

## Facultative associations of two sympatric lycaenid butterflies with *Camponotus compressus* – field study and larval surface ultrastructure

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### Abstract

The present study focused on the associations of two sympatric lycaenid species, *Chilades pandava* Horsfield, 1829 and *Euchrysops cnejus* Fabricius, 1798 with their respective host plants and the lycaenid tending *Camponotus compressus* Fabricius, 1787 ants by conduction of field studies and by examination of the ultrastructure of the larval myrmecophilous organs. The study revealed two facultative association complexes: ants - the defoliating *Cl. pandava* larvae - *Cycas revoluta* (Thunb.) plants and ants - the pod-boring *E. cnejus* larvae - cowpea plant, *Vigna unguiculata* (L.) Walp. The association of *Cl. pandava* was strongly synchronized with its host plant phenology and relatively less strongly with its late-arriving ant partner since the young, curled up leaves provided resources only to the caterpillars. The provision of resources to both the ants and the lycaenids by the cowpea plants contributed to the synchronization of *E. cnejus* association with the early arriving ants as well as the host plant. Presence of a single type of setae in *Cl. pandava* and of two types of setae in *E. cnejus* larvae indicates their facultative adaptations for resisting attack by their host ants. Ultrastructural similarity in the dorsal nectary, pore cupola and tentacle organs suggest that the basic myrmecophilous organs are conserved in these two lycaenid species.

**Keywords:** ants; *Euchrysops cnejus*; *Chilades pandava*; scanning electron microscopy; myrmecophilous organs.

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### Introduction

The myrmecophilous butterfly family Lycaenidae accounts for approximately a quarter of the global butterfly species richness (Pierce *et al.*, 2002). About 60% of the lycaenid myrmecophiles are associated with several ant species (Pierce *et al.*, 2002). The association between ants and the lycaenid larvae ranges from facultative (Saarinen & Daniels, 2006; Bächtold *et al.*, 2014; Hojo *et al.*, 2014) to obligate (Als *et al.*, 2002; Pierce *et al.*, 2002; Steiner *et al.*, 2003; Martins *et al.*, 2013). Many species of lycaenids are involved in food for-protection mutualistic relationships with ants. Myrmecophily involves both behavioural as well as morphological adaptations of the lycaenid caterpillars which possess a suite of anatomical structures for maintaining association with ants (Fiedler *et al.*, 1996; Pierce *et al.*, 2002; Trager & Daniels, 2009). Ant attendance of third/fourth

instar larvae is primarily sustained by gustatory and/or semiochemical mediation involving at least three types of ant-associated organs: the pore cupola organs (PCOs) present across the abdomen; the dorsal nectary organ (DNO) on the seventh abdominal segment; and a pair of tentacle organs (TOs) on the eighth abdominal segment (Kitching & Luke, 1985; Leimar & Axen, 1993; Axen *et al.*, 1996; Hojo *et al.*, 2008, 2009). These serve primarily as appeasement organs and help to avoid predation from the ants (Dupont *et al.*, 2016).

The myrmecophilous lycaenid caterpillars are tended by the associated ant species, usually on the larval host plants, where the herbivorous larvae encounter the plant-visiting worker ants (Pierce *et al.*, 2002). Lycaenids demonstrate considerable variations in their host plant range and their larval stages

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are specialist feeders of tender foliage or inflorescence (Fiedler, 1996). Hence, the host plant phenology and seasonal predictability in the availability of the larvae preferred plant resources (food and/or shelter) is likely to play an important role in ant-lycaenid-host plant association.

A large number of facultative ant-lycaenid associations involve plant-visiting ants belonging to the genus *Camponotus* (Saarinen & Daniels, 2006; Bächtold *et al.*, 2014; Hojo *et al.*, 2014). *Camponotus compressus* is distributed across Africa and Asia and is widespread in many parts of India (Agarwal & Rastogi, 2010; Bharti *et al.*, 2016; Ekka & Rastogi, 2017). Our preliminary observations revealed the association of *C. compressus* with caterpillars of two sympatric lycaenid butterflies: *Chilades pandava* Horsfield and *Euchrysops cnejus* Fabricius. While the larvae of *Cl. pandava* are defoliators of cycads, plants belonging to family Fabaceae are also preferred host plants (Robinson *et al.*, 2010; Marler, 2012). *E. cnejus* larvae are pod-boring pests which prefer various species of legumes belonging to the Fabaceae family (Robinson *et al.*, 2010; Tiple *et al.*, 2011). The respective locally available host plants of *Cl. pandava* and *E. cnejus* were *Cycas revoluta* and *Vigna unguiculata*.

Elucidation of myrmecophily requires a basic understanding of the natural history of ant-lycaenid-host plant complex as well as the ultrastructural details of the specialized myrmecophilous organs possessed by the fourth instar lycaenid larvae as adaptations related to their association with ants. Ant, lycaenid and the host plant association involves three partners but the emphasis of majority of studies has been mainly on the ant-lycaenid myrmecophilous aspects (Pierce *et al.*, 2002; Fiedler, 2012). For survival, the lycaenid larvae need both food and protection from enemies. Only few studies have examined the influence of host plants on myrmecophilous associations (Fiedler, 1996). Since lycaenid juveniles feed on various types of host plants, the species specific role of host plant phenology on the extent of larval dependence on each of its two associates: the host plant and the ant body guards, needs to be deciphered. Concurrently, it is also essential to examine if the ultrastructural details of the myrmecophilous

organs are influenced by variations in the larval association with ants. In view of the constraints imposed by the narrow host plant range of *Cl. pandava* and *E. cnejus*, we hypothesize that the strength of the myrmecophilous associations would be affected by the availability of the host plant mediated resources (food and/or shelter) to the ants and/or the lycaenids. The association of the same ant species with two sympatric lycaenids, each utilizing its specific host plant, provides a very good model system to test this hypothesis. Therefore, the present study addresses the following two questions: (i) How is the association between *C. compressus* ants, each of the two sympatric lycaenids and the respective host plants, influenced by host plant phenology? (ii) Are there ultrastructural differences in the myrmecophilous organs of the two sympatric lycaenid species?

## Materials and Methods

### Study site and systems

The field observations were carried out in the Botanical Garden of Banaras Hindu University campus, Varanasi (25°18' N and 80°1' E, 76 m above the mean sea level) in Uttar Pradesh, India.

There were two study systems: *Camponotus compressus* - *Chilades pandava* - *Cycas revoluta* complex and *Camponotus compressus* - *Euchrysops cnejus* - *Vigna unguiculata* complex. *Cy. revoluta*, a palm-like tree with a stout trunk and a crown formed by large, evergreen and pinnate leaves (Jones, 2002), is one of the host plant of the tropical lycaenid, *Cl. pandava* commonly known as the plains cupid or cycad blue is native to southern Asia (Moore *et al.*, 2005). The young leaves are circinately coiled (Raju & Rao, 2011). The life cycle of this lycaenid is known to consist of the egg, four larval instars, the pupal stage and the adult butterfly (Raju, 2009). The caterpillars feed on the tender emerging fronds of *Cy. revoluta* plants and cause extensive damage to the leaves (Moore *et al.*, 2005; Marler, 2012; Marler & Lawrence, 2012). *Cl. pandava*, therefore has become a conspicuous and serious pest on native (Raju, 2009) and horticultural cycads (Wu *et al.*, 2010). Other host plants of *Cl. pandava* are *Bauhinia* spp., *Butea monosperma* (Lam.) Taub., *Desmodium*

*dalbergiodes* Roxb. and *Acacia* sp. (Robinson *et al.*, 2010; Nitin *et al.*, 2018). The natural distribution of this butterfly spans Indo-Asia, including India, Sri Lanka, Sundaland, Philippines, Taiwan (Igarashi & Fukuda, 2000), Japan, Guam, Madagascar, Mauritius, Egypt, and the United Arab Emirates (Moore *et al.*, 2005; Wu *et al.*, 2010).

*V. unguiculata*, commonly known as cowpea, is an annual crop plant. It bears extrafloral nectaries on the stipules of the trifoliate leaves and also at the base of the inflorescence. The plant grows to a height of about 50-60cm and the flowers are borne in the leaf axils, in clusters of two to four (Kuo & Pate, 1985). *V. unguiculata* is the host of another common lycaenid, the gram blue butterfly, *E. cnejus* that is widely distributed in India, Malayan subregion, extending to Australia and the South Sea Islands (Varshney & Peter, 2015). It has been reported on pod-bearing host plants belonging to the family Fabaceae including those belonging to the genus *Vigna*, *Butea monosperma*, *Desmodium dalbergiodes*, *Acacia* sp., *Phaseolus* sp., *Cajanus cajan* (L.) Millsp. (Robinson *et al.*, 2010). Life cycle of *E. cnejus* is known to consist of the egg stage, four larval instars, the pupal and the adult butterfly stage (Akand *et al.*, 2015).

#### Ant-lycaenid-host plant association

Field observations, during the growth season of the respective host plants, were carried out for 2 years, in each case. To monitor *C. compressus* - *Cl. pandava* - *Cy. revoluta* complex, observations were conducted on the cycas host plants (n = 15) from April to September, (2015 & 2016) while observations pertaining to *C. compressus* - *E. cnejus*- *V. unguiculata* complex were carried out on the cowpea plants (n = 30), from March to August (2015 & 2016).

The occurrence of ants and lycaenids on each species of host plants were recorded by the standard visual scanning method (as per the method of Agarwal & Rastogi, 2009). Each host plant was visually scanned for 5 mins (from 8:00 - 11:00 h) for the presence and activity of ants and the lycaenid caterpillars. The observations were carried out four times a month. The area in the vicinity of the plants was examined (4 times

a month) and the number of *C. compressus* satellite nests and the distance of each, if any, from the host plants were recorded.

#### Scanning electron microscopy

The fourth instar caterpillars (n = 5, in each case) of *Cl. pandava* and *E. cnejus* were respectively collected from the infested new leaves of cycas plants and from the cowpea plant pods. The caterpillars were prepared for scanning electron microscopy by using the method of Kumari *et al.* (2012) with minor modifications. Caterpillars were rinsed in distilled water and fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, at pH 7.4 for 2–2.5 hours at 4°C. Following fixation, the caterpillar samples were washed in 0.1 M sodium cacodylate buffer (pH 7.4) for three times each for 1 hour at 4°C and dehydrated at 4°C with graded acetone in ascending concentrations. After absolute acetone treatment the material was kept at 37°C for 48 hours. The caterpillar samples were then attached to stubs, coated with gold using Sputter Coater (SC7620, Quorum Technologies Ltd., UK) and examined with a scanning electron microscope (EVO® LS 10 Zeiss, Germany). Results were recorded using an Intel Pentium IV D computer (Model dx2280 MT, Hp Compaq, USA).

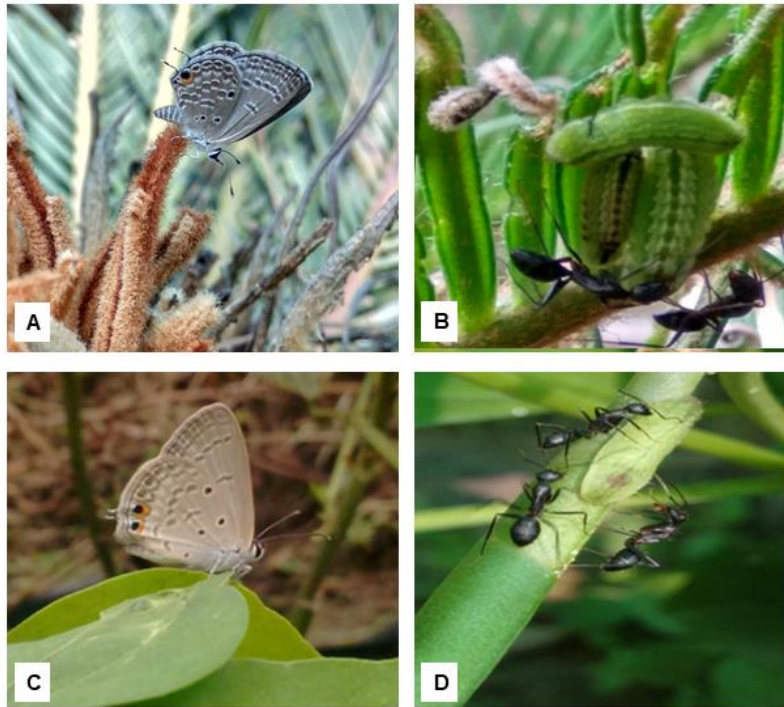
## Results

#### Ant-lycaenid-host plant association

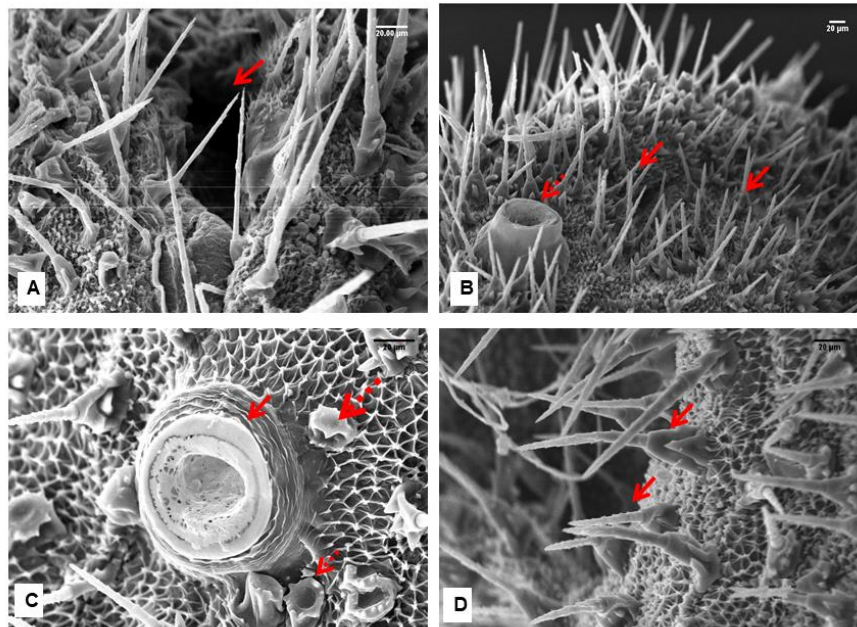
As members of *C. compressus* - *Cl. pandava* - *Cy. revoluta* complex, the *Cl. pandava* caterpillars were found only on the tender, young, unfurled fronds of *Cy. revoluta*. These newly emerged fronds were recorded on the *Cy. revoluta* plants for 15-20 days only during the months of April and September, each year. The minor caste workers of *C. compressus* were recorded on the new foliage only after the occurrence of the (first and/or second instar) *Cl. pandava* caterpillars on the cycas plants (Fig. 1B).

As components of the *C. compressus* - *E. cnejus* - *V. unguiculata* complex, the minor caste worker ants visited the extrafloral nectaries of the young (pre-flowering) cowpea plants even before the occurrence of the early (first and/or second) instar caterpillars on the plants. Later, interactions of *C. compressus* with the third/

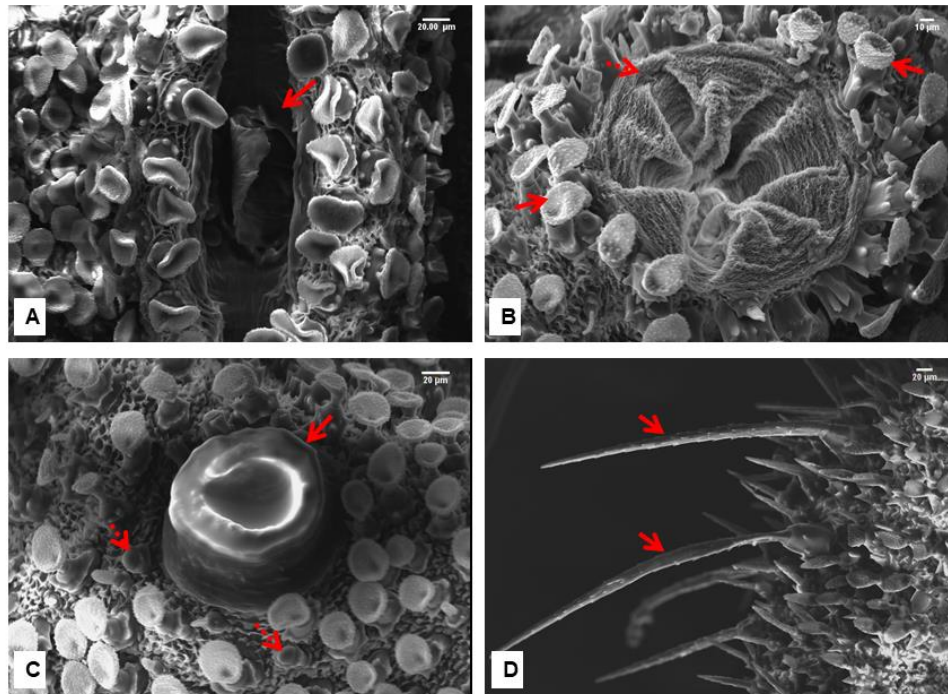
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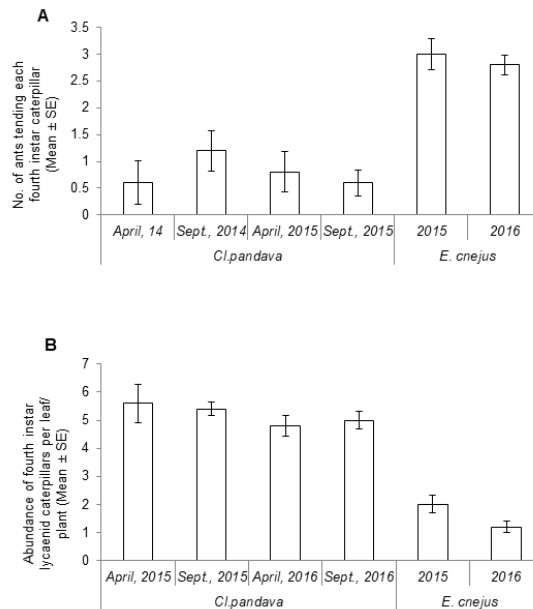
**Figure 1:** **A.** *Chilades pandava* butterfly on *Cycas revoluta* young leaf; **B.** *Camponotus compressus* worker ants tending *C. pandava* caterpillars on a cycas leaf; **C.** *Euchrysops cnejus* butterfly on the leaf of *Vigna unguiculata*; **D.** Caterpillars of *E. cnejus* on the cowpea pod.



**Figure 2.** Scanning electron micrographs of the IV instar larva of *Chilades pandava*: **A.** Dorsal nectary organ (arrow); **B.** Retracted tentacle organ (broken arrow) surrounded by setae (arrows); **C.** Spiracle (arrow) surrounded by pore cupola organs (broken arrows); **D.** Stellate based setae (arrows) on the abdomen.



**Figure 3.** Scanning electron micrographs of the IV instar larva of *Euchrysops cnejus*: **A.** Dorsal nectary organ (arrow); **B.** Retracted tentacle organ (broken arrow) surrounded by disc-shaped setae (arrows); **C.** spiracle (arrow) surrounded by pore cupola organs (broken arrows); **D.** Stellate based long setae (arrows) on the abdomen.



**Figure 4: A.** Number (Mean ± SE) of *Camponotus compressus* ant attendants on fourth instar caterpillars of *Chilades pandava* and *Euchrysops cnejus*; **B.** Abundance (Mean ± SE) of fourth instar lycaenid caterpillars of *Cl. pandava* per *Cycas revoluta* leaf and of *E. cnejus* per *Vigna unguiculata* plant.

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**Table 1.** Field study of ant-lycaenid-host plant association between *Camponotus compressus* ants and lycaenids: *Chilades pandava* (on *Cycas revoluta*) during April & September and with *Euchrysops cnejus* (on *Vigna unguiculata*) during March-August, 2015–2016. Control (ant-excluded), Experimental (ant-included).

Parameters	<i>Cycas revoluta</i> (perennial)	<i>Vigna unguiculata</i> (annual)
<b>First occurrence of <i>Camponotus compressus</i> on the plants</b>	8.33 ± 0.88 days (range: 7-10 days) after emergence of new leaves	36.66 ± 4.41 days (range: 35-45 days) after plant emergence from seed
<b>First occurrence of lycaenid larvae on the plants</b>	5.0 ± 0.57 days (range: 4-6 days) after emergence of new leaves	55.66 ± 2.96 days (range: 50-60 days) after plant emergence from seed
<b>Time of satellite nest occurrence within 100m<sup>2</sup> of host plant</b>	April, 2015: 12.33 ± 1.45 days Sept., 2015: 10.33 ± 1.45 days April, 2016: 11.66 ± 1.45 days Sept., 2016: 11.66 ± 1.85 days (after emergence of new leaves)	2015: 65.33 ± 3.52 days 2016: 67.66 ± 3.84 days (after plant emergence from seed)
<b>Number of satellite nests associated with each lycaenid-harbouring host plant (Mean ± SE)</b>	April, 2015: 0.75 ± 0.55 (range: 1-2) Sept., 2015: 0.5 ± 0.28 (range: 0-1) April, 2016: 1.0 ± 0.40 (range: 1-2) Sept., 2016: 1.0 ± 0.57 (range: 1-2)	2015: 0.50 ± 0.43 (range: 1-2) 2016: 0.62 ± 0.26 (range: 1-2)
<b>Distance of satellite nests from each host plant (Mean ± SE)</b>	April, 2015: 26.33 ± 13.84 cm (range: 12.5-54 cm) Sept., 2015: 24.33 ± 5.6 cm (range: 13-30 cm) April, 2016: 23.26 ± 3.93 (range: 15.4-27.2 cm) Sept., 2016: 34 ± 11.66 (range: 11.8-47 cm)	2015: 89.90 ± 42.7 cm (range: 47.2-218 cm) 2016: 66.72 ± 33.08 cm (range: 26.3-210 cm)

fourth instar *E. cnejus* caterpillar were recorded during the flowering/fruiting period of the plant (Fig. 1D). The number of ant attendants on fourth instar caterpillars was higher in case of *E. cnejus* as compared to *Cl. pandava* (Fig. 4A). Abundance of fourth instar lycaenid *Cl. pandava* caterpillars was high on *Cy. revoluta* as compared to that of *E. cnejus* on *V. unguiculata* plants (Fig. 4 B).

Satellite nests (range: 1-2) of *C. compressus* colonies were recorded at or near the base of the lycaenid caterpillar-harboring, cycas and cowpea plants (Table 1) after the arrival of the lycaenids on the respective host plants.

### Scanning electron microscopy

The scanning electron microscopy of the ultrastructure of the abdomen of the fourth instar lycaenid caterpillars of *Cl. pandava* and *E.*

*cnejus* revealed the presence of three types of myrmecophilous organs, in each case: DNO was visible as an opening on the dorsal portion of the seventh abdominal segment (Fig. 2A, 3A), a pair of retracted TOs (Fig. 2B, 3B) were located on the eighth abdominal segment and PCOs were wart-like glandular structures distributed throughout the larval abdomen (Fig. 2C, 3C). Other observed structures included a pair of spiracles (Fig. 2C, 3C), prominently visible as round structures on each of the seventh and eighth abdominal segments and presence of setae on the abdomen (Fig. 2D, 3D). Only a single type of long and stellate base setae (Fig. 2D) were recorded on the body of *Cl. pandava* larvae while two types of setae: stellate based short disc-like setae (Fig. 3B) and long tactile setae (Fig. 3D) were present on the body of *E. cnejus* larvae.

## Discussion

The results of the field study of the two types of ant-lycaenid-host plant complexes indicate facultative associations in both the cases under study, involving spatiotemporal synchronization between the lycaenid, their respective host plants and *C. compressus* ants. It has been reported that *Cl. pandava* and *E. cnejus* facultatively associates with *Camponotus* sp. as well as other ant species (Eastwood & Fraser, 1999; Heath & Claassens, 2003). The results also indicate that the ant-lycaenid-host plant associations are strongly influenced by two important host plant related factors, the presence and/or absence of the: i. food for the ants, and ii. food and shelter for the lycaenid caterpillars.

*Cl. pandava* caterpillars were recorded on the cycas plants much before the ant visits were recorded on the plants. The association of *Cl. pandava* was found to be more strongly synchronized with its host plant phenology and relatively less strongly with the late-arriving *C. compressus* ant partners since the host plant offered no food at all for the ant partner. The tender tightly curled up fronds of the cycas apparently provided not only food but also shelter to the early stages of *Cl. pandava* caterpillars. The vulnerable early instar caterpillars remained concealed within the young, circinately coiled leaflets of the fronds. However, the host plant phenology imposed a constraint on the lycaenid since there was only a short window period (range: 15-20 days) in the availability of these resources to the *Cl. pandava* juveniles, during the months of April and September of each year. Thus, there was a fine-tuned synchronization of the larval developmental period with the bi-annual emergence of young fronds. The late instar larvae were exposed to their enemies later when the leaves gradually matured, hardened in texture and unfurled. At this stage the third and/or fourth larvae were tended by the late-visiting *C. compressus* ants.

In contrast, the presence of 2 types of extrafloral nectaries in *V. unguiculata* consistently provided food to the worker ants and thereby ensured their presence on the plants, even before the arrival of the lycaenid caterpillars. While the seeds of the developing pods of the cowpea plants served as food, the

pods provided shelter to the early vulnerable instars of *E. cnejus*. The lycaenid caterpillars are reportedly susceptible to parasitoids (Gupta *et al.*, 2014). Therefore, the developing larval instars could obtain an enemy-free space within the pods and on emerging out from the pods could obtain protection by the already arrived ant guards which were present in close vicinity, feeding at the plant provided extrafloral nectaries.

Various studies have reported that lycaenid caterpillars occur predominantly on the plants where ants are present (Seufert & Fiedler, 1996; Kaminski *et al.*, 2012). Evolution towards myrmecophily in Lycaenidae is correlated with the utilization of nitrogen-rich host plants as nitrogen can enhance their overall fitness and survival and the amount of nitrogen required to complete an insect's life cycle may vary greatly among species (Pellissier *et al.*, 2012). Cycas plants associate with nitrogen fixing cyanobacteria within specialized roots enabling the plants to maintain a homeostasis of leaf nitrogen concentration throughout heterogeneous soil conditions and herbivory pressures (Marler & Dongol, 2016). We suggest that the nitrogen concentrations and texture of the cycas young leaves may be optimal for the plant-feeding larval stages as compared to older leaves. Moreover the coiled leaflets conceal the vulnerable early instars and account for the preference of the larvae for freshly emerged fronds. The cowpea seeds are also reported to have high protein content (Gupta *et al.*, 2014).

The field observations revealed that the *C. compressus* colonies exhibit similar behavioural responses in terms of establishment of satellite nests in the vicinity of the lycaenid-harboring host plants in both the cases thereby revealing the propensity of attending ants to construct temporary nests in the vicinity of lycaenid-harboring plants. The satellite nest construction occurred after the arrival of the lycaenids on the plants in both the cases. *C. compressus* being a polydomous ant species (Kumari *et al.*, 2016) apparently utilizes this strategy to maximize its access to the highly attractive, DNO secretion produced by the tended caterpillars of both the lycaenid species.

This is the first study of the ultrastructure of the myrmecophilous organs of

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*Cl. pandava* and *E. cnejus*. The SEM observations revealed similarities in the three basic myrmecophilous organs, (DNO, PCOs and TOs) of the last instar larvae of each of the two sympatric lycaenid butterfly species involved in food for defence association with the same species of carpenter ant, *C. compressus*. Evidently, all the three important myrmecophilous organs have been conserved in these two lycaenid species even though they belong to different genera. These basic myrmecophilous organs are needed to pacify ant workers to facilitate ant attendance and association with the lycaenids (Fiedler, 1991; Pierce *et al.*, 2002; Kaminski *et al.*, 2012).

Our results revealed the presence of two morphologically distinct types of setae. The stellate based short disc-like setae along with long setae were located on the abdomen of *E. cnejus* while only a single type of long-stellate based setae were distributed throughout the abdomen of *Cl. pandava* caterpillars. Setae occur on larvae of many members of the Lycaenidae (Ballmer & Pratt, 1988). The setae vary in shape, density and distribution among lycaenid species (Kitching & Luke, 1985; Ballmer & Pratt, 1991). Earlier studies have shown that the modified setae are involved in larval myrmecophily and may be of various shapes such as club-shaped (Fiedler, 1991; Tautz & Fiedler, 1992), dome shaped (Kitching & Luke, 1985), mushroom-like or dendritic (Tautz & Fiedler, 1992).

The perforated pore-like structures, the PCOs were distributed on the abdomen and more number of PCOs were recorded around the DNO and TOs of both the lycaenid species. It has been reported that the PCOs are universally present on majority of lycaenid larvae with tightly clustered distribution around DNO and TOs (Kitching & Luke, 1985; Fiedler, 1991; Pierce *et al.*, 2002; Kaminski & Freitas, 2010). The PCOs are found to exude ant attractant or appeasement substances that suggestedly contain polypeptides and/or free amino acids (Hojo *et al.*, 2014). These are said to be the earliest myrmecophilous adaptations and help in avoiding ant attack (Fiedler *et al.*, 1996; Pierce *et al.*, 2002).

SEM studies revealed DNO as an opening like structure located on the dorsal

surface of the seventh abdominal segment of the larva, in each species. This organ was found to be surrounded with setae and a large number of PCOs. The presence of DNO is widely observed in lycaenid larvae and is probably a primitive condition. Our results support earlier studies (Pierce *et al.*, 2002; Hojo *et al.*, 2008; Dupont *et al.*, 2016) indicating its important fundamental role in ant-lycaenid association. Droplets of an aqueous solution containing sugars and amino acids are known to be secreted by the DNO when the larvae are stimulated by the antennation of ants (Wada *et al.*, 2001; Daniels *et al.*, 2005). Recent work on the Japanese species, *Narathura japonica* Murray, 1875, has shown that the DNO secretions can also manipulate attendant ant behaviour via the dopaminergic pathway (Hojo *et al.*, 2015).

Our study also revealed the presence of the retracted TOs on the eighth abdominal segment as reported in the previous studies (Pierce *et al.*, 2002; Hojo *et al.*, 2008; Dupont *et al.*, 2016). These tentacles are everted when palpated by ants, showing a corona of spiny setae. The TOs of both the lycaenid species were similar to the TOs reported from various other lycaenid species such as *Hemiargus hanno* Stoll, 1790, *Parrhasius polibetes* Stoll, 1782 and *Liphyra brassolis* Westwood, 1864 (Kitching & Luke, 1985; Duarte *et al.*, 2001; Kaminski *et al.*, 2012; Dupont *et al.*, 2016). Some studies have proposed that the TOs may release a volatile substance that attract and alert attendant ants (Axén *et al.*, 1996). However, a recent study by Gnatzy *et al.* (2017) has shown that the tentacle hairs are typical insect mechanoreceptors, each innervated by a small bipolar sensory cell with a tubular body in the tip of the outer dendritic segment and no glandular structures were found on TOs.

All the three myrmecophilous organs studied are thus exocrine in nature and are found to secrete substances that entice, alarm, appease, feed, and/or manipulate attending ants (Pierce *et al.*, 2002; Hojo *et al.*, 2015). These secretions are said to be responsible for the suppression of ant aggression, maintenance of standing-guard, and ant-mediated defensive measures. Ant workers are found to provide an enemy-free space for the vulnerable caterpillars thereby aiding in larval defence against predators,



parasites and parasitoids (Atsatt, 1981; Fiedler *et al.*, 1996; Gupta *et al.*, 2014).

The plant-visiting *C. compressus* minor caste ants apparently contribute facultatively towards enhancement of the survival of the lycaenid larvae in both the species. It is well established that ant association has exerted a strong selection pressure on lycaenid larval morphology (Pierce *et al.*, 2002). Long and densely distributed setae form flexible armour and reportedly are adaptations of the facultative lycaenid species to avoid predation and resist attack by their host ants (Dupont *et al.*, 2016). The differences in the type of larval setae of the two species appear to be adaptations for entraining ant attendance and may indicate the behavioural shifts and differences in the larval survival strategies, although more research is needed to elucidate the role of the two types of setae. The species specific differences in the host plant phenology and differential contribution of resources to the lycaenid and its ant partners influences the synchronization of lycaenid larval developmental period on the plant with its ant body guards. The host plant attributes appear to be significant in facilitation of food and shelter to the vulnerable lycaenid stages and in making the association more strongly ant-dependent (tritrophic) in case of ant-*E. cnejus*-cowpea host plant complex as compared to that between *C. pandava* and the ants. The study thus highlights the differences in the selection pressures on the two sympatric lycaenid species associated with the same ant species.

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#### Disclosure statement

No potential conflict of interest was reported by the authors.

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