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Review

Sexual ecological behavioral phases varied among blister beetles (Coleoptera: Meloidae)

Tutankhamun Sawiris Al-Fayed

Faculty of Science, Al-Azhar University, Cairo, Egypt. E-mail: sawiris0987@yahoo.com.

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The Meloidae (blister or oil beetles) are widely distributed in the world. They have serious impacts, whether agronomic, veterinary or medical. The present review discussed several aspects in the behavioral ecology of Meloidae. The sexual behavior phases varied among meloid species including searching for mate, approaching and some physical contacts ending in mating. Cantharidin usually be employed as a nuptial gift in the courtship. Courtship may be repeated and the assortative mating may be taken place. Mate-guarding was, also, recorded for certain species. The present work comprehensively reviewed, also, the feeding tactics, defensive measures and cleaning antennae among the non-sexual behavioral patterns of Meloidae. An intensive attention was paid to the phoresy behavior focusing on triungulin structural adaptation for phoresy, scenarios of phoresy and phoresy as dispersal way as well as a taxonomic tool. The uses of sexual and egg-laying behavior in the systematics of Meloidae had been presented.

Key words: Courtship, nuptial gift, cantharidin, oviposition, phoresy, defensive behaviour, cleaning behaviour, physiology.

INTRODUCTION

About 40% of all described insect species are beetles classified in the order Coleoptera (Hammond, 1992). The order includes species more than any other insect order (Powell, 2009). Some estimates put the total number of species, described and undescribed at as high as 100 million, but a figure of one million is more widely accepted (Chapman, 2006). The Meloidae (blister beetles or oil beetles) is a family of coleopterans with a wide spread distribution in the world except for New Zealand and Antarctica (Arnett et al., 2002). They inhabit widely distributed regions especially of warmer and drier climates (Booth et al., 1990). Meloidae comprises approximately 3000 species in 120 genera (Dettner, 1997).

Several ecological phenomena of the blister beetles, such as population dynamics, seasonal abundance and activity, behavioral ecology, and the effect of various biotic and abiotic environmental factors, had been studied (Leppla, 1970; Houck and O'Conner, 1991; Ruiz et al., 1994; Mafra-Neto and Jolivet, 1994; Nikbakhtzadeh and Tirgari, 2002; Zhu et al., 2005). Also, various bionomic activities and interrelationships of the family had been described in different parts of the world (Linsley and MacSwain, 1942; Selander, 1960, 1984, 1986; Pinto and Selander 1970; Pinto, 1972 b; Erickson and Werner, 1974 a,b,c; Selander, 1988; Mahal et al., 1989; Doumbia, 1992; Bologna and Alsoisi, 1994; Bologna and Pinto, 1995; Senthil-Kumar et al., 1996; Bologna and Di Giulia, 2002). More ecological information, in general, can be found in the literature (Atkins, 1980; Matthews and Kitching, 1984; Schowaller, 2006; Prakah, 2008; Speight et al., 2008; Matthews and Matthews, 2010; Kaptan et al., 2011; Ananthakrishnan and Sivaramakrishnan, 2012). The present review aims to discuss several aspects of behavioral ecology, including sexual and nonsexual patterns and phoresy, as well as the sexual behaviour as a dispersal way and as a tool for systematics of the family.

SEXUAL BEHAVIOR OF MELOIDAE

In the past few decades research has demonstrated that many insect species rely heavily on learning to decide about a variety of behaviors, including diet choice, predator avoidance, spatial orientation and social interactions (Dukas, 2001; Greenspan and van Swinderen, 2004). The role of learning in insect sexual behaviour, however, has been either neglected or considered negligible (Alexander et al., 1997; Dukas, 2006). Insects are especially suited for research of behavior because they are readily available in large quantities and have a short lifespan and learning is involved in processes determining sexual selection and incipient speciation (Gibson and Langen, 1996; Beltman et al., 2004) and many research programs on these processes have used insects as model systems (Coyne and Orr, 2004; Andersson, 1994). On the other hand, characters associated with reproduction play an important role in the diversification of sexually reproducing organisms (Arnqvist, 1998; Panhuis et al., 2001; Gage et al., 2002; Emlen et al., 2005). In insects, courtship behaviour often includes the extensive use of the antennae, as reported from cockroaches (Roth and Barth, 1967), crickets (Murakami and Itoh, 2003), true bugs (Ho and Millar, 2001; Rowe et al., 2006), beetles (Tallamy et al., 2002), butterflies (Friberg et al., 2008) and hymenopterans (Cheng et al., 2004; Steiner et al., 2010).

Courtship and mating behavioral patterns

For Meloidae in different parts of the world, the literature contains a plenty of the description of courtship and copulation entailing in pumping male aedegus into female genitalia (Eisner et al., 1996a; Pinto, 1974, 1975a,b, 1977a,b; Pinto et al., 1996; Turco et al., 2003; Turco and Bologna, 2005). During the descriptive study of sexual behaviour of 11 species of the genus *Pyrota*, Selander (1964) observed the adults exhibiting little aggressive behavior, and courtship involved prolonged physical contact between the sexes and male orients himself behind the female to perform a series of acts (such as leg grasp, palpal insertion beneath her elytra, lifting of her body, posterior antennation). For some details on certain meloid species, the male courtship behaviour in the blister beetle *Linsleya convexa* (LeConte) was recognized in three phases but the antennae of the male were not used in stimulating the female in any of the phases (Selander and Pinto, 1967). Features of male courtship behavior in *Pleuropompha* spp. were distinguished including the performance of all acts, such as the genital presentation from a position completely off and behind the female (posterior position), and the occurrence of a unique non-tactual display termed antennal fanning (Pinto, 1973). During courtship in the Nuttall blister beetle *Lytta nuttalli* Say, the male assumed an active role because he mounted above the female and repeated a cycle of three stereotyped, stimulatory activities: antennal manipulation, abdominal vibration, and attempted genital insertion (Gerber and Church, 1973). Sexual behaviour of the desert blister beetle *Lytta vulnerata* (LeConte), *Epicauta ochrea* (LeConte) and jagged blister beetle *Tegrodcra erosa* Lee was observed by Pinto and Mayor (1986). Also, Bologna and Marangoni (1986) described the sexual behaviour of 5 species of *Meloe* including the interspecific interactions, homosexual behaviour in males and females of the black blister beetle *Meloe proscarabaeus* Linnaeus and violet oil beetle *Meloe violaceus* Marsham. Yang et al. (2001) described the courtship and mating behavior of the dark-black blister beetle *Epicauta mannerheimi* (Maklin) and Chinese blister beetle *Mylabris phalerata* (Pallas). The sexual behaviour of *M. proscarabaeus* was observed in the fields of El-Frarafra oasis, Egypt (Ali et al. 2005). In this beetle species, males are attracted to females by sex pheromone emitted by females. Courtship may start primarily since male touched the antenna of the female partner. The male jumped on the female dorsal side rapidly and held female by fore- legs while female's abdomen was held by male mid- and hind-legs. Male abdominal tip flexed below the abdominal tip of the female and widely opened the female genitalia aperture for the entrance of the apical fleshy part of aedeagus (El-Skeikh 2007).

The repeated copulation was documented for several meloid species. In the blister beetle *L. nuttalli*, females had been copulated at least once before the first oviposition and usually again within 24 h after each oviposition. The first copulation stimulated oocyte maturation and probably also deposition of the first batch of eggs (Gerber and Church (1976). In the blister beetle *Tricrania stansburyi* (Haldeman), individuals mated more than once as they emerged from host nests (Torchio and Bosch, 1992). Random pairing was artificially made between 50 males and 50 females of the dark-black blister beetle *Epicauta mannerheimi* (Maklin) in the laboratory. One beetle mated 1.5 times on average. Each of males mated 0～4 times, and each of female ～2 times (Yang et al., 2005). In addition, both sexes of the darken blister beetle *Meloetyphlus fuscatus* Waterhouse mated more than once (Garófalo et al., 2011) which was observed for the black blister beetle *M. proscarabaeus* under laboratory conditions (Ghoneim et al., 2012a).

The size-preference was reported in the context of copulation among different animal species. There is abundant evidence that many traits do indeed affect an animal’s probability of obtaining a mate, and the quality of mate that is obtained (Andersson, 1994). One aspect of the phenotype that is often implicated in this respect is the body size. An animal’s body size may influence its mating success *via* various processes (Clutton-Brock, 1991). If either sex strongly prefers mating partners of a particular size, this behaviour may substantially modify the relationship between mating success and body size (Jennions and Petrie, 1997). Mate choice based on the body size can have numerous consequences. One such consequence is the possibility of size-assortative mating: that is, larger males will tend to mate with larger females and smaller males with smaller females (Cooper and Vitt, 1997). Among the blister beetles, the black-crossed yellow blister beetle *Tegrodera aloga* Skinner did not exhibit assortative mating, even though it formed large mating aggregations, individuals varied greatly in size, males donated a large. The absence of assortative mating in this species might occur (Alcock and Hadley, 1987). As observed in field and laboratory, both sexes of the Arizona blister beetle *Lytta magister* Horn preferred larger mates. Small beetles were left with no choice but to mate among themselves (Brown, 1990a). Brown (1990b) studied the mating system of *T. aloga* and observed males courting larger females more frequently than small females, suggesting that males prefer big mates. His results suggested that assortative mating may occur under certain conditions and may be due to large-phenotype mating advantages.

One of the most interesting post-copulatory behaviors of male is the mate-guarding that is, physically preventing other males from mating with his female before fertilization (Parker, 1970; Alcock, 1994). Mate guarding, which may increase a male’s paternity assurance, is a commonly observed behavior in insects (Alcock, 1994). Many studies have examined what characteristics of the male, female, or their social environment affect a male's guarding duration, and potentially his ability to guard successfully (for details, see: Sillen-Tullberg, 1981; Sih et al., 1990; Arnqvist, 1992; Brown and Stanford, 1992; Stoks et al., 1997; Knox and Scott, 2006). The environmental conditions, such as temperature, may affect a male's ability to guard a female effectively (Switzer et al., 2008). Saeki et al. (2005) examined the effect of the social environment on post-copulatory mate guarding duration in Japanese beetles, *Popillia japonica* in a laboratory experiment. Yamamura (1986) predicted that a male should guard his mate when the sex ratio is male-biased, when density is high, and when the female lays eggs soon after the copulation. Brown and Stanford (1992) described alternative post-mating tactics of males of the blister beetle *Nemognatha nitidula* Enns since males at the oviposition site guard their mates for an extended period after mating, whereas males that secure copulations at open flowers (the foraging site) forgo mate guarding.

Cantharidin as a nuptial gift in courtship

Nuptial feeding includes any form of nutrient transfer from the male to the female during, or directly after courtship and/or copulation. In insects, this may take the form of nuptial gifts of food captured or collected by the male, parts, or even the whole of the male's body, or glandular products of the male. There has been considerable debate over the selective pressures responsible for the evolution and maintenance of nuptial feeding in insects (Trivers, 1972; Simmons and Parker, 1989). A summary of different hypotheses for the function of nuptial gifts in insects was presented by Gwynne (1997). For more information, see Parker and Simmons (1989), Boggs (1995), Vahed (1998) and Gwynne (2008).

The function and intrinsinc role of cantharidin (haemolymph exudation through leg joints or/and antennal pores) in the courtship behaviour of the family Meloidae has been never fully established. McCormick and Carrel (1987) suggested that cantharidin might be used by female when selecting a mate at close range. Pinto (1974, 1975b) was, in fact, the first to consider male cuticular pores on antennae as being involved in the courtship behaviour of species from the genera *Linsleya* and *Tegrodera*. According to Alcock and Hadley (1987), *T. aloga* individual males donated a large, cantharidin-containing spermatophore to their mates, and body size was correlated with the size of the cantharidin-producing accessory glands. Studies on the blister beetle *Epicauta nyassensis* (Haag-Rutenberg) showed a correlation between density of cuticular pores and cantharidin titer of the scape and pedicel segments. There are many canal-shaped structures in the male scape stretching from the antennal haemolymph to the antennomere surface. Female may be able to discriminate the opposite sex with abundant reserves of cantharidin prior to mate (Nikbakhtzadeha et al., 2007a,b). Also, Nikbakhtzadeh et al. (2008a) calculated the cuticular pore density in antennae of the meloid adult beetle *Cyaneolytta* sp. and suggested that a natural system has developed in the females enabling them to select the mate with high titers of cantharidin. In addition, the involvement of "cantharidin" in courtship behaviour has been already confirmed for certain canthariphilous insects (Eisner et al. 1996 a, b; Frenzel and Dettner, 1994; Frenzel et al., 1992; Hemp et al., 1999).

Egg-laying behavior

The oviposition and egg-laying behavior is, also, one of the most intensively studied behaviour in Meloidae. In nature, each meloid species may attack only a single species or genus of solitary wild bees, grasshoppers, crickets, or wasps (For review, see Ghoneim, 2013). The adult females dig or excavate burrows (or cylindrical holes) in the ground close to the nests or burrows of the host. Generally, the eggs are deposited in the soil within a tubular chamber at a depth of 3 to 4 cm normally in clusters or batches. The female covers the eggs after oviposition with a protective matrix (Pinto and Selander, 1970; Church and Gerber, 1977a,b; Patnaik et al., 1993; Pinto et al., 1996).

Mating in some meloid species often continues for many hours since a pair of the shiny metallic blister beetle *Lytta cyanipennis* (LeConte), in USA, lasted over 11 hours. Adults mate end-to-end; they continue feeding on flowers during mating, often pulling in opposite directions, but rarely become disengaged (Selander, 1960). The excavating oviposition chambers or holes had been recorded for the variegated blister beetle *Meloe variegates* in which pregnant females dig holes at 2 to 3 cm deep in the ground and each lays several batches of yellow eggs (Bohac and Winkler, 1964). In Egypt, *M. proscarabaeus* had been observed, in the field, excavating the egg chambers during January. Female used its mandibles and fore- and hind-legs for digging a chamber of 5x5 cm diameter and 4 × 6 cm deep (El-Sheikh, 2007). Several meloid beetles in different states in USA, such as Clematis blister beetle (*Epicauta cincerea* Fabricius), ashgray blister beetle (*Epicauta fabricii* LeConte), margined blister beetle (*Epicauta. funebris* Horn) and Florida blister beetle (*Epicauta floridensis* Werner), as well as nectar-sucking blister beetle *Nemognatha nemorensis* Hentz, pale blister beetle *Nemognatha pallida* Dillon, orange blister beetle *Zonitis vittigera* (LeConte) were observed ovipositing egg masses in the ground or under stones (Meloinae) or on the food plant of adults (Nemognathinae) (Selander and Fasulo, 2010). Also, Dattagupta and Nath (2010) described the mating and egg-laying behaviour of *M. phalerata* in India.

NON-SEXUAL BEHAVIOR

Feeding tactics

Host plant quality is a key determinant of the fecundity of herbivorous insects and also affects the insect reproductive strategies (Caroline and Simon, 2002). Different host plants can also play an important role in population increase and outbreaks of polyphagous insect pests (Singh and Parihar, 1988). Some studies revealed that insects significantly show sex-specific differences in feeding behaviors and adult nutritional requirements (Erhardt and Rusterholz, 1998; Cornelius et al., 2000; Rusterholz and Erhardt, 2000). Feeding activity of some meloid species was recorded by Selander (1969) where adults are seldom found dispersed generally through an area of food plant, but rather tend to aggregate which make them to be agricultural pest.

For some details, adult feeding activity of *L. convexa* was studied (Selander and Pinto, 1967) and feeding preference of the orange blister beetle *Mylabris pustulata* (Thunb) was recorded (Shukla and Upadhyaya, 1972). Field investigation of naturally occurring densities of three-striped blister beetle *Epicauta occidentalis* Werner and *E. funebris* in USA was achieved. Several plant parameters, such as alfalfa stem height, stem density, and developmental stage may partially influence the occurrence of *E. occidentalis* on the alfalfa cultivars or experimental lines (Zhu and Higgins, 1994). In Egypt, Ali et al. (2005) recorded some field observations on the feeding activity of the black blister beetle *M. proscarabaeus*. Immediately after emergence, adult beetles were seen moving in swarms to faba bean (*Vicia faba*) fields where they disperse and starting to feed for a period of up to 50 days. Under laboratory conditions, the feeding activity of the gloomy blister beetle *Rhabdopalpa atripennis* Fabricius was studied on the host plant *Luffa cylindrica*. Both normal and 24 h starved adults of *R. atripennis* fed on the leaves of *Luffa cylindrica* more than other plant parts both in light as well as dark condition (Shukla and Singh, 1982). The food preference of the blister beetle *Epicauta atomaria* Germar to different species of passion fruit *Passiflora* spp., in free choice and no choice tests was evaluated by Junior et al. (2007). The plant species *P. laurifolia* and *P. alata* had been found resistant to *E. atomaria*, expressing the type of resistance of no preference for feeding. Ghoneim et al. (2012 b) investigated the adult food preference of *M. proscarabaeus* to some host plants, under multiple-choice conditions. On using *Vicia faba* as a comparison purpose, the feeding interest of adults was estimated in 1.04 for *T. alexandrinum*, 2.26 for *Lactuca sativa*, and 0.15 for *Pisum sativum*.

Concerning the feeding behaviour of larvae, particularly the first instar larvae (triungulins), larvae of the species belonging to tribes Epicautini and most Mylabrini are predaceous on grasshopper (Acridoidea) egg-pods while larvae of the remaining tribes in the family feed on the provisions and immature stages of various aculeate Hymenoptera, particularly wild bees (Apoidea) of different families. A few genera of tribes Lyttini (*Australytta*) and Mylabrini (*Ceroctis*) attack other aculeate hymenopterans (Vespoidea and Sphecoidea), and larvae of few *Epicauta* are reported to feed on eggs of their own species or of other congeners (Selander, 1981, 1982a,b). Among Lyttini, the extreme adaptation to phoresy on carabid beetles and the possible trophic specialization to feed on termite eggs occur in the genus *Cyaneolytta* (Di Giulio et al., 2003) but also the trophic adapation to feed on Masaridae wasps by larvae of *Australytta* (Bologna, 2003). In the tribe Mylabrini, almost all described species are predators on the Acridodidea cocoons; probably this is a derived condition in the subfamily, but very few taxa, particularly *Ceroctis*, mirror the plesiomorphic feeding habit, but feeding on Sphecidae rather than on Apoidea (Bologna and Di Giulio, 2011). However, the phoresy will be discussed thereafter.

Defensive measures

Insects suffer a wide variety of enemies, including vertebrate and invertebrate animals. To protect themselves, they have a wide range of defense mechanisms including mechanical defenses, cryptic morphology, mimicry, structural characters and retreating (Huheey, 1984; Nation, 2002; Gullan and Cranston, 2005; Eisner et al., 2005; Meyer, 2005). There is a great variation in the presence and absence of chemical defensive weapons among insect orders and families to even within families (Pasteels et al., 1983). Many compounds are derived from the main food source of insect larvae, and occasionally adults, whereas other insects are able to synthesize their own toxins (Howse, 1984). In reflex bleeding, insects dispel their blood, haemolymph, or a mixture of exocrine secretions and blood as a defensive maneuver. Reflexive bleeding occurs in specific parts of the body (Blum, 1981).

Meloid beetles have been attacked by some insects and other natural enemies. It was reported that some blister beetles such as *Meloe* spp. are attacked by *Pedilus* (Pedilidae) (LeSage and Bousquet, 1983) and/or by some species of Miridae (Pinto, 1978). Also, the dark blister beetle *Epicauta murina* (LeConte) and *E. fabricii* are attacked by *Pedilus lugubris* (Pyrochoridae)(Williams and Young, 1999). A curious behavior was recorded by Mafra-Neto and Jolivet (1994) because some of *Aristobrotica angulicollis* (Chrysomelidae) were found feeding on the meloid beetle *Epicauta aterrima*; some individuals were observed preying adult meloids that had fallen from the plant and remained immobile, engaging in thanathosis or similar behavior (Moura, 2011). However, the majority, if not all, species of Meloidae usually exhibit a defensive behaviour such as a chemical strategy. Haemolymph is often discharged, as a defensive vehicle, and in many cases it contains highly toxic compounds which have been synthesized either *de novo* by the beetle itself (Blum, 1981) or *via* bacterial symbiosis. When attacked or disturbed, adults of blister beetles release haemolymph droplets in so called "reflex bleeding". The highly toxic material, "cantharidin" in the haemolymph, is a well defensive reaction against the aggressive creatures. Cantharidin is considered responsible for the repellent properties of meloid haemolymph against a wide variety of predators (Carrel and Eisner, 1974). Although the haemolymph droplets (containing cantharidin) have been discharged from adults, larvae exude a milky solution containing cantharidin out of their mouth (Alexander, 1984).

Apart from cantharidin and palasonin the corresponding non-toxic imides cantharidinimide and palasoninimide could be identified in various body parts of the meloid beetle, *Hycleus lunata* (Dettner et al., 2003). While the Indian shrub *Butea frondosa*, contains (S)-(–)-palasonin of high enantiomeric purity, palasonin from *H. lunata* shows a low ee with the (R)-(+)-enantiomer (20–50ee) prevailing. Despite this difference between the insect-derived and the plant-produced product, an uptake of palasonin from hitherto unknown plant sources in the environment of *Hycleus* appears to be highly unlikely; however, palasonin may be produced by oxidative demethylation of cantharidin (Fietz et al., 2002).

Cleaning antennae

In insects, grooming behavior seems particularly useful because it is a widespread and prominent part of their behavioral repertory. There is variation in the behavior patterns and the structures used for grooming in insects. Oral cleaning of the legs and antennae is common in the orthopteroids, and is thought to be the primitive condition for insects (Jander, 1966). Cleaning behaviour in cockroaches involves chewing movements of the mouthparts (Smith and Valentine, 1986). However, Lipps (1973) provided an excellent review of grooming literature. In addition, comparative studies of several orders had been based on grooming behavior (Hlavac, 1975; Valentine and Glorioso, 1979). In order Coleoptera, Valentine (1973) divided the grooming movements into 3 categories: 1) cleaning: appendages are passed through the mouth; 2) rubbing: with one or more legs; and 3) positioning: involving adjustment of the elytra, wings, or abdomen.

Antennal cleaning of the meloid adults is one among the reported behavioral patterns and habits in this family. The male courtship behavior in the flattened blister beetle *Phodaga alticeps* LeConte includes stimulation of the female partner consisting of periodically curling the antennae around those of the female and at the same time stimulating her maxillary palpi with the middle legs (Pinto, 1972b). The antennal cleaning behaviour for *L. convexa* was described (Selander and Pinto, 1967). In the tribe Meloini (Meloinae), males and females show antennation during the pre-copulatory phase of the courtship behaviour (Bologna, 1991a). Turco et al. (2003) described the cleaning behavior of five species in the genus *Cerocoma*. They provided a morphological analysis by scanning electron microscopy of sexually dimorphic anatomical features of antennae, maxillary palpi, and forelegs, involved in cleaning and sexual activities. Turco (2005) described this behaviour, also, for the three-spotted blister beetle *Lydus trimaculata* Fabricius. In addition, Li et al. (2009) discussed the biological function of sensilla on the antennae of the blister beetle *Epicauta chinensis* Laporte using the scanning electron microscopy and discriminated the different types, quantity and distribution in males and females.

PHORESY OF MELOIDAE

For dispersal, many living species are unable to leave a host, crawl around, and find a new host, so they must rely on external factors to be transmitted. Biotical factors may be important in passive transport and the process, by means of which an animal is passively transported by a selected carrier of different species, is known as "phoresy" (Macchioni, 2007). Shortly, phoresy is a phenomenon in which an animal actively seeks and attaches to another animal in order to disperse (Athias-Binche, 1994). Phoresy, as a transferring behaviour, may be, also, used for migration of arthropod animals (Binns, 1982). Phoresy was, generally, reviewed among the entomophagous insects (Clausen, 1976).

Because several blister beetles are poor flyers, different theories have been provided for explanation of their dispersal ecology. Various studies have shown that many blister beetles use phoresy to locate their food source (Saul-Gershenz and Millar, 2006). This tactic can also enable the species to disperse further than it would be able unaided (Houck and O'Commor, 1991). One of the most wonderful behaviors attracting the attention of many entomologists in the world is the bee-beetle interrelationship. Some thought that correlation no more than "phoresy", that is the beetle triungulins attach themselves to the hairs of the host bee body in order to be transported to the bee nest in which they feed on eggs and provision. On the other hand, some believed that the interrelationship should include more aspects and has a greater significance, as discussed hereafter. It is worthy to mention that the larval behaviour had been reported in the literature for some meloid species such as *M. proscarabaeus* (Selander, 1981; Di Giulio and Bologna, 2007), short-necked oil beetle *Meloe brevicollis* Pans. and rugged oil beetle *Meloe rugosus* Marsham (Klausnitzer and Rauch, 2000), and Ethiopian blister beetle *Cyaneolytta fryi* (Wollaston) (Selander, 1987).

What is the correct term, parasite or predator, in blister beetles? Although Luckmann and Assmann (2005) reported that the knowledge of the ecology of host-parasite interaction of most species is scanty, evaluation of the relevant literature indicates plenty of the research works on this bee-beetle association in nature (Danielyan and Nalbandyan, 1971; Erickson and Werner, 1974 a,b; Erickson et al., 1976; Liakos and Katrali, 1984; Quintero and Canales, 1987; Blochtein and Wittmann, 1988; Bologna et al., 1990; Sharouzi, 1996; Paulmier et al., 1999; Hafernik and Saul-Gershenz, 2000; Topolska et al., 2001; Saul-Gershenz and Miller, 2006). Also, although many reports referred to such interrelation as "host-parasite", we think the correct description is ″prey-predator″ because the beetle first instar larvae (triungulins) usually predate on the eggs and/or larvae in the bee nests or burrows, and may feed also on its provision like honey and pollen. However, we will use the commonly referred term of this interrelation that is "host-parasite"!

Historical viewpoint

Historically, phoresy of meloid beetles and some other insects have been known since the mid-1800s (Newport, 1851) and were summarized by Beauregard (1890). The parasitic relationship of Meloidae with Hymenoptera was earlier since the description provided by DeGeer (1775) (*cf.* Clausen, 1940). Newport (1845) determined that the triungulins were carried into bees' nests and latter described the older instars from cells of the hymenopterous *Anthophora*. Fabre (1857) studied the oil beetle *Apalus muralis* Foerster developing in the cells of *Anthophora*. Many of the meloid species not yet associated with a bee host have apparently narrow host-plant associations as adults (Enns, 1956; MacSwain, 1956; Werner et al., 1966). Erickson et al. (1976) published a synopsis of bee hosts of the meloid larvae. Some taxa are highly host specific, and eggs may or may not be deposited on the same plants of hosts. The plants upon which eggs are deposited may help locate the host bee, because first instar nemognathine beetles attach to bees visiting these plants and are carried back to the bee's nest. However, Engel (2005) investigated an Eocene ectoparasites of bees and concluded the occurrence of phoretic meloid triungulins in middle Eocene (Lutetian) Baltic amber. The most bee species are probably potential hosts although many host-parasite relationships remain unknown (Stephen et al., 1969). In spite of the prevalence of phoresy in Meloidae, some are non-phoretic as reviewed herein.

Phoresy prevalence in Meloidae

The available literature reported this ecological phenomenon in some meloid species in the Old World. Two blister beetles, *M. variegatus* and *M. proscarabaeus*, had been observed as important ectoparasites of honey bees in the Province of Gilan and other parts in Iran (Tahmasebi and Esmaili, 1991). The meloid beetle *Stenoria hessei* (Schaum) was recorded in South Africa for the first time as a parasitoid of the solitary bee *Othinosmia* (*Megaloheriades*) *schultzei* (Kuhlmann and Timmermann, 2009). In France, a scarce incident of the triungulin presence of *M. proscarabaeus* was found in the honeybee (*Apis mellifera* Linnaeus, Hymenoptera: Apidae) colonies. In the honeybee colony, the larvae of *M. proscarabaeus* nourish on the stored food and the bee's eggs. As well as, a parasite of the honey bee was recognized only as larvae of *M. variegatus*, which fed on the honeybee's haemolymph (Chorbinski and Tomaszewska, 2004). In Loire-Atlantique, pictures taken by Mahe (2008) showed how the triungulins of *Stenoria analis* (Schaum) cling to the males of the ivy bee *Colletes hederae* Schmidt and Westrich (Hymenoptera: Colletidae) to reach the nest of host bees where the larvae will complete their life cycle. A male of the ivy bee brought into contact with the triungulins became infested over its whole body. During copulation, the triungulins transfer to the female attaching themselves to the back of her thorax. Once she has forty and more triungulins the female bee cannot fly properly any longer, and will starve to death. The triungulins will probably die as well (Moenen, 2009).

For reviewing some meloid species in the New World, the Hopping's blister beetle *Lytta hoppingi* Wellman larvae are nest parasites of solitary bees in USA (Selander, 1960). A parasitic relation of the blister beetles *Sitaris muralis* Forster on *Anthophora* bee (Hymenoptera: Anthophoridae) had been described by Richards and Davis (1977). The black oil beetle *Meloe niger* Kirby infested 4 to 31% of alkali bee *Nomia melanderi* Cockerell (Hymenoptera: Halictidae) nest cells in the Touchet Valley (southeastern Washington, USA) during the period 1973 to 1976, before control by pit-fall trapping (Mayer and Johansen, 1978). In USA, also, parasitism of the blister beetle *T. stansburyi* was accomplished through phoresy by triungulins and the entire host cell provision was consumed by the first five instars (sixth and seventh instars did not feed) (Torchio and Bosch, 1992). Some meloid larvae had been reported as parasitoids on a variety of hosts (mostly bee larvae and grasshoppers) in the Columbia River basin (USA-Canada) (Johnson, 1995). In southern Brazil, the blister beetle *Tetraolytta gerardi* (Pic) was recorded developing in the nests of the bee *Monoeca haemorrhoidalis* (Smith) (Hymenoptera: Apidae) (Bologna and Pinto, 2007). In Brazil, also, the reproductive biology of the meloid beetle *M. fuscatus*, a kleptoparasite of the bee *Eulaema nigrita* Lepeletier (Hymenoptera, Apidae) nests, was investigated. The adult parasites were never observed trying to leave the host nests. The triungulins of the meloid beetle *M. fuscatus* most likely transfer to female bees during mating and were transported to the nests of the bee *E. nigrita* to consume the bee egg and the larval food stored in the cell (Garófalo et al., 2011).

Thus, the majority of reported works obviously denoted the attacking and feeding of invasive blister beetles on the bee progeny and/or provision. Erickson et al. (1976**)** recorded some potential bee hosts for the beetle species of subfamily Nemognathinae. Among the 6 apoid host families listed, Anthophoridae and Megachilidae were most frequently cited. On the other hand, Erickson and Werner (1974a) discussed the life history of 4 species of bee-associated Nearctic Meloinae under the laboratory conditions and concluded that the immature of these beetles are polyphagous because eggs or larvae of bees were not necessary for normal development.

Triungulin adaptations and devouring capability

As reported by Di Giulio et al. (2005), the triungulins of South American blister beetle *Epispasta abbreviata* (Klug) are highly adapted for phoresy on bees and resemble the triungulins of several other phoretic genera in the subfamily Meloinae. Phoretic larvae have several common structural features that allow the presumption of phoresy even if behaviour is not observed (Selander, 1985). These structures include the well sclerotized body and modifications of the head and legs which are adapted for grasping the setae of its host (MacSwain, 1956; Pinto and Selander, 1970; Selander, 1985).

To imagine how damage can be caused to host bees by the phoretic meloid larvae, some meloid species require only the pollen contents of one bee's larval cell to complete their development, but others need more and attack several cells. In doing so, larvae of these species frequently kill and consume the immature stages of the host bee as well as consuming their pollen stores (Selander, 1960). Triungulins of *Meloe* spp. are sometimes so numerous that they can kill the bees simply by overloading. The triungulins, safe from their hosts, are transported by them right into the hives. Once inside the colonies, the triungulins drop off, attack and devour eggs, brood (*Meloe franciscanus* Van Dyke), honey (*M. proscarabaeus*) and pollen. Some, like the larvae of the variegated blister beetle *Meloe variegatus* Donovan, are even capable of sucking the haemolymph of adult bees which succumb with convulsive movements (Bailey and Ball, 1991).

Scenarios of phoresy

Now, we discuss the nature of the beetle-bee interrelationship. Simply, the eggs of a blister beetle hatch in the soil holes or burrows in the vicinity close to the same host plant of a foraging bee. Soon after hatching, the triungulins climb up the plants reaching to blossoms and aggregate in huge number waiting the adult bee visit. During the nectar sucking and pollen collecting by bees, the triungulins cling themselves to the hairs of bees' thoraces. This is shortly the proposed story of how the triungulins find their way to the nests or burrows of the host bees. For more details, Askew (1971) declared that the bee-beetle interrelationship has been described as "phoresy", the term which means the ride of an organism on another one for transporting to certain site or location. It is important to remember that not all blister beetle species are phoretic because some are non-phoretic (as will be discussed later). Also, it may be fruitful to note that larvae of several blister beetle species of the genus *Cyaneolytta* are phoretic on carabid beetles (Di Giulio et al., 2003). Nevertheless, it seems that the bee-beetle interrelationship is not just a phoresy but more complex process since Saul-Gershenz and Millar (2006) reported a well developed, multistep phoretic system in which the passenger species not only rides on the host but activity lures the host to it by mimicking the host's sex pheromone and subsequently parasitize the host's nest. Such study system comprised the blister beetle *Meloe fransciscanus* VanDyke and its host, the solitary bee *Habropoda pallida* Timberlake (Hymenoptera: Anthophoridae), which inhabit sand dunes in the deserts of the southwestern United States. The larval aggregations of the blister beetle cooperate to exploite the sexual communication system of their hosts by producing a chemical cue that mimics the sex pheromone of the female bee. Male bees are lured to larval aggregations, and upon contact (pseudocopulation) the beetle larvae attach to the male bees. The larvae transfer to female bees during mating and subsequently are transported to the nests of their hosts.

Almost similar story was narrated for the European blister beetle *S. analis* with the Ivory solitary bee *Colletes hederae* Schmidt and Westrich (Hymenoptera:

Colletidae). Their observations suggested that clusters of newly hatched beetle triungulins sexually deceive the patrolling males of their host. Males of the bee *C. hederae* usually emerge a few days or weeks before the females, and engage in very conspicuous male-male competitions to access virgin females emerging from their underground natal cell. The formation of these spectacular “mating balls” suggests that female sex pheromone might be responsible for mate location and recognition in this species. Newly hatched triungulins of *S. analis* remained at their emergence site and formed coherent groups that triggered approaching flights of patrolling *C. hederae* males. A few males of the bee instantaneously approached the larval clusters of the beetle and attempted copulation (that is, pseudocopulation) with the latter, collecting small groups of triungulins on their body in the process (Vereecken et al., 2006). Results of Vereecken and Mahe (2007) illustrated that the bee *C. hederae* males are drawn to larval aggregations of the beetle *S. analis* by means of an olfactory cue, in a manner reminiscent of approaching flights to emerging, conspecific females. This hypothesis constitutes a striking parallel to results of another study carried out on the American blister beetle *Meloe fransciscanus* (Hancok) and its host, the solitary bee *H. pallida*. In this context, Hafernik and Saul-Gershenz (2000) described triungulins grouping together and releasing sex pheromone-mimicking compounds that triggered pseudocopulations of male bees with the larval aggregations. Once on board the male bee, the beetle larvae are then transferred onto the body of conspecific female bees during “genuine” copulations, and they are ultimately brought back to the bee’s nest as the female bee discharges its pollen load to provision its brood cells.

Phoresy as a dispersal way

Phoresy behaviour of Meloidae as dispersal way had attracted the attention of many researchers because the available literature contains many reports about it. In their taxonomic work on the West Indian meloid fauna, Selander and Bouseman (1960) hypothesized the phoresy as an important factor in the dispersal of the Meloidae which gains support from the fact that the West Indian meloid fauna is composed of two distinct groups, one of which is constituted by the genera *Tetraonyx, Cissites, Pseudozonitis*, and *Nemognatha* (the subfamily Nemognathinae) sharing a number of specialized characters besides phoresy. The early blister beetle *Apalus bimaculatus* Linne develops in the nests of the solitary bee *Colletes cunicularius* (Hymenoptera: Colletidae) (Notini, 1942) and needs a dense population of the bee for successful reproduction (Cederberg, 2003). There are no studies showing that the beetle larva of *A. bimaculatus* uses their solitary bee *C. cunicularius* hosts to disperse, but the presence of the phoresy strategy in several related species (Bologna and Pinto, 2001) make it plausible that this also occurs in *A. bimaculatus* (Bologna et al., 2008). The dispersal of the blister beetle *A. bimaculatus* may be closely linked to the dispersal of the bee *C. cunicularius* (Ahlbäck, 2010).

Non-phoretic Meloidae

In spite of the phoretic behaviour of triungulins has been recorded among the majority of Meloidae, some meloid genera or species have been recorded as non-phoretic. Generally, al1 blister beetles of the oceanic islands have phoretic first instar larva (Bologna and Marangoni, 1990) but the *Hycleus rufipalpis* (Escalera) is the first non-phoretic species of the Macaronesian Islands (Bologna, 1992). The Old World tribe Cerocomini have non-phoretic triungulins which are actively reaching the host’s nest where they develop to adult stage (Turco and Bologna, 2007). The blister beetles in subgenus *Micromeloe* would be the second non-phoretic subgenus within the tribe Meloini next to *Physomeloe* (Luckmann and Scharf, 2004). As reported by Di Giulio and Bologna (2007), in the subfamilies Tetraonycinae, Nemognathinae and Meloinae, the phoresy phenomenon evolved several times independently, giving rise to different larval types, with many morphological convergences, but Nemognathinae still show a non-phoretic triungulin larva in the basal tribe of Stenoderini. Within the Meloinae there are different types of non-phoretic triungulins in all 7 tribes, with a wide variety of morphological adaptations connected to different feeding strategies. According to its morphology, the triungulin of *Trichomeloe* is not phoretic, but probably reaches the nest of a bee species, as in other Lyttini genera (Bologna and Di Giulio, 2008).

Behavioral patterns as tools for the systematics of Meloidae

The study of sexual and egg-laying behaviour patterns had been largely utilized in phylogenetic analyses and classification of meloid beetles (Selander, 1960, 1965, 1982 a,b, 1984, 1987; Selander and Pinto, 1967; Mathieu, 1967; Church, 1967**;** Selander and Mathieu, 1969; Pinto and Selander, 1970; Gerber and Church, 1973; Pinto, 1973, 1974, 1980, 1991; Pinto and Mayor, 1978; Bologna and Marangoni, 1986; Pinto and Adriean, 1986; Pinto et al., 1996). For some examples, Church (1967) studied the egg-laying behaviour of 11 species from the subfamily Lyttinae and suggested some relationships among species of the genera *Lytta, Linsleya* and *Epicauta*. The courtship behaviour of *Negalius, Phodaga* and *Cordylospasta*, three closely related genera of blister beetles, was compared (Pinto, 1972 a). On the basis of courtship behavior, Pinto (1975a) revised the taxonomy of three North American species of the genus *Epicauta* and separated from one another and from the Maculata group, the two-thorny blister beetle *Epicauta bispinosa* Werner*, Epicauta punctipennis* Werner and

Epicauta cazieri Dillon. The description of courtship behavior in the 3 allopatric species of *Tegrodera* was found similar to that in Eupompha and Pleurospasta (Pinto, 1975b). The sexual behaviour of another meloid genus, *Cysteodemus*, was described by Pinto (1977a). Pinto (1977b) expanded the study to compare the sexual behaviour in 18 species, representing all 8 genera of the subtribe Eupomphina. Early in the present century, Turco (2005) described the sexual behaviour of the blister beetle *Lydus trimaculatus* Fabricius and provided some information on courtship of other six species of different genera of the tribe Lyttini, in the field. The courtship behavior of *Meloe decorus* Brandt and Erichson and *S. muralis* was described by Lückmann (2005). He showed, also, the differences to other subgenera within the genus *Meloe*.

Some classification works of Meloidae were based on the phoretic behavior (Pinto et al., 1996; Bologna et al., 2001; Bologna and Pinto, 2001). In his review of the family, MacSwain (1956) summarized the triungulin structure in four subfamilies, Tetraonycinae, Horiinae, Nemognathinae and Meloinae. Phoresy was the only justification for separating Meloinae from a fifth subfamily, Lyttinae. As defined by MacSwain and certain earlier authors (BoÈving and Craighead, 1931), Meloinae was restricted to the Holarctic genus *Meloe* Linnaeus. Selander (1964) collapsed MacSwain's five subfamilies into two, Nemognathinae and Meloinae, the latter including *Meloe* and numerous non-phoretic taxa. Although no longer according *Meloe* subfamily status, Selander continued to emphasize phoresy by placing the genus in its own tribe, Meloini (Bologna and Pinto, 2001). Some genera of the tribe Nemognathini, such as *Stenoria*, show impressive adaptations to the phoresy, such as the evolution of a “trident” claw (claw and lateral modified setae), which totally parallels that of some *Meloe* (subgenera *Lampromeloe, Meloe, Treiodus*) (Bologna and Di Giulio, 2011).

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