Review of Literature

Ants (Family: Formicidae) are the most abundant group of insects and have powerful defence mechanisms such as acid taste, aggressive biting, painful sting, and group defense (Wilson, 1971). Ants are generally not subject to predation (Hölldobler and Wilson 1990; McIver and Stonedahl, 1993; Furst et al., 2012). The worker ants of most species are aggressive, each well-armed with a sting and/or a powerful bite (Hölldobler and Wilson, 1990: Marlier et al., 2004; Allon et al., 2012). Ants are often distasteful, and have the amazing ability to recruit their nest-mates to help when they are attacked (Witte et al., 2010). These features along with their high abundance in the terrestrial ecosystems make them intimidating to many predators (Mooney, 2006; Katayama et al., 2015). Ants therefore, constitute ideal models for other, less well protected species, to mimic. They are the ideal models in mimicry rings. Behaviour is an important part of multi-modal signals. Constant waving of antennae is a common feature of ants. Ants are also characterized by their jerky and zigzag movements. These ant behaviours are commonly seen in some of the ant mimics (Cushing, 1997). In ants, the primary method of communication involves chemical and, to a lesser extent, tactile cues (Hölldobler and Wilson, 1990, 2009). Acoustics also plays a role among the adults of four ant sub-families (Ponerinae, Nothomyrmecinae, Pseudomyrmecinae, Myrmicinae) that can stridulate (Markl, 1973; Taylor, 1978), and others that drum the substrate, by inducing specific behaviours in receiving individuals (Markl, 1965; Barbero et al., 2009) or by amplifying or modulating the effects of pheromones (Markl and Hölldobler, 1978; Baroni-Urbani et al., 1988; Hölldobler, 1999).

In most species of ants, winged sexual castes mate during or following a flight at a species-specific time of the day and the inseminated females lose their wings and start new colonies (McCluskey, 1992). In ant colonies a significant proportion of old workers remain in
the nest and some newly emerged ones rapidly develop to become foragers (Sendova-Franks and Franks, 1993). Ant colonies are efficiently policed against intruders, ranking them among the most impenetrable and inhospitable of places for the majority of arthropods and thus they provide ‘enemy free space’ in an area effectively devoid of predators. Among arthropods, an estimated 10,000 species are myrmecophilous to some degree (Elmes, 1996), exploiting the various resources that ant colonies have to offer. In the general sense, any organism that is dependent on ants at least during part of its lifecycle is a myrmecophile. Different myrmecophilous species interact with the ants in different ways, ranging from parasitism to mutualism. While some involve obligate associations, (for instance many hemipterans are inquiline, meaning that they can only survive inside ant nests. Most of these associations are facultative and opportunistic (Stadler and Dixon, 2008; Moore et al., 2011).

Myrmecophilous associations have been best studied in temperate butterfly species belonging to family Lycaenidae. Many lycaenid caterpillars produce nectar by specialized organs and communicate with the ants through sound and vibrations (Pierce et al., 2002). The association with ants is believed to reduce the parasitisation of the butterfly caterpillars (Baumgarten and Fiedler, 1998). Rettenmeyer et al., (2011) listed over 300 animals that depend on a single army ant species, Eciton burchellii. Most of these species are inquilines, including mites, beetles, scuttle flies, and bristletails. Army ant myrmecophiles are not only extremely diverse taxonomically, they are also abundant. Among coleopterans the myrmecophilous ladybird beetle, Coccinella sp. was recorded with the red wood ant, Formica rufa group (Majerus, 1989; Sloggett et al., 2002; Mynhardt, 2013). Four species of beetles, Morica hybrida, Pimelia integra, P. monticola, and Tentyria incerta are reportedly specialized in the use of ant-nest debris as an important source of food while Aphodius baeticus, uses the ant nests principally as a mating arena (Sanchez-Pinero and Gomez, 1995).
Many plant-visiting and honeydew-producing homopterans such as aphids (Auchenorrhyncha and Sternorrhyncha), scale insects (Coccidae), mealybugs (Pseudococcidae), and treehoppers (Membracidae) are reported to be myrmecophilous (Hölldobler and Wilson, 1994). Very little information is available about spider myrmecophiles. Some myrmecophilous spiders are documented to be ant predators (Hölldobler 1971; MacKay 1982; Porter and Eastmond, 1982).

In the order Lepidoptera, many blue butterflies belonging to family Lycaenidae, show acoustic (Fiedler, 1991; Agrawal and Fordyce, 2000; Barbero et al., 2009a, b) and chemical mimicry (Thomas, 1983) to their respective host ants. Chemical mimicry helps butterfly larvae to mimic the ant larvae. Ants primarily use chemical communication (Thomas, 1983) to identify themselves as members of the colony and to indicate their reproductive status. This system can be exploited by parasites, which imitate the chemicals produced by the ants and thereby gain access to the ant nest. In the case of the caterpillars of the *Maculinea rebeli* butterfly (the Mountain Alcon blue), the mimicry is so precise that *Myrmica schencki* ants that come across a caterpillar will pick it up and bring it back to the nest, as though it was an ant larva (Thomas, 1983). In case of acoustic mimicry (Barbero et al., 2009a, b) *M. rebeli* caterpillars make a hissing noise, similar to the sound made by alarmed *Myrmica* workers. Ants make this hissing sound by rubbing together two parts of their bodies: one part carrying a ‘plectrum’ and the other a ‘file’. Hence, *M. rebeli* caterpillars are suggested to have similar structures. The sounds made by the queens and the workers are quite distinct, and different from alarm ‘hissing’. The differences are entirely due to the shapes of the ‘plectrum’ and the ‘file’. The noises made by the queen prompts the workers to take up a guard behaviour, whereas the noises made by a worker do not, suggesting that the sounds enable the ants to identify the social status of the insect that produced them (Barbero et al., 2009).
Myrmecomorphy in spiders is generally regarded as a type of Batesian mimicry in which spiders gain protection from predators through their resemblance to aggressive or unpalatable ants (Cushing, 1997; Nelson et al., 2004; Jackson et al., 2008; Yamasaki and Ahmad, 2013; Corcobado et al., 2016). Mimicry is a common phenomenon within the order Araneae comprising spiders. Some spiders resemble bird droppings, bark, or sand surfaces. However, some mimic ants or beetles, and jumping spiders in the genus Synemosyna (Cushing, 1997) are unusually good ant mimics. About 80% of spiders showing Batesian mimicry imitate ants (Cushing, 1997). Some species of spiders show transformational mimicry (Bhattacharya, 1939) during their development, wherein different instars mimic different ant species of a variety of colours and sizes. Ant-mimicking spiders are also known to exhibit colour polymorphism (Reiskind 1965; Cutler 1980), multiple mimetic forms within a species have been found in other spider families such as Clubionidae (Reiskind, 1970).

Myrmecomorphic spiders exhibit various types of morphological adaptations (Reiskind 1972, 1977; McIver and Stonedahl, 1993). These morphological adaptations include a variety of colour and body-form modifications that give the spider the appearance of having three body segments instead of two and of having long, narrow legs instead of shorter, more robust legs. Mandibles, compound eyes and even stings are sometimes mimicked by the spiders through modifications in the chelicerae, pigmentation in the cuticle, or special positioning of the spinnerets. The overall body of spider myrmecomorphs is much narrower than non-mimics, and this apparently reduces their fecundity. Female myrmecomorphs lay fewer eggs per egg sac than non-mimetic spiders of similar size (Edmunds, 1978; Wanless, 1978; Bradoo, 1980; Boevé, 1992). However, myrmecomorphs may compensate for this limitation by laying more number of egg sacs so that their life-time fecundity may be about equal to that of non-mimetic spiders. Spiders show three types of
morphological mimicry: (i) Simple one stage mimicry (Cushing, 1997; Ceccarelli, 2013) (ii) Transformational mimicry, where different stages use different ant models as their mimicry models; Bhattacharya, 1939; Ceccarelli, 2013) and (iii) Polymorphic mimicry (Reiskind, 1965; Cutler, 1980). Myrmeicum gounelley exhibits transformational mimicry since it mimics two different ant species according to the developmental stage of the spider. Spiderlings have triangular abdomens and closely mimic the small, Crematogaster limata. Adult M. gounelley are strikingly similar in shape and colour to Camponotus femoratus. In polymorphic mimicry, mimic species show polymorphism and different colour morphs often mimic different ant species. Synemosyna aurantiaca, showspolymorphism but lacks sexual dimorphism in its mimicry. Yellow morphs closely resemble yellow Pseudomyrmex ants, such as P. javidulus and P. oculatus while the black morphs mimic black Pseudomyrmex ants, such as P. gracilis. Myrmeicum bifasciatum is also polymorphic: yellow morphs mimic yellow Megalomyrmex ants, and black morphs resemble black Camponotus species. Myrmeicum cf. velutinum and Myrmeicum sp. are ponerine-like spiders that mimic Ectatommu lugens and Pachycondyla unidentata, respectively (Oliveira, 1988). The mimics have elongate ponerine like abdomens and are found in the same microhabitats as their models. Ant-mimicking spiders such as Peckhamia picata face reduced aggression not only from the ant model, Camponotus nearcticus but also from the spider - hunting specid wasps, both of which use chemical cues for prey identification (Uma et al., 2013).

Some species of ant–mimicking spiders show behavioural mimicry such as locomotor mimicry (Pekár and Jarab, 2011; Nelson and Card, 2016; Shamble et al., 2017). Many species of spiders are reported as accurate or inaccurate mimic (Edmunds, 2000; Pekár and Král, 2002; Nelson and Card, 2016). A number of studies have tried to understand the evolution of imperfect mimicry (Kikuchi and Pfennig, 2010; Penney et al., 2012). Some studies indicate that avian predators such as pigeons rank hoverfly mimics which use wasp as
the model in a broadly similar order as that used by human beings, indicating that imperfect mimicry is not just a human illusion (Dittrich et al., 1993). More interestingly avian predators are found to show lower willingness to attack imperfect insect prey (Veselý et al., 2013).

Among Acari, the phoretic mites belonging to the genus *Planodiscus* attaches itself to the tibia of its host ant, *Eciton hamatum*. The cuticular sculpturing of the mite's body is nearly identical to that of the ant's leg (Holldobler and Wilson, 1990).

Insects belonging to order Orthoptera are very different in morphology to ants but in some species like *Macroxiphus siamensis* (Family: Tettigoniidae), young larvae are ant-mimicking and thus differ in both appearance and behaviour from older ones and from adults (Helfert and Sanger, 1995). Structural modifications together with significantly placed markings make them look remarkably like ants; the resemblance with the model is achieved by the following features: the primary colouration is black and the head is round like an ant.

Many species of mantids (Family: Mantidae) have first nymphal instars which mimic ants (Edmunds, 1976) and the fact that *Sphodromantis lineola* first nymphal instars have a positive association with the ants of genus *Oecophylla* indicates that ant mimicry is of defensive importance. *Tarachodes afzelii* not only has ant-mimicking nymphs but also lives amongst and feeds on ants. The nymphs of the ghost mantis, *Phyllocrania paradoxa*, look like black ants to repel predators (Thomasinelli, 2002).

The stick insect, *Extatosoma tiaratum* (Phasmatidae) resembles dried thorny leaves as an adult but hatches from the egg as a replica of a *Leptomyrmex* ant with a red head and black body (Key, 1994). The long end is curled up to make the body shape appear ant-like, and the movement is erratic, while the adults move differently.

*Franklino thrips* (belonging to order Thysanoptera) females are predatory myrmecomorphs which exhibit mimicry in both behaviour and body form (Stannard, 1976; Mound and Reynaud, 2005). Ant-like appearance in some *Franklino thrips* species is
achieved through the basal abdominal segments being constricted and sharply white in contrast to the dark brown of the rest of the body (Mound and Reynaud, 2005). Ant mimicry also occurs in other genera of Aeolothripidae, where it has arisen independently. It includes Aeolothrips albicinctus in Europe, A. bicolor in North America, the Australian species, Desmothrips reedi, Allelothrips and seven species from Africa and India and Stomatothrips with eight species from the Americas (Mound and Reynaud, 2005).

Ant mimicry in insects belonging to the Order Hemiptera is well documented (Knight, 1941; Mciver and Stonedahl, 1987; Aldrich, 1988; Schuh and Slater, 1995; Schwartz and Cassis, 2003; Curcic et al., 2004). However, most studies are limited to their morphology and taxonomy (Knight, 1941; Mciver and Stonedahl, 1987; Schuh and Slater, 1995; Curcic et al., 2004). The nymphs of both sexes become more slender and ant-like with age. Late instar males are less ant-like because of the greatly increased size of the meso- and metathoracic wing pads. A wingless hemipteran, Myrmecoris gracilis looks like an ant and feeds on ant larvae. Pithanus maerkeli is also an ant-like bug. Another species, Systellonotus triguttatus, in which nymphs and females strongly resemble ants, is often found in the vicinity of ants (Curcic et al., 2004). Dulichius inflatus (Alydidae) closely resembles ants of the genus Polyrhachis. The nymphs of Himacerus mirmicoides look like ants. Ant-mimicry in family Coreidae is shown by the first instars of the Coreid bug (Aldrich, 1988) which mimic ants to gain protection (Aldrich, 1988). Another example of Batesian mimicry is shown by some species of bugs belonging to family Lygaeidae in which the body colour and behaviour of the mimics is like the black ant (Schuh and Slater, 1995). These lygaeids have ant-like waist, along with body colour patterns similar to their ant model (Schuh and Slater, 1995).

Among coleopterans many species of beetles show different types of ant mimicry but Batesian (Fisher 1931; Wheeler, 1931; Hespenheide, 1984; Maruyama et al., 2003; Wheeler et al., 2009) and chemical mimicry are most common among them. The clerid’s resemblance
to pseudomyrmecines is also enhanced by an erratic antlike movement. Clerid males are about the same size as worker ants, whereas the larger females are about the same size as dealated queens. The ants, *Pseudomyrmex pallidus* and *P. seminole* are found to co-occur with the clerid. Many parasitic Staphylinidae that march with army ants strikingly resemble their hosts. An outstanding example is *Ecitomorpha nevermanni*, whose colour varies to match the colour variation of its host, *Eciton burchellii*. *Ecitomorpha velutinus* mimics *Camponotus sericeiventris* ants. Several other cerambycids also resemble ants. The Central American *Mallocreaspinicollis* (Bates, 1862) and *Diphyrama singularis* (Bates, 1862) closely resemble the stinging ants. *Pseudomyrmecion ramalium* Bedel (1885) closely resembles *Crematogaster scutellaris* in size and colouration and lives in close vicinity to the ant nest (Monné and Hovore, 2005). In North America beetles belonging to certain genera including *Anthoboscus*, *Cyrtophorus* and *Tillomorpha* are ant mimics (Monné and Hovore, 2005). *Cyrtinus pygmaeus* resembles *Lasius niger americanus*, and *Michthisoma heterodoxum* mimics small workers of *Camponotus pennsylvanicus* (Wheeler, 1931; Monné and Hovore, 2005). The ant beetle, *Thanasimus formicarius* (Cleridae) mimics ants belonging to the genus *Formica* (Wheeler, 1931; Monné and Hovore, 2005).

Dipterans belonging to the family Richrdiidae, mainly show Batesian mimicry (Pie and Del-Carlo, 2002). A species belonging to the genus *Sepsisoma* (Richrdiidae) shows a clear ant like appearance, particularly resembling the Formicine ant, *Camponotus crassus*, very common on plants bearing extrafloral nectaries (Pie and Del-Carlo, 2002). A myrmecophilous syrphid hoverfly known as *Microdon mutabilis*, lives in one part of its range with *Formica lemani*, the host ants and in other parts with another host ant, *Myrmica scabrinodis* (Elmes et al., 1991; Elmes et al., 1999; Schönrogge et al., 2002).

In ant-ant mimicry, an ant species shows mimicry with its respective ant model (Ito et al., 2004). In Malaysia, worker ants belonging to the genus *Camponotus* are found on the
foraging trail of the Myrmicine, *Crematogaster inflata* (Ito *et al*., 2004). The body size and colouring of *Camponotusbendigensis* are found to be similar to *Myrmecia fulvipes* ants (Merrill and Elgar, 2000.) The latter ant species has a painful venomous sting. The distribution of the two species largely overlaps. *Polyrhachis rufipes* is often found on the trails of *Gnamptogenys menadensis* in the Oriental tropics (Gobin *et al*., 1998). *Polyrhachis rufipes* is a commensal of *G. menadensis*. The workers of *P. rufipes* can follow the trails of *G. menadensis* and thus reach sugar sources even though *P. rufipes* workers are also attacked and repelled by *G. menadensis* workers from feeding sites.

In temperate regions, velvet ants are wasps, (belonging to family Mutillidae) that sometimes look like ants (Wheeler, 1983). Velvet ants are often covered with hairs giving them a velvet-like appearance. Both velvet ants and true ants belong to the same order Hymenoptera. For example, *Pappognatha myrmiciformis*, mimics the ant, *Camponotus sericeiventris* (Wheeler, 1983). It was earlier hypothesized that the resemblance might enable wasp females to enter the nest of *C. sericeiventris* and parasitize the brood (Wheeler, 1983). However, a recent study suggests that the larvae of the parasitoid feed on myrmecophilic (ant loving) beetles that live within the ant colonies (Brothers *et al*., 2000).

Although many species of ants in India are strongly predatory (Agarwal *et al*., 2007) some species are sugar-loving and visit plants for the EF nectar (Agarwal and Rastogi, 2008, 2009). A study on ant-myrmecophyte association revealed that the composition of the extrafloral nectar is important in influencing the association (Shenoy *et al*., 2012). A few studies on Batesian mimics of ants have been carried out in India (Tikader, 1973; Bradoo, 1980; Sharma, 2012). The morphs of the salticid spider, *Myrmarachne plataleoides* are apparently able to discriminate between the female constructed silken retreats of symatric colour morphs (Borges *et al*., 2007). Another study has shown that ant-mimicking praying mantis, *Euntissa pulchara* can discriminate between two closely related mimetic prey
(Ramesh et al., 2016). Ant-like jumping spiders have been reported from Sri Lanka (Benjamin, 2015). However, most studies conducted in India, till date, on the myrmecomorphic arthropods are only at the preliminary level. Very few field and laboratory investigations have been conducted on myrmecophilous and myrmecomorphic arthropod diversity associated with a common and abundant ant species. Furthermore, studies relating to the behavioural ecological basis of such associations are still lacking.