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Full Length Research Paper

Embryonic and postembryonic development of blister beetles (Coleoptera: Meloidae) in the world: A synopsis

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Blister (oil) beetles, family Meloidae, are distributed throughout the world except for New Zealand, Antarctica and most Polynesian islands. They are characterized by their complex biology including hypermetamorphosis and diapause. The present review discusses the embryonic development of several meloid species belonging to various genera. Concerning the postembryonic development, this work reviews the life histories of some meloid species focusing on the adult longevity, preoviposition period and oviposition period. It reviews, also, the adult reproductive potential of several species and pays some attention for the immature stages, particularly the larvae of bee- and grasshopper-associated beetle species. Trials had been achieved for maintaining laboratory colonies of some meloids in different parts of the world for which failure was reported more than success. In addition, the present work shed some light on the diapause in Meloidae as an escape in time from the unfavorable environmental conditions.

Key words: Blister beetles, embyogenesis, hypermetamorphosis, triungulin, longevity, oviposition, fecundity, fertility, diapause.

INTRODUCTION

The family Meloidae (order Coleoptera) is commonly known as oil or blister beetles. Meloid species are widespread throughout the world except for New Zealand and Antarctic (Arnett et al., 2002). Distribution of meloid genera over the different zoogeographical regions was shown by Bologna (1991a, b). As reported few years ago, Meloidae contains more than 3000 species of 120 genera (Dettner et al., 1997; Arnett et al., 2002) and primarily inhabit the temperate and arid regions, as well as the sub-tropical and tropical savannas or other open habitats (Bologna and Di Giulio, 2011).

The Meloidae is one of the most interesting of all Coleoptera families on account of the remarkable biology; hypermetamorphic, that is, the first instar larva is active and campodeiform, while the subsequent larval instars are sedentary and scarabaeiform. The larvae are semi-parasitic predators, usually feeding either in the nests of bees on the larvae and food stores, or on the egg cases (oothecae) of grasshoppers (Selander, 1987; Bologna and Pinto, 2002). Postembryonic development includes 7 larval instars and 5 distinctive phases. The first instar larva has usually received the name of triungulin (more recently planidium) because of the peculiar shape of pretarsus, specialized in some genera for climbing and holding the host (Gillott, 1995; Di Giulio and Bologna, 2007).

Adult beetles can be recognized by morphological characteristics such as soft body, bright coloration, rather elongate, head deflexed with narrow neck, pronotum not carinate at sides, heteromerous tarsi, and smooth integument (Borror et al., 1981, 1989; Bologna, 1991a, b; Arnett et al., 2002). They are phytophagous, and certain groups, on account of their moderate size and swarming behavior, can cause considerable damage to crops by feeding on the foliage or flower heads (Greathead, 1963; Booth et al., 1990). Thus, a species may often be beneficial to agriculture as a larva, helping to control grasshopper populations, yet be a pest as an adult (Mayer and Johansen, 1978).

Diapause is a behavioral and physiological characteristic of blister beetles. It is a delay in development in response to regularly and recurring periods of adverse environmental conditions (Tauber et al., 1986). Understanding of diapause as a “process”, rather than as a “status”, is now widely accepted by the research communities with insects (Tauber et al., 1986; Danks, 1994; Hodek, 2002). Generally, diapause in insects is a dynamic process consisting of several distinct phases (Kostal, 2006). The dynamism during diapause is manifested in the changing responses to temperature, photoperiod, humidity, hormonal treatment and other factors, as observed in numerous laboratory and field experiments (Okuda, 1990; Nakamura and Numata, 1997; Koveos and Broufas, 1999; Tanaka, 2000; Gray et al., 2001; Fantinou et al., 2003; Higaki and Ando, 2005). The present work on Meloidae aims to review various biological parameters focusing on the embryonic development, postembryonic development and the diapause in several species belonging to various genera.

EMBRYONIC DEVELOPMENT

Before now, egg formation and development in insects had been studied (Margaritis and Mazzini, 1998; Waring, 2000; Woods and Bonnecaze, 2006). The egg shell, or chorion, of an insect is a complex of several layers. It is synthesized within the ovariole by the follicular epithelium that surrounds the oocyte and begins once vitellogenesis takes place, that is, the uptake of yolk proteins (Margaritis, 1985; Zissler, 1992). Choriogenesis is a period of intense protein synthesis, and before chorion gene expression, the follicle cells undergo several rounds of DNA replication without cell division to increase the DNA content and their synthetic capability (Klowden, 2007). Following the union of the sperm from male and the egg in female, the newly formed zygote undergoes cleavage within the patterned environment that is present in the egg (Klowden, 2007). Further information about oogenesis and vitellogenesis through the successive stages of embryogenesis can be obtained from the studies of Anderson (1972), Bownes et al. (1988), Tautz and Sommer (1995), Sander (1996), Kawamura (2001), Davis and Patel (2002), Hamdoun and Epel (2007), and Klowden (2007). The mechanism of egg hatching process can be understood based on the observations of Bianchi (1962) for the big-eared blister beetle *Cissites auriculata* (Champion) starting from the collapse of the chorion along the mid-ventral line of the embryo and ending in splitting of chorion in a straight line backwards from the head along the middle of the longitudinal depression, and soon the body of the triungulin is pushed forward through the split.

Incubation period of the insect eggs is usually the interval that elapsed between the time of egg laying and egg hatching. This period may be used as an indicator of the embryonic developmental rate. In the case of blister beetles, the major part of embryogenesis occurred in the incubation period. Egg incubation period ranges from 4 to 6 days in the case of *Zonitis immaculata* (Olivier) to 4 weeks in other meloid species, under normal temperature conditions, or up to 5 months in species that oviposit during colder seasons or that overwinter in the egg stage (Cros, 1928). Eggs of the Nuttall blister beetle *Lytta nuttalli* Say, green blister beetle *Lytta viridana* LeConte and shiny metallic blister beetle *Lytta cyanipennis* (LeConte), in the field (under 15 to 30°C), appeared to take about 2-3 weeks as incubation period (Church and Gerber, 1977). For the blister beetle *Mylabris impressa stillata* (Baudi) under laboratory conditions (28°C, 100% RH and total darkness), Nikbakhtzadeh et al. (2008) recorded two weeks of incubation period. The triungulins (the first larval instars) of the meloid beetle *Meloetyphlus fuscatus* hatched from eggs 18-20 days after oviposition (Garófalo et al., 2011). For the black blister beetle *Meloe proscarabaeus* Linnaeus, a field study was carried out by El-Sheikh (2007). Depending on his results, the shortest incubation period (23 days) was measured for those eggs laid in January (17°C, 30% RH) but the longest period (30 days) lasted for those eggs laid in December (21°C, 36% RH). Under the laboratory conditions (23±2°C, 46±10% RH, 12L: 12D photoperiod), Ghoneim et al. (2012) studied the effects of food quality on the incubation period, and consequently conceivable embryonic developmental rate, of the same beetle. The embryonic developmental duration was remarkably shortened after parent feeding on the Egyptian clover *Trifolium alexandrinum* but prominently prolonged after feeding on lettuce *Lactuca sativa*. This reflects some effects of parent food on the embryonic developmental rate which was faster after feeding on *T. alexandrinum* but slower after feeding on *L. sativa*, than that rate after feeding on the broad bean *Vicia faba*.

For more intensive studies on the embryonic developmental stages in family Meloidae, only a few species attracted the attention of researchers. As reported in the available literature, the most interesting meloid species is *L. viridana*, the embryonic development of which was described by Rempel and Church (1965). They observed porous vitelline membranes of the newly laid eggs and believed it to be the first record of this phenomenon in insects. Also, the structure of vitelline membrane of the same species was carefully examined under both the light microscope and electron microscope (Gerrity et al., 1967). The structure of the chorion and micropyles of the embryo of *L. viridania* was investigated by Sweeny et al. (1968) who discussed the peculiar characteristics of the egg structures compared with those of other insect eggs, and their significance in connection with water conservation, respiration and sperm entry. Chromatin elimination occurs in most of the embryonic tissues of *L. viridana* during the first to fifth period of embryogenesis (Rempek and Church, 1969a). In a complementary work, Rempel and Church (1969b) studied the blastoderm, germ layers and body segments of the embryo of the same blister beetle. With regard to the appendiculation of its embryo, Church and Rempel (1971) inquired about the origin of the segmental appendages including the coelomic sacs, enteron rudiments, nerve ganglia, tracheal invaginations and serosal cuticle. More details on this beetle had been provided for the cephalic apodemes and head segmentation (Rempel and Church, 1971). However, the development of respiratory system in the embryos was studied in details by Rempel and Church (1972).

In addition, the structure and development of the larval visual system in embryos had been shown by Heming (1982) as well as the structure and development of larval antennae in these embryos (Heming, 1996). Besides, the formation of stomatogasteric nervous system and endocrine system in the embryo was described by Rempel et al. (1977). In another species belonging to the genus *Lytta*, Church et al. (1970) used the scanning electron microscope to examine the structure of micropyles of *L. nuttalli* in which it was also noted that other efforts were made to study vitellogenesis and egg membrane formation (Sweeny et al., 1970). As described by Sidhra et al. (1983), the cephalic neuroendocrine system in the orange blister beetle *Mylabris pustulata* (Thunberg) includes neurosecretory cells in the brain, a pair of corpora cardiaca and corpora allata.

POSTEMBRYONIC DEVELOPMENT

The change that occurs when an insect develops from an immature stage to an adult stage is called “metamorphosis,” literally meaning “change in form”. Insects show three major metamorphic strategies for reaching the adult stage, with the degree of metamorphosis dependent on the degree of divergence between the immature and adults (Speight et al., 2008). As highlighted by Barnes et al. (2001), both molting and metamorphosis are under the control of a suite of hormones, two of the most important being juvenile hormone (JH) and ecdysone (ecdysteroids). When JH levels are reduced, molting results in the appearance of the adult directly in exopterygotes, or *via* pupation in endopterygotes. Ecdysone, on the other hand, is itself under the control of another hormone, prothoracicotrophic hormone (Hinton, 1963; Wigglesworth, 1973; Whitten, 1976; Cole, 1980; Bernays, 1986; Reynolds and Samuels, 1996; Truman and Riddiford, 1999; Nijhout, 2003; Klowden, 2007; Mirth and Riddiford, 2007).

The family Meloidae attracts the attention of entomologists because of its hypermetamorphic development that is known as the occurrence of two or more larval forms in the larval stage of each species. Also, the larval stage wholly or partially is predacious on eggs of other insects. However, the pioneering contribution to the knowledge of the Meloidae biology was the gorgeous monograph prepared by Beauregard (1890) and the extensive earlier studies on the larval biology that were carried out by Auguste Cros between 1910 and 1943, and which was published by Paoli (1937). Some other early accounts of the biology of the family were published by Newport (1851), Parker and Boving (1924), Ingram and Doglas (1932), Clausen (1940), Horsfall (1943), etc. Like other holometabolous insects, beetles’ life passes through four developmental stages: egg, larva, pupa and adult. The life cycle duration varies considerably among species of Meloidae.

The development of three-striped blister beetle *Epicauta lemniscata* (Fabricius), as for example, from egg to adult lasts 35-50 days and 3 generations may be produced annually (Ingram and Douglas, 1932). Each of the red-striped oil beetle *Meloe majalis* Linné and the striped blister beetle *Epicauta vittata* (Fabricius) has 2 generations annually (Cros, 1924a). On the other hand, the oil beetle *Apalus muralis* (Forster) has only one generation every 2 years.

As previously mentioned, blister beetles have an attractive phenomenon during the larval stage which is usually known as “hypermetamorphosis” in addition to another phenomenon “diapause”. This complex developmental process had been understood only some decades ago, but its details still vary among the species of different genera in different subfamilies. Detailed biological information about various species of the blister beetles are provided by Selander and Bohart (1954), Crowson (1960), Selander and Bauseman (1960), MacSwain (1961), Kifune (1961), Selander (1981, 1982a), Singh and Moore (1985), Whitehead (1991), El-Khouly (1992), Luckmann and Kuhlmann (1997), Topolska et al. (2001), etc. Herein, the most important outlines of the life history and biology of Meloidae are reviewed with some reference to the well studied variation through different developmental events starting from the egg deposition by adult females to the adult emergence. The majority of the following information had been driven by the field observations because the laboratory rearing of meloid species is still difficult.

Adult stage

After the termination of the pupal stage in the soil, adults emerge during a season differing from a part to another in the world and according to the species. For the rugged oil beetle *Meloe rugosus* Marsham, Whitehead (1991) recognized adults in months of September, October, November, December, January, February and April, and emergence took place in synchronous waves during September and October. Also, the periodicity of *M. rugosus* adult emergence occurs in the same period of the black blister beetle *M. proscarabaeus* (El-Shiekh, 2007). El-Shiekh (2007) reported, in a field study on this species in Egypt, a gradual increase of the emergence reaching its maximal level in the last week of January after which it decreased reaching the minimum in the third week of March.

Adult longevity varies among species and genera, and also varies in the same species, according to the sex and emergence time. Adults of the blister beetle *Tricrania stansburyi* (Haldeman) apparently did not feed and were short-lived (1-2 weeks) (Torchio and Bosch, 1992). Females of *M. proscarabaeus* survived 100-128 days but males survived 87-116 days under field conditions (El-

Sheikh, 2007). Ghoneim et al. (2012) recorded different data for the same beetle, under laboratory conditions because the total longevity of females was longer than that of males, regardless of the host plant. They investigated the differential effect of host plants on the adult female longevity. A lengthening effect of *L. sativa* was detected (89.4±1.84 days) while shortening effect was found by feeding on *T. alexandrinum* (22.70±0.95 days) or *V. faba* (27.50±1.43 days). On the other hand, Selander and Fasulo (2000) reported that adult of the meloid beetle *Nemognatha plazata* Fabricius commonly live three months or more. In nature, new adult generally rests for three or four days following emergence and their feeding begins at the adult age of 4-6 days but sexual behaviour normally appears at a mean age of about 10 days (Adams and Selander, 1979; Nikbakhtzadeh, 2004). The minimum age of males within tribes Epicautini, Lyttini and Mylabrini at first courtship is 6 days (Pinto, 1991). A periodical activity in nature was conducted by adults presumably in response to varying conditions of temperature and humidity. In hot arid areas, it has been found that adults tend to remain on or near the ground, under dense foliage for the greater part of the day (Adams and Selander, 1979). For the blister beetle *M. impressa stillata* under laboratory conditions, Nikbakhtzadeh et al. (2008) found that adult females are alive for several months and produce egg masses periodically.

Pre-oviposition period of meloid adult females varies according to the species, locality, and environmental conditions. This gestation (or ovarian maturation) period is short, being only a few days, and in some cases eggs are laid on the day of adult emergence. As regards *M. proscarabaeus*, such period may vary according to the emergence time of aestivated beetles because they emerged in mid-November and started to lay eggs 49 days postemergence, while about 48-57 days are needed by beetles which have emerge from late November to nearly mid-December in Egypt (El-Shiekh, 2007). Under laboratory conditions, the preoviposition period of the same species was affected by the food quality because feeding of parents on *T. alexandrinum* resulted in a shorter period (5.33±1.12 days) but feeding on *L. sativa* resulted in considerably longer period (8.70±1.16 days), in comparison with the measured period after feeding on *V. faba* (6.65±1.59) (Ghoneim et al., 2012). *Oviposition period* is relatively short of 2-4 weeks in most Meloidae but in the case of *M. proscarabaeus*, adults emerged from mid-November to nearly late December and commenced egg deposition during early January to nearly the beginning of February. Generally, adult females spend 3.1-3.6 days for oviposit (El-Sheikh, 2007). Under laboratory conditions, the oviposition period of the same beetle was affected by the food quality because it was estimated in 7.68±2.32 days after parent feeding on *V. faba* and slightly shortened after feeding on *T. alexandrinum* or *L. sativa* (Ghoneim et al., 2012).

Fecundity is one fundamental indicator of an animal's reproductive success. Simply, the more eggs that an adult female produces during her lifetime, the higher the probability should be that at least some of her offspring will live to reproduce (Speight et al., 2008). In reality, quality and quantity of eggs will influence the offspring survival (Rossiter, 1994). The energy and resources available for egg production are largely a function of the size of adult laying the eggs (Riddick, 2006), which in turn is related to pupal size (Bauerfeind and Fischer, 2005), and a function of food collected and assimilated by the juvenile (nymphal or larval) stage. The egg production varies within the family Meloidae, and this variation appears to be associated with proximity of hosts for the larvae. For example, in those meloids that attack locust egg pods, females deposit their clutches in the general vicinity of such egg pods. The total number of eggs deposited by these meloids is 10 or more times lower than that in bee parasitic meloids, whose larvae wait in flowers for a bee visitation so that they can hitch a ride back to the bee nest (Hinton, 1981).

Meloid species which develop on eggs of Locustidae usually produce a comparatively small number ranging from < 100 to several hundreds. These eggs are laid in batches (or masses) in shallow burrows in the hard dry soil of the host's breeding area (Clausen, 1940). As aforementioned, the number of eggs produced per female in species that attack bees is considerably larger. Probably owing to the greater hazards encountered by young larvae before they reach the host nests. Each of the blister beetles *Meloe cicatricosus* Leach and *Meloe autumnalis* Olivier lay 3000 or more eggs. A single batch of eggs of the violet oil beetle *Meloe violaceus* (Marsham) contains 3000-4000 eggs, and several additional batches, containing smaller numbers, were laid by the same female (Cros, 1930a). The red-striped oil beetle *M. majalis* was recorded to lay several thousand eggs in each batch (Cros, 1912a). Among the genus *Meloe*, each of the variegated blister beetle *Meloe variegatus* Donovan females lay 10000 eggs (Bohac and Winkler, 1964). Erickson and Werner (1974) studied the immature life histories of 4 species of bee-associated Nearctic Meloinae under laboratory conditions. They succeeded to obtain eggs from sexually mature adult females where each one laid two or more small egg masses. The total output of eggs was estimated to no fewer than 22800 eggs. The first batch usually contained the largest number of eggs, while those following were successively smaller. Egg batches of *L. nuttalli*, *L. cyanipennis* and *L. viridana* contained an average of 320, 340 and 390 eggs, respectively (Church and Gerber, 1977). As recorded by Selander (1986a), under laboratory conditions, the number of eggs per mass is quite constant within females but varies with the body size among females. Further, it varies inversely with the egg size among species. In Epicautina, Mylabrina and many Nemognathinae, the number of eggs is on the order of 50 to a few hundred. In some of the tribes such as Meloini and Lyttini, it may be as high as three or four thousand. Fecundity of the blister beetle *T. stansburyi* was high (>900 eggs per female) (Torchio and Bosch, 1992). Luckmann and Assmann (2005) studied the reproductive biology of nine meloid beetles from Central Europe. They recorded the total reproductive potentiality with up to 40000 eggs. Furthermore, the number of laid eggs strongly related to the way by which the triungulins find their host. Also, three types of reproductive strategy could be distinguished within these meloids. For rearing the blister beetle *M. impressa stillata*, under laboratory conditions, Nikbakhtzadeh et al. (2008b) found that the eggs were deposited in compact masses. The number of eggs per mass varies with body size, but was usually 30 to 40. The black blister beetle *M. proscarabaeus* was reported to have approximately 1000 ovarioles per ovary (Büning, 1994). This high reproductive potential is translated into enormous bouts of egg laying, in which the beetles dig a hole and therein deposit their immense pile of eggs (as many as 4218 eggs oviposited in one location in *M. cicatricosus* (Fabre, 1857). In comparison, females of *M. proscarabaeus* were reported to have very low fecundity because they usually lay 1995-2290 eggs/female in the field (El-Shiekh, 2007) while females of the meloid beetle *M. fuscatus* had a high fecundity (more than 8,000 eggs) (Garófalo et al., 2011).

In connection with the effect of food quality on the female fecundity, some observations on the fecundity of *M. pustulata*, maintained on two different food plants *Ipomoea cornea* and *Ipomoea tuberosa* under laboratory conditions were recorded (Manoharan et al., 1987). Beetles reared on the food plant *I. cornea* laid 144±30.80 eggs while those reared on the food plant *I. tuberosa* laid only 93±38.87 eggs. The difference in fecundity was attributed to the protein concentration in the host plant. In another laboratory study, feeding of adult beetles of *M. proscarabaeus* on each of the three host plants (namely, *V. faba, T. alexandrinum* and *L. sativa*) affected the female fecundity because feeding on *V. faba* resulted in fecundity of 1499.5±14.18 eggs in a single egg mass while feeding of *T. alexandrinum* induced the females to be more fecund and feeding on *L. sativa* deleteriously reduced the fecundity (Ghoneim et al., 2012).

Concerning the number of egg masses (or batches), female *L. nuttalli* deposited more than one egg batch under the laboratory conditions. The largest number of batches deposited by a female was 5. Batches laid by one female were of the same size, and each batch represents one gonadotropic cycle (Gerber and Church, 1976). Under laboratory conditions, also, the total output of each female of *C. auriculata* was often divided into two or more small masses; but in the field, each female usually deposited all her eggs in a single mass, adding to it from day to day. The first mass was estimated to contain no fewer than 22,800 eggs. Another mass contained about 9,000 eggs (Bianchi, 1962). Also, the adult female of *M. proscarabaeus* usually laid only one egg batch throughout its life under laboratory conditions (Ghoneim et al., 2012).

Immature stages

'Hypermetamorphosis' usually occurs as an adaptation of the ontogeny of certain parasitoid insects, notably the beetle families Meloidae and Ripiphoridae, the fly family Acroceridae, certain members of the Bombyliidae, the parasitic wasp family Eucharitidae, and the order Strepsiptera (Richards and Davies, 1977). Larval development in the family Meloidae is complicated because of the production of different larval forms. The larvae of first instar are called "triungulins" (or triungulinids) and are very highly mobile. In most species of this family, larvae disperse almost immediately after hatching, but in certain species, there is a tendency for them to remain in mass for some time around the egg shells (Pinto and Selander, 1970). In typical examples, the first-instar larval morphology is campodeiform (elongated, flattened, and active) and in this form, it does not feed. On locating its host, it undergoes ecdysis, changing its skin and adopting a scarabaeiform (grub-like) or vermiform (maggot-like) morphology (Johnson and Triplehorn, 2004).

Various ways of the meloid triungulins to gain access to hosts, on which they develop, can be discussed herein. In the case of species specializing for feeding on bees' brood, the adult females lay eggs in the burrows or soil holes usually in the immediate vicinity of their hosts' nests. Triungulins cannot be induced to enter the nest or burrow of their host bees directly, but rather entry was by carriage on the body of the adult bees (Parker and Boving, 1924). Species that oviposit entirely apart from the host bee have triungulins that frequently show a tendency to climb upwards the same host plants of bees and may congregate in large numbers onto the blossoms and wait the visit of foraging adult bees (Evans and Hogue, 2006). These triungulins have well-developed claws and adult-like legs by which they attach or cling themselves to the host bodies particularly with the hairs of thoracic region or to the abdominal intersegmental folds. The carrier bee transports the beetle triungulins back to the bee nests or burrows. This carriage may be not more than a phoresy or may be in another association (Cros, 1927a, b, d). On the other hand, some species of Meloidae attack egg-masses of acridid grasshoppers because they are specialized predators on their eggs (Selander and Fasulo, 2000). Striped blister beetle, *E. vittata*, is closely associated with grasshoppers that produce large egg-pods, particularly two-striped grasshopper, *Melanoplus bivittatus* (Say) and differential grasshopper, *Melanoplus differentialis* Thomas. Also, crickets and wasps had been recorded for some other beetle species. Furthermore, triungulins of a few meloid species evidently prey on the eggs of some blister beetles (Selander, 1981). Phoretic larvae of the African meloid beetle *Cyaneolytta fryi* (Wollaston) appear to be associated with bees, although morphological studies indicated that they are phoretic on the ground beetles, Carabidae (Bologna et al., 1990). In such cases, the way of triungulins to their host burrows is much simpler because they are already in the soil in the breeding grounds of the host and thus are dependent only on their own searching to find the egg masses. Only 1-2 eggs of host are consumed before the first moult of the blister beetle (Clausen, 1940).

Subsequent larval development and metamorphosis varied among the different species and genera of Meloidae. Considering the bee-parasitizing meloids, after reaching the nest of the host bee, the triungulins begin to feed on the eggs. Triungulins moult to the first time right after the host eggs have been consumed. The next instar larvae can float freely on the honey while feeding on it along with the immature bee larvae provision (pollen and others) inside the host bee nest (Cros, 1935; Evans and Hogue, 2006). Then, the developing triungulins moult into active grub-like larvae (feeding on the same food) of 3rd, 4th, and 5th instars. For some details, various scenarios can be appreciated. After hatching, the first instar larvae of the genus *Epicauta* will seek out grasshopper egg masses. The larvae will develop through 5-9 instars and overwinter in the last instar. However, during the adverse environmental conditions, larvae will delay the development for two or more years (Adams and Selander, 1979). More or less, another developmental pathway is followed by the molesten blister beetle *Lytta molesta* (Horn). Once the triungulin parasitizes an appropriate host nest, later the instars become progressively less active, until the 6th instar or pseudopupa has a thick exoskeleton and functionless legs. Larvae hibernate over winter in the pseudopupal form, and in the spring, it moult into the final, seventh, larval instar (Borror et al., 1989). Typically at this point, all of the host bee's pollen stores (and probably the bee larvae itself) are consumed by the meloid larvae during the previous year, and therefore the 7th instar does not feed. The 7th instar instead quickly transforms to the true pupa, completing metamorphosis and emerging in the spring, presumably timed with their bee host species' emergence (Hardwicke et al., 2009).

Continuing to discuss the development scenarios, a field study on the life history of the striped blister beetle, *E. vittata* feeding on grasshopper eggs, was carried out at warm temperature by Capinera (2003). Overwintering, also, may occur in the fifth instar, followed by pupation in the spring. Alternatively, larvae may display 6th and 7th instars before pupation, with the 6th instar persisting for about 230 days and the 7th for 6-14 days. The seventh instar is found from April through July at about the same time other individuals are pupating or emerging as adults. On some Iranian species of the subfamily Meloinae, Nikbakhtzadeh (2004) described another senario. Larvae fed during the first instar (triungulin phase) moulted into four or five following instars, in which the larva was grub-like in appearance (first grub phase). On completing feeding, the first grub larva prepared a cell in the soil apart from the grasshopper egg pod on which it fed and typically became, at ecdysis, a heavily sclerotized, and immobile coarctate larva. This larva entered diapause and passed the winter or other unfavourable period of the year in the coarctate phase. When it is close to the beginning of the next season, the larva is ecdysed again into a grub-like form (second grub phase). This phase, which entailed only one instar, was followed shortly by pupation and adult emergence. The first field study on black blister beetle *M. proscarabaeus* in Egypt was achieved by El-Shiekh (2007) who recorded 3 distinct larval phases of 7 larval instars in a certain scenario. Phase I included the 1st and 2nd larval instars (triungulins) feeding on bee-eggs and brood and it lasted 14.2±0.2 days. Phase II was represented by scarabaeiform larvae produced from the triungulins entering a rapid growth through the 3rd, 4th and 5th instars and lasting 13.2, 13.8 and 13.6 days, respectively. Phase III included the 6th and 7th (137-146 days) larval instars. The 7th instar larvae entered an aestival diapause during May, June, July, October, under the adverse conditions. On the other hand, Selander and Fasulo (2010) studied the larval development of *Epicauta* spp. which passed through 4 distinct phases: the first instar (triungulins) phase reached its feeding site and ecdysed into scarabaeiform larvae entering a period of rapid growth (first grub phase) and lasted until the end of the 5th or 6th instar. The larvae moulted again to become scarabaeiform (second grub phase). Then several alternative developmental pathways were identified depending on the ambient conditions. When the pupal stage was taken into account, the pupae of striped blister beetle *E. vittata* greatly resembled an adult, though the wings and legs were tightly drawn to the ventral surface. As reported by Capinera (2003), the pupal duration in this species is 9-13 days. They are found naturally in May-August. For *M. proscarabaeus*, the pupal stage lasted 60.3-69.3 days in the field (El-Shiekh, 2007).

REARING AND COLONY MAINTENANCE IN THE LABORATORY

Bianchi (1962) tried to rear the big-eared blister beetle *C. auriculata* on fresh bee-bread obtained from nests of the local carpenter bee *Xylocopa* sp. in Honololu (Hawaii). The larvae took little interest in the food and were never observed feeding on it and died within two or three days. Selander and Mathieu (1964) succeeded to rear *Pyrota mutata* Gemminger, *Pyrota niyrovittata* (Haag-Rutenberg) and *Pyrota palpalis* Champion on a diet of honey bee provisions and larvae, under labroratory conditions, until the coarctate phase or beyond. The first instar larvae of blister beetle *Linsleya convexa* (LeConte) failed to feed on the eggs of the grasshopper *M. differentialis* (Selander and Pinto, 1967). The immature life histories of four species of bee-associated Nearctic Meloinae under laboratory conditions were studied (Erickson and Werner, 1974). Unfortunately, a laboratory colony could not be established although several food materials were offered and a paste consisting of mixed pollen (from honey bees), honey, and a mold inhibitor was found to be the most acceptable. Selander (1986) described a rearing technique which was developed over a period of many years as an extension and refinement of procedures used initially by W.R. Horsfall in rearing *Epicauta* spp. in Arkansas (USA). His laboratory study was successful in complete and, often, extensive rearing of nearly 50 species of *Epicauta*. For the blister beetle *Psalydolytta pilipes* Maklin, attacking the pear millet (*Pennisetum glaucum*) in fields in north-west Mali (Africa), Grunshawa et al. (1994) obtained eggs from the field captured adults beetles and successfully reared the hatching larvae, feeding on egg-pods of a grasshopper, through to coarctates only.

In the present century, Zhu et al. (2005) tried to rear the Chinese blister beetle *Mylabris phalerata* Pallas in China under laboratory controlled conditions. The adaptable temperature for artificial mass rearing was ≥28°C. Nikbakhtzadeh et al. (2008) carried out an intensive work for establishing a laboratory colony of the medically important blister beetle *M. impressa stillata* in Iran but they unfortunately failed to achieve their aim. In Egypt, Ghoneim et al. (2012a) carried out some attempts to maintain a continuous culture of the black blister beetle, *M. proscarabaeus*. The triungulins were provided with clutches (honey, eggs, larvae, and provision) of honey bee (*Apis mellifera*, Hymenoptera: Apidae) but they did not take interest in food and eventually died. Similar attempt was done using the egg-pods of the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae) buried in soil, and the same negative result was obtained. However, the available literature, to this study, contains no reports of the complete success for establishing continuous colony and raising successive generations of a blister beetle. Such failure may be attributed to the delicacy and complicated system of the beetle which need much efforts and time, as well as to the cannibalistic behaviour among larvae under laboratory conditions (Nikbakhtzadeh et al., 2008).

DIAPAUSE IN MELOIDAE

Under unfavorable environmental conditions, an insect would not survive. Many species initiate a series of metabolic changes well before the unfavorable conditions actually occur. Unlike migration, which is an escape in space, diapause is an escape in time, allowing the insect to withstand the unfavorable conditions while remaining in place (Danks, 1987). For some details, insect diapause is a dynamic process consisting of several distinct phases which vary considerably from one taxon of insects to another. However, the induction phase, preparation phase, the maintenance phase and the termination phase had been discussed by several authors (Hegdekar, 1979; Chapman, 1998; Kostal, 2006). The insect diapause is affected by certain environmental stimuli and physiologically regulated by certain hormones. Photoperiod is the most common environmental factor inducing the onset of diapause in temperate-zone insects (Tauber et al., 1986; Huffaker and Gutierrez, 1999; Saunders, 2002). In many insects, temperature is another important factor affecting diapause, especially in insects living in warehouses and underground while diapause in soil-inhabiting insects can be influenced by soil temperature, moisture and oxygen (Lee and Denlinger, 1990). Diapause in the tropics poses several challenges to insects that are not faced in temperate zones (Denlinger, 1986). With regard to neuroendocrine regulation, there are several key hormones involved in the regulation of diapause: JH, diapause hormone, and prothoracicotropic hormone (Brown and Chippendale, 1978; Yin and Chippendale, 1979; Horie et al., 2000; Denlinger, 2002). Insects must reduce their metabolism without the aid of cold temperatures and may be faced with increased water loss due to high temperatures. The diapause phases can be characterized by particular sets of metabolic processes and responsiveness of the insect to certain environmental stimuli (Chapman, 1998; Kostal, 2006).

The *larval diapause* in the blister beetles *Pyrota mutata* Gemminger, *Pyrota niyrovittata* (Haag-Rutenberg) and *Pyrota palpalis* Champion was studied under laboratory conditions (Selander and Mathieu, 1964). Nagatomi (1968) attributed the diapause to the temperature of pre-cold season (before winter) under which all beetles do not operate upon the elimination of diapause, that is, the temperature necessary for the termination of diapause in all of the individuals. According to Selander and Weddle (1969), species of the genus *Epicauta* have both an extended and abbreviated pattern of postembryonic development. The former involves, successively, a triungulin or dispersal phase (the 1st instar), a first grub or feeding phase encompassing 3-5 instars (4 or 5 in Meloinae), a coarctate or resistant phase normally characterized by diapause, and an active second grub phase immediately preceding pupation. Larvae following the abbreviated pattern develop directly from the first grub phase to the pupal stage, without diapause. With few exceptions, larvae of *Eipicauta segmenta* (Say) reared at 27°C followed the extended pattern and diapaused as coarctates, while those reared at 35°C followed the abbreviated pattern. As reported by Selander and Weddle (1972), the thermal stimulation was sufficient to terminate diapause in coarctate larvae of the blister beetle *Epicauta segmenta* (Say). In Iran, Nikbakhtzadeh (2004) reported that the meloid larvae fed during the first instar (triungulin phase) and the four or five following instars appeared in a grub-like form. On completing feeding, the first grub larva became, at ecdysis, a heavily sclerotized, and immobile coarctate larva. This larva entered diapause and passed the winter or other unfavourable period of the year in the coarctate phase. In Egypt, diapause of the black blister beetle *M. proscarabaeus* was recorded by El-Shiekh (2007) who recorded the heavily sclerotized 7th instar larvae which remained immobile for 137-146 days in the soil. The 7th instar larvae entered an aestival diapause during May, June, July, and October, under the adverse conditions. In China, the effect of environmental conditions on diapause in the blister beetle *M. phalerata* was investigated by Zhu et al. (2006).

Depending on their results, the early larval instars, particularly, the second larval instar, appeared to be more important for diapause induction than the latter instars. When the last instar larvae were kept at 26°C or more, they did not enter diapause but when they were kept under 25°C, they entered diapause, regardless of the soil water content and photoperiod. After two years, Zhu et al. (2008) determined the effect of temperature upon the difference in development characters between the same blister beetle and its acridid prey *Chondraris rosea rosea*. They suggested that the development of the beetle was seasonal synchronizing with the development of its prey, and diapause of the beetle synchronized its development and its prey.

In USA, Selander and Fasulo (2010) studied *Epicauta* spp. in which a diapause period was recorded because the 6th instar larvae moulted into scarabaeiform and then several alternative developmental pathways were identified depending on the ambient conditions. In Japan, Shintani et al. (2011) carried out a study on the bean blister beetle *Epicauta gorhami* Marseul which undergoes larval diapause in the 5th instar as a pseudopupa. The effects of temperature, photoperiod and soil humidity on larval development were examined, using egg pods of *Locusta migratoria* L. as food.

With regard to the *egg diapause* in blister beetles, the diapause incidence of *Mylabris cichorii* Linnaeus offspring was evaluated by exposing parents' generation and offspring to different photoperiods and temperatures in order to determine the best conditions for diapause induction and termination (Gao et al., 2011). The results revealed that diapause of *M. cichorii* eggs could be induced by short photoperiod and could be terminated by low temperature (10°C) treatment for 10 days. They concluded that photoperiod is the critical environmental factor in the induction of egg diapause. The *pseudopupal diapause* in the same blister beetle was studied in Japan to determine the effects of temperature and photoperiod on its termination.

Diapause was terminated by exposure to low or high temperature, but not by transfer to long-day conditions. The optimal low temperature for diapause termination was 10-15°C, but a higher or lower temperature was less effective (Terao et al., 2012).

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