultative myrmecophiles associate with multiple ant genera and subfamilies. A number of exceptions exist to these broad generalizations (Eastwood and Fraser 1999; Fiedler 2001; Glasier et al. 2018). For example, the obligately ant-associated

Australian lycaenid, *Jalmenus eichhorni*, is attended by ants from different genera during the day and night (Dunn 2007). Larvae of a congener, *J. evagoras*, are typically associated with only a few ant species in the genus *Iridomyrmex* but during “breakout” periods of high abundance can readily be found associating with other genera (Pierce and Nash 1999).

Like other conditional interactions with ants, caterpillar-ant associations vary spatially and temporally, ranging from **mutualisms**, where both parties derive net fitness benefits from their interaction, through to **parasitisms**, where one party (in this case usually the ants) pays a fitness cost due to the association. Many appear to be commensal or only mildly parasitic in the sense that caterpillars benefit while ant fitness seems largely unaffected.

Many insects produce secretions that serve as a food source to attract and maintain a standing guard of ants and are described as being **trophobiotic**. We refer to lycaenid and riodinid caterpillars that do this as **ant-attended**. We use the term **non-trophobiotic** to describe caterpillars that are not actively ant-attended. The term “myrmecoxenous” has been used as a substitute for “non-trophobiotic” in recent literature but confusingly describes either a symphile, an insect that is a guest in ant nests (Nichols 1989), or a non-myrmecophile, an insect that is simply not ant-associated (Kitching and Luke 1985; Paul 1977), so we have avoided using it here.

Parasites found in ant nests often belong to groups that prey on ant-attended hemipterans and thus already possess appropriate defensive and feeding-related adaptations to coexist with ants (Eisner et al. 1972; Malicky 1970; Pierce 1995). These include numerous genera within the subfamily Miletinae [Lycaenidae], *Shirozua* [Lycaenidae], a few riodinids, *Eublemma* [Erebidae], Cyclotornidae, and perhaps *Stathmopoda* [Tineidae] and *Baratrachedra* [Coleophoridae]. This pattern is not confined to Lepidoptera: ant brood and trophallaxis feeding have been reported in species from nearly every prominent hemipteran-associated arthropod group, including ladybug beetles (Orivel et al. 2004; Vantaux et al. 2010), flower flies (Hölldobler and Wilson 1990), green lacewings (Tauber and Winterton 2014; Tauber et al. 2020), and even certain aphids themselves (Salazar et al. 2015).

Many butterfly and moth larvae have ant associations that have been potentially overlooked because the relationship is defined largely by its absence: these are cases where ants cannot detect or appear indifferent to the caterpillars. These caterpillars typically only associate with ants near nests and food sources—habitats that are hotspots for lepidopteran ant associates more generally. For example, a veritable menagerie of potentially ant-associated Lepidoptera lives on the African ant-acacia *Vachellia drepanolobium*, the dominant tree species in the “black cotton” vertisols of East African savannas. Eighteen species of Lycaenidae, some attended by ants, were documented on these ant-plants at field sites in Kenya and Tanzania over a 5-year period (Fig. 1) (Baker et al. 2016; Martins et al. 2013; Whitaker et al. 2019). Numerous species of Tineidae, Tortricidae, Sesiidae, Blastobasidae, Gelechiidae, and Geometridae have been reared from the swollen thorn ant domatia of *V. drepanolobium*, and many others feed in the tree canopy (Adamski 2017; Agassiz 2011; Agassiz and Bidzilya 2016; Agassiz and Harper 2009; Agassiz and Kallies 2018; Baker et al. 2016; Hocking 1970). Some of these species are polyphagous and have

Fig. 1 Lycaenid larvae, almost certainly *Kipepeo kedonga* (formerly known as *Chilades kedonga* (Parmentier et al. 2014)) that were abundant in swollen thorns of *Vachellia drepanolobium* in Suyian, Kenya. (Photo by Dino Martins)



Fig. 2 The brown silk envelope on the left was built by a tortricid caterpillar feeding inside a thorn domatium of *Vachellia drepanolobium* occupied by *Crematogaster mimosae* in Kitengela, Kenya. (Photo by Naomi Pierce)



been described as having greater abundance in the absence of ants (Agassiz 2011), and we would not describe these ones as being ant-associated. The majority are not sufficiently well known to be able to characterize them as ant-associated or not.

A few specialist myrmecophiles have nonetheless been documented on ant-plants. For example, larvae of *Hystrichophora* (Tortricidae) build strong, membranous, dome-like shelters within hollowed-out *V. drepanolobium* domatia that are frequently shared with ants (Fig. 2) (Agassiz 2011). Caterpillars of *H. griseana* are common on trees inhabited by colonies of *Crematogaster mimosae* or *C. nigriceps*, but they are almost never found on trees inhabited by colonies of *Tetraponera penzigi* (Baker et al. 2016). Similarly, caterpillars of *Syssphinx mexicana* (Saturniidae), *Rosema dentifera* (Notodontidae), and *Coxina* spp. (Erebidae) specialize on Central American acacias, *Vachellia cornigera*, and its relatives, which are inhabited by aggressive *Pseudomyrmex* ants, whose defenses the caterpillars are able to overcome (Janzen 1967; Janzen 1984; Janzen and Hallwachs 2021). The larvae of *Dyops* spp. (Noctuidae) are essentially immune to ant attack and feed on various species of Urticaceae, including *Cecropia* ant-plants defended by *Azteca* ants (Janzen and

Hallwachs 2021; Ramos et al. 2018). Many other species reported from ant-plants may prove to be ant-associated upon further investigation. Tunnels and silk shelters built by *Stenoma charitarca* (Oecophoridae), and leaf rolls built by *Acrospila gastralis* (Crambidae), allow caterpillars to persist on *Maieta guianensis* plants occupied by *Pheidole* ants (Vasconcelos 1991), much as certain crambid larvae are protected from ants within leaf rolls on *Tococa* ant-plants (Michelangeli 2003). The database of macrocaterpillar food plants of the Area de Conservacion Guanacaste, Costa Rica (Janzen and Hallwachs 2021), does not indicate whether caterpillar host plants were actually occupied by ants but nonetheless includes dozens of butterfly and moth species that have been exclusively reared from ant-plant species, such as *Lygropia cernalis* (Crambidae) from *Triplaris melaenodendron*, *Conchylodes nolckenialis* (Crambidae) and *Munona robuschendorfi* (Erebidae) from *Cordia alliodora*, and *Macalla* sp. (Pyralidae) from *Cecropia obtusifolia*. Many Lycaenidae and Riodinidae also prominently infiltrate ant-plants (e.g., DeVries and Baker 1989; Eastwood and Fraser 1999; Heredia and Robbins 2016; Heredia and Robbins 2016; Kaminski 2008b; Kaminski et al. 2010a; Kaminski et al. 2012b; Kaminski et al. 2020a; Maschwitz et al. 1984; Sands 1986; Shimizu-Kaya et al. 2015).

Many caterpillar species that do not directly interact with ants are polyphagous and occur on different host plants only as they become occupied by ants. For example, the obligate ant associations of many species in the butterfly tribe Liptenini (Lycaenidae) only became evident based on the observation that the large, attractive adults had only been observed around arboreal *Crematogaster* nests (see discussion below). Similarly, *Homodes* (Erebidae) are large and unusual caterpillars that occur on a wide variety of host plants but generally only when the plants are also patrolled by *Oecophylla* ants (see discussion below) (Fiedler 1991; Holloway 2005; Leong and D’Rozario 2012; Lokkers 1990). This kind of “cryptic” association probably exists even in less charismatic lepidopterans, such as leaf mining micromoths (compare Bily et al. (2008)).

Dejean et al. (2017) undertook the most extensive study to date of the extent of ant-caterpillar associations in tropical habitats. Defoliator and nectarivorous caterpillars were collected and reared from 50 to 100 m transects of the extrafloral nectary-bearing plant *Alchornea cordifolia* along forest edges in Cameroon, each transect exclusively dominated by one of five species of aggressive ants. Each of the tree-nesting species *Crematogaster striatula*, *Oecophylla longinoda*, *Tetramorium aculeatum*, and *Camponotus brutus* were represented by 30 transects, along with 10 transects dominated by the ground-nesting species *Myrmecaria opaciventris*. Of the 22 species of caterpillar found, only 1 was found with more than 1 ant species, although many were collected from numerous transects. All species showed distinct specializations to coexist with ants, including some parasites that could solicit trophallaxis or appeared to feed within ant nests. This study may be the first to systematically document the full spectrum of defoliator and nectarivorous caterpillars on a host plant dominated by specific ant species and shows that previously unknown ant associations across diverse lepidopteran families can be uncovered by careful observations in tropical habitats.

Synopsis of Caterpillar-Ant Associations

Tineidae and Psychidae

Diverse species of Tineidae and Psychidae are known to scavenge exclusively within ant nests, encased with debris or protected by silk webbing, and some of these probably feed on ant brood or food resources. Pending genus-level phylogenies that may reveal additional origins, ant associations appear to have originated independently in at least three tineid clades, represented respectively by the genera *Myrmecozela*, *Setomorpha*, and *Amydria*, as well as in the psychid genera *Iphierga* and *Ardiosteres*; see Regier et al. (2015) for a higher level molecular phylogeny of 62 representatives of the main lineages within Tineoidea (Ahn et al. 2014; Gray 1974; Hinton 1951; Kistner 1982; Parmentier et al. 2014; Robinson and Nielsen 1993; Sanchez-Pena et al. 1993). Caterpillars in the Palearctic and Oriental genus *Ippa* (Tineidae) have been found in ant nests of *Crematogaster* (Myrmicinae), *Polyrhachis*, *Lasius*, *Dolichoderus*, and *Anoplolepis* (Formicinae) (Hinton 1951; Hölldobler and Kwapich in review). *Ippa* caterpillars build a flattened protective case, and while *I. dolichoderella* larvae in Java are only known to consume brood, *I. conspersa* larvae in Japan also feed on adult ants (Hinton 1951; Hölldobler and Kwapich in review). Although not obligately ant-associated, the free-living larvae of *Perisceptis carnivora* (Psychidae) in Panama build portable defensive cases and frequently feed on worker ants (Davis et al. 2008).

Tortricidae

Malaysian caterpillars of *Semutophila saccharopa* (Tortricidae) live in silk shelters constructed on bamboo and associate with ants from at least seven genera in a manner similar to aphids. Ants feed on the sugar-rich anal droplets provided by the caterpillars. The caterpillars prefer to excrete waste in the presence of ants, but the droplets can be withdrawn back into the anus and jettisoned several centimeters away from the larval shelter if ants remain unavailable (Maschwitz et al. 1986).

Cyclotornidae

In the Australian family Cyclotornidae, which comprises the single genus *Cyclotorna*, larvae start out as external parasites of ant-attended leafhoppers or scale insects (Fig. 3) (Dodd 1902, 1912; Pierce 1995). Second-instar larvae of *Cyclotorna monocentra* are flattened and produce an anal secretion that attracts ants. Workers of *Iridomyrmex purpureus* carry them into the nest, where they feed on brood until leaving to pupate under bark (Epstein et al. 1999; Pierce 1995). The *Cyclotorna* larvae will die if their anal secretions are not removed by ants (Hinton

Fig. 3 This was one of several *Cyclotorna* (Cyclotornidae) larvae found in a *Camponotus* nest in Western Australia. (Photo by Jean Hort)



1951). Epipyropidae, the apparent sister group to Cyclotornidae (Hall et al. 2004; Heikkilä et al. 2015), are ectoparasites of planthoppers and cicadas (Hemiptera) but are not known to interact with ants (Pierce 1995).

Coleophoridae and Oecophoridae

Many *Batrachedra* (Coleophoridae) prey on scale insects, but larvae of the Indonesian species *B. myrmecophila* feed on ant brood in nests of *Polyrhachis dives*, protected from ants by portable cases (Hinton 1951; Pierce 1995). While several *Stathmopoda* spp. (Oecophoridae) feed on scale insects (Pierce 1995), one Australian species builds webs in *Oecophylla* nests where it may feed on ants (Downes and Edwards 2016).

Pyralidae

Many Pyralidae are associated with ants. Larvae of the Brazilian *Pachypodistes goeldii* (Chrysauginae) chew *Dolichoderus gibbosus* nest cartons, which they use to construct a protective case, and may also feed on the brood (Hinton 1951; Pierce 1995). Adults of this species are covered in long, loose setae that are likely to help freshly eclosed adults escape attack by ants (Kistner 1982). An Australian species, *Stenachroia myrmecophila* (Galleriinae), may feed on *Crematogaster* brood (Hinton 1951; Pierce 1995). Larvae of other unidentified pyralids have been found in *Dinomyrmex* nest debris in Borneo (Orr et al. 1996) and in *Oecophylla* nests in Cameroon (Dejean et al. 2017). Caterpillar silk weaving may also help herbivorous Pyralidae coexist with ants. Dejean et al. (2017) found an unidentified species of pyralid that uses silk to cordon off young leaves of *Alchornea cordifolia* inhabited by *Crematogaster striatula*. Caterpillars of another unidentified pyralid species were found only on *A. cordifolia* occupied by *Oecophylla longinoda*, in communal

caterpillar nests resembling *Oecophylla* nests from which they emerge at night to feed when the ants are less active. *Crematogaster* ants were recently found nesting within a shelter built by larvae of *Triphassa* (Pyralinae) on an *Erica imbricata* heath in South Africa [iNaturalist #23039584]. More work will be needed to determine if this remarkable relationship is coincidental or occurs regularly.

Other than Lycaenidae and Riodinidae, species of Tineidae and Pyralidae are the most prominent caterpillar guests in ant nests (Table 1). These species are herbivores, detritivores, and parasites and include the only caterpillars found in colonies of ants, such as leaf-cutter ants [Attini], that do not harvest nectar from plants and hemipterans (Kistner 1982; Robinson and Nielsen 1993; Sanchez-Pena et al. 2003). Other species of Tineidae and Pyralidae feed within social wasp, bee, termite, and even communal spider nests (Ahn et al. 2014; Brandl et al. 1996; Davis and Davis 2007; Deyrup et al. 2004; Kistner 1982; Pierce 1995). Most Lepidoptera found within human dwellings also belong to these two families (Bertone et al. 2016; Linsley 1944). Flexible diets, along with defenses that help larvae avoid aggression, may be among the factors that help these families to thrive alongside diverse host ant associates, and more species will undoubtedly be found in association with ants as new life histories are uncovered.

Crambidae

In the family Crambidae, at least two lineages in the largely phytophagous subfamily Spilomelinae may be associated with ants. *Cirrhochrista saltusalis* (Spilomelinae: Margaroniini) caterpillars have been found alongside *Pheidole* ants and *Oboronia punctatus* caterpillars (Lycaenidae) within debris nests constructed by the ants on flowerheads, but this cohabitation may be an unusual occurrence (Lamborn 1911; Lamborn et al. 1914). Immature stages remain unknown from most Wurthiini, but several feed on brood of arboreal ants, in addition to a single phytophagous species (Mally et al. 2019). *Niphopyralis aurivillii* (Spilomelinae: Wurthiini), a possibly chemical mimic of host ants known from Java, feeds on the brood of *Polyrhachis bicolor* and may help maintain the silken nest structure (Hinton 1951; Pierce 1995). Another species found in Java, *N. myrmecophila*, feeds on *Oecophylla smaragdina* brood and has a flattened portable case for protection (Hinton 1951). *Niphopyralis chionesis* is suspected to prey on brood of *Oecophylla smaragdina* in Australia (Pierce 1995), and Dejean et al. (2017) found a related larva feeding on *Oecophylla longinoda* eggs in Cameroon (Fig. 4).

Erebidae

Larvae of lichen moths (Erebidae: Lithosiini) secrete toxins that protect them from ants (Chialvo et al. 2018; Palting 2020). Ayre (1958) observed hundreds of British Columbian *Crambidia casta* larvae that sheltered and pupated in *Formica* nests,

Fig. 4 (a, b) Caterpillar on an *Oecophylla* nest in Guinea, near Conakry. Larvae of this undescribed species near *Niphopyralis* (Crambidae) feed voraciously on weaver ant eggs (Dejean et al. 2017). (Photo by Piotr Naskrecki)



although this behavior has not been found in other populations of this species (Palting 2020). Larvae of another small lichen moth found in Japan, *Nudina artaxidia*, are obligate associates of *Lasius* ants and feed on honeydew from scale insects, along with lichen (chapter frontispiece) (Komatsu and Itino 2014).

Many *Eublemma* spp. (Erebidae: Boletobiinae) feed on scale insects, where they are concealed from attending ants by a portable protective casing (Dejean et al. 2016; Lamborn et al. 1914; Pierce 1995; Susilo and Susilo 2015). In Cameroon, Dejean et al. (2016) found that *Eublemma albifascia* lays eggs on ant nests, and first-instar caterpillars are carried into *Oecophylla longinoda* brood chambers by workers. Subsequent instars are fed by ants and steal from trophallaxis between workers, and ants groom their bodies and drink their anal secretions. The larvae acquire colony odors and do not require physical protection from host ants (Dejean et al. 2016). Dejean et al. (2017) found 359 caterpillars of *Eublemma albifascia* in only four colonies of *Oecophylla longinoda*. Due to their intense trophallaxis requirements, *Eublemma albifascia* parasites generally cause the death of the queen through neglect, though their numbers are regulated by some parasitoid wasps (Dejean et al. 2016). Eclosed adults are mostly ignored and, if occasionally attacked, are protected by long, dense scales (Dejean et al. 2016).

Fig. 5 (a, b) A weaver ant-mimicking *Homodes* larva (Erebidae) in Singapore. (Photo by Lionel Lim. Soh Kam Yung [K. Y. Soh] provides another full-habitus view at iNaturalist #37480826)



In a few wasmannian ant mimics, the same specialized tactile structures are used to integrate with ants and to scare off other predators (von Beeren et al. 2018; Kronauer and Pierce 2011). A few Oriental and Australasian species of the genus *Homodes* (Erebidae: Boletobiinae) occur on a wide range of host plants but never far from *Oecophylla smaragdina* weaver ants (Fiedler 1991; Holloway 2005; Leong and D’Rozario 2012, iNaturalist #65316827, iNaturalist #27728866). These caterpillars are excellent mimics of *Oecophylla* ants at both the front and the back, with a false head on the posterior abdomen and long clubbed setae resembling ant appendages (Fig. 5). Waving these setae not only deters visual predators but appears to placate *Oecophylla* workers (video at <https://www.facebook.com/watch/?v=1938845709677099>) (Entomological Network of Singapore 2017). Structurally similar, possibly glandular setae are found on the thorax and abdomen of related larvae documented on iNaturalist, which are not known to be ant-associated [e.g., iNaturalist #21087410, iNaturalist #38085822, iNaturalist #21414510]. Lokkers (1990) found ant-mimicking looper moth caterpillars in north Queensland exclusively on *Oecophylla*-occupied trees, which may have been larvae of *Homodes* or another group with a similar life history.

Fig. 6 *Stauropus* larva (Notodontidae) feeding on *Salix* in Italy. The elongated thoracic legs help early-instar larvae mimic ants and in some cases are used to communicate with ants. (Photo by Paolo Mazzei)



Notodontidae

Phytophagous larvae of *Stauropus* and *Neostauropus* (Notodontidae) have enlarged mesothoracic and metathoracic legs used to mimic ants in early instars, and spiders once larvae become larger, with a terrifying threat display (Fig. 6) (Poulton 1890; Pratt et al. 2016). In Britain, photographer Andy Newman experimentally brought together first-instar *Stauropus fagi* larvae and *Formica* ants and discovered that larvae were ignored after waving their mesothoracic legs and contacting the ants' antennae [http://www.andynewman.org/html/lobster_moth.html]. Dejean et al. (2017) discovered related larvae in Cameroon that use their enlarged mesothoracic legs to solicit trophallaxis from associated *Oecophylla longinoda* ants. The larvae also fed on young leaves and extrafloral nectaries. An unidentified larva of this species from southern Nigeria may have also been described by Farquharson et al. (1922). Larvae of Afrotropical *Amyops ingens* strongly resemble *Stauropus* larvae and have much shorter, but still notably elongated, thoracic legs of unknown function [(iNaturalist #11244196, iNaturalist #11446507)]. Perhaps they are used to handle soft-bodied Hemiptera or honeydew as in some Lycaenidae and Riodinidae (DeVries and Penz 2000; Dejean et al. 2017). The biology of these fascinating Notodontidae remains largely undocumented; more research is needed to understand their ecology and diversity.

Papilionoidea (Hesperiidae, Nymphalidae, Pieridae)

With over 900 well-documented and more than 4000 inferred myrmecophilous species, the butterfly families Lycaenidae and Riodinidae account for an overwhelming proportion of caterpillar-ant associations (Table 2). At least a few butterfly species in other families are also ant-associated. Malaysian *Lotongus calathus* caterpillars



Fig. 7 Glistening droplets on spines of larva of *Phoebis philea* (Pieridae) feeding on *Senna mexicana* being inspected by an unidentified ant, with a second ant feeding on an extrafloral nectary nearby. The droplets are thought to be defensive but may in some cases (depending on the ant species, host plant, and location) be strikingly attractive to ants (e.g., photo of *Catopsilia pyranthe* surrounded by *Anoplolepis gracilipes* ants at <http://pureoxygengenerators.blogspot.com/2017/10/some-nature-finds.html>). (Photo by James Spencer, kindly provided by Nadia Spencer)

(Hesperiidae) build leaf shelters that are always shared with nesting *Dolichoderus* ants (Igarashi and Fukuda 1997). Chemically protected larvae of Neotropical *Vettius tertianus* (Hesperiidae) are usually found living with predatory ants in ant gardens, although not enough is known of their biology to conclude whether or not they are true myrmecophiles (Orivel and Dejean 2000).

Ants gathering to drink from leaf exudates generated by herbivores are not uncommon, although rarely analyzed, and result in facultative ant interaction with caterpillars of various butterfly and moth species (Fiedler 1991; Larsen 2005). For example, Young (1978) observed ants using their antennae to stroke a larva of the nymphalid butterfly *Mechanitis isthmia* in Costa Rica, whereupon the larva would withdraw from the leaf edge and allow the ants to drink exudates from the newly cut surface. Diverse ants commonly drink from the feeding sites of *Catopsilia* larvae (Pieridae), and some ant species appear to find the caterpillars themselves more attractive than the leaf exudates (Williams 1995-2020, iNaturalist #10726006 iNaturalist #15027508, <http://pureoxygengenerators.blogspot.com/2017/10/some-nature-finds.html>, <https://www.flickr.com/photos/129254524@N06/16162943814/>). Larvae of many Pieridae and Saturniidae produce potent secretions to deter ants, and occasional reports suggest that the secretions themselves are consumed by ants under rare circumstances (Fig. 7) (Fiedler 1991; Hinton 1951; Smedley et al. 2002).

Ant Association in the Lycaenidae and Riodinidae

Throughout Lepidoptera, only the families Lycaenidae and Riodinidae contain ant-associated taxa that number more than a few dozen species. The ability to actively attract ants with food rewards and sophisticated signaling may help account for their surprisingly massive radiation compared with other ant-associated larvae whose interactions are more limited and rarely involve food rewards. Non-trophobiotic myrmecophiles are limited to ant “hotspots,” where enemy-free space is strongest and unique resources are available: either around ant-attended hemipterans, within ant nests, on ant-plants, or within the arboreal territories of highly aggressive ants like *Oecophylla*. Correspondingly, trophobiotic organs in Lycaenidae and Riodinidae that obligately occur around ant-tended hemipterans and ant nests are often lost or modified, most notably in the lycaenid subfamilies Miletinae and Poritiinae and in riodinids like *Aricoris arenarum* (Kaminski et al. 2020b; Shimizu-kaya et al. 2013).

Recent comparative analyses using a well-resolved tribal level phylogeny of butterflies indicate that ant association arose once in the ancestor of the Lycaenidae nearly 80 mya, twice more recently in its sister family, the Riodinidae, once in the subtribe Eurybiina, and once in the Nymphidiini (Espeland et al. 2018). Thus, similar traits used in ant-caterpillar associations appear to have arisen independently at least three times in these two butterfly families.

Adaptations of Adults

Ant-related visual and chemical cues are used during mate finding and oviposition by many ant-associated Lycaenidae and Riodinidae (e.g., Atsatt 1981b; Casacci et al. 2019b; Dejean et al. 2017; DeVries 1997; Elgar and Pierce 1988; Elgar et al. 2016; Fiedler and Maschwitz 1989a; Fiedler and Maschwitz 1989b; Fraser et al. 2002; Kaminski et al. 2013; Heath 1997; Henning 1983; Kaminski and Carvalho-Filho 2012; Martins et al. 2013; Pierce 1984; Pierce and Elgar 1985; Pierce and Nash 1999; van der Poorten and van der Poorten 2016; Pringle et al. 1994; Seufert and Fiedler 1996; Williams 1995-2020), even in species that are facultatively ant-attended (Mota and Oliveira 2016; Wagner and Kurina 1997) or non-trophobiotic (Bächtold et al. 2014; Fiedler and Maschwitz 1989b; Funk 1975; Sáfíán and Collins 2014; Sáfíán and Larsen 2009; Rodrigues et al. 2010). Many obligate ant associates will not oviposit unless ants are present (e.g., Heath 1997). Chemical eavesdropping on ants is widespread among myrmecophiles, and lycaenid adults may detect ant pheromones as well as visual cues (e.g., Adams et al. 2020; Kaliszewska et al. 2015; Sáfíán and Larsen 2009; Williams 1995-2020). Visual and chemical cues are also used by non-myrmecophiles to avoid ovipositing near ant territories (Freitas and Oliveira 1996; Van Mele et al. 2009; Sendoya et al. 2009).

Phengaris (= *Maculinea*) is one of two lycaenid genera with species whose larvae are obligately phyto-predaceous, with eggs laid on specific plant hosts that serve as

food for the early instars and that later drop to the ground to be carried by workers into the ant nest, where they feed on the brood or solicit regurgitations to complete development. Recent research on ovipositing females of *Phengaris* species has started to resolve a longstanding puzzle regarding whether or not these parasitic butterflies use ants as cues to locate oviposition sites (Carleial et al. 2018; Casacci et al. 2019b; Czekes et al. 2014; van Dyck and Regniers 2010; Fürst and Nash 2010; Musche et al. 2006; Patricelli et al. 2011; Thomas and Elmes 2001; Wynhoff et al. 2008; Wynhoff et al. 2015). Apparently *Myrmica* ants nesting at the base of *Origanum vulgare* plants (Lamiaceae) damage the roots and thereby induce the plants to release defense-related volatile organic compounds, or VOCs, including the monoterpeneoid carvacrol and its isomer thymol. Ovipositing females of *Phengaris arion* can detect these compounds and use them to identify plants with appropriate ant hosts located beneath them (Pech et al. 2007; Patricelli et al. 2015). The larvae of other species of *Phengaris* also feed on host plants in the Gentianaceae and Rosaceae (Als et al. 2004), and it seems likely that a similar mechanism exists on other host plants whereby damage to plant roots caused by ant colonies nesting underground may induce the release of VOCs that attract ovipositing females. Cues from a number of different plant families may be used by ovipositing females in this way, but this remains to be tested.

Chemical signals seem to mediate ant interactions with adults of many lycaenid and riodinid butterflies, generally with ants that are also associated with caterpillars (Atsatt 1981a; Farquharson et al. 1922; Fiedler and Maschwitz 1989a; Pierce et al. 2002). These semiochemicals may be particularly important in species that pupate within ant nests (Elfferich 1998; Lohman 2004). Various adult Lycaenidae and Riodinidae are inspected or groomed by ants (DeVries 1984; Fiedler and Maschwitz 1989b; van der Poorten and van der Poorten 2016, iNaturalist #36616206, iNaturalist #5526494, iNaturalist #62627204, iNaturalist #56774612, iNaturalist #66838365). Adults of most Poritiinae and Miletinae (Lycaenidae) feed exclusively from extrafloral nectaries and carbohydrate-rich insect exudates, both frequently attended by workers of the same ant species that are associated with their own larvae (Figs. 8 and 9) (Atsatt 1981a; Callaghan 1992b; Cottrell 1984; Dejean et al. 2017; Farquharson et al. 1922; Fiedler and Maschwitz 1989b). Certain Riodinidae may have similar habits (Torres and Pomerantz 2016).

Adaptations of Caterpillars and Pupae

Before pupation, and in some species whenever not feeding, larvae of diverse Riodinidae (e.g., DeVries 1997; Kaminski and Carvalho-Filho 2012; Kaminski et al. 2020b; Ross 1966) and Lycaenidae enter special shelters built for them by ants (e.g., Eastwood et al. 2005; Eastwood et al. 2008a; Ekka and Rastogi 2019; Webster and Nielsen 1984) or the ants' nests themselves (e.g., Benyamini and Bálint 1995; Bury and Savchuk 2015; Mizuno et al. 2019; Wagner 1995). These cohabitation behaviors appear to co-opt existing ant behaviors widely used to shelter

Fig. 8 *Lachnocnema* butterflies (Lycaenidae: Miletinae) collecting honeydew from ant-attended scale insects in Gorongosa National Park, Mozambique. (Photo by Piotr Naskrecki)



Fig. 9 An adult *Miletus biggsii* (Lycaenidae: Miletinae) perches among aphid-tending dolichoderine ants in Thailand. (Photo by Henrik Petersen. A related *Logania malayica* perches similarly among myrmicine ants in another photo at iNaturalist #50360170)



hemipterans. Many caterpillars in seasonally arid and cold regions enter underground ant nests, likely to escape unfavorable conditions. The need to escape the increasingly dry conditions and the associated risk of fires that occurred during the aridification of Africa in the Miocene may have been an important driver leading to the relatively large number of obligately parasitic relationships found in the dry savanna habitats of southern Africa and Australia. These regions are also hotspots for myrmecochorous plants, those plants with seeds dispersed by ants (Lengyel et al. 2010), possibly for similar reasons, although the phosphorus-poor soils of these regions are also likely to have been important (see discussion below) (Westoby et al. 1982). Larvae of a number of species have been reported to follow ant trail pheromones, but only a few cases of this behavior have been experimentally confirmed (Dejean and Beugnon 1996; Fiedler et al. 1996).

Hinton (1951) noted that ant-attended larvae, even within ant nests, may be attacked if ants are sufficiently alarmed by an intruder. Most lycaenid larvae can

retract their head beneath a sclerotized prothoracic plate and are ventrally flattened, shielding vulnerable body parts (Ballmer and Pratt 1988; Fiedler 1991; Malicky 1969; Malicky 1970; Pierce et al. 2002). Larvae that live in close proximity with ants may have a wrinkled cuticle up to 20 times thicker than that of other Lepidoptera to avoid harm from the occasional bite (Bächtold and Alves-Silva 2013; Fiedler 1991; Gnatzy et al. 2017; Malicky 1969; Malicky 1970). In general, those with facultative associations with ants have thicker cuticles than those with obligate associations, although this depends in part on the mandible size of the ant associates (Dupont 2012). Lycaenid caterpillars also generally lack the thrash reflex to disturbance found in other Lepidoptera, which can elicit enhanced attack from ants (Bächtold and Alves-Silva 2013; Fiedler 1991).

Ant-attended Lycaenidae and Riodinidae possess a variety of multimodal “ant organs” to attract and signal to ants via chemicals or stridulation. Cuticular hydrocarbons and similar substances protect lycaenid larvae from most ant aggression, as described in a later section. In addition, many ant-associated lycaenid and riodinid caterpillars are attractive to ants, which groom and antennate various parts of their bodies. Ants are often drawn to specific parts of lycaenid larvae bearing dense single-celled epidermal glands that Malicky (Malicky 1970) described in English as “perforated cupola organs” (PCOs). Kitching (g 1983) translated Malicky’s original “*porenkuppeln*” (Malicky 1969) as “pore cupola organs” (PCOs), and this term has been adopted generally. PCOs are also found in many pupae (e.g., Duarte et al. 2001; Fiedler 1989b; Fiedler and Seufert 1995; Hinton 1951; Malicky 1970; Pierce and Nash 1999). PCOs or putative homologs have been found in the larvae of all Lycaenidae and Riodinidae that have been examined (Dupont et al. 2016; Fiedler 1991; Mota et al. 2014; Nielsen and Kaminski 2018; Pierce et al. 2002; Santos et al. 2014). As a result, Pierce et al. (2002) suggested that PCOs may represent a key preadaptation for the radiations of myrmecophilous Lycaenidae and Riodinidae. The ant-associated functions of these organs are likely to be convergent given what we now know about the phylogeny of these groups. The function of PCOs in non-myrmecophilous caterpillars has not been carefully explored: PCOs are widespread among caterpillars of non-myrmecophilous Riodinidae as well as the non-myrmecophilous family Hesperidae, where they were originally called “lenticles” (DeVries 1991c; Franzl et al. 1984).

Larval PCOs are often concentrated around spiracles and secretory organs (e.g., Downey and Allyn 1979; Fiedler 1991; Kitching and Luke 1985; Mota et al. 2014; Mota et al. 2020; Pierce and Nash 1999). Many Lycaenidae also have a higher density of PCOs on thoracic segments that are attractive to ants (Pierce and Nash 1999). Comparing related species or different populations of a single species, PCOs may be more numerous or productive in larvae that are more closely ant-associated (e.g., Ballmer and Pratt 1991; Kaminski et al. 2013).

In addition, a large number of wedge-shaped, dendritic, mushroom, and other highly modified setae appear important to ant interactions of various larvae and pupae (DeVries et al. 1986; Downey and Allyn 1979; Duarte et al. 2001; Dupont et al. 2016; Fiedler 1989a; Fiedler 1991; Hall and Harvey 2001; Hall et al. 2004; Kaminski and Carvalho-Filho 2012; Kaminski et al. 2013; Kaminski et al. 2020b;

Fig. 10 *Plebejus idas* larva (Lycaenidae: Polyommataini) in Italy with everted tentacle organs (on left), attended by *Lasius emarginatus* ants. (Photo by Paolo Mazzei)



Pierce et al. 2002). The presence of dendritic setae appears to be strongly correlated with the ants' interest in larvae (Ballmer and Pratt 1991). These specialized setae are generally concentrated near PCOs and other secretory organs and may help disperse secretions to arouse ants (Ballmer and Pratt 1991). Others are mechanoreceptors that respond to attending ants (Tautz and Fiedler 1992).

Tentacle organs (TOs) are paired, typically eversible structures on the eighth abdominal segment of many riodinid and lycaenid larvae that are operated hydrostatically by specialized muscles (Fig. 10) (Basu and Kunte 2020; Gnatzy et al. 2017; Hinton 1951; Vegliante and Hasenfuss 2012). While TOs are potentially part of the lycaenid and riodinid ground-plan, they are absent in the riodinid subfamily Nemeobiinae, the lycaenid subfamilies Poritiinae and Lycaeninae, all of the Miletinae except the genus *Aslauga*, and a few other genera (Campbell and Pierce 2003; Fiedler 1991; Pierce et al. 2002). Their function is usually defensive and often specialized to signal to ants as discussed below.

Vibratory Signaling

Larvae of various Lepidoptera produce vibratory signals to deter predators, defend larval territories, or attract additional larvae (see Yack, Ch. 7) (e.g., Bura et al. 2009; Bura et al. 2011; Dookie et al. 2017; Fletcher et al. 2006; Sanetra and Fiedler 1996; Yack et al. 2001; Yadav et al. 2017). Stridulations are a widespread method for ants to recruit nestmates for foraging or defense and have correspondingly been adapted by some larvae to attract attention (Schönrogge et al. 2017). One of the earliest reports of larval stridulation came from naturalist Charles O. Farquharson, who noted a sensation like an electric shock from touching different lycaenid caterpillars (Farquharson et al. 1922). Substrate-borne acoustic signals produced by numerous lycaenid and riodinid larvae encourage ant attendance and are similar to those made

by attending ants (e.g., Fiedler et al. 1996; Lin et al. 2019; Riva et al. 2017; Schurian and Fiedler 1994; Travassos and Pierce 2000). Larval sounds or sound-producing organs have been observed in all examined ant-attended lycaenid and riodinid larvae and are only known to be absent in some non-myrmecophilous Riodinidae and New World Lycaenidae of the tribe Eumaeini (DeVries 1990; DeVries 1991d). Some non-trophobiotic larvae are able to produce sounds, but all belong to genera that facultatively associate with ants (Elfferich 1998; Pierce et al. 2002; Riva et al. 2017).

The few described sound production mechanisms in lycaenid larvae are all stridulatory (Hill 1993; Schönrogge et al. 2017; Schurian and Fiedler 1994). The stridulatory organ of both the larva and pupa of *Arhopala madytus* is located between the fifth and sixth abdominal segments (Hill 1993), as is the stridulatory organ of most lycaenid pupae (Downey 1966). However, in the pupa, the file (sixth segment) is posterior to the stridulatory plate (fifth segment), whereas in the larva of *A. madytus*, their placements are reversed. The discrete organs giving rise to these substrate-borne vibrations have proved difficult to identify in many species. In the Australian lycaenid, *Jalmenus evagoras*, they seem likely to consist of rings of tiny, serially repeating teeth and scrapers occurring between each pair of larval abdominal segments. When the larva is calling, these areas can be seen to vibrate using high speed video (Pierce et al. 2002; Travassos and Pierce 2000).

Pupae of Lycaenidae and Riodinidae also produce several types of vibrations, including “chirping” noises audible to humans, using plate-and-file stridulatory mechanisms located on membranes between abdominal segments 4 and 7 (Downey and Allyn 1973; Downey and Allyn 1978). In addition, “tooth-cast” systems, in which one opposing structure of the sound-producing organ is an imprint of the other, are found in diverse Lycaenidae (Downey and Allyn 1973), as in pupae of Nymphalidae and Papilionidae (Dolle et al. 2018). Acoustic signals play an important role in ant recruitment and appeasement by myrmecophilous Lycaenidae and Riodinidae but are also widespread in non-myrmecophilous pupae, presumably serving as deimatic displays to startle predators as in other Lepidoptera (Dodd 1916; Dolle et al. 2018; Downey and Allyn 1973; Elfferich 1998; Lin et al. 2019; Pierce et al. 2002; Travassos and Pierce 2000).

Lycaenidae

The Lycaenidae contain over 5000 species in more than 400 genera distributed worldwide (Eliot 1973; Espeland et al. 2018; Pierce et al. 2002). Although different species vary in the relative strength and context of ant association, all lycaenid subfamilies have species that are either ant-attended or form some kind of regular association with ants (Table 2).

Curetinae

The lycaenid subfamily *Curetinae* consists of a single genus (*Curetis*) of 18 species and is distributed from India to the Solomon Islands (Eliot 1990). The genus is significant inasmuch as it is sister to all other Lycaenidae and may illustrate plesiomorphic traits shared with riodinids but lost in other lycaenids (Espeland et al. 2018). *Curetis* larvae can produce loud substrate-borne vibrations (Fiedler et al. 1995). *Curetis* TOs are housed in large, sclerotized cylinders, which evert long filamentous processes when the larva is disturbed, exciting nearby ants (videos at <https://www.youtube.com/watch?v=2AAg26XDtgM>, https://www.youtube.com/watch?v=zhSX_7edW44) (DeVries 1984). Much like those of some non-trophobiotic riodinids described below (Nielsen and Kaminski 2018), *Curetis* TOs evert and appear to emit repulsive chemicals, in response to ants and other attackers including parasitoid flies and wasps (video at https://www.youtube.com/watch?v=LUKxmq3_6MU) (Ballmer 2015; DeVries et al. 1986; Fiedler et al. 1995; de Niceville 1890; van der Poorten and van der Poorten 2016). Ants usually show little interest in *Curetis* larvae but often accompany them to drink from leaf exudates where larvae have been feeding (Fig. 11) (DeVries 1984; Fiedler et al. 1995).

The remaining Lycaenidae form a clade that is ancestrally ant-attended (Espeland et al. 2018). Most species of the subfamilies Aphaeinae, Theclinae, and Polyommatainae have a dorsal nectary organ [DNO], a unique slit-like glandular invagination on the 7th abdominal segment that produces attractive secretions for ants and appears in the 2nd or 3rd instar (Daniels et al. 2005; Fiedler 1991; Hinton 1951; Pierce et al. 2002). A superficially similar abdominal invagination found in *Curetinae* may be a vestigial DNO or perhaps simply a muscle attachment site (DeVries et al. 1986). The DNO contains 2–4 individual glands, which structurally and developmentally resemble modified setae (Hinton 1951; Malicky 1970; Newcomer 1912; Pierce and Nash 1999; Vegliante and Hasenfuss 2012). Muscles around the DNO usually allow it to push upward and extrude liquid droplets or retract and suck back these secretions (video at <https://www.youtube.com/>

Fig. 11 *Curetis thetis* (*Curetinae*) larva with ants in Sri Lanka. (Photo by Nuwan Chathuranga)



[watch?v=fCho3Vrt2bU](#)) (Basu and Kunte 2020; Pierce and Nash 1999). Larvae of many obligately ant-attended species have been reported to die in captivity from mold and/or infection without ants to remove built-up secretions around the opening of the DNO (Cottrell 1984; Hinton 1951; Williams 1995-2020).

Caterpillars of some species have been shown experimentally to deploy their DNO secretions strategically, increasing the rate of droplets provided when they are vulnerable or under perceived attack and decreasing per capita secretions in larger larval aggregations (Agrawal and Fordyce 2000; Axen and Pierce 1998; Axén et al. 1996; Leimar and Axén 1993). Caterpillars may also increase secretion rates when more ants are present; this might allow them to retain a larger retinue of ants (Axén 2000; Fiedler and Hagemann 1992). Curiously, the dorsal nectary organ remains functional in many parasites that enter the ant nest such as *Niphanda fusca* and species of *Phengaris*, suggesting that secretions from the DNO in these species may contain essential substances enabling them to manipulate attendant ants.

The TOs of species in the Aphnaeinae and the Theclinae-Polyommatainae assemblage appear to secrete volatile chemicals that excite ants to defend the larva (Casacci et al. 2019b; Fiedler 1991; Fiedler et al. 1996; Henning 1983; Pierce et al. 2002). Lycaenid TOs are most frequently everted to attract ants when caterpillars are disturbed or are traveling to a new location or when ant-caterpillar interactions first begin (Axén et al. 1996; Fiedler et al. 1996; Fiedler and Hagemann 1992; Leimar and Axén 1993). Secretions from the tentacle organs of lycaenids have been difficult to detect and/or characterize chemically (Gnatzy et al. 2017; Pierce and Nash 1999). The TOs of the Japanese species *Shirozua jonasi* (Theclinae: Theclini) were described to contain dendrolasin (Yamagushi and Shirozu 1988), a compound found in some ant alarm pheromones (Hölldobler and Wilson 1990). Although the chemicals involved are unknown, extracts from the TOs of *Aleiodes dentatis* (Aphnaeinae) were shown to elicit an alarm response from workers of the attendant ant species (Henning 1983). Alarm pheromones are also mimicked by many myrmecophilous rove beetles and wasps (Stoeffler et al. 2007; Thomas et al. 2002).

In terms of delivery, some authors have speculated that the tentacle organs of Lycaenidae might disperse chemical signals that are coated on their long, finely branched apical setae when the tentacle is withdrawn into an evagination formed by the cuticle (Fiedler et al. 1996; Fiedler et al. 1995; Hinton 1951; Kitching and Luke 1985; Pierce and Nash 1999; Sanetra and Fiedler 1996). Additional research is warranted, as Gnatzy et al. (2017) carefully examined the histology of these setae and found no evidence that they were glandular in nature.

The Theclinae-Polyommatainae Assemblage

Theclinae and Polyommatainae are both polyphyletic as traditionally defined but together form a well-supported monophyletic group (Espeland et al. 2018). The Theclinae-Polyommatainae assemblage is widespread, including over 4000 species in nearly 350 genera. Larvae are mostly phytophagous and ant-associated, but

Fig. 12 The larvae of several species of *Hypolycaena* (Theclinae: Hypolycaenini) are attended by *Oecophylla* ants, such as this *H. erylus* in Malaysia being accompanied as it travels. (Photo by Masatoshi Sone)



several lineages are non-mymecophilous (Table 2, Fig. 12, videos at <https://www.youtube.com/watch?v=G5SlcA0WXnk>, <https://www.youtube.com/watch?v=43vmltWoSdo>].

With over 1300 species that typically only form facultative ant associations, the tribe Polyommattini is the largest tribe of Lycaenidae. Only a few obligately ant-associated taxa are known in this tribe outside of the two unique genera, *Lepidochrysops* and *Phengaris* (Polyommattini). Larvae of the some 130 species of Afrotropical *Lepidochrysops* typically feed on flowers until the 3rd instar, when they begin to mimic ant brood and are carried by workers of species of *Camponotus* (subfamily Formicinae) into the nest to feed on brood and/or engage in trophallaxis (Heath and Claassens 2003; Henning 1983).

Like *Lepidochrysops*, the approximately ten species of Palearctic *Phengaris* (= *Maculinea*) are also phyto-predaceous. The larvae of different species of *Phengaris* initially feed on flowers and in the fourth instar are carried by *Myrmica* workers (subfamily Myrmicinae) into the nest, where different larvae, even those derived from eggs laid in the same year, will remain parasitic for either 1 or 2 years (Elmes et al. 2019; Thomas et al. 1998; Witek et al. 2006). Acceptance of *Phengaris* by host ants is mediated by specialized chemical mimicry of ant hosts (Akino et al. 1999; Casacci et al. 2019b; Casacci et al. 2019a; Nash et al. 2008; Schönrogge et al. 2004; Solazzo et al. 2013). Although most *Phengaris* feed directly on ant brood, a group of “cuckoo” species have larvae that specialize on trophallaxis (Als et al. 2004; Thomas and Elmes 1998). Both predatory *Phengaris arion* and cuckoo *Phengaris rebeli* are nest parasites whose larvae have been reported to produce acoustic signals resembling those of their host ant queens and giving them extreme priority in feeding and protection (Barbero et al. 2009a; Barbero et al. 2009b; Barbero et al. 2012; Sala et al. 2014; Thomas et al. 2013). Most *Phengaris* species can parasitize nests of multiple ant species, although local populations are often strongly specialized on different hosts (Pech et al. 2007; Tartally et al. 2019; Ueda et al. 2016; Witek et al. 2011; Witek et al. 2008; Sielezniew et al. 2010; Thomas et al. 2013). *Phengaris arion* has become a classic conservation success story, after recognition of its

obligate relationship with a single ecologically restricted *Myrmica* species in the UK facilitated the reintroduction of the caterpillar species (Thomas et al. 2009).

First-instar larvae of East Asian *Niphanda fusca* (Niphandini) feed on aphid honeydew, but later-instar larvae enter *Camponotus* nests, where they chemically mimic male ants and are fed by workers (Hojo et al. 2014a; Hojo et al. 2009). Larvae of *Phengaris*, *Lepidochrysops*, and *Niphanda fusca* that enter the ant nest in later instars have an unusual growth pattern, growing more than ten times as much once in the ant nest as would be predicted from their earlier stages (Elmes et al. 2001). Two Afrotropical species of *Anthene* (Lycaenesthinae) are parasites in nests of species of *Crematogaster* (Williams 1995–2020). A few related larvae—Tropical Asian *Chilades lajus* (Polyommata) and Afrotropical *Triclema lamias* (Lycaenesthinae)—may prey on aphids and scale insects (Farquharson et al. 1922; Pierce 1995). Many other plant-feeding species supplement their larval diet with hemipteran honeydew under certain conditions (Fig. 13) (e.g., Pierce and Elgar 1985).

Only a few other parasitic species can be found within the remaining tribes that are currently non-monophyletically grouped as Theclinae. All 11 species of the Australian genus *Acrodipsas* (Eastwood and Hughes 2003; Miller and Lane 2004; Sands and Sands 2015) and a few species within the mostly phytophagous and highly ant-associated genera *Ogyris* and *Arhopala* are brood predators in ant nests (Braby 2000; Fiedler 2012; Pierce 1995). Palearctic *Shirozua* larvae mostly feed on hemipterans and their excretions but also sometimes on *Lasius* or *Camponotus* ant trophallaxis (Fiedler 2012; Pierce 1995; Zhou and Zhuang 2018). *Shirozua jonasi* may enter ant nests to pupate, and adults are protected by dense cotton-like hairs (Cottrell 1984).

Although widely distributed, over 90% of the approximately 1096 species in the tribe Eumaeini are found in the Neotropical region, and all are either non-myrmecophilous or facultatively so, usually only sporadically ant-attended. The Old World taxa are clustered in a single clade consisting largely of the species-rich sections *Callophrys*, *Erora*, and *Satyrium*. Their huge radiation appears to be associated with intense sexual selection, as males have a great diversity of secondary sexual traits such as brush organs associated with the genitalia and androconial

Fig. 13 A fourth-instar larva of *Jalmenus daemeli* (Theclinae: Zesiini) feeds on secretions from a margarodid scale, while both are tended by workers of *Iridomyrmex rufoniger*. These Australian caterpillars are usually herbivorous but may facultatively feed on honeydew secretions. (Photo by Naomi Pierce)



Fig. 14 Cycad-feeding *Eumaeus* larvae (Theclinae: Eumaeini), such as these *E. toxea* in Nayarit, Mexico, are toxic and not ant-associated. (Photo by Juan Cruzado Cortés)



wing scent pads and patches that waft pheromones (Valencia-Montoya et al. [In review](#)). Caterpillars of several genera are aposematically colored or bear defensive tubercles and scoli, resembling Limacodidae (Fig. 14) (e.g., Kaminski et al. [2010b](#); Silva et al. [2014](#)). Some respond to disturbance by curling their body or hanging off the substrate on a silk thread, behaviors otherwise unknown in Lycaenidae (Fiedler [1991](#); Silva et al. [2014](#)). The approximately 175 species in the detritivorous Neotropical subtribe Calycopidina have never been reported with ants, but limited evidence suggest that some species might be facultatively ant-associated (Duarte and Robbins [2010](#); Nishida and Robbins [2020](#), supplemental table from Schär et al. [2018](#); Silva et al. [2014](#)).

A number of studies have looked at the developmental effects of ant attendance on caterpillars of the Theclinae-Polyommatainae assemblage. Different attendant ant species differ in their impact on survival and development (Fraser et al. [2001](#); Kaminski and Rodrigues [2011](#); Mizuno et al. [2019](#); Trager and Daniels [2009](#); Saarinen and Daniels [2006](#); Wagner [1993](#)). The costs and benefits of ant attendance are also borne differently by males and females, probably based on differing physiological demands on adults of each sex to ensure reproductive success (Mizuno et al. [2019](#); Pierce et al. [1987](#)). Measured effects of ant attendance on developmental times and adult sizes vary extensively between different species (Baylis and Pierce [1992](#); Cushman et al. [1994](#); Fiedler and Hölldobler [1992](#); Fiedler and Hummel [1995](#); Fiedler and Saam [1994](#); Fraser et al. [2001](#); Kaminski and Rodrigues [2011](#); Mizuno et al. [2019](#); Pierce and Nash [1999](#); Pierce et al. [1987](#); Robbins [1991](#); Saarinen and Daniels [2006](#); Trager et al. [2013](#); Wagner [1993](#)). The methods employed in quite a few of these studies involve placing ants and larvae together in disturbed laboratory environments in order to create an “ant-attended” treatment. Controlled experiments using intact ant colonies containing queens and with naturally foraging workers tending caterpillars feeding on live host plants are difficult to carry out, but they seem likely to yield different results from treatments in which individual workers are simply enclosed with caterpillars feeding on cuttings to simulate natural tending. For example, field versus laboratory experiments found

different effects on developmental times of facultatively ant-associated larvae of *Glaucopsyche lygdamus* (Fraser et al. 2001; Pierce and Eastal 1986).

Leguminous host plant use is broadly correlated with ant attendance within the Theclinae-Polyommatae assemblage (Fiedler 1995; Pellissier et al. 2012a; Pierce 1985). The relationship may not be causal, but protein-rich foods could help caterpillars produce nitrogen-rich secretions for ants. For example, individual larvae of *Jalmenus evagoras* larvae are tended by more ants per capita when they are fed higher-quality host plants that have been treated with nitrogenous fertilizer than when feeding on lower-quality control plants (Baylis and Pierce 1991). Similarly, feeding on flowers may lead to greater larval growth and in some cases has been shown to increase the volume of DNO secretions (Burghardt and Fiedler 1996; Collier 2007; Pierce and Eastal 1986; Wagner and Kurina 1997). The distribution of legumes and their symbiotic bacteria might also exert indirect effects on Lycaenid biogeography (Steidinger et al. 2019). Feeding on Fabaceae appears to be an ancestral state of all phytophagous Lycaenid subfamilies with the exception of the Lycaeninae (Boyle et al. 2015; Espeland et al. 2018; Fiedler 1991). Thus, the correlation between ant attendance and legume feeding might be more appropriately viewed as one where species that switch to less nutritious food sources are unlikely to remain ant-attended (Fiedler 1995).

Lycaeninae

The approximately 110 species of Lycaeninae, which form a sister group to the Theclinae-Polyommatae assemblage, have an unusually wide, disjunct distribution that includes all major zoogeographic regions. All described species of Lycaeninae lack a dorsal nectary organ and tentacle organs, but larvae and pupae possess stridulatory organs and sometimes enter ant nests (Bascombe et al. 1999; DeVries 1991d; Downey and Allyn 1973; Fiedler 1991; Gibbs 1980; Heath and Claassens 2003; Yago et al. 2010). Furthermore, a few species have been reported possibly to rely on ants for oviposition, and these caterpillars may also be somewhat attractive to ants (Ballmer and Pratt 1991; Fiedler 1989a; Funk 1975; Oliver 2007).

Miletinae

The Lycaenid subfamily Miletinae is notably missing from the Neotropics and western Palearctic (and has only one species in the Nearctic). All 190 species in 13 genera are thought to be entomophagous, eating either ants, their regurgitations, or ant-associated hemipterans and their secretions (Fig. 15, video at <https://www.youtube.com/watch?v=ZmCz2UxKaHA>) (Cottrell 1984; Eliot 1986; Kaliszewska et al. 2015; Pierce 1995). Many adult Miletinae have an especially long, sclerotized abdomen and legs, possibly to protect against the occasional ant bite while alighting and/

Fig. 15 This ant-associated *Lachnocnema laches* larva (Miletinae) feeding on treehopper nymphs was reared in South Africa. (Photo by Suncana Bradley)



or ovipositing among hemipteran prey that are being tended by ants (Cottrell 1984; Pierce 1995).

Ants intensively palpate and display interest in the larvae of many Miletinae, but larvae lack dorsal nectary organs, and only species in the Afrotropical genus *Aslauga* possess tentacle organs (Bascombe et al. 1999; Claassens and Heath 1997; Cottrell 1984; Dejean et al. 2017; Lohman and Samarita 2009; Pierce et al. 2002). Most appear obligately ant-associated (Table 2). Larvae of Oriental and Palearctic *Spalgis* and *Taraka* spp. and Nearctic *Feniseca tarquinius* appear facultatively ant-associated and are protected by silk shelters or cuticular hydrocarbons of ant-attended prey (photos at iNaturalist #57006925 and iNaturalist #14834663) (Cottrell 1984; Lohman et al. 2006; Youngsteadt and Devries 2005). Larvae of *F. tarquinius* produce vibratory signals that may be ant-related (Mathew et al. 2008).

Kaliszewska et al. (Kaliszewska et al. 2015) found that the subfamily of hemipteran-attending ant is strongly conserved phylogenetically within Miletinae, whereas hemipteran host preference can be quite broad (Fiedler and Maschwitz 1989b; Lohman and Samarita 2009). For example, lycaenids in the genus *Miletus* appear to associate only with species of ants in the genus *Dolichoderus*, which adults use to find their hemipteran prey. All 27 species in the southern African genus *Thestor* are thought to parasitize ants in the genus *Anoplolepis* (Formicinae), particularly *A. custodiens* (Claassens and Dickson 1980; Clark and Dickson 1971; Pringle et al. 1994). While the larvae of the majority of Miletinae feed on Hemiptera, later instars may occasionally be carried into the ant nest, where they feed on ant regurgitations and sometimes also ant eggs and detritus (Clark and Dickson 1960; Clark and Dickson 1971; Heath and Claassens 2000; Heath and Claassens 2003; Heath and Pringle 2004; Williams and Joannou 1996).

Caterpillars of the sister genera *Liphyra* and *Euliphyra* inhabit the nests of weaver ants in the genus *Oecophylla* (Fig. 16). Oriental *Liphyra brassolis* and *Liphyra grandis* feed voraciously on ant brood and are protected from occasional

Fig. 16 *Liphyra brassolis* larva (Miletinae) displaying its highly sclerotized, tank-like dorsum on the outside of an *Oecophylla* nest in Queensland, Australia. (Photo by Martin Lagerwey)



attack by a thick, bulky “chain link” integument derived from modified setae (Braby 2000; Dupont et al. 2016; Pierce 1995). African species of *Euliphyra* also coax trophallaxis, intercept trophallaxis between workers, and steal brood within *Oecophylla* nests (Dejean et al. 2017; Fiedler 2012). *Liphyra* pupae are entirely enclosed within the hardened exuviae of the last larva instar, or puparium, and *Euliphyra* pupae only partially emerge during larval-pupal ecdysis (Eltringham 1913). *Euliphyra* larvae have been shown experimentally to find *Oecophylla* nests by following ant trail pheromones (Dejean and Beugnon 1996), and *Liphyra* probably do this as well (Common and Waterhouse 1981; Pierce et al. 2002). Larvae of *Liphyra*, along with those of *Thestor*, have short, stubby antennae used to seek and manipulate prey (Dupont et al. 2016). Adult *Liphyra* are protected upon eclosion by a thick vestiture of greasy, loose scales that slip off in the mandibles of vicious attacking ants, similar to several other species that pupate in ant nests (Atsatt 1981a; Cottrell 1984; Dodd 1902; Hinton 1951; Pierce 1995).

The Miletinae likely constitute the largest radiation of entomophagous lepidopterans (Cottrell 1984; Pierce 1995), and ant association may be linked to the success of this dramatic dietary shift. Body plan constraints may limit the success of predatory caterpillars, except around concentrated food resources or in situations where there are few competing predators (Pierce 1995)—ant brood and ant-attended hemipterans meet both of these conditions. The reverse dietary shift in spiders follows the same principle: the only two spider species with known specializations for plant-feeding are found on well-defended ant-plants with few other herbivores (Meehan et al. 2009; Nyffeler et al. 2016; Painting et al. 2017).

Aphnaeinae

The Aphnaeinae, which along with the Poritiinae are sister to the Miletinae (Espeland et al. 2018), are a largely African subfamily that seems to have been ancestrally associated with *Crematogaster* ants and legume feeding (Boyle et al.

Fig. 17 *Cigaritis takanonis* larvae (Aphnaeinae) tended by *Crematogaster* ants in South Korea. (Photo by iNaturalist user clurarit)



2015). All species whose life histories are known appear obligately ant-associated (Fig. 17, Table 2). Moreover, at least one species in each of nine genera is aphytophagous, feeding on hemipterans or the eggs, brood, or regurgitations of ants (Boyle et al. 2015; Pierce 1995; Sanetra and Fiedler 1996). One species, *Aleiodes pallida*, is known to feed in early instars on species of *Aspalathus* (Fabaceae), but Heath and Claassens (Heath and Claassens 2000) were able to rear final-instar caterpillars of this species in observation nests of the formicine ant, *Lepisiota capensis*, where caterpillars selectively ate only the ant eggs and not the brood. Additional evidence suggests that several other species of *Aleiodes* may share this ability to shift from eating plants to eating ant eggs in the final instar. Other species, with exclusively parasitic larval habits, appear in several otherwise phytophagous genera (Basu and Kunte 2020; Fiedler 2012; Heath and Claassens 2003; Pierce 1995). Many Aphnaeinae depend on the presence of a specific species of ant to oviposit (Heath 1997). Dish organs or dew patches are dish-like depressions found on the anterior abdomen in several ant-attended genera of Aphnaeinae that appear to produce reward secretions (Basu and Kunte 2020; Clark and Dickson 1971; Cottrell 1984; Vegliante and Hasenfuss 2012). Several authors note that caterpillars of different species of Aphnaeinae will die if ants are not present to remove secretions from the dew patches and the DNO to prevent them from growing moldy (e.g., Heath 1997; Williams 1995-2020). Tentacle organs of aphnaeine larvae are often housed in protruding cylindrical bases and can be deployed almost like a cat-o'-nine-tails to shoo away overly persistent ants from the DNO (video at <https://www.youtube.com/watch?v=Qkd23Pmucmk>) (Fiedler 1991).

Poritiinae

The Poritiinae are a subfamily of Lycaenid butterflies with non-trophobiotic caterpillars. The approximately 729 species are divided into two clades: the small Asian tribe Poritiini and the large African tribe Liptenini (sometimes split further). Among

these, the Liptenini are notable for their lichenivorous diet, although larvae of *Deloneura* have also been recorded feeding on honeydew near ants (Heath and Claassens 2003; Williams 2006). Larvae of some species feed on lichens growing on bark, rocks, or sticks along the ground and may not be found around ants (Larsen 2005; Williams 2006). While poritiine larvae in the generally open habitats of southern Africa are generally facultatively ant-associated (with the exception of *Deloneura*), most species in the wetter forests of West Africa seem to be obligately ant-associated (Bampton 1995). Adults of many species are only found around individual colonies of arboreal *Crematogaster* ants (Larsen 2005; Sáfián 2015b), and caterpillars of several genera have been reared from ant-infested trees (Callaghan 1992a; Dejean et al. 2017; Jackson 1937; Sáfián 2015a; Sáfián and Collins 2014; Sáfián and Larsen 2009). Over 50% of Poritiinae belong to genera that appear to contain obligate ant associates (Table 2). Obligately ant-associated poritiines tend to be rare, and some species have only ever been found in association with a single arboreal ant colony, raising considerable conservation concern (Larsen 2005; Williams 1995-2020). The lack of obligate ant association in some genera of Poritiinae is perhaps a secondary loss—except for the Poritiini that remain understudied, all major lineages of Poritiinae include species apparently only found on trees along with their associated ant species. Together, the subfamilies Miletinae, Aphnaeinae, and Poritiinae probably constitute the largest single radiation of obligately ant-associated Lepidoptera.

All caterpillars of Poritiinae are covered in long bristles that appear to repel ants (Callaghan 1992b; Dejean et al. 2017). They are probably also chemically defended, as larvae of many species interact with ants with no sign of overt conflict (Farquharson et al. 1922; Sáfián and Collins 2014; Sáfián and Larsen 2009). Ants are repelled from many liptenine caterpillars, perhaps because they secrete toxic chemicals. Some species form large larval aggregations, and others appear to be aposematic (Sáfián 2015a; Sáfián and Larsen 2009). Tussock moth caterpillars (Erebidae: Lymantriinae) protected by defensive glands are sometimes found near poritiine caterpillars in Africa and may similarly be associated with arboreal ant colonies (Farquharson et al. 1922; Hinton 1951). These lymantriine and poritiine caterpillars are visually similar and possibly form a Müllerian mimicry complex (Farquharson et al. 1922).

Riodinidae

Riodinidae are sister to Lycaenidae, and while the 153 genera of Riodinidae are distributed worldwide, more than 1400 species are found in Central and South America. The *ca.* 120 Old World species are concentrated in Southeast Asia (Espeland et al. 2015; Seraphim et al. 2018). Most Riodinidae are not known to be ant-associated and possess long setae and chemical defenses that prevent ants from getting too close (e.g., Ballmer and Pratt 1988; DeVries 1988a; Fiedler 1991; Kaminski 2008a; Mota et al. 2014; Nishida 2010; Vélez-Arango et al. 2010). Larval

Fig. 18 Aposematic *Emesis aurinna* larva (Riodiniinae: Emesidini) in Costa Rica. (Photo by Karl Kroeker)



aggregation and aposematism are also widespread among riodinids (Fig. 18) (Allen 2010; Callaghan 1986; Janzen and Hallwachs 2021; Nishida 2010). Recorded ant associations are limited to the tribe Nymphidiini and subtribe Eurybiina of the tribe Eurybiini, both of which are in the strictly Neotropical subfamily Riodiniinae (Espeland et al. 2015). Almost a thousand riodinid species belong to genera that are non-trophobiotic and generally not known to be ant-associated (Table 2).

Eurybiini

In ant-attended larvae of the subtribe Eurybiina of the riodinid tribe Eurybiini, modified TOs, called tentacle nectary organs (TNOs), evert to release a drop of fluid that ants eagerly drink (Horvitz et al. 1987). However, larvae of the subtribe Mesosemiina, sister to the subtribe Eurybiina (Espeland et al. 2018; Seraphim et al. 2018), have never been found with ants, and their TOs are protected by defensive bristles (Nielsen and Kaminski 2018; Vélez-Arango et al. 2010). Nielsen and Kaminski (2018) found that TOs of these larvae evert and extrude a droplet of liquid when attacked by various predators including wasps, biting midges, and lacewing larvae. Ants that came into contact with this liquid cleaned themselves and shunned the larva (Nielsen and Kaminski 2018). Larvae of Symmachiini (Riodiniinae), which are not ant-associated, also possess tentacle organ openings that may prove to have a similar function (Seraphim et al. 2018).

Nymphidiini

In the riodinid tribe Nymphidiini, all known larvae are ant-associated and typically secrete liquid droplets from glandular tissue within the tentacle organs for ants to imbibe (Fig. 19) (Callaghan 1986; DeVries 1988b; DeVries 1997; DeVries and

Fig. 19 Ant-attended *Synargis calyce* larva (Nymphidiini) in Brazil. (Photo by Kel Silva)



Penz 2000; Hall and Harvey 2001; Kaminski 2008b; Kaminski and Carvalho-Filho 2012; Kaminski et al. 2016; Kaminski et al. 2013; Mota et al. 2020; Ross 1964; Torres and Pomerantz 2016). The TNOs may be everted most often when the larva is vulnerable or attending ants have only started to arrive (DeVries 1988b).

In a handful of related Nymphidiini, a pair of metathoracic anterior tentacle organs (ATOs) induce alarm in attending ants, sensitizing them to future threats much like the TOs of Lycaenidae (DeVries 1988b, 1997; Kaminski and Carvalho-Filho 2012; Kaminski et al. 2016; Penz and DeVries 2006). Brush-like setae at the apex of the ATOs likely help disperse volatile chemicals (DeVries 1997; Ross 1964). DeVries (1988b) found that the ATOs are important for these larvae to maintain the attention of attending ants and activate most often when the larva is initiating contact or vulnerable. Some phylogenetically earlier-branching Nymphidiini have thoracic PCO clusters that appear homologous in position to the anterior tentacle organs and similarly excite ants (Kaminski et al. 2013).

Balloon setae, swollen structures on the prothorax, may play a role in myrmecophilous interactions in some Nymphidiini that lack ATOs (Kaminski 2008a; Penz and DeVries 2006). However, balloon setae appear to serve a largely defensive function and are shared by many non-myrmecophilous caterpillars (Fig. 20) (Hall et al. 2004; Kaminski et al. 2013; Mota et al. 2014). While *Zabuella paucipuncta* (Nymphidiini) lacks ATOs, a unique cervical gland that is exposed when ants antennate the balloon setae causes the ants to react in alarm (DeVries et al. 2004).

Adaptations for ant attendance have largely been lost in the riordinid genus *Stalachtis* (Nymphidiini), but caterpillars remain facultatively ant-associated, and their cuticle appears attractive to diverse ants, much as in some non-trophobiotic lycaenids (Espeland et al. 2015; Seraphim et al. 2018, <https://www.flickr.com/photos/142712970@N03/33322969114>, <https://www.flickr.com/photos/142712970@N03/40459961724>, <https://www.flickr.com/photos/142712970@N03/38713147222/>, <https://www.flickr.com/photos/142712970@N03/27298752638/>, <https://www.flickr.com/photos/142712970@N03/34660951953/>, <https://www.flickr.com/photos/142712970@N03/48374845847/>).

Fig. 20 Non-myrmecophilous *Caria ino* larva (Riodininae: Riodinini) in Texas, displaying orange balloon setae. (Photo by Joseph Connors IV)



Vibratory signals in ant-attended riodinid larvae are produced through several different mechanisms. Larvae of ant-attended Eurybiini produce sound by rubbing small teeth on the cervical membrane against granulations on the head (DeVries and Penz 2000; Travassos et al. 2008). Larvae of ant-attended Nymphidiini produce sounds using vibratory papillae, small rodlike structures on the prothorax that rub against granulations on the head. Larvae can adjust the beat frequency of the vibratory papillae, with higher rates attracting more ants. Vibratory papillae of *Thisbe irenea* beat fastest when the larva is stressed, traveling, or during initial contact with ants (DeVries 1988b).

Riodinidae in several genera have independently evolved hemipteran diets (DeVries 1997; Mota et al. 2020). Many species in both Eurybiini and Nymphidiini cohabit with ants, including a single species, *Aricoris arenarum*, in which the first two instars steal honeydew from ant-attended hemipterans and solicit trophallaxis, and later instars feed by trophallaxis within *Camponotus* nests (DeVries 1997; Kaminski et al. 2020b; Robbins et al. 1996). Another riodinid caterpillar was recently found preying on ant brood in arboreal nests of *Neoponera villosa* (Rocha et al. 2020). As in the Lycaenidae, adults of aphytophagous Riodinidae frequently have greasy wings that may help them to escape ants (DeVries 1997; Espeland et al. 2015; Hall and Harvey 2002), and the greasiness of wings has been used to successfully predict larval diet in at least one instance (Hall 2007; Mota et al. 2020). The TNOs no longer secrete rewards in ant-associated hemipterophagous riodinids, but still signal to ants (Kaminski et al. 2020b; Mota et al. 2020), much as nectary organs have been lost in the predatory lycaenid subfamily Miletinae. The predatory larvae of Neotropical *Pachythone* spp. (Mota et al. 2020) are also remarkably convergent in appearance and adaptive morphology to the ecologically similar larvae of Afrotropical *Aslauga* spp. (Lycaenidae: Miletinae) (Dejean et al. 2017).

Mutualism and Manipulation: Caterpillar-Ant Trophobiosis in Lycaenidae and Riodinidae

All ant species known to tend trophobiotic caterpillars are agricultural in the sense that they also harvest plant extrafloral nectar and the honeydew produced by Hemiptera (DeVries 1991b; Eastwood and Fraser 1999; Fiedler 2001, 2006; Pierce and Elgar 1985). They include genera such as *Iridomyrmex*, *Oecophylla*, *Camponotus*, and *Crematogaster* that are among the most dominant ants in the regions where they occur, with wide distributions and large colony sizes that are often polydomous in structure. Caterpillars may take advantage of ant preadaptations to harvest carbohydrate rewards, which are essential resources for ants in many environments (Blüthgen and Fiedler 2002, 2004; Blüthgen et al. 2003; Davidson et al. 2003; Dejean et al. 2007; Grover et al. 2007; Kaspari et al. 2020; Kaspari et al. 2012; Pohl et al. 2016; Ribas and Schoereder 2004). Although biochemically modified to attract ants in many species, hemipteran honeydew is an excrement, produced whether attendant ants are present to collect it or not (Stadler and Dixon 2005). *Semutophila saccharopa* (Tortricidae) are the only caterpillars that produce sugar-rich excrement for ants in a manner similar to aphids. In contrast, lycaenid and riodinid larvae produce secretions tailored specifically for their ant associates and released from specialized exocrine glands. This distinction is an important one because exocrine glands provide opportunities for lycaenids and riodinids to fine-tune their secretions to manipulate ant behavior, without necessarily providing nutritious rewards.

Ants, although they confer substantial overall benefit to aphid populations, sometimes consume honeydew-producing hemipteran mutualists, particularly when alternative carbohydrate sources are available (Offenberg 2001; Shibao et al. 2009; Silveira et al. 2010; Stadler and Dixon 2005). In contrast, ants have been rarely reported to attack lycaenid larvae except under unnatural circumstances in captivity. Ants suffer a serious opportunity cost when they invest in protecting caterpillars rather than preying on them, especially facultatively ant-attended lycaenids whose secretions may provide poor-quality rewards. The striking absence of overt ant predation also suggests that lycaenid caterpillars must be able to manipulate ants, at least sufficiently to avoid aggression (Fiedler 1998a; Fiedler et al. 1996).

A number of lycaenid larvae mimic the cuticular hydrocarbon (CHC) profiles of host plants or ants or conceal themselves entirely by lacking recognizable molecules (Barbero 2016; Inui et al. 2015; Lima et al. 2020; Lohman 2004; Morozumi et al. 2019), much as reported for different honeydew-producing hemipterans (Endo and Itino 2013; Silveira et al. 2010). This “cloak of invisibility” can ensure that a caterpillar is not attacked by the ants, even if it is not actively tended. CHC mimicry of ants plays an intimate role in the adoption of parasitic species like *Phengaris* by host ants, as reviewed by Barbero (2016) and Casacci et al. (2019b). Chemical disguise may be observed in other groups when more lycaenid species are studied, but it is clearly not universal (Hojo et al. 2014a; Omura et al. 2009). Other mechanisms might also exist to avoid ant predation. Pupae of facultatively ant-attended *Lycaeides*

argyrognomon, which sometimes cohabit with *Camponotus* or *Formica* host ants, have been found to subdue ant aggression through the presence in their cuticle of several long-chained aldehydes not seen in larvae (Mizuno et al. 2018).

DNO and TNO secretions contain amino acids and carbohydrates and have been studied in about ten species (Cushman et al. 1994; Daniels et al. 2005; DeVries 1988b; Pierce and Nash 1999; Pierce et al. 2002; Wada et al. 2001). Secretions of obligate or steadily ant-attended larvae have a higher nutritive content than those of less myrmecophilous species (Daniels et al. 2005).

Aphid mimicry may be one way that facultatively attended larvae attract ants. Melezitose is an aphid gut compound that serves as an attractant for aphid-attending ant workers and is a major component of the nectary secretions in *Polyommatus icarus* and *Zizeeria knysna* [Polyommataini], one of the few well-studied species whose caterpillars are weakly attended (Daniels et al. 2005; Depa et al. 2020; Detrain et al. 2010; Vantaux et al. 2011).

Hojo et al. (2015) determined that the facultatively ant-attended Japanese lycaenid *Arhopala* (= *Narathura*) *japonica* produces DNO secretions that manipulate the dopaminergic pathway in the brains of their attendant ants, workers of *Pristomyrmex punctatus*. Reduced levels of dopamine are correlated with a reduction in worker activity levels (thereby increasing their fidelity to the caterpillar) and heightening aggression toward intruders. Specialized cuticular hydrocarbons (CHCs) of *A. japonica* act as a signal to host ants that they learn to associate with reward after attending larvae (Hojo et al. 2014a).

The parasitic species *Niphanda fusca* has larvae that secrete primarily only trehalose and glycine for host *Camponotus japonicus* ants (Hojo et al. 2008; Wada et al. 2001). Glycine alone is ignored by ants at low concentrations but acts as a manipulative “umami” taste enhancer substance when added to trehalose, increasing host ant interest in this specific sugar (Hojo et al. 2008; Wada et al. 2001). The relative simplicity of this “umami” mechanism for taste enhancement (i.e., the coupling of an amino acid or small peptide with a sugar reward) makes it an attractive candidate for further research into how and why lycaenid caterpillars can be so extremely attractive to their associated ants. However, these same taste preferences are not shared by the closely related *Camponotus obscuripes*, indicating that lycaenid secretion components may be specialized to individual ant species (Hojo et al. 2008).

By comparing the foraging behavior of colonies of the attendant ant species, *Iridomyrmex mayri*, fed on high-protein, high-carbohydrate, or mixed diets, Pohl et al. (2016) showed experimentally that the nutritional state of the attendant ant colony influenced the number of attendant workers foraging on larval secretions from the Australian lycaenid, *Jalmenus evagoras* (Fig. 21). Workers from colonies fed on either carbohydrate- or protein-restricted diets were inconsistent in their compensatory behavior. Those on low-carbohydrate diets compensated by foraging more on sugars, but those on low-protein diets did not show compensatory behavior by foraging more on amino acids. However, workers from colonies that were diet restricted were significantly more interested in foraging on secretions from the larvae than those from well-fed colonies. Workers were not strongly attracted to the

Fig. 21 *Jalmenus evagoras* larval aggregation (Theclinae: Zesiini) in Victoria, Australia. (Photo by Ron I. Greer)



amino acid serine, which had been thought to be the primary amino acid in *Jalmenus evagoras* larval secretions (Pierce 1984) nor did they show an “umami” response when serine was coupled with sugar. More recent analysis suggests that glutamine rather than serine is the primary amino acid in *J. evagoras* larval secretions (Zemeitat 2017), and further work will be necessary to explore the relationship between larval secretions and ant attendance. The chemical composition of liquid secretions produced by different species of ant-attended larvae varies depending on the species and seems likely to be shaped at least in part by the feeding preferences of the ants that attend each caterpillar species (Daniels et al. 2005; Pierce 1984).

Certain obligate lycaenid-ant associations may provide sufficient fitness benefits to both partners under some conditions to warrant being classified as mutualists (Cushman et al. 1994; Fiedler and Maschwitz 1988; Fiedler et al. 1996). For example, caterpillar secretions from the Australian *Jalmenus evagoras* confer a net benefit in terms of positive growth rates (potentially resulting in a greater production of alates) for colonies of its most common ant associate, *Iridomyrmex mayri* (Pierce et al. 1987).

However, even associations with larvae of *Jalmenus evagoras* may sometimes be detrimental to ants. Under experimental conditions, small ant colonies grew faster when allowed to collect secretions from *Jalmenus evagoras* larvae, but colonies provided with only one larva grew significantly faster than colonies given access to five larvae, although this may have been because larvae were allowed to aggregate on the host plants (Nash 1990; Pierce and Nash 1999). Subsequent experiments showed that once small groups of workers and brood passed below a minimum ratio of workers to brood, workers would consistently chose to tend *J. evagoras* larvae and neglect their own brood, allowing them to perish (Merrill 1997; Pierce and Nash 1999). As has been demonstrated for symbioses more generally, whether the relationship is mutualistic or parasitic varies spatially and temporally and is influenced by a number of factors (Madeiros et al. 2018; Thompson 2005; Warren et al. 2019). In the case of caterpillar-ant interactions, this context dependency can include the size of the ant colony, the availability of alternative resources, the number of caterpillars, and the relative cost of their defense.

In certain contexts, manipulation can stabilize mutualisms (Heil et al. 2014; Sachs 2006). However, the manipulation and asymmetry seen in typical lycaenid-ant associations suggest that despite their superficial similarity to honeydew-secreting insects such as aphids, the majority of phytophagous lycaenids might best be viewed as only rarely mutualistically associated with ants and more often mildly parasitic upon them. This association could also help to explain why lycaenids are unusually prone to shifts to overt parasitism and obligate aphytophagy (Sachs and Simms 2006). A number of different ant species are obligately dependent upon associated plants, fungi, and even hemipterans, but it is perhaps significant that none are known to be obligately associated with caterpillars (Chomicki and Renner 2015; Eastwood and Fraser 1999; Ivens 2015).

Because many non-trophobiotic and trophobiotic caterpillars associate with the same species of ants, the primary advantage for trophobiotic caterpillars seems to be that they can attract ants with additional food rewards, not simply that they are able to appease them. There are many reasons why myrmecophilous lycaenids may utilize ants for defense rather than relying on toxic secondary compounds or other means of caterpillar protection. Different circumstances in combination with factors such as larval size or feeding activity can influence predation risk for non-myrmecophilous caterpillars (Berger et al. 2006; Bernays 1997; Dmitriew 2011; Gotthard 2000; Mänd et al. 2007). Selection will favor conditional ant association for protection if maintaining an ant guard is both possible and metabolically less expensive than other means of defense (see discussion below) (Mizuno et al. 2019; Wagner 1993). Different attending ant species can confer significantly different levels of protection (Fraser et al. 2001), but predation or parasitism rates are typically many-fold higher in the absence of ants, both for facultative and obligate ant associates (Atsatt 1981a; Forister et al. 2017; Kaminski et al. 2010a; Rodrigues et al. 2010; Peterson 1993; Pierce and Eastal 1986; Pierce and Mead 1981; Thomas et al. 2020; Weeks 2003). For example, the obligately ant-associated juveniles of the Australian lycaenid, *Jalmenus evagoras*, suffered nearly 100% mortality from parasites and predators when ants were experimentally removed (Pierce et al. 1987), and even the facultatively attended larvae of the North American lycaenid, *Glaucopsyche lygdamus*, were shown experimentally in one field season to suffer up to a 12-fold difference in mortality without ants (Pierce and Eastal 1986).

Highly specialized parasitoids and predators may seek out myrmecophilous caterpillars by using chemical or vibrational cues from their associated ants to locate their prey (e.g., Dejean et al. 2016; DeVries 1991b; Elgar et al. 2016; Fiedler et al. 1992; Pierce and Nash 1999; Thomas and Elmes 1993; Thomas et al. 2002). In situations like this where specialized enemies use attendant ants to find their prey, selection might favor the loss of ant association. Ant associations in plants and insects are prone to frequent loss or modification, and Lepidoptera are no exception (Chomicki and Renner 2015; Sachs and Simms 2006; Stadler and Dixon 2005; Weber and Keeler 2013; Yao 2014). For example, several Australian species in the obligately ant-associated lycaenid genus *Hypochrysops* have likely either lost ant association (*Hypochrysops byzos*, *H. pythias*) or become facultatively associated with them (*H. polycletus*) (Braby 2000). In another Australian genus, *Ogyris*, while most

species have caterpillars that are never found without ants, often with only a single genus or species, the clade containing *Ogyris amaryllis*, *O. oroetes*, *O. olane*, and *O. barnardi* has lost or greatly reduced facultative ant associations (Eastwood and Fraser 1999; Schmidt and Rice 2002). The *Taraka-Spalgis-Feniseca* clade (Lycaenidae: Miletinae) and several genus-groups of Poritiinae represent other cases where phylogenetic studies will probably reveal extensive secondary loss of obligate ant associations. Ant associations appear lost most frequently in facultatively ant-associated groups of the Theclinae-Polyommatainae assemblage, a pattern also observed in facultative associations more generally (Chomicki et al. 2020).

Like many classic symbioses, ant-caterpillar associations typically have additional hidden partners. Hemipteran-ant mutualisms often benefit host plants (Campbell et al. 2013; Pringle et al. 2011; Styrsky and Eubanks 2007), and host plants may similarly benefit when lycaenid and riordinid caterpillars attract ants that drive away other herbivores and deposit nutrients, as recently documented for *Euchrysops cnejus* caterpillars attended by *Camponotus* ants on *Vigna* plants in India (Ekka et al. 2020).

Abiotic Effects, Obligate Associations, and Biogeography

One of the more significant insights gained in recent years from a worldwide consideration of the drivers of interspecies symbiosis (e.g., Kaspari 2020; Steidinger et al. 2019) is the importance of abiotic factors in determining the distribution of species interactions such as those seen between caterpillars and ants. Pierce (1987) pointed out a striking pattern in the biogeographic distribution of lycaenid-ant interactions: obligate interactions are considerably more common in the Southern Hemisphere, particularly Australia and Southern Africa, compared to those in the Northern Hemisphere, including the Nearctic and Palearctic. These patterns appear to extend into wet tropical Africa and Southeast Asia, where life histories of Lycaenidae are comparatively less well-documented. All but one tribe of lycaenids has representatives in both hemispheres, and thus this pattern cannot be explained by a single vicariance event involving ant-associated and non-associated lineages. Rather, it is due to a heterogeneous distribution of tribes with different levels of ant association, with Poritiinae, Aphnaeinae, Miletinae, and strongly ant-associated genera of Theclinae-Polyommatainae generally limited to the Afrotropical, Oriental, and Australasian regions. In the same way, ant-associated Riordinidae and other Lepidoptera are almost entirely limited to the Neotropical, Afrotropical, Oriental, and Australasian regions (Table 1).

Two nonexclusive explanations for this pattern include (1) climate differences and (2) bottom-up effects of soil micronutrients and precipitation that affect plants, microbes, and species that interact with them (e.g., Steidinger et al. 2019). For example, the phosphorus-poor soils of southern Africa and Australia have been evoked as potentially playing a role in the high percentage of ant-dispersed myrmecochorous plants in these areas (Westoby et al. 1982). Research has accumulated

over the past 25 years in what Kaspari has called “ionic ecology” (Kaspari 2020), demonstrating the importance of the stoichiometry of essential elements like Na, P, Cl, K, Mg, and Ca that flux across membranes of organisms at different trophic levels.

Functional mechanisms involving different species are complex and undoubtedly vary depending upon the circumstances, but numerous experiments at a variety of spatial scales focusing on invertebrates ranging from termites (with a rich gut microbiome) to caterpillars (largely devoid of a gut microbiome) have shown that levels of accessible environmental sodium either from direct access through soil or “mud puddles” or indirectly through plant tissues consumed by herbivores can have an enormous effect not only on the abundance and distribution of invertebrates but also on the entire network of parasites and predators interacting with them (Baker et al. 2020; Kaspari 2020). The significance of these results in considering caterpillar-ant interactions seems especially clear given the trophobiotic nature of most of their associations. Coping mechanisms are required in habitats with soils that are poor in phosphorus: an essential, rare, and limited nutrient needed for ribosomes, ATP, and nucleic acids. For insects with gut microbiota, movement into the cell can be facilitated by bacteria with surface proteins that can cotransport Na-P across membranes (Werner and Kinne 2001). This means that sodium can be at a premium for organisms with microbial associations like ants because of its role in facilitating cotransport of phosphates into cells of their symbionts (Kaspari 2020). A growing body of research has shown that the availability of sodium and phosphorus can place constraints on ant growth (Bujan et al. 2016; Goitía and Jaffé 2009; Kaspari et al. 2008, 2009, 2020). Any mechanism that could enhance sodium acquisition and/or facilitate sodium ion transport might be especially favored in regions where soils have low phosphorus or sodium.

For plants, this could be achieved through extrafloral or floral nectars or through seeds with attractive eliasomes. For caterpillars, this could perhaps be achieved with secretions and could explain the appearance of obligate, intense ant associations in arid habitats with low phosphorus soils such as those found in central Australia and Southern Africa. The same ability to attract and manipulate ant partners would not exist in habitats with well-fertilized soils because ants might not be limited by essential micronutrients in the same way. This difference in soil fertility could also help to explain in part why ant plants are restricted to the tropics. For example, although the genus *Macaranga* is widely distributed in the Old World tropics, the clade containing ant plants occurs in West Melanesian rainforest, a region also characterized by phosphorus-poor soils (Davies et al. 2001). Similarly, natural variation as well as experimental manipulations in nutrient exposure of obligately associated ant plants ranging from *Cordia* and *Cecropia* in the Neotropics to *Macaranga* and *Vachellia* in the Old World tropics have resulted in differences in plant growth rates and turnover of ant inhabitants (Folgarait and Davidson 1995; Heil et al. 2001; Pringle et al. 2013).

Aridification has played an additional role in affecting ant associations, both by driving caterpillars to seek shelter and possibly food in ant nests (Espeland et al. [in review](#)) and by generating extremes in the distribution of soil micronutrients over a

large spatial scale (Bui et al. 2014). It seems no coincidence that relatively high levels of ant association are observed in caterpillar-ant interactions in Australia, Southern Africa, and the Cerrado of Brazil.

Finally, differences in soil composition across large spatial scales may have also played a more important role in shaping ant association across landscapes of the Southern Hemisphere including Australia and Southern Africa because weathering and erosion processes have taken place in the absence of the kind of severe, cyclical history of glaciation observed in the Northern Hemisphere (Hopper 2009). This explanation has the advantage of accounting for different levels of obligate association in similar temperate climates of the Western Palearctic (Fiedler 1998b) versus in Australia (Pierce 1987).

Experimental evidence suggests that seasonal temperature fluctuations can break up established partnerships by disrupting ant ecological partitioning. Ant territorialism on caterpillar host plants seems to facilitate obligate ant-caterpillar association, as exemplified by species of aggressive, tropical, arboreal *Oecophylla* and *Crematogaster* found with diverse specialized Lepidoptera. Ecologically dominant ant species typically have the most abundant and aggressive workers, and their large colonies create stable, high-quality habitats for myrmecophiles (Eastwood and Fraser 1999; Fiedler 1991; Fiedler 2001; Fiedler 2006; Hölldobler and Wilson 1990). The combined suitability of a host plant to feed on and enemy free space afforded by the ability to appease otherwise threatening ants can create “ecological islands” of opportunity for obligately specialized myrmecophilous Lepidoptera, and this can have strong effects on their subsequent diversity through restriction of population size and/or structuring of populations (Eastwood et al. 2006; Pellissier et al. 2012; Pierce et al. 2002; Schär et al. 2018). This helps explain why New World *Eciton* and Old World *Dorylus* army ant species, although the former have the most diverse myrmecophile communities known, do not have caterpillar associates—their lepidopteran interactions are restricted to a few species of Papilionidae, HesperIIDae, and Nymphalidae whose adults use ant columns to find nitrogen-rich bird droppings (Ivens et al. 2016; Kistner 1982; Rettenmeyer et al. 2011). The foraging strategies of army ants afford little opportunity for caterpillars, which are relatively sedentary and typically herbivores, to form stable associations (Pierce 1995; Powell et al. 1998). Ant partners in temperate regions might also be less desirable due to the various documented effects of climate on colony traits and community structure (Dunn et al. 2010; Dunn et al. 2009; Kaspari and Vargo 1995; Kaspari et al. 2000).

Besides making suitable ant partners difficult to find, climate fluctuations in temperate areas might increase caterpillar developmental times and reduce access to nutritious host plants (Fiedler 2006; Pellissier et al. 2012a). These hypotheses are supported by the observation that obligate ant associates in temperate areas generally spend most of their life cycle within ant nests, where nutritious food sources, favorable microclimates, and attendant ants are always available (Fiedler 2006). Caterpillar life histories are generally more specialized and diverse in the tropics (Dyer et al. 2007; Forister et al. 2015). Further studies are needed to elucidate the underlying ecological causes.

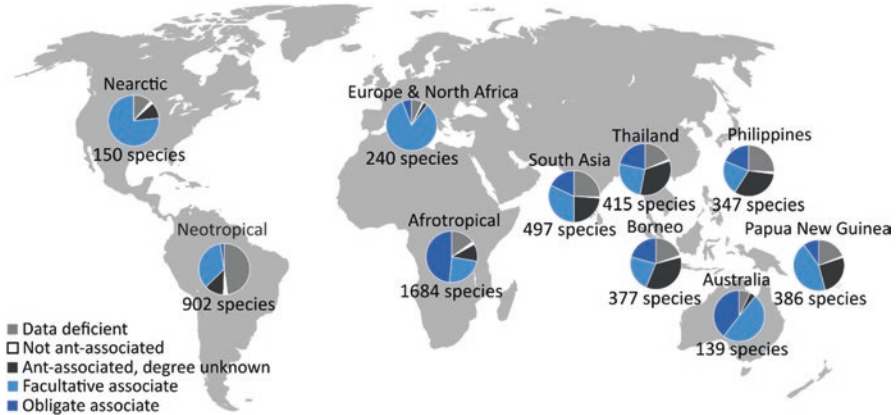


Fig. 22 Geographical distribution of ant associations in Lycaenidae. Known and inferred lycaenid life histories reported in Table 2, or the lack thereof, were cross-referenced with regional catalogs in (Braby 2000; Ek-Amnuay 2012; van Gasse 2013; Hardy and Lawrence 2017; Lamas et al. 2004; Opler 1992, 1999; Parsons 1999; Seki et al. 1991; Tshikolovets 2011; Williams 1995-2020). Facultative associates are often more widely distributed than obligate associates, and they may comprise an increasingly large fraction of total species when looking at small, disturbed, or isolated regions

Whether based on climate, soils, the availability of required ants, or other factors, only non-myrmecophilous or flexible, facultative ant associates in the families Lycaenidae and Riodinidae are found extensively beyond the Old World and New World southern zoogeographic regions (Fig. 22). The Lycaenidae are thought to have originated in the Old World tropics, where extant phylogenetic diversity remains heavily concentrated (Espeland et al. 2018). Only five lycaenid groups occur substantially beyond the Old World tropics and subtropics into the Palearctic, and all five have also entered the New World through Beringia or across the Atlantic (Fric et al. 2019; Gompert et al. 2008; Vila et al. 2011): the *Spalgis-Taraka-Feniseca* clade [Miletinae], the subfamily Lycaeninae, and the tribes Theclini, Eumaeini, and Polyommataini of the Theclinae-Polyommatainae assemblage. Except for a handful of obligately associated species of Polyommataini found within otherwise facultatively associated genus groups, species in these groups are all largely facultatively ant-associated or not ant-associated (Table 2, Fig. 23). The Riodinidae have diversified primarily in the Neotropics. A single lineage within the subfamily Nemeobiinae has colonized the Old World, most likely via Beringia, with a secondary return to the Neotropics of the genera *Styx* and *Corrachia* (Espeland et al. 2015). None of the over 300 species in this subfamily are known to be ant-associated (Table 2). It is tempting to conclude that strongly ant-associated butterflies have been unable to disperse between the Old World and the New World due to the challenge of finding suitable ant partners, especially when confronted with climatic conditions found in temperate regions.

Obligately myrmecophiles' double reliance on associated ants and food sources may make them especially sensitive to disturbance and vulnerable to extinction

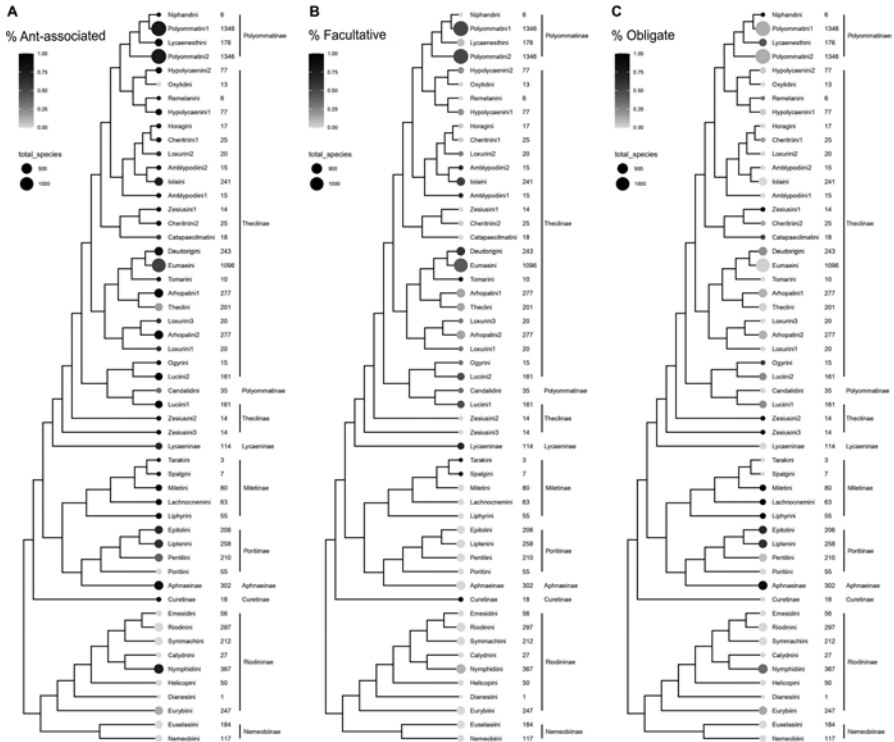


Fig. 23 Phylogenetic tree of extant Lycaenidae and Riodinidae based on data from Espeland et al. (Espeland et al. 2018), showing (a) distribution of species with larval ant association overall, (b) distribution of facultative larval ant associations, and (c) distribution of obligate larval ant associations (from data summarized in Table 2). The size of each circle is proportional to the number of species represented. Percentages correspond to the number of records known or inferred from congeners divided by the total number of species, with groups where life history information such as degree of obligacy is unavailable scored as 0%. Tribes that were rendered non-monophyletic appear multiple times in the tree (e.g., the Polyommataini). We have illustrated the same species counts and ant association proportions next to each appearance as current phylogenies do not allow us to break down these data further. (Figure prepared by João Tonini)

(Chomicki et al. 2020; Geyle et al. 2021; Koh et al. 2004; Pierce 1995; Pierce et al. 2002). Invasive ant species, habitat disturbance and destruction, and climate change are particular concerns (e.g., Braby et al. 2021; Geyle et al. 2021). Over 60% of the threatened Lycaenidae and Riodinidae on the IUCN Red List are recorded as obligate ant associates or predicted to be obligate ant associates based on congeners (Table 2) (IUCN 2020). Among the obligately ant-associated species, those that are “aphytophagous,” having at least one life stage obligately dependent on animal rather than plant tissue for nutrition, are particularly vulnerable. Species of Lepidoptera with this rare life history trait comprise only 400 species at most, representing only about 0.25% of the estimated 160,000 species (Pierce 1995). However, aphytophagous species are greatly overrepresented on the IUCN Red List

of Threatened Species of butterflies, appearing almost two orders of magnitude more likely to be included in the categories of “Extinct,” “Critically Endangered,” and “Endangered” than are herbivorous species (IUCN 2020). Most obligate ant associations remain poorly studied. Moreover, countless groups of ant-associated caterpillars likely remain undiscovered, as nearly two-thirds of currently known myrmecophile groups are known from only a single species, almost entirely in the tropics (Table 1). Surprising and unique forms of ant association continue to be described regularly (e.g., Agassiz and Kallies 2018; Dejean et al. 2017; Komatsu and Itino 2014; Ramos et al. 2018; Rocha et al. 2020). Future experiments will need to measure the abundance and distribution of myrmecophiles in different regions and habitats to let us estimate their true global diversity, document their often-unbelievable biology, and ensure their future.

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