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BLUES' ASSOCIATION WITH ANTS - A STRANGE SUSTAINING PHENOMENA

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Introduction

Larvae that can survive ant encounters and colonise ant territories, whether on host plants or inside ant-built structures, may benefit from a variety of advantages, such as reduced competition, enemy-free space, and favourable microclimates (Saarinen and Daniels, 2006). Pierce et al. (2002) and Casacci et al. (2019) recently reviewed on ant associations with the lepidopteran families lycaenidae and riodinidae. Over 70% of the species in the large butterfly family lycaenidae appear to be ant-associated, making them the largest single group of myrmecophile lepidopterans (Tables 1 and 2). Two more ant associate radiations account for 20% of the species in the closely related butterfly family riodinidae. Over the course of 10 million years, these butterfly groups have evolved a wide range of adaptations. This study is quite novel in terms of the mechanism facilitating these fascinating interactions.

Table 1.

Family	Ant-associated group	Degree of association and type of relationship with ants	No. of ant-associated species	Distribution
Psychidae	*Iphierga* , *Ardiosteres* (may constitute more than one distinct group of ant associates)	Obligate. Larvae feed on debris or ants in *Iridomyrmex* or other nests	3 species	Australia
Tineidae	Myrmecozelinae (in part may constitute more than one distinct group of ant associates)	Obligate. *Myrmecozela ochraceella* feed on *Formica* nest material and possibly also ants. *Ippa* are carnivorous and along with others occur with diverse ant groups	>8 species in >3 genera	Europe to New Guinea
	Setomorpha melichrosta	Obligate (?). Larvae feed on plant materials in fungus gardens of *Atta* and *Acromyrmex* leaf-cutter ants	1 species	New World tropics/subtropics
	Amydria anceps	Obligate. Feed on fungal substrate accumulations outside of *Atta* nests	1 species	Mexico

Family	Ant-associated group	Degree of association and type of relationship with ants	No. of ant-associated species	Distribution
Tortricidae	*Hystrichophora* spp.	Obligate (?). Larvae feed within *Vachellia* ant-plant domatia	3 species	East Africa
	Semutophila saccharopa	Facultative (?). Trophobiotic relationship	1 species	Malaysian peninsula
Sesiidae	*Osmanthedon domaticola*	Facultative (?). Larvae feed on *Vachellia* ant-plant domatia within silk shelters	1 species	East Africa
Cyclotornidae	*Cyclotorna* spp.	Obligate. Ant-attended and parasitic within ant nests	12 species	Australia
Coleophoridae	*Batrachedra myrmecophila*	Obligate. Preys on ant brood	1 species	Java
Oecophoridae	*Stathmopoda* sp.	Obligate (?). Known from *Oecophylla* nests	1 species	Australia
Pyralidae	*Pachypodistes goeldii*	Obligate. Larvae feed on *Dolichoderus* ant nest cartons	1 species	Brazil
	Stenachroia myrmecophila	Obligate. Larvae may feed on *Crematogaster* brood	1 species	Australia
	Gen. sp.	Obligate (?). Found in *Dinomyrmex* nest	1 species	Borneo
	Gen. sp.	Obligate (?). Found in *Oecophylla* nest	1 species	Cameroon
	Gen. sp.	Facultative (?). Found only on plants with *Crematogaster*	1 species	Cameroon
	Gen. sp.	Facultative (?). Found only on plants with *Oecophylla*	1 species	Cameroon
Crambidae	*Niphopyralis* and allies	Obligate. Feed on *Oecophylla* eggs and brood	4 species	Australia, Java, and Cameroon
Noctuidae	*Dyops* spp.	Facultative. Larvae feed on *Cecropia* ant-plants defended by *Azteca* ants	>10 species	Central and South America
Erebidae	*Coxina* spp.	Facultative (?). Larvae feed on *Acacia* ant-plants	1 species	Central America
	Eublemma albifascia	Obligate (?). Larvae feed on *Oecophylla* regurgitations	1 species	Cameroon
	Homodes spp.	Obligate (?). Larvae feed on foliage around *Oecophylla ants*	>6 species	Tropical Asia and Australia
	Nudina artaxidia	Obligate (?). Larvae feed from ant-attended scale insects	1 species	Japan
Notodontidae	*Rosema dentifera*	Facultative (?). Larvae feed only on *Acacia* ant-plants	1 species	Central America
	Gen. sp. (near *Stauropus*)	Obligate (?). May solicit trophallaxis from *Oecophylla*	1 species	Cameroon
Saturniidae	*Syssphinx mexicana*	Facultative (?). Larvae feed only on *Acacia* ant-plants	1 species	Central America
Hesperiidae	*Lotongus calathus*	Obligate (?). Larvae build nests always shared with ants	1 species	Malaysia
Pieridae	*Catopsilia* spp.	Facultative. Larvae regularly attract ants to excretions and leaf exudates	>3 species	Africa and tropical Asia

Family	Ant-associated group	Degree of association and type of relationship with ants	No. of ant-associated species	Distribution
Lycaenidae	Lycaenidae	See Table 2. Most form trophobiotic relationships with ants	>3830 species estimated	Widespread globally
Riodinidae	Eurybiina (Riodininae: Eurybiini)	See Table 2. All appear to form trophobiotic relationships with ants	>35 species estimated	South America
	Nymphiidini (Riodininae)	See Table 2. Most form trophobiotic relationships with ants	> 273 species estimated	Central and South America

(Pierce and Dankowicz, 2022)

Table 2

	No. 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)
Poritiinae	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)
Eurybiini	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, Riodinini, and Helicopini	615	NA, NT	0 (0)	0 (0)	0 (0)	0 (0)	72 (484)	0 (0)

(Pierce and Dankowicz, 2022)

Myrmecophily

The ability to form symbiotic relationships with ants, known as 'myrmecophily,' is an ancestral trait shared by butterfly members of the Lycaenidae (Lepidoptera) family, commonly known as the 'blues,' 'coppers,' 'hairstreaks and 'metal marks' (Fiedler, 1995). The blues have one of the most fascinating life-cycles as it has close relationship with ants.

The level of association with ants ranged from facultative to obligate, mutually beneficial, manipulative, and parasitic.

Degree of association

1. **Facultative:** Larvae in the facultative association are only seldom attended by ants; they are not required to be cared for by numerous genera or species of ants. Eg:The tending ants (*Camponotus compressus*) partially cleared the frass-filled larval feeding hole in order to obtain the sugary substance secreted by

the lycaenid (*Deudorix isocrates*) (Kumar et al., 2017).

2. **Obligate:** Because of the significant risk of predation or for other reasons, larvae in the obligatory association are invariably connected with a certain genus or species of ants. Without ants, larvae would not be able to survive. Eg: *Crematogaster hodgsoni* ants are obligately associated with all stages of lilac silverline, *Apharitis lilacinus*. Female *A. lilacinus* ants lay eggs at the entrance to the nest of *C. hodgsoni* ants, sometimes on sand and away from plants. From hatching to eclosion, caterpillars and pupae are completely dependent on ants and must be constantly attended. Caterpillars do not feed on plant tissue at all, instead relying on ant regurgitated food (Basu & Kunte 2020).
3. **Mutualism:** A mutualistic relationship between two species is one that benefits both parties. Eg: The larvae of butterflies secrete nutritious 'larval nectar' (rich in sugars and amino acids) from their Dorsal Nectary Organs (DNO) to ants. In exchange, the larvae are protected from ant attack, and ants aggressively protect the larvae from other predators (Hojo et al., 2015).

Various ant genera associated with the larvae of *C. pandava* (Chaudhary & Kumar, 2021)

Caterpillars control ant behaviour through the use of multimodal signals such as chemical, acoustic, and tactile signals, which we will discuss further.

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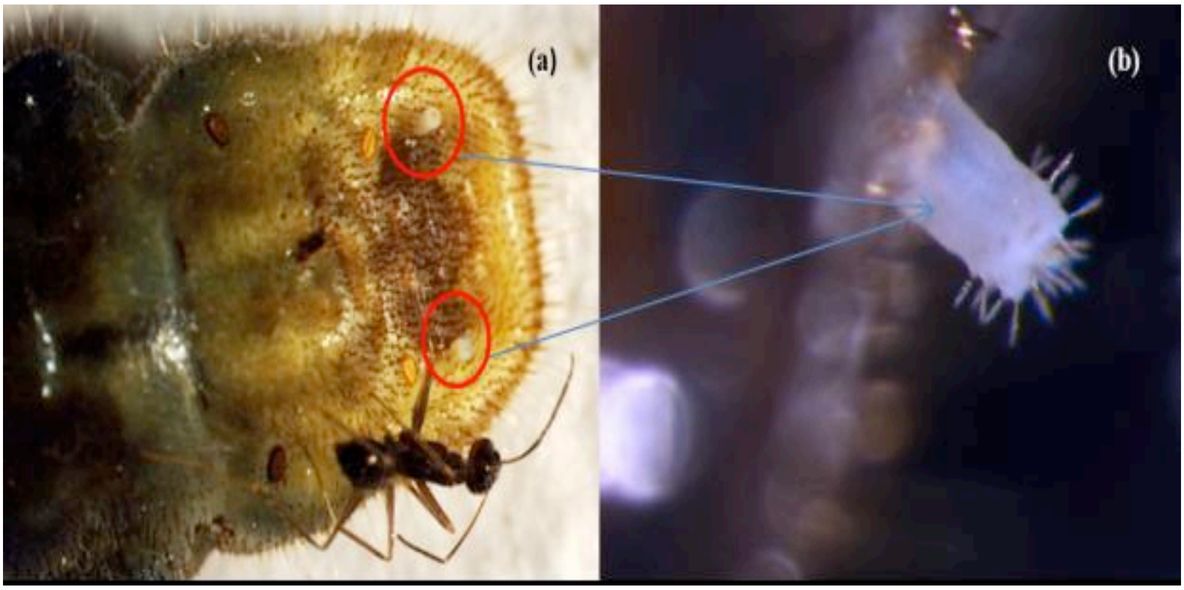
1. Chemical signal

a) Pore cupola organ (PCO)

Pheromone secreting single-celled epidermal gland found on all lycaenid sp. larvae emit chemicals to pacify ants that would otherwise attack soft-bodied larvae. PCO enabled a critical innovation that allowed ancestral lycaenids to take advantage of enemy free space in the presence of ants.

b) Dew patches and Dorsal Nectary Organ (DNO)

DNO, also known as the "honey bee gland," is located on the 7th abdominal segment and produces nutritious secretions (rich in carbohydrates such as sucrose, glucose, arabinose, fructose, maltose, trehalose, and lactose, followed by free amino acids and trace amounts of methionine) for ants (Daniels et al., 2005). It also has the potential to change the level of dopamine in the attending ant's brain, causing them to slow their locomotion.



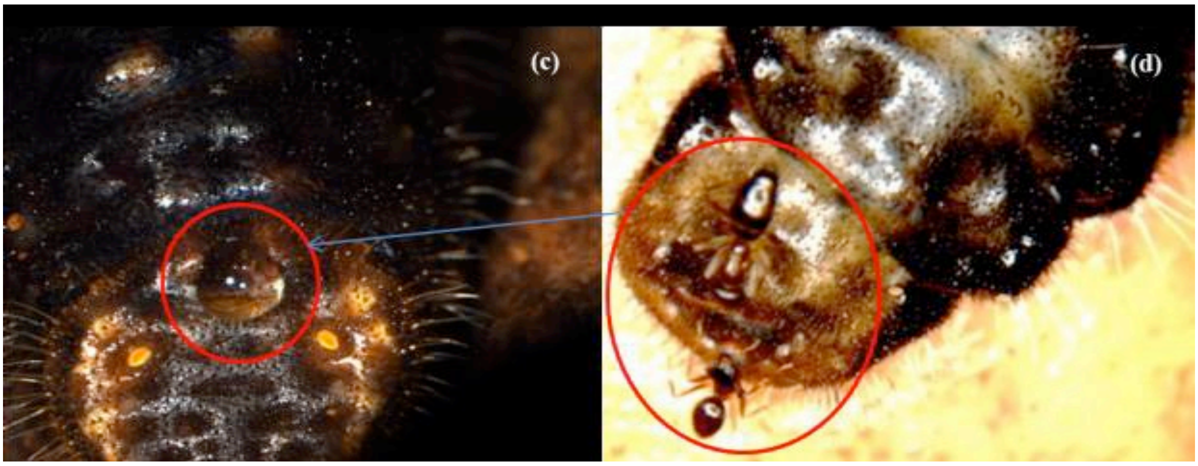
(Kumar et al., 2017)

2. Acoustic signals

Idle myrmecophile pupae communicate with ants via substratum-borne acoustic signals produced by stridulating chitinous micro-ridges at the segmental ends (Travassos & Pierce, 2000). In some cases, the larvae mimic the sound of queen ant which enable the ants into service.

3. Tactile/Tentacle signal

A pair on the eighth abdominal segment, compass to direct caterpillars toward ant aggression. Once the caterpillars are alarmed, volatile substances eluted from the tip of this organ attract and alert the ants (Ekka et al., 2020).



(Kumar et al., 2017)

4. Other associated morphology

Caterpillars have thick, convoluted skin/dermis to protect themselves from ant attack. The pro-thoracic plate and endplate were also thick and chitinous, suggesting that they serve as protective shields for the sensitive head and abdominal ends. The foregut, on the other hand, was remarkably narrow, which could be related to the caterpillar's reliance on trophallaxis, which eliminates the heavy digestive machinery found in caterpillars that must digest tough vegetation *viz*., *Apharitis lilacinus*, which feeds on the regurgitated food provided by *Crematogaster hodgsoni*.

Functional understanding

Traditional dissection and staining methods destroy connecting muscles and nerves, making detailed internal structures or functional morphology of these organs difficult to characterize (Vegliante & Hasenfuss, 2011). It is also unknown how these organs interact with the surrounding anatomical systems. To address these limitations, microtomography (MicroCT) was developed, which sheds light on internal and functional morphology. Basu and Kunte. (2020) used this technique to delineate the internal, native morphology of specialised larval dew patches, nectar glands, and tactile ciliary organs that mediate interactions between *Crematogaster* ants and *Apharitis lilacinus* butterfly caterpillars.

Conclusion

The association of blue butterflies with their ant hosts is one of the nature's wonders. Functional morphologies of insect adaptations have always been thought to be important, but they have been difficult to study due to technological limitations. Applications of similar MicroCT analysis may range from soft tissue mechanics in insect larvae and relative organ development through insect metamorphosis to predator-prey interactions and arms races. Understanding the morphology and behaviour of lycaenids can help us understand the interactions and survival needs of organisms. It would be preferable if aspiring entomologists showed an interest in comprehending such marvellous ecological relationships of various insects.

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