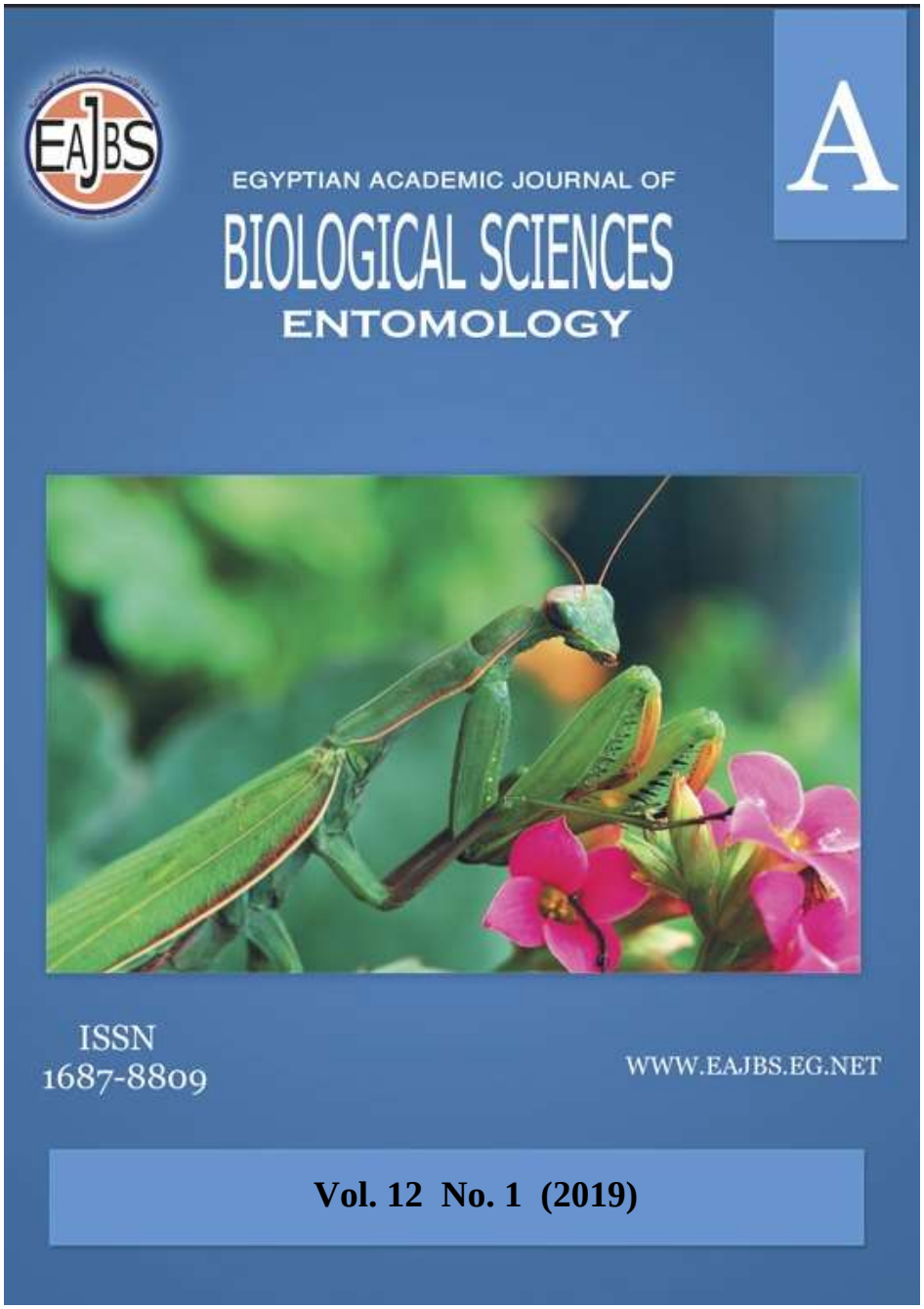

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Characterization of Qualitative and Quantitative Haemogram Parameters in Insects: Current Concepts and Future Prospects.

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ABSTRACT

Since the circulating hemocytes are involved in the key physiological functions in insects, knowledge of these haemocytes is necessary to physiologists, toxicologists and biochemists. The present article was prepared to aim at updating the identification of hemocyte types and discussing different terminological and technical difficulties. It focused, also, on most important quantitative parameters of haemogram and discussed various factors influencing their values. In this review, we described, also the origin of circulating hemocytes during embryonic and the postembryonic development as well as intensively reviewed the categorization of hemocyte types in several insect species of different orders. The controversial terminology and technical difficulties of the hemocyte identification were discussed. It was emphasized that none of the individual methods was satisfactory for all cell types within a given insect but a combination of techniques should be used. The present chapter included only on the major quantitative parameters of haemogram, such as the total haemocyte count (THC), blood volume (BV) and mitotic index. It shed some light on the interrelationship between THC and BV. In addition, the endocrine control of THC and BV had been reported. The interrelationships between BV and osmotic pressure as well as between mitotic index and THC had been discussed. Heartbeat rate was reported to depend on different factors but the control mechanisms for the insect heart are not fully elucidated.

List of Initials & Abbreviations:

20-hydroxyecdysone (20E), absolute haemocyte count (AHC), adipohemocytes (ADs), blood volume (BV), coagulocytes (CGs), corpora allata (CA), corpora cardiaca (CC), crystal cells (CRs), cystocytes (CCs), differential haemocyte count (DHC), fluorescence microscopy (FM), granulocytes (GRs), haemolymph volume (HV), juvenile hormones (JHs), lamellocytes (LMs), light microscopy (LM), mitotic index (MI), monoclonal antibodies (MAb), neurosecretory cells (NSCs), oenocytoids (OEs), plasmatocytes (PLs), podocytes (POs), prohemocytes (PRs), scanning electron microscopy (SEM), sessile cells (SCs), spherulocytes (SPs), thrombocytoids (TCs), total haemocyte count (THC), transmission electron microscopy (TEM), vermiform cells (VRs).

Contents:

1. INTRODUCTION

Insects have an open type of circulatory system. A pale colored fluid called 'haemolymph' (insect blood) circulates in the haemocoel (body cavity) bathing different organs and tissues (Jones, 1977; Wigglesworth, 1979; Gupta, 1979). Haemolymph, like the blood of higher animals, comprises two main components, the plasma and the corpuscles. The circulating cells in the insect haemolymph are called 'haemocytes'. They are morphologically distinct cell types and comparable to vertebrate leucocytes (Mead *et al*., 1986; Kerenhap *et al*., 2005; Pandey and Tiwari, 2012).

In insects, there are several types of hemocytes. The most common types are prohaemocytes (PRs), plasmatocytes (PLs), granulocytes (GRs), spherulocytes (SPs), adiphohaemocytes (ADs), coagulocytes (CGs) and oenocytoids (OEs). It is important to emphasize that not all these hemocyte types exist in all insect species (Lavine and Strand, 2002; Meister and Lagueux, 2003; Lamprou *et al*., 2007; Wang *et al*., 2010; Manachini *et al*., 2011). However, their characteristic features are slightly different in various insect species (Gupta, 1979; Kanost *et al*., 2004; Meister, 2004; Ribeiro and Brehelin, 2006; Browne *et al*., 2013).

Insect hemocytes are initially produced from the median mesoderm during embryogenesis (Ratcliffe *et al*., 1985; Tepass *et al*., 1994; Strand, 2008) and the majority of these cells circulate freely in haemolymph (circulating hemocytes), but a significant number, called 'sessile hemocytes', can be found associated with internal organs (fat body, gut, digestive system or dorsal tube) (Hillyer and Strand, 2014; Hillyer, 2016). On the other hand, origin of the hemocyte types seen during the postembryonic development is less clear. Maintenance of circulating hemocytes has been attributed to both the mitosis (cell division) of hemocytes already in circulation as well as to the release of hemocytes from hematopoietic organs (Feir, 1979; Ratcliffe *et al*., 1985; Gillespie *et al*., 1997; Lavine and Strand, 2002; Holz *et al*., 2003; Tan *et al*., 2013; Grigorian and Hartenstein, 2013). These organs provide the correct cellular and molecular environment for the control of cell proliferation and

differentiation (Koch and Radtke, 2007; Martinez-Agosto *et al*., 2007). Also, different hemocyte types are thought to be produced *via* the differentiation of circulating prohaemocytes and *via* linear transition of prohaemocytes to plasmatocytes and subsequent differentiation into other hemocyte types (Beaulaton, 1979; Yamashita and Iwabuchi, 2001).

For last few decades, the worldwide research on insect circulating haemocytes has received much attention (Wigglesworth, 1959; Jones, 1962; Gupta, 1979; Hall, 1983; Lavine and Strand, 2002; Ribeiro and Brehelin, 2006; Suhail *et al*., 2007; Strand, 2008; Shaurub, 2012; Soares *et al*., 2013; Siddiqui and Al-Khalifa, 2014; Kwon *et al*., 2014; Ghoneim *et al*., 2015a,b, 2017) because these cells perform different physiological functions, such as cell development and differentiation; metabolic processes; endocrine regulation; reproductive potential; transport of essential biological materials between cells, tissues and organs; coagulation to prevent loss of blood; preservation of an insect homeostasis; defense reactions against parasites and pathogens invading the insect body cavity (phagocytosis, encapsulation and nodulation); detoxification of metabolites and other foreign bodies, as well as synthesis, storage, distribution of nutritive materials and hormones to various tissues throughout the insect body and wound healing (for some details, see: Garcia and Rosales, 2002; Lavine and Strand, 2002; Ceraul *et al*., 2003; Zhou *et al*., 2004; Ling *et al*., 2005; Figueiredo *et al*., 2006; Ribeiro and Brehelin, 2006; Wood and Jacinto, 2007; Singh *et al*., 2008; Strand, 2008; Glenn *et al*., 2010; Pandey *et al*., 2010, 2012; Siddiqui and Al-Khalifa, 2012a; Chavan *et al*., 2017). In addition to these functions, insect hemocytes are responsible for clearing apoptotic cells during development (Kurtz, 2002) and they are regarded as an excellent model system for the study of cell communication (Manogem *et al*., 2015). However, some of the important reviews dealing with various aspects of hemocytes (*viz*., categories, function, cellular responses, *etc*.) are those of Rizki (1962), Rowley and Ratcliffe (1981), Arnold (1982), Gupta (1985), Brehelin and Zachary (1986), Lackie (1988), Ribeiro and Brehelin (2006), Izzetoğlu and Karaçali, (2010), Pandey and Tiwari (2012), Shauraub (2012), Izzetoglu (2012), Siddiqui and Al-Khalifa (2014), Er *et al*. (2017).

Since hemocytes are involved in the key insect physiological functions, circulating hemocytes provide an excellent model system to study the cell development, differentiation and their role in the immune system (Hoffmann, 1995; Lavine and Strand, 2002; Rosales, 2011; Pandey and Tiwari, 2012). Also, hemocytes are found to show changes in their types, number and configuration as a response to different stresses. Therefore, knowledge of normal haemocytes of an insect is necessary to physiologists, toxicologists and biochemists (Qamar and Jamal, 2009; Liu *et al*., 2013) and the insect haemogram is suggested to be a useful tool for investigation of toxic effects of the insecticidal materials on biocontrol agents (Patton, 1983; Kohlmaier and Edger, 2008; Qamar and Jamal, 2009). The main objective of this article was to update the identification of insect hemocyte types and discuss different technical difficulties opposing their characterization. It focused, also, on the most important quantitative parameters of haemogram in insects and reviewed various factors influencing their values.

2. Categorization of Circulating Hemocyte Types in Insects:

Classification, identification and categorization of hemocyte types are important for understanding their functions in insects, such their fundamental importance in the preservation of insect homeostasis, especially with regard to the cellular defense reactions and management of nutritional elements and other crucial

physiological functions, as previously mentioned.

2.1. Variation in Number and Types of Circulating Hemocytes:

It is interesting to give some historical information about the hemocyte classification and characterization. Hollande (1911) firstly attempted to classify and categorize the insect hemocytes after the earlier research works, particularly those of Cuenot (1897) and Kollmann (1908). Then, Wigglesworth (1939) followed each of Hollande's categories. Yeager (1945) identified ten hemocyte classes containing 32 different types in the Southern armyworm *Prodenia eridania*. Some years later, Jones (1962) reduced this number to nine distinct cell types, and his generalizing work earned a special place in the history of hemocytes, since his classification was the basis used by most researchers thereafter. The same author described eight hemocyte types in insects: PRs, PLs, GRs, Cystocytes (CCs), OEs, ADs, Podocytes (POs), and Vermiform cells (VRs). With this classification, this author established a system to give an order to more than 70 names for hemocyte types used by earlier investigators. Later, Price and Ratcliffe (1974) examined the hemocytes of 15 representative insect orders and distinguished six different types distributed in those orders: PRs, PLs, GRs, spherulocytes (SPs), CCs and OEs; however, CCs were absent in Lepidoptera. Using phase contrast microscopy, Sharma and Dutta (1979) recorded the presence of ten categories of hemocytes: PRs, PLs, GRs, CCs, COs, SPs, ADs, OEs, POs and VRs in the grasshoppers *Chrotogonus trachypterus* and *Acrida exaltata*. Although, Gupta (1979) recognized seven main types of haemocytes in various insect orders, namely PRs, PLs, GRs, SPs, ADs, OEs and Coagulocytes (CGs), while Gupta (1994) merged the category CGs with that of GRs. Although Brehelin and Zachary (1986) proposed a new system with nine hemocyte types, the classified categories of haemocytes ranged, generally, from four to seven (Gupta, 1979) or between three and nine (Wigglesworth, 1959; Arnold, 1972, 1974). However, some authors described three to eight hemocyte types in several insect orders by means of the transmission electron microscopy (TEM)(Ratcliffe and Rowley, 1979; Al-Khalifa and Siddiqui, 1985).

As reported in the available literature, the main types of hemocytes are PRs, GRs, PLs, SPs and OEs. These hemocyte types have been described in insect species of diverse orders, including Lepidoptera, Hymenoptera, Coleoptera and Diptera (Ayaad *et al*., 2001; Rizk *et al*., 2001; Zohry, 2006; Ribeiro and Brehelin, 2006; Annuradha and Anuadurai, 2008; Manfredini *et al*., 2008; Hassan *et al*., 2013; Shaurub *et al*., 2014; Hwang *et al*., 2015; Vogelweith *et al*., 2016; Ghoneim *et al*., 2015a, 2017; Shaurub, and Sabbour, 2017; Sadeghi *et al*., 2017; Chavan *et al*., 2017) as well as Dictyoptera (Chiang *et al*., 1988), Heteroptera (Sanjayan *et al*., 1996), Hemiptera (George and Ambrose, 2004; Ruiz *et al*., **2015**) and Orthoptera (Al-Robai *et al*., 2002; Barakat *et al*., 2002; Tanani, 2010; Ghoneim *et al*., 2015b; Kaidi *et al*., 2017). Until now, types, functions, and density of hemocytes remain different across insect orders (Lavine and Strand, 2002; Strand, 2008). However, variable number and types of hemocytes can be reviewed as follows.

2.1.1. Two Types of Hemocytes:

Early Lepesme (1938) distinguished only two haemocyte categories in haemolymph of adults of the desert locust *Schistocerca gregaria*: Proleucocytes and Phagocytes. Two types only could be identified in the migratory grasshopper *Melanoplus sanguinipes*: PLs and GRs (Gurwattan *et al*., 1991; Meranpuri *et al*., 1991). Hypsa and Grubhoffer (1997) characterized two distinct hemocyte types in

the kissing bug *Triatoma infestans*: OEs and PLs. In the common vinegar fly *Drosophila melanogaster*, Crozatier and Meister (2007) reported that two different types of mature hemocytes are produced by the embryonic hematopoiesis: PLs and CRs.

2.1.2. Three Types of Hemocytes:

As reported by George and Ambrose (2004), many workers have agreed that insects have three basic fairly well-defined haemocytes, namely PRs, PLs and GRs. Three main types of haemocytes could easily be differentiated by phase-contrast microscopy in the American cockroach *Periplaneta americana*: GRs, PLs and CGs (Laekie *et al*., 1985). Saxena and Agarwal (1979) identified three haemocyte categories in the poultry louse *Lipeurus lawrensis tropicalis*: PRs, GRs and OEs. Three types of circulating hemocytes were characterized by light microscopy (LM) and TEM from larval haemolymph in the paper wasp *Polistes dominulus*: PRs, PLs and GRs (Manfredini *et al*., 2008).

2.1.3. Four Types of Hemocytes:

Four types of haemocytes were identified in many insect species (Osman *et al*., 1984; Mahmoud and Yousuf, 1985; Masconi *et al*., 1989; Peter and Ananthakrishnan, 1995). Some authors (Akai and Sato, 1979; Mahmood and Yousaf, 1985; Masconi *et al*., 1989) recognized four haemocyte types in the migratory locust *Locusta migratoria*, the two-spotted cricket *Gryllus bimaculatus* and *P. americana*. In the 5th instar hoppers and adults of the rice grasshopper *Hieroglyphus nigrorepletus*, Khan *et al*. (1984) reported the occurrence of PRs, PLs (spherical, oval and fusiform in shape), GRs and OEs. Later, in the same insect, Ahmad (1988) and Ahmad and Khan (1986) confirmed these hemocyte types. Islam and Roy (1982) identified four types of haemocytes in the desert cricket *Schizodactylus monstrosus*: PRs, PLs, ADs, and SPs, while Islam and Roy **(**1984) observed five hemocyte types in the same insect: PRs, PLs, GRs, ADs and SPs. Four haemocyte types were identified in the last instar female nymphs of the brown spotted locust *Cyrtacanthacris tatarica*: PRs, SPs, GRs and PLs (John and Ananthakrishnan, 1995).

Based on the morphological criteria, Uckan and Sak (2010) identified four hemocyte types in haemolymph of the last instar larvae of the ichneumonid parasitoid *Pimpla turionellae*: PRs, PLs, GRs, and ADs. Four hemocyte types were distinguished in larvae of the Amazon black flies *Ectemnaspis rorotaense* and *Ectemnaspis trombetense*: PRs, GRs, OEs, and PLs (da Silva *et al*., 2015). Four hemocyte types were found in the haemolymph of 5th instar larvae of the grapevine moth *Eupoecilia ambiguella*: GRs, OEs, PLs and SPs (Vogelweith *et al*., 2016). Using light microscopy, differential interference contrast microscopy scanning electron microscopy (SEM) and TEM, Khosravi *et al*. (2016) identified four hemocyte types in larvae and pupae of the rose sawfly *Arge ochropus* for the first time: PRs, PLs, GRs, and OEs. Recently, four main categories of circulating hemocytes were identified in 4th instar larvae of the corn stem borer *Sesamia cretica*: PRs, PLs, GRs and OEs (Sadeghi *et al*., 2017). Also, Kaidi *et al*. (2017) distinguished four types of hemocytes in *L. migratoria*, namely PRs, PLs, CGs and GRs

2.1.4. Five Types of Hemocytes:

Five haemocyte types were identified in different insect species, such as the tobacco hornworm *Manduca sexta* (Horohov and Dunn, 1982; Miller and Stanely, 2000), the Usherhopper *Poekilocerus bufonius* (Al-Robai *et al*., 2002) and the Asian

corn borer *Ostrinia furnacolis* (Jian *et al.*, 2003). For more insect species, Dunphy and Nolan (1980) identified five types of hemocytes in the larvae, prepupae, and pupae of the spruce budworm *Choristoneura fumiferana*: PLs, GRs, SPs, OEs and PRs. Ghosh *et al*. (1984) recognized five different hemocyte types in the adult females of the grasshopper *Oxya hyla hyla*: PRs, PLs, GRs, SPs and CGs. Ahmad (1988) described the PRs, PLs, OEs, ADs and POs in haemolymph of the middle-aged larvae of 3rd, 4th, 5th and 6th instars, prepupae, pupae and adults of the Bihar hairy caterpillar *Spilosoma oblique*.

In the late two decades, Vivekananthan *et al*. (2010) used the Olympus LM to observe five types of hemocytes in 4th and 5th instar nymphs and adults of the common sand grasshopper *Chorthippus brunneus*, *viz*., PRs, PLs, GRs, SPs and ADs. Using a combination of LM and TEM, Zhang *et al*. (2012) characterized five hemocyte types in pupae of the small white butterfly *Pieris rapae*: PRs, GRs, PLs, OEs and CGs. Khosravi *et al*. (2012) used SEM to identify five types of hemocytes in all larval instars of the carob moth *Ectomoyelois ceratoniae*: PRs, PLs (with several morphological forms), GRs, SPs, and OEs. Ajamhassani *et al*. (2013) identified five hemocyte types in haemolymph of the 4th instar larvae of the fall webworm *Hyphantria cunea*, without ADs, whereas Zibaee and Sendi (2011) used LM and recognized six types: PRs, PLs, GRs, OEs, SPs and ADs in the same insect. Five hemocyte types had been reported in the Mediterranean flour moth *Ephestia kuehniella*: PRs, PLs GRs, EOs and SPs (Ghasemi *et al*., 2013a) while Ghasemi *et al*. (2013b) distinguished two additional morphotypes, namely VEs and POs in haemolymph of this species. Recently, Çelik *et al*. (2017) identified five hemocyte types in larval haemolymph of the smaller wax moth *Achoria grisella*: GRs, PLs, SPs, PRs and OEs. Based on shape and size of soma and nucleus, general appearance and staining of cytoplasm, degree of vacuolization, type, number, size and affinities of staining inclusions, Perveen and Ahmad (2017) identified five different haemocytes in the haemolymph of giant honeybee *Apis dorsata*: PRs, PLs, GRs, OEs and SPs.

2.1.5. Six Types of Hemocytes:

Six hemocyte types were characterized in different insect species (Jones, 1962; Ashhurst and Richards, 1964; Gupta, 1985; Gurwattan et *al.*, 1991; Miller and Stanely, 2000; Lavine and Strand, 2002): PRs, GRs, PLs, ADs, SPs and OEs. For some detail, hemocyte types in the American bollworm *Helicoverpa* (*Heliothis*) *armigera* were firstly characterized by LM and TEM as six different types, *viz*., PRs, PLs, GRs, SPs, OEs and CGs (Essawy *et al*., 1985). In their investigation on hemocytes of the same insect, Kalia *et al*. (2001) with phase contrast microscopy observed ADs, which had not been previously reported but considered as CGs (Essawy *et al*., 1985) or GRs (Gupta, 1994). Six types of hemocytes were identified in the sugarcane borer *Diatraea saccharalis* (Falleiros *et al*., 2003) and the lemon butterfly *Papilio demoleus* (Jalali and Salehi, 2008). Six hemocyte types were distinguished in all developmental stages of the variegated grasshopper *Zonocerus variegates*, namely PRs, PLs, GRs, SPs, OEs and ADs (Ademolu *et al*., 2010). In haemolymph of the velvet bean caterpillar *Anticarsia gemmatalis* larvae, six types of hemocytes were identified: PLs, GRs, PRs, SPs, OEs and VRs (Andrade *et al*., 2003a, 2010). Using LM, Zibaee and Sendi (2011) recognized six types in hemocytes of the lesser mulberry snout moth *Glyphodes pyloalis*: PRs, PLs, GRs, OEs, SPs and ADs. Basing on their size, morphology and dye-staining properties, six types of circulating hemocytes were classified in the white-spotted flower chafer *Protaetia brevitarsis seulensis*, *viz*., GRs, PLs, OEs, SPs, PRs, and ADs (Kwon *et al*., 2014).

2.1.6. Seven Types of Hemocytes:

Seven types of hemocytes had been described in various insects (Gupta, 1985; Brehelin and Zachary, 1986). Azambuja *et al*. (1991) characterized and compared different morphological types of hemocytes in six triatomine species, *viz*., *Rhodnius prolixus*, *Rhodnius neglectus*, *Rhodnius robustus*, *T. infestans*, *Panstrongylus megistus*, and *Dipetalogaster maximus*. Seven hemocyte types were identified by phase-contrast microscopy: PRs, PLs, GRs, OEs, ADs, CCs and giant cells. All seven types of hemocytes are not present in all species. For example, ADs and OEs were not observed in *P. megistus* and *P. infestans*, and the giant cells were rarely found in any of the species studied. Hemocytes in the 5th instar larvae and pupae of the soybean semilooper *Plusia orichalcea* were observed to be: PRs, PLs, GRs, ADs, SPs, CGs and OEs (Pathak and Saxena, 1994). On the basis of the fine structure, seven distinct types of circulating hemocytes: PRs, GRs, CGs, ADs, PLs, OEs and SPs were reported in the gypsy moth *Lymantria dispar* (Butt and Shields, 1996). Recently, Raveen and Nalini (2017) identified seven haemocyte types in the adult haemolymph of the dragonfly *Bradinopyga geminata*, *viz*., PRs, PLs, GRs, OEs, ADs, SPs and VRs.

2.1.7. Eight Main Types of Hemocytes:

Eight distinct haemocyte types: PLs, GRs, PRs, SPs, OEs, ADs, POs and VEs were observed in the haemolymph sample collected from 4th larval instar to pupal stage of the lawn armyworm *Spodoptera mauritia* (Manogem *et al*., 2015, 2016).

2.1.8. Variable Hemocytes in Selected Economic Insects:

In this context, special attention should be paid to selected species of the most economically important insects. With regard to the pink bollworm *Pectinophora gossypiella*, Clark and Chadbourne (1960) identified four categories of haemocytes in the haemolymph of last (4th) instar larvae: PLs, SPs, CCs and Proleucocytoids, while Raina and Bell (1974) distinguished seven types in the same larval instar: PRs, PLs, GRs, SPs, ADs, OEs and POs. Two years later, Raina (1976) used some ultrastructural characteristics and described only five types of hemocytes in the mature last instar larvae (PRs, PLs, GRs, SPs and OEs) because the author could not distinguish ADs or POs. Recently, Ghoneim *et al*. (2017) used LM and identified six main types in the haemolymph of full grown larvae, *viz*., PRs, PLs, SPs, OEs, GRs and ADs.

In connection with the Egyptian cotton leafworm *Spodoptera littoralis*, Harpaz and Zelcer (1969) distinguished four hemocyte types in the larval haemolymph; PLs, GRs, ADs and OEs. Also, Kislev *et al*. (1969) differentiated four major types: ADs, GRs, OEs and PLs. Other researchers identified different four types of hemocyte, such as PLs, GRs, SPs and OEs (Gelbič *et al*., 2006); PLs, GRs, PRs and SPs (Abd El-Aziz, 2015) or PLs, GRs, PRs and OEs (Asiri, 2017). On the other hand, many authors (Zohry, 2006; Hassan *et al*., 2013; Shaurub *et al*., 2014; Ghoneim *et al*., 2015a; Abou-Taleb *et al*., 2015) reported five types of the circulating hemocytes in last (6th) instar larvae.

In respect of the tobacco cutworm (Asian army worm) *Spodoptera litura*, Saxena *et al*. (1988) described nine types of hemocytes: PRs, PLs, VRs, POs, GRs, OEs, SPs, ADs and CGs because they considered VRs and POs as separate hemocyte types. Kurihara *et al*. (1992) used the phase contrast microscopy to categorize the circulating hemocytes into seven categories: PRs, PLs, GRs, SPs, OEs, POs, and granular plasmatocytes because POs and VRs were classified in the same class as the

"podocytes". Sharma *et al*. (2003) identified only five distinct haemocyte types in the 6th instar larvae, *viz*. PRs, PLs, GRs, SPs and OEs. Also, Zhu *et al*. (2012) distinguished five different types of hemocytes in 5th instar: PRs, PLs, GRs, OEs, and SPs.

Concerning the greater wax moth *Galleria mellonella*, an earlier study was conducted by Ashhurst and Richards (1964) who identified five types of hemocytes in larvae: PRs, PLs, ADs, OEs, and SPs. A year later, Shrivastava and Richards (1965) reported the presence of at least three types of hemocytes; PRs, GRs and PLs. Identification of each type by LM had often been perplexing, especially for GRs which were difficult to be distinguished from PRs (Ling *et al*., 2003; Ling *et al*., 2005). Also, three hemocyte types in haemolymph of larvae were observed under fluorescence microscope: PLs, GRs, and PRs (Izzetoglu, 2012). Basing on the size, morphology, detection by molecular probes, dye-staining properties, and their role in the immune response, five hemocyte types could be distinguished by some researchers (Altuntaş *et al*., 2012; Kurt and Kayis, 2015; Blanco, 2016): PRs, PLs, GRs, OEs and SPs. Basing on the morphological criteria, Sezer and Ozalp (2015) identified five hemocyte types in the pupal haemolymph: PRs, PLs, GRs, SPs and OEs. On the other hand, Wu *et al*., (2016) used cytological and morphological analyses for differentiation of four types of hemocytes; PLs, GRs, SPs and OEs. Recently, Er *et al*. (2017) distinguished four types of circulating hemocytes in the last instar larvae: GRs, PLs, PRs and OEs.

With regard to the black cutworm *Agrotis ipsilon*, Abd El-Aziz and Awad (2010) identified five types of haemocytes in the 4th larval instar, *viz*., PRs, PLs, GRs, SPs and ADs. Also, Shaurub and Sabbour (2017) distinguished five types of haemocytes in the last instar larvae: PRs, PLs, GRs, SPs and OEs. Moreover, Ali (2011) distinguished eight types in haemolymph of the 4th and 6th larval instars, *viz*., PLs, GRs, ADs, SPs, OEs, CCs and Spindle cells (SNs). Abd El-Wahed (2011) described eight types of haemocytes in the haemolymph of the 4th and 6th larval instars: PRs, PLS, GRs, SPs, ADs, OEs, SNs and CCs. Recently, Abdel-Hakim and El-Mandarawy (**2017**) identified eight types of haemocytes in haemolymph of last instar larvae: PRs, PLs, GRs, ADs, SPs, OEs and CCs and SNs. In addition to *A. ipsilon*, five different hemocyte types, *viz*., PRs, PRs, GRs, SPs and OEs were identified in the larval haemolymph of the turnip moth *Agrotis segetum* (Ayvali and Gul, 1988).

In respect of *S. gregaria*, the literature sources reported an early study of haemocytes conducted by Mathur and Soni (1936). They recorded four distinct types of haemocytes, *viz*., mother cells, proleucocytes, granular leucocytes and phagocytes. Two years later, Lepesme (1938) distinguished only two haemocyte categories in haemolymph of adults: Proleucocytes and Phagocytes. Some authors (Al-Hariri and Suhail, 2001; Al-Hariri and Suhail, 2001; Teleb, 2011) recognized five hemocyte types: PRs, PLs, GRs, OEs and SPs, while others (Laekie *et al*., 1985; Tanani, 2010; Ghoneim *et al*. (2015b) identified only three types in the haemolymph of last instar nymphs and adults: PLs, GRs and CGs. Recently, Kaidi *et al*. (2017) identified four types of hemocytes, namely PRs, PLs, CGs and GRs

Among silkworms, Nittono (1960) early classified the circulating hemocytes in the mulberry silkworm, *Bombyx mori* into six types, *viz*., PRs, PLs, GRs, SPs, OEs and imaginal SPs (observed only in the adult stage, but occasionally in pharate adults). Forty years later, the same **six** types of hemocytes were identified in adults of the same species by Balavenkatasubbaiah *et al*. (2001). On the other hand, less number of hemocyte types had been reported since many authors (Jones, 1962; Akai and Sato, 1973; Han *et al*., 1998; Ling *et al*., 2003a; Saad, 2005; Nakahara *et al*.,

2009; Tan *et al*., 2013; Liu *et al*., 2013; Essawy and Saad, 2013; Ganie *et al*., 2015a, b; Ahamad *et al*., 2016) distinguished five types: PRs, PLs, GRs, SPs and OEs. A lesser number was differentiated by Gupta (1979): PRs, PLs, SPs and OEs. He also described two subclasses of PRs as macronucleocytes and micronucleocytes, depending on their size. Four types of circulating haemocytes were also differentiated in this species of silk worms: GRs, OEs, PLs and SPs (Strand, 2008; Hori *et al*., 2012).

Some attention should be paid to the hemocyte types in other silkworms. Hemocytes of selected stages of the Cecropia silkmoth, *Hyalophora cecropia* (from 1st instar larvae to 4-day-old adults) had been early examined by Lea and Gilbert (1966) who compared them with those of the Ailanthus silkmoth, *Samia cynthia* and the Polyphemus silkmoth, *Antheraea polyphemus*. These authors described five classes and two subclasses of hemocytes in all species: PRs, SPs, OEs, PLs (of several morphological types) and ADs (two subclasses). In the haemolymph of 4th and 5th instar larvae of the Eri silkworm, *Philosamia ricini*, Bhagawati and Mahanta (2012) identified five types of haemocytes: PLs, GRs, ADs and PRs. Recently, Talukdar *et al*. (2018) identified the haemocyte types in the same larval instar of *Ph. ricini*. In the haemolymph of 5th instar larvae of the Muga silkworm *Antheraea assama*, Baishya *et al*. (2015a) and Bardoloi *et al*. (2016) identified five hemocyte types in haemolymph of all larval instars of the same silkworm: PR, PL, GR, SP and OE. In the haemolymph of 5th instar larvae of the tasar silkworm, *Antheraea mylitta*, Pandey *et al*. (2010) identified six types of hemocytes: PRs, PLs, GRs, SPs, OEs and ADs. In addition, VRs and POs were occasionally observed in smears of moulting phase of late 5th instar larvae.

Within mosquitoes, Hall (1983) reviewed what little is known about the structure of mosquito hemocytes and their possible functions. Ten years later, Zahedi (1993) identified three basic types of haemocytes in the common mosquito vector of filariasis *Armigeres subalbatus*, namely PLs, CCs and PRs. Castillo *et al.* (2006) used a combination of morphological and functional markers to distinguish three hemocyte types, *viz*., GRs, OEs and PRs, in haemolymph of larvae, pupae and adults of the African malaria mosquito *Anopheles gambiae* and the yellow fever mosquito *Aedes aegypti*. Using LM and TEM, Hillyer and Christensen (2002) described four distinct hemocyte types in *Ae. aegypti*: GRs, OEs, ADs and thrombocytoids (TCs). They believed GRs and OEs as true circulating hemocytes, but ADs and TCs have likely adhered to fixed tissues. In the adult haemolymph of the same mosquito, Araujo *et al*. (2008) recognized six circulating hemocyte types, *viz*., PRs, ADs, GRs, PLs, OEs and TCs. Some authors (Gad and El-DaKheel, 2009; Wang *et al*., 2011) reported four types of haemocytes in larval haemolymph of the filarial mosquito *Culex quinquefasciatus*: PRs, GRs, PLs and OEs. Also, four haemocyte types were identified in *Culex pipiens* larvae: PRs, PLs, GRs and OEs (Zahran and Gad, 2013).

Among dipterous flies, four types of haemocytes were early described in the flesh fly *Sarcophaga falculata*: PRs, GRs, OEs and phagocytes (Dennel, 1947). Jones (1956) examined the haemocytes of the flesh fly *Sarcophaga bullata* by phase contrast microscopy and observed only three types: PLs, GRs and SPs. Abozenadah (2010) classified the hemocyte types of the 2nd instar larvae of the house fly *Musca domestica* into five types: PRs, PLs, GRs, SPs and OEs. Pal and Kumar (2014) reported that the larval haemolymph of three flies, the flesh fly *Sarcophaga ruficornis*, *M. domestica* and the oriental latrine fly *Chrysomya megacephala*, possess five types of haemocytes: PRs; PLs; GRs; SPs; OEs. In addition, VRs were found in the haemolymph of *S. ruficornis* and ADs in the haemolymph of *M.*

domestica. Kaaya and Otieno (1981) observed three classes of haemocytes (PRs, PLs and GRs) in haemolymph of the tsetse flies *Glossina morsitans morsitans* and *Glossina pallidipes*. In addition to these three types, a category of spindle cells was observed in haemolymph, especially in the newly emerged adults. Based on their unusual morphology, as well as on their inverse relationship with the number of the filamentous plasmatocytes (TCs), it was suggested that these spindle cells might be precursors of TCs observed mostly in older *Glossina*. A year later, Kaaya and Ratcliffe (1982) studied the haemocytes in *G. morsitans*, the stable fly *Stomoxys calcitrans*, the blue blowfly *Calliphora erythrocephala* and the common green bottle fly *Lucilia sericata* and morphologically characterized seven types of haemocytes: PRs, PLs, TCs, GRs, ADs, OEs, and spindle cells. By TEM, these authors were able to observe only PRs, PLs and SPs. Using the Giemsa stain under SEM; Silva *et al*. (2002) distinguished six well-defined hemocyte types in haemolymph of the West Indian fruit fly *Anastrepha obliqua* at the beginning and end of the 3rd larval instar: PRs, PLs, GRs, ADs, OEs and SPs.

Concerning the fly *D. melanogaster*, many researchers (Whitten, 1964; Rizki *et al*., 1980; Shrestha and Gateff, 1982; Rizki and Rizki, 1992; Lanot *et al*., 2001) described five main types of hemocytes in larvae: PLs, POs, Crystal cells (CRs), Lamellocytes (LMs) and sessile cells (SCs). Under TEM, Yu (1976) distinguished five types of haemocytes: PRs, PLs, GRs, CRs and OEs. On the basis of the expression or lack of expression of blood cell antigens, Kurucz *et al*. (2007) defined four hemocyte types: CRs, PLs, LMs and precursor cells. Other authors (Meister and Lagueux, 2003; Meister, 2004; Strand, 2008; Ribeiro and Brehelin, 2006; Wood and Jacinto, 2007; Liu *et al*., 2013; Salazar-Jaramillo *et al*., 2014) reported only three main classes of circulating hemocytes in larvae: PLs, CRs and LMs. In the same fly, Crozatier and Meister (2007) reported that two different types of mature hemocytes are produced by the embryonic hematopoiesis: PLs and CRs. Both types persist into the larval stage beside the larva itself possesses a hematopoietic organ (the lymph gland), where PLs and CRs are differentiated from PRs. Hemocytes in the cherry vinegar Fly *Drosophila suzukii* were morphologically similar to those of *D. melanogaster* (Kacsoh and Schlenke, 2012). Early, Rizki (1953) investigated the haemocytes in three larval instars of a neotropical species, *Drosophila willistoni*, and classified into six types: PLs, POs, SPs, OEs, CRs and Nematocytes. Recently, Bozler *et al*. (2017) identified and described, in detail for the first time, a novel hemocyte, type-II Nematocytes, in larvae of numerous *Drosophila* species, such as *Drosophila falleni* and *Drosophila phalerata*. They found that these remarkable cells are distinct from previously described hemocytes due to their anucleate state (lacking a nucleus) and unusual morphology.

Within beetles and weevils, McLaughlin and Allen (1965) classified and described four hemocyte types in the boll weevil *Anthonomus grandis*: PRs, PLs, SPs and ADs. Giglio *et al*. (2008) observed four morpho-types of haemocytes in the ground beetle *Carabus* (*Chaetocarabus*) *lefebvrei*. Also, four types of haemocytes were identified in the rice hispa beetle *Dicladispa armigera*: PRs, PLs, GRs and SPs (Phukan *et al*., 2008). On the other hand, five types of circulating hemocytes were observed in the elm leaf beetle *Xanthogaleruca luteola*: PRs, PLs, GRs, OEs and SPs (Kohan *et al*., 2012). Under SEM and LM, Firlej *et al*. (2012) identified five hemocyte types in haemolymph of the Asian lady beetle *Harmonia axyridis*: PLs, GRs I, GRs II, OEs, and SPs. Recently, Agarwala (2017) identified five hemocyte types in all postembryonic stages of the giant ladybird beetle *Anisolemnia dilatata*: PRs, PLs, GRs, SPs and OEs. Five types of hemocytes were identified by Suhail *et*

al. (2007) in the ladybird beetle *Coccinella septempunctata*. Sahayaraj and Kombiah (2010) characterized five types of haemocytes in haemolymph of the banana rhizome weevil *Cosmopolites sordidus*: GRs, PRs, PLs, OEs and CCs. Moreover, Al-Khalifa and Siddiqui (1985) studied the haemocytes in four beetle species, the leather beetle *Dermestes vulpinus,* the hide beetle *Dermestes maculates,* the scarab beetle *Hybosorus illegari* and the whirligig beetle *Dineutes aerius*. They distinguished six hemocyte types in these species: PRs, PLs, GRs, SPs, OEs and ADs. Also, Hwang *et al*. (2015) identified six circulating hemocytes in larvae of the Japanese rhinoceros beetle *Allomyrina dichotoma*: GRs, PLs, OEs, SPs, PRs and ADs. Recently, Chavan et al. (2017) identified seven types of haemocytes in haemolymph of the tenebrionid beetle *Platynotus belli*, *viz*., PRs, PLs, GRs, OEs, ADs, SPs and CGs.

Considering the red palm weevil *Rhynchophorus ferrugineus*, six types of haemocytes were reported by some authors (AI-Khalifa and Siddiqui, 1999; Siddiqui and Al-Khalifa, 2012b): PRs, PLs, GRs, OEs ADs and CCs. A lesser number of hemocyte types was reported because Manachini *et al*. (2011) and Hamadah and Tanani (2017) identified only five hemocyte types: PLs, GRs, PRs, OEs and SPs. Moreover, Mastore *et al*. (2015) observed three main hemocyte populations in the late stage of last instar larvae: GRs, PLs and larger OEs.

Within the hemipterous bugs, Hypsa and Grubhoffer (1997) characterized two distinct hemocyte populations in the haemolymph of *T. infestans*: OEs and PLs. By LM and TEM, Berger and Slavíčková (2008) classified the hemocytes in the adult linden bug *Pyrrhocoris apterus* into four distinct types: PRs, GRs, PLs and SPs. Using phase contrast microscopy, four types of hemocytes were identified in the haemolymph of adult females of the cochineal bug *Dactylopius coccus*: GRs, PLs, PRs and OEs (Caselín-Castro *et al*., 2008). Five hemocyte types, *viz*., PRs, PLs, GRs, CCs and OEs, were distinguished in adult haemolymph of the reduviid bugs *Acanthaspis pedestris* (Ambrose and George, 1996), *Catamiarus brevipennis* (Ambrose and George, 1994) and *Rhynocoris kumarii*: (George, 1996; George and Ambrose, 2004). Also, Sanjayan *et al*. (1996) observed five types of haemocytes in the haemolymph of both 5^{th} instar nymphs and adults of the darth maul bug *Spilostethus hospes*: PRs, PLs, GRs, ADs and SPs. Similarly, Qamar and Jamal (2009) identified five hemocyte types in the 5^{th} instar nymphs and adults of the red cotton bug *Dysdercus cingulatus*: PRs, PLs, ADs, GRs and OEs. Moreover, Barracco and Loch (1989) identified six hemocyte types in the reduviid bug *Panstrongylus megistus*: PRs, PLs, GRs, CGs, OEs and ADs. With Giemsa stain, Ruiz *et al*. (2015) could classify hemocytes in both 4^{th} and 5^{th} nymphal instars of the reduviid bugs *R. prolixus* and *R. robustus* into six types: PRs, PLs, GRs, OEs, SPs and ADs.

With regard to aphids, the comparative identification of hemocyte numbers in aphids is a complicated task because of some technical problems, such as the polymorphism, low cell number, quantity of debris and symbionts in the haemolymph. Therefore, prior studies on hemocytes are scarce and mainly based on LM (Boiteau and Perron, 1976; Behura and Dash, 1978; Behura and Bohidar, 1983; Behera *et al*., 1999; Patro *et al*., 2005; Poirié and Coustau, 2011). Boiteau and Perron (1976) described six hemocyte categories in the aphid *Macrosiphon euphorbiae*: PRs, OEs, PLs, GRs, SPs and wax cells. In the pea aphid *Acyrthosiphon pisum*, Laughton *et al*. (2011) described three hemocyte categories: PRs, GRs and OEs. Schmitz *et al*. (2012) used morphological, histological, ultrastructural and functional criteria to characterize five main hemocyte types in haemolymph of the same aphid: PRs, GRs, and the non-previously described PLs, as well as two additional categories, SPs and wax cells. However, the number and identification of hemocyte

types in insects, and even in the same insect species, is a subject of great debate owing to some reasons which will be discussed in the following section.

2.2. Controversial Terminology and Technical Difficulties of the Hemocyte Identification:

Insect hemocytes are often classified according to their morphological, histochemical, and functional characteristics (Strand, 2008). However, their nomenclature and classification have been ambiguous and controversial, owing to their variable morphologies, the development stages of an insect and various influencing environmental factors, besides diversity of insects (see the previous section). Moreover, many workers (Gardiner and Strand, 2000; Lavine and Strand, 2002; Brayner *et al*., 2005; Ribeiro and Brehelin, 2006) used different terminology to classify the same hemocyte type. Therefore, some of the major problematic aspects should be discussed herein.

The used nomenclature or terminology for hemocytes has often complicated comparisons of hemocyte categories in different insect orders (Nardi, 2004; Huang *et al*., 2010). For example, the larval hemocytes of Lepidoptera are typically identified by field or phase microscopy whereas this conventional method of hemocyte classification has been the source of frequent controversy in other insect orders (Ling *et al*., 2003a); since the hemocyte terminology based on morphological features which often differ from order to order. There are over 70 different names used for just 6-9 hemocyte types (Ratcliffe *et al*., 1985). Thus, there is a need to develop a more uniform terminology for naming hemocytes in different insect species (Strand, 2008).

On the other hand, the non-uniformity and considerable differences in haemocyte classification in insects may arise from several causes, such as differences in experimental treatments, observation of living haemocytes as opposed to fixed specimens, morphological changes of haemocytes after withdrawal, and the tendency of some workers to simplify haemocyte classification (Arnold, 1972; George and Ambrose, 2004). Also, the number, type and morphology of haemocytes vary with the developmental stages of the test insects and their physiological conditions, i.e., there is an inherent variability of haemocyte types within a species as well as among closely related species (Gupta, 1979; Chapman, 1998; Beetz *et al*., 2008). Also, the hemocyte classification is often influenced by some factors affecting the haemolymph physical properties or biochemical composition (Carrel *et al*., 1990). In addition, the differences in number and type of identified hemocytes in insects may be attributed to several technical difficulties and the characters adopted by other researchers (Giulianini *et al*., 2003; George and Ambrose, 2004; Ribeiro and Brehelin, 2006). Moreover, many erroneous descriptions of certain hemocytes may be attributed to the rapid transformation during or soon after haemolymph collection (Brehélin and Zachary, 1986). Experimentally, a comprehensive classification of hemocyte types is difficult because of the different appearances of them under different culture conditions (Brehélin and Zachary, 1986).

Izzetoglu (2012) reported confusion between various haemocyte types, such as PRs and PLs as well as GRs and ADs. In some detail, PRs are commonly regarded as precursor cells (Brehelin and Zachary, 1986), but their differentiation into the other hemocyte types is still uncertain. The assumption that there are different sub-types of PRs which differentiate into other hemocytes explains why some of these cells are difficult to be distinguished from other hemocytes (Nevermann *et al*., 1991). Lai-Fook (1973) could not identify the PRs of the Brazilian skipper *Calpodes ethlius* by the light microscopy (LM) but she could distinguish them from the other cell types

only by the TEM. Also, some authors (Price and Ratcliffe, 1974; Ratcliffe and Price, 1974) reported different difficulties for distinguishing the PLs and GRs by the TEM. The PLs of *C. ethlius* (Lai-Fook, 1973) and of *G. mellonella* (Neuwirth, 1973), in contrast to their GRs, do not contain grana and, therefore, are easily identified, even though grana-containing transients have been described by Neuwirth (1973). In addition, Coagulocytes (labile hyaline haemocytes) in insects are highly unstable cells and have been degranulated spontaneously *in vitro*, their cytoplasm becoming hyaline before they eventually disintegrate (Gregoire, 1970; Price and Ratcliffe, 1974).

In a comparative study of LM, SEM and TEM of hemocytes in the German cockroach *Blatella germanica*, Chiang *et al*. (1988) pointed out that all hemocyte types can be recognized exclusively by TEM. Fluorescence microscopy (FM) for hemocyte classification is particularly well suited to perform structure-function analysis of living cells using vital staining with fluorescent probes. This method is more precise than the conventional method of hemocyte identification using bright field or phase contrast microscopy (Canete *et al*., 2001). Among the commonly used fluorescent probes, acridine orange (AO) is one of the most widely used dyes for analysis of cell viability and selective visualization of organelles and dead cells (Canete *et al*., 2001; Foglieni *et al*., 2001). Ling *et al*. (2003a) found that AO could be used to classify the circulating hemocytes of *B. mori*. This method is extremely useful for the discrimination of specific cells that are difficult to identify by ordinary LM. In addition, the antibody and genetic markers have been characterized in selected species that more reliably distinguishes different hemocyte types from one another (Lavine and Strand, 2002; Ribeiro and Brehelin, 2006; Manfredini *et al*., 2008).

In his valuable article, Davis (2007) described a computer-assisted (i.e., using image analysis software) technique for counting hemocytes in the large milkweed bug *Oncopeltus fasciatus* that is both objective and automated and that yields data within seconds. Indeed, the main advantage that this method offers over hemocytometer counts is its increased efficiency. Given the recent attention to insect immunity by researchers, this method may prove valuable in future studies that rely on hemocyte counts.

Thus, none of the individual methods for studying the various morphological types of haemocytes was entirely satisfactory for all types of cells within a given insect (George, 1996). Various techniques often yield profound different information about types, number, distribution and functions of haemocytes (for more detail, see Lebestky et al., 2000; Lebestky *et al*., 2000; Lanot *et al*., 2001; Lavine and Strand, 2002; Pandey *et al*., 2003; George and Ambrose, 2004; Dean *et al*., 2004; Ling *et al*., 2005; Ribeiro and Brehelin, 2006; Tiwari *et al*., 2006; Gandhe *et al*., 2007; Wood and Jacinto, 2007; Pandey *et al*., 2008, 2010; Qamar and Jamal, 2009; Pandey and Tiwari, 2011; Pandey and Tiwari, 2012).

In conclusion, there is a need to develop a more uniform terminology for naming hemocytes in different insect species. The hemocyte classification in the haemolymph of an insect species should be revised several times. Also, there is no single technical method to distinguish the haemocyte types but a combination of morphological characteristics, ultrastructural features, immunochemical identification, functional typescripts, genetic markers and computer-assisted technique. Monoclonal antibodies (MAb) should also be tried as a tool for identifying the different categories of circulating haemocytes but such studies are scanty. In using the MAb as specific markers of antigens shown to be specific to a

haemocytes must be based on studying its signal pathways activated during differentiation. Another approach is lectin labeling and it also has a similar limitation as labeling by MAbs.

3. Hemocyte Population Dynamics:

Haemogram is a statement of the haemocyte population picture in an insect at a given time. It is a quantitative (Total haemocyte count, THC) and qualitative (Differential haemocyte count, DHC) expression of the haemolymph and its constituent inclusions (Jones, 1962; Wheeler, 1963; Jones, 1967a,b; Arnold, 1972). Haemogram parameters include, also, haemolymph (blood) volume, mitotic index and cytological features of hemocytes. It is important to point out that the insect haemogram serves as a good indicator of the insect physiology during growth and adulthood (Giglio *et al*., 2008), as well as the environmental adaptability in each developmental stage of insects (Sharma *et al*., 2008; Ghasemi *et al*., 2013a; Bardoloi *et al*., 2016).

Prior to further discussion of the hemocyte population dynamics, it is important to emphasize that the insect hemocytes constitute up to 10% of the blood volume (Wheeler, 1963) and even higher percentage in insects preparing for metamorphosis (George and Ambrose, 2004). A great deal of data has been accumulated to explain the THC and DHC changes in the haemocyte population of various insect species during growth and development (Pathak, 1986).

3.1. Variation of Total Hemocyte Population:

As previously mentioned, THC represents an important quantitative parameter of haemogram. Experimentally, THC is usually measured in the number of circulating hemocytes per cubic millimeter. Also, THC varies not only according to the insect species but also depending on different biological, physiological and environmental factors. For example, a remarkable variation in the quantitative profile of haemocyte types of the same species was found in relation to development, eclosion, sex, and reproductive phases (Sanjayan *et al*., 1996). Any change in THC of particular insect directly or indirectly affects the insect (Essawy and Saad, 2013). However, the most important factors influencing the THC will be discussed later in the present section.

Different THC values can be reviewed in various insect species as follows. Among the early studies of THC in insects are those of Mathur and Soni (1936) who recorded the THC in the haemolymph of *S. gregaria* adults as 6500 cells/mm^3 and Tauber and Yeager (1936) who counted the THC in the Jamaican field cricket *Gryllus assimilis* ranging from 15,000 to 275,000 cells/mm^3 and in *P. americana* ranging from 15000 to 60000 cells/mm^3. Three decades later, Gupta and Sutherland (1968) counted THC in *P. americana* from 7996 to 27796 cells/mm^3. Mall and Gupta (1979) estimated THC of the red pumpkin beetle *Aulacophora foveicollis* in an average of 5500 cells/mm^3. The THC in adult females of the grasshopper *Oxya hyla hyla* was 80200±105·8 cells/mm^3 (Ghosh *et al*., 1984). Hassan (1985) recorded THC of normal larvae of the yellow stem borer *Tryporyza incertulas* in an average 22475 cells/mm^3. As reported by Kurihara *et al*. (1992), THC in haemolymph of *S. litura* larvae was 1.4-2.1x10^4/µl. THC of the 5^{th} instar nymphs of *S. hospes* averaged to 3263 cells/mm^3 but THC was slightly less in the 0-day old adults (Sanjayan *et al*., 1996).

In the last two decades, the available literature contains many reported results of research concerning the variable THC value in different insect species. THCs of the West Indian fruit fly *Anastrepha oblique*, at the beginning and end of the 3^{rd}

instar larvae, were determined as 147.0±10.6 and 210.0±144.5 cells/µl of haemolymph, respectively (Silva *et al*., 2002). In the Usherhopper *Poekilocerus bufonius*, Al-Robai *et al*. (2002) determined THCs in the nymphal stage and adult males and females as: 1300/mm^3, 892/ mm^3 and 838/mm^3, respectively. George and Ambrose (2004) determined the THC in adults of the reduviid bug *Rhynocoris kumarii* as 8900±305.532 cells/$mm^{\mathbf{3}}$ (7250-11000). Sabri and Tariq (2004) determined THC of the red pumpkin beetle *Aulacophora foveicollis* in 4372 cells/$mm^{\mathbf{3}}$. In the healthy adults of the rice hispa beetle *Dicladispa armigera*, the THC varied between 5055 and 5950cells/mm^3 (Phukan *et al*., 2008). Jalali and Salehi (2008) recorded the THC in 2nd instar larvae of *P. demoleus* as 2008.0cells/$mm^{\mathbf{3}}$, in 4th instar larvae as 9244.0/ $mm^{\mathbf{3}}$, in the late prepupae as 12326cells/$mm^{\mathbf{3}}$ and in newly formed pupae as 6688cells/ $mm^{\mathbf{3}}$. The THC in nymphal instars (4th and 5th) and adults of both males and females of *C. brunneus* were 2,375 cells/mm^3, 3,202 cells/mm^3, 3,150cells/mm^3 and 3,364 cells/mm^3, respectively (Vivekananthan *et al*., **2010**). Sendi and Salehi (2010) determined THC of 17864±1264.6 cells/mm^3 in 4-day old of 4th larval instar, 5261±316.7 cells/mm^3 in prepupae and 4328±763.5 cells/mm^3 in 1-day old pupae of *P. demoleus*. Teleb (2011) determined the THC in normal 5th (last) nymphal instar of *S. gregaria* as 7800±130.4 cells/mm3 at 1-day old and increase at the 3rd and 5th days (8890±710 and 9380±128.1 cells/mm^3, respectively). In the 96 h-old 5th instar larvae of *S. litura*, THC was measured as $12.6x10^{\mathbf{3}}$ cells mL^{-1} (Zhu *et al*., 2012). THC in the normal larvae of *G. mellonella* was determined as $227.33x10^{\mathbf{4}}$ cells/mL (Kurt and Kayis, 2015).

Within the last two years, Manogem *et al*. (2016) determined the THC in haemolymph of 0-day old 6th (last) instar larvae of the lawn armyworm *Spodoptera mauritia* as 1.3860±3.1199 cells/mm^3 and in the 1-day old last instar larvae as 1.2540±4.1548 cells/mm^3. The THC was found to be $5.17±0.08x10^{\mathbf{3}}$per $mm^{\mathbf{3}}$ in adult females of *C. brunneus* (Jain and Ahi, 2016). Ghoneim *et al*. (2017) estimated THC in the haemolymph of full grown larvae of *P. gossypiella* in an average of 7213±716.91 cells/$mm^{\mathbf{3}}$ (6 hr full grown larvae) and 10138±918.67 cells/$mm^{\mathbf{3}}$ (48 hr full grown larvae). Chavan *et al*. (2017) estimated the THC in haemolymph of normal larvae of the tenebrionid beetle *Platynotus belli* in an average of 26233.33±251.66 cells/$mm^{\mathbf{3}}$. As recorded by Perveen and Ahmad (2017) in the giant honeybee *Apis dorsata*, THCs were 45,875 cells/$mm^{\mathbf{3}}$ in larvae and 43,850 cells/$mm^{\mathbf{3}}$ in pupae. In adults, it was almost seven times less (6470 blood cells/$mm^{\mathbf{3}}$) than both the larval and pupal stages.

3.2. Factors Influencing the Total Hemocyte Population:

Most research has sought to increase our understanding of what factors influence the insect hematological parameters. These hematological parameters are rapidly changed as response to biotic and/or abiotic factors. Early, Jones (1962) reported that both internal and external factors affect the total hemocyte population (THC), depending on age, instar, sex, size and method of detection in different organs and systems depending upon their mode and functions. Also, nutrition, stage and instar may influence the hemocyte population from one form to another. Crossley (1968) reviewed the humoral control of insect hemocyte populations. He suggested that the changeable number of the circulating haemocytes can be a result of a dynamic balance between four factors: (a) mitosis of circulating haemocytes, (b) death or fragmentation of circulating haemocytes, (c) release or retention of haemocytes at haemocytic reservoirs and (d) release of sessile haemocytes from haemocytopoietic tissues.

Some years later, some of these suggested factors had been substantiated, since

many authors (Wigglesworth, 1973; Mahmood and Yousuf, 1985; Romosen and Stofolano, 1998; Gardiner and Strand, 2000; George and Ambrose, 2004; Ling *et al*., 2005; Okazaki *et al*., 2006; Ribeiro and Brehelin, 2006) reported that the THC has been found to normally vary depending upon the insect species *in situ*, the developmental stage and its physiological conditions, as well as the age, sex, variance in studying haemocytes, and the used technique. In many insect species, fluctuations in the hemocyte populations are influenced by the release of hemocytes from the hemapoietic organ and attachment of the cells to internal tissues (Tu *et al*., 2002; Okazaki *et al*., 2006).

In general, the hematological parameters are rapidly changed as response to biotic factors, i.e. infection by pathogens or infestation by parasitoids, and abiotic ones, i.e., wounding, age, eclosion, sex, insecticidal compounds and starvation (Sanjayan *et al*., 1996; Gillespie *et al*., 2000; Sharma *et al*., 2008; Mowlds and Kavanagh, 2008). In this context, another point of interest is the stress to which the insect has been subjected (Silva *et al*., 2002; Andrade *et al*., 2003b; Mochiah *et al*., 2003). The THC in circulation markedly changes after the triggering of an immune response to stress (Ratcliffe *et al*., 1985). Recently, Khosravi *et al.*, (2016) reduced the influencing factors in two factors: the first factor is the generation time of cells, and the second factor is the longevity of cells. In the following sections, we will review the currently available results of works concerning the influencing factors on the hemocyte population dynamics in different insects.

3.2.1. Variation in Hemocyte Population Due to the Developmental Stage:

In normal insects, variations in the hemocyte population have been remarkably demonstrated during the active growth period and as such, THCs have progressively increased during the larval stage culminating prior to the pupation. Depending on the literature sources, some of the early studies were conducted by Tauber and Yeager (1935, 1936) on THCs in normal insect species of different orders. These authors reported that the THCs in the nymphs of hemimetabolous insects were lower compared to those of the respective adults. In contrast, the larval THCs were higher than those of the adult stage in holometabolous insects. In the holometabolous insects, the haemocytes increase in number at a relatively constant rate during the growth of larvae and reach the peak in the pre-pupae. Then, THC declines very rapidly at pupation and eventually falls to a minimal level during the pupal stage (for reviews, see Wigglesworth, 1965; Jones, 1977; Gupta, 1979; Hazarika and Gupta, 1987; Han and Gupta, 1989; Hazarika *et al*., 1994; Siddiqui and Al-Khalifa, 2014).

In some detail, Nittono (1960) reported that the THC was definitely higher in larvae of *E. kuehniella* than in other developmental stages. Also, THC reached its peak in 5^{th} (last) larval instar of *B. mori* and later declined to reach its lowest level after adult emergence. In the tsetse flies *Glossina morsitans* and *G. pallidipes*, THCs significantly dropped during the first 48 hrs following the adult emergence (Kaaya and Otieno (1981). Nishi (1982) recorded a gradual increasing of THC in *S. litura* from the 5^{th} instar to the late 6^{th} instar (pre-pupae) and a subsequent decrease was recorded during the pupal stage. As observed by Jalali and Salehi (2008) and Sendi and Salehi (2010), THC in the swallowtail butterfly *Papilio demoleus* steadily increased during the larval instars, attaining its peak in the late 5^{th} (prepupae) instar and then decreased in prepupae and steeply declined in the pupae. As recorded by Pal and Kumar (2014), THCs in three cyclorrhaphous dipteran flies, *S. ruficornis*, *M. domestica* and *C. megacephala* showed an increasing trend throughout the larval stage, attaining a peak value in the freshly formed puparium but declining thereafter. In the lawn armyworm *Spodoptera mauritia*, THC increased in the haemolymph

during the later larval instars and declined during the pupal stage. Then, it reached its lowest level after adult emergence (Manogem *et al*., 2015). In the rose sawfly *Arge ochropus*, the pattern of THC changed during development and reached its peak in prepupae and then declined slowly in the pupal stage (Khosravi *et al*., 2016). In *A. assama*, THC increased continuously from 1st to 5th instar larvae and recorded a steep decline in the pupal stage (Bardoloi *et al*., 2016).

In contrast, a decreasing tendency of THC level was recorded during the larval period in *A. gemmatalis* (Andrade *et al*., 2003b). Also, Ademolu *et al.* (2010) reported that the adult stage of *Z. variegates* had significantly higher THC than that of other developmental stages. In the pentatomid bug *Chrysocoris purpureus*, THC continuously increased throughout the developmental period and reached a peak in the adult stage (Pugazhvendan and Soundararajan, 2012). As recorded in *A. dorsata* by Perveen and Ahmad, (2017), THC in the normal larvae was 45,875cells/mm^3 but slightly less in pupae and almost seven times less (6470cells/mm^3) in adults.

It is important to shed some light on the variation of THC in the larval stage of the same insect, because the continuous increase of THC during the successive larval instars is a widespread phenomenon in many insects. For examples, THC reached its peak at every moult during the larval stage of *B. mori*, but the highest THC was attained in 5th instar (Nittono, 1960). In the same insect, Wago and Ichikawa (1979) recorded a gradual increase in THC from the 1st to the 3rd instar and a remarkable increase from the 4th to the 5th instar larvae. In the bug *Halys dentata*, THC decreased before and after ecdysis but increased only in the mid instar (Bahadur and Pathak, 1971). In the red cotton bug *Dysdercus cingulatus*, THC reached a peak during the intermoult period and prior to metamorphosis into 5th instar nymphs (Zaidi and Khan, 1975). According to Arnold and Hinks (1976), the THC increased from 6000 mm^3 to 20,000 mm^3 from the 2nd to the 6th instar larval instar of the clear dart moth *Euxoa declarata*. Increasing THC during larval development in *C. fumiferana* was reported by Dunphy and Nolan (1980). In the West Indian fruit fly *Anastrepha oblique*, Silva *et al*. (2002) determined THCs at the beginning and end of 3rd instar larvae as 147.0±10.6 and 210.0±144.5 cells/µl of haemolymph, respectively. Vivekananthan et al. (2010) recorded increasing THC by the nymphal instar processing in the common sand grasshopper *Chorthippus brunneus* (2,375cells/mm^3 and 3,202cells/mm^3 in 4th and 5th larval instars, respectively). In the carob moth *Ectomoyelois ceratoniae*, THC increased with the successive larval instars (Khosravi *et al*., 2012). In the Mediterranean flour moth *Ephestia kuehniella*, THC was significantly higher in the late 4th and 5th instar larvae and prepupa than that in the early 4th and 5th instar larvae (Ghasemi *et al*., 2013b). Recently, Ghoneim *et al*. **(**2017) recorded increasing THC in *P. gossypiella* in the last larval instar toward the prepupae.

On the contrary, Kitano (1969) noticed that the THC in the early 5th instar larvae appeared to be higher than that in the late 5th instar larvae of *P. rapae*. No significant difference existed between the THC of 1st and 2nd nymphal instars of the variegated grasshopper *Zonocerus variegates* (Ademolu *et al*., 2010). Abozenadah (2010) recorded increasing THC during the first part of the 2nd larval instar of *M. domestica* and deceased THC in the second part. She determined 25685±245, 26335±211, 18855±230 cells/ mm³ and 16040±284, at 6, 12, 24 and 48hr, respectively.

Taking the previously reported results into consideration, it is necessary to explicate the fluctuation of THC in the developmental stages of insects. Some conceivable scenarios can be provided herein. (1) Hemocytes are known to be

involved in different physiological functions, such as the intermediary metabolism, such as protein synthesis, transport of nutrients, phenol metabolism, and growth stimulation. Due to active growth during the larval instars, intermediary metabolism should be higher and therefore needs the services of a large THC (Crossley, 1979; Patton, 1983; Sanjayan *et al*., 1996; Ribeiro and Brehelin, 2006; Chavan *et al*., 2017). This scenario was, also, substantiated by some authors, such as Pugazhvendan and Soundararajan (2012) who pointed out that the increasing THC throughout the postembryonic developmental stages is correlated with an increasing demand for the nutrient supply, cellular defense and production of an immunologic factor. (2) The increasing THC in insects is important for inducing their ability to withstand the environmental stresses (Mahmood and Yousuf, 1985). (3) THC increases during the larval stage and attains its peak by end of the last instar (prepupa) and then declines in the pupa. The reason seems to be an elevated rate of mitosis that characterizes all other tissues during this period of active growth (Jalali and Salehi, 2008). (4) Many authors (Kunkel, 1981; Gupta, 1986; Bardoloi and Hazarika, 1995) reported that as the larva metamorphoses from one instar to another, the body size increases and consequently the physiological demand increases. To address this demand, THC increases in the haemolymph. On the other hand, endocrine control of the THC fluctuation during the developmental stages of insects will be discussed later in the present review.

3.2.2. Variation in Hemocyte Population Due to the Sex, Age and Reproductive Status:

Although Sanjayan *et al*. (1996) reported no significant difference between THCs in two sexes of *S. hospes* at one day prior to the copulation, THC may vary between the sexes of the same species in many insects. In some insects, the males show significantly higher THC than the females of the same age, whereas in other insects, the reverse is true. In some detail, females of many insects were found to contain higher THC than their male congeners of the age. Arvy *et al*. (1949) studied the THCs in mantids and found that the females had a higher THC than the males. Depending on the results obtained by Akram (1970), females possess more THCs than those of males of some insects, such as the house cricket *Acheta domesticus*, *G. assimilis* and the grasshopper *C. trachypterus*. Bharvaga *et al*. (1980) recorded higher THC in females than that in males of the red cotton bug *Dysdercus cingulatus*. In *G. bimaculatus*, THC was measured in a range of 29000–46600 cells/mm^3 in females but 26050-42250 cells/mm^3 in males (Mahmood and Yousuf, 1985). Lindsey and Altizer (2008) showed that females of the monarch butterfly *Danaus plexippus* had greater average THC than males. In *C. brunneus*, Vivekananthan *et al*. (2010) recorded higher THC in adult females (3,364/mm^3) than adult males (3,150/mm^3). The THC of the adult females of the pentatomid bug *Chrysocoris purpureus* was higher (6660±440 cells/mm^3) than that of the adult males (4420±165 cells/mm^3)(Pugazhvendan and Soundararajan, 2012)..

On the contrary, some authors (Muhammad, 1961; Hoffmann, 1970) reported that the adult males possess more THC than that of adult females of some insects, such as *L. migratoria migratoriodes* and some grasshoppers. Al-Hariri and Suhail (2001) observed the higher value of THC in adult males (10330cells/mm^3**)** of *S. gregaria* than that in adult females (8690cells/mm^3). In the same locust, Teleb (2011) determined higher THC in 1-day old adult males than that of adult females of the same age (10520±198.5 and 8560±231.5 cells/mm^3, respectively). In *P. bufonius*, Al-Robai *et al*. (2002) determined higher THC in adult males (892cells/mm^3) than that in adult females (838cells/mm^3).

In addition, the dependence of THC on the sex is associated with the developmental stage. The spruce budworm *C. fumiferana* represents an example, since the THC was greater in female larvae than in the male larvae during the 4th instar but was higher in the males during the 5th and 6th instars. Also, THC reached its peak in the prepupal phase of females but in the early pupal stage of males (Dunphy and Nolan, 1980).

The age of an insect, as a factor influencing the hemocyte population in insects was early reported by Gilliam and Shimanuki (1967). The high THC in the young adult bees of *A. mellifera* decreased with age (Amdam *et al*., 2004; Schmid *et al*., 2008; Alaux *et al*., 2010). Trawinski (2016), also, examined the THC in young honey bee workers. Interestingly, 5-day old bees had higher THCs compared to THCs observed in 12 day old bees. In contrast, Wilson-Rich *et al*. (2008) recorded lower THC in the newly emerged adult bee workers compared to the foraging bee workers. Abozenadah (2010) determined variable THC in the 2nd (penultimate) instar larvae of *M. domestica* depending on the age, as follows: 25685±245 cells/mm³ at 6hr, 26335±211 cells/mm³ at 12hr, 16040±284 cells/mm³ at 24hr and 18855±230 cells/mm³ at 48hr. The adult mosquitoes contain slightly more than 1,000 circulating hemocytes at the time of emergence but this number drops with age, falling to 800 or less by their 6th day after eclosion (Castillo *et al*., 2006). Also, Hillyer and Strand (2014) reported that the mosquito adult female harbors anywhere between 500 and 4,000 hemocytes, and this number decreases with the age in females maintained on sugar water.

With regard to the reproductive status, as influencing factor on the THC in insects, the maximal value of THC was recorded before mating in the males and prior to the laying of each egg batch by the females of some insects (Siddiqui and Al-Khalifa, 2014). In *B. germanica*, Hazarika and Gupta (1987) suggested that a higher THC in female was related to its periods of oviposition. As recorded by Sanjayan *et al*. (1996) for *S. hospes*, a 50% decrease in THC was observed during the adult eclosion from the 5th larval instar. Then, THC gradually increased. Upon mating, THC decreased in males but increased in females to almost double that of males. These results indicated that the THC not only undergo definite changes during moulting but also must be associated with the process of maturation of the oocyte in the females. The high THC in the adult females of *Ch. purpureus* seemed to be associated with the reproductive function of these females (Pugazhvendan and Soundararajan, 2012).

3.2.3. Variation in Hemocyte Population Due to the Circadian Rhythm:

Most animals show circadian rhythms in their behavior. The circadian patterns are, also, reflected in the physiology of various systems in many insects (Lipton and Sutherland, 1970; Brady, 1974). Biochemical changes were reported in the haemolymph following a definite diurnal periodicity (Kannan and Ravindranath, 1980) and similar rhythms in the mitotic activities of hemocytes have also been reported in some insects (Jones and Liu, 1968).

Depending on the available literature, it is evident that all hemocytes do not circulate at the same time; some remain to adher to the tissue surfaces. Their appearance in and disappearance from the circulation also seems to follow a definite rhythm (Maheswari and Sehgal, 1979). The changes in the haemogram of a nocturnal, sand burrowing cricket *Schizodactylus monstrosus* had been investigated by Islam and Roy (1982) during different hours of day and night. They found that the THC varied depending on the daily rhythm, since THC appeared to be much lower during the day than at night. This might be due to synchronized mitosis of the

undifferentiated hemocytes or release of sessile hemocytes from the temporary hemocyte reservoirs (Crossley, 1975). In this context, a study on the periodicity of differential haemocyte counts in the giant cockroach *Blaberus giganteus* before and after dark may be important. In this study, Arnold (1969) reported changes in the proportions of SPs and GRs during the light-dark cycle in 25% of the insects but found no change in the proportion of PRs and PLs. He could not demonstrate convincing evidence for a diurnal response but noted that 'there is a potential for periodicity in the haemocyte complex and a need to consider it in the planning of experiments'.

3.2.4. Variation in Hemocyte Population Due to the Physical Conditions and Habitat Topography:

It has been reported by various workers that temperature affects the THC; since low temperature treatment leads to a decrease of THC, while high temperature enhances the THC increase (Tiwari and Shukla, 2000). On the other hand, Rosenberger and Jones (1960) found that starvation of *P. eridania* at low temperatures does not affect the THC in haemolymph but does so at high temperatures. However, there are several articles demonstrating the effects of temperature on the hematology of lepidopterous species. For examples, chilling of the African monarch *Danaus chrysippus* larvae caused a decline in the THC while heating elicited an increase in the number of the circulating cells (Pandey *et al*., 2008). The incubation of *G. mellonella* larvae at 4 or 37 °C for 24 h led to an increase in THC (Mowlds and Kavanagh, 2008). Rearing the 5th instar larvae of *A. mylitta* under high temperature promoted to increase the THC but low temperature treatment led to clumping of the circulating hemocytes (Pandey *et al*., 2010).

Ghasemi *et al*. (2013a) reported that the changes in temperature, like other abiotic factors, may affect the cellular immune responses of insects, including the changed THC. In the same year, Ghasemi *et al*. (2013b) assessed the effects of heat and chill stresses on hemocytes of 2-day old 5th instar larvae of *E. kuehniella*. They revealed that high temperature (40 °C) caused a significant increase in THC, principally PLs, OEs. In contrast, chilling (4 °C) led to a significant reduction in THC, proportion of PLs with an increase in counts of OEs. The increase in THC of *E. kuehniella* larvae exposed to high temperature may be attributed to the more mitotic rate of hemocytes and more importantly increased hemocyte proliferation of hemopoietic organs. These authors, also, reported that the release of hemocytes attached to the internal organs of heat exposed larvae of *E. kuehniella* into the haemolymph circulation can be another reason for the increase in THC.

As previously mentioned, the high THC induces the ability of insects to withstand external environmental stresses (Mahmood and Yousuf, 1985). It seems that exposing the insects to high temperatures can increase the environmental fitness of larvae through a similar mechanism to thermoregulatory behaviour by increasing THC (Ghasemi *et al*., 2013b).

Another point of interest in this respect is the interrelationship between the voltinism of some insects and THC in their haemolymph. To the best of our knowledge, only one study had been conducted in which Ganie *et al*. (2015b) studied the voltinism of *B. mori* and the fluctuated THC in the haemolymph of different breeds under temperate climatic conditions of Jammu and Kashmir. They used bivoltine breeds and multivoltine breeds. The observations of high THC in the multivoltine breeds of *B. mori* may be attributed to their high haemolymph content which in turn contributes to their higher survival under adverse climatic conditions, while in case of bivoltine breeds, the high THC values during spring are attributed to

higher feeding efficiency coupled with quality mulberry leaf during the same season. Another reason that could be assigned to the higher THC values in multivoltine breeds was probably the release of more haemocytes from the hematopoietic organs.

To investigate the effect of the habitat topography on the hemocyte population, especially the circulating PLs and GRs, in insects, Baishya *et al*. (2015b) carried out a study on the 5th instar larvae of *A. assama* reared at four different sericulture farms situated at different altitudes. The mean circulating PLs and GRs were highest at Khanapara (55.5 m ASL), whereas their numbers gradually decreased in altitude at Nongpoh (464 m ASL), Tura (657 m ASL), and Kalimpong (1,247 m ASL). This may be attributed to the average environmental temperatures observed at different altitudes, which might affect the overall hemocyte load of larval stages reared at those altitudes. The increased numbers of immunocytes (PLs and GRs) at lower altitudinal broods, when compared to those observed at higher altitudinal broods probably correspond to the growing demand for the cellular immunity (Bardoloi and Hazarika, 1995). For some detail, the high THC at the higher temperature may be attributed to the loss of body fluid due to desiccation. In addition, at the higher temperature, probably as a defense mechanism, hemocytes (including PRs and GRs) get detached from tissue surfaces and increase their rate of multiplication leading to higher hemocyte production so as to promote cellular defense to the silkworm larvae, which are supposed to be more prone to infections at higher temperatures. Similarly, declining THC in lower temperature (higher altitudes) may be attributed to clumping of hemocytes due to chilling stress and thus making the hemocytes unavailable in circulating haemolymph (Pandey *et al*., 2010).

3.2.5. Variation in Hemocyte Population Due to the Nutritive Factor:

As reported in the currently available literature, the nutritive content of the diet or the host plant composition affects the THC in haemolymph of the feeding insects. For examples, the haemolymph of *A. mellifera* adult workers contained higher THC after feeding on a diet deficient in protein than those fed a rich protein source (Alaux *et al*., 2010). The cabbage looper *Trichoplusia ni* larvae reared on broccoli had more THC than those reared on cucumber (Shikano *et al*., 2010). Effect of the host plant or diet on THC was investigated in *S. gregaria* nymphs by Barakat *et al*. (2016). They recorded that the nymphs fed on clover had the highest THC, while those fed on grass had the lowest THC. Bardoloi *et al*. (2016) reared the larvae of *A. assama* on two host plants. They recorded a significant difference in THC in the later instars (4th and 5th instars) and pupae suggesting the impact of host plant on THC in haemolymph. Also, Vogelweith *et al*. (2016) found that the THC in 5th instar larvae of *E. ambiguella* varied depending on the diet. Responses of the reduviid predator *Rhynocoris marginatus* to six prey species of different insect orders had been investigated by Sahayaraj *et al*. (2016). Depending on this study, THC was greater in the predator reared on larvae of Lepidoptera, followed by those reared on adults of Heteroptera and lowest THC was recorded in those reared on adults of Coleoptera. Recently, Tungjitwitayakul and Tatun (2017) recorded that the THC in 5th instar larvae of the Eri-silkworm *Samia cynthia ricini* reared on cassava leaves was significantly higher (2.45±0.33 x10^{4} cells/ml) than that in larvae reared on the artificial diet (1.61±0.12 x10^{4} cells/ml). The effects of nutrient supplementation of *B. mori* last instar larvae with the mineral salt compounds (potassium sulphate and sodium sulphate) were studied by Essawy and Saad (2013). The larvae were fed on the salt-treated mulberry leaves on the first day. During 5th day of the feeding period, the salts individually enhanced the THC in larvae. Also, the biosalt mixture enhanced the THC during the feeding period.

An increase in the THC was reported in *Leptinotarsa decemlineata* (Arvy *et al*., 1948) and *P. eridania* (Yeager, 1945; Rosenberger and Jones, 1960) during starvation. On the other hand, a decrease in the THC was seen in the starved larvae of *B. mori* (Nittono, 1960) and in *G. mellonella* (Shapiro, 1966). Thus, it is apparent that there was an increase of the THC in some insects and decrease in others following starvation. For the above changes in THC, variations in the blood volume were thought to be responsible.

Storage of different nutrients, like carbohydrate, lipid and amino acids by the hemocytes and their role in maintaining the normal nutrient balance during different stress conditions are well documented (Munson and Yeager, 1944; Arnold, 1952, 1970). The alterations in the number of circulating hemocytes, maintaining a relationship with the alteration of nutrient levels in the haemolymph, demonstrates the role of stored food materials in the hemocytes (perhaps by releasing them into the haemolymph) to balance the nutrient level in the haemolymph during periods of acute energy need, since these nutrients were reported to serve as an immediate fuel source during exercise in the cricket *S. monstrosus* (Islam and Roy, 1983).

It is well known that under adverse conditions and at the time of experimental stress, particularly when metabolic water is not available, fluid from the tissue spaces is added to the circulating haemolymph (Shapiro, 1979; Gupta,1985), thus increasing the hemocytes.

With regard to the differential haemolymph counts (DHCs), Szymas and Jedruszuk (2003) examined the influence of different diets on the haemolymph of *A. mellifera* adult workers. They found that a lack of protein in the diet caused a significant increase in the count of GRs and a significant decrease in the counts of other types. Also, Vogelweith *et al*. (2016) found that the DHC of each hemocyte type in 5^{th} instar larvae of *E. ambiguella* varied among diets.

From the defense mechanism point of view, many authors (Lazzaro and Little, 2009; Babin *et al*., 2010; Vogelweith *et al*., 2011; Ponton *et al*., 2011) recognized now the nutrition as a critical factor in immune defense and resistance of insects. Experimentally, many authors (Pletcher *et al*., 2002; Kapari *et al*., 2006; Ayres and Schneider, 2009) demonstrated that food deprivation affects immune responsiveness. Klowden (2007) suggested that GRs are involved in the nutrient transport. Thus, it could be hypothesized that food deprivation or poor quality food induces a nutritive stress, reducing the proportion of GRs and affecting the encapsulation process against foreign bodies.

3.2.6. Variation in Hemocyte Population Due to the Behavioral Patterns:

As far as our literature survey could ascertain, no information was available on the examination of varied THC depending on the behavioral activities except a study conducted on the desert cricket *S. monstrosus* (a nocturnal carnivorous insect, showing intraspecific aggressiveness) by Islam and Roy (1984). As recorded by these authors, THC was 16,400±320/mm^3 blood at the initiation of fighting. The THC showed an 85% increase after 20 min of continuous fighting. They attributed the increasing THC during the early periods of fighting to the considerably higher number of sessile hemocytes releasing into the circulation than that in later periods. This indicated that such intraspecific aggressiveness accompanied by vigorous exercise was also an external factor that caused the release of sessile hemocytes into the circulation.

3.2.7. Variation in Hemocyte Population Due to the Measuring Technical Method:

As previously reviewed (section 'Controversial terminology and technical

difficulties of the hemocyte identification'). For some detail, Tauber and Yeager (1935) found that the number of haemocytes in the haemolymph of unfixed insects is always lower in comparison with that in the haemolymph of a fixed insect. The reason for such variation is the adhesion and coagulation of haemocytes at the site of withdrawal. More than two decades later, this information was substantiated by some authors (Nittono, 1960; Wheeler, 1961) who reported that the unfixed plasma in some insects rapidly coagulates and/or mechanical agitations of the blood drop *in vitro* or of the circulating blood at the withdrawal site lead to intense sticking of living hemocytes, therefore, significantly fewer hemocytes are available for determining THC than if plasma coagulation and/or clumping of cells are prevented by chilling or fixing the insects in either hot acetic acid vapors or hot water. As observed by Matsumoto and Sakurai (1956), the THCs in three successive drops of haemolymph from unfixed *Bombyx* larvae diminished by 883 cells between the first and second drop, and by 587 cells between the second and third. These authors suggested that these decreases were due to the adhesion of hemocytes near the withdrawal site. Wigglesworth (1956) counted a lower THC in the haemolymph of unfixed *R. prolixus*, compared to that counted in the haemolymph of a heat-fixed *R. prolixus*. However, it has been found that in the unfixed and unfed *R. prolixus* larvae, the first drop of haemolymph contains more hemocytes than the second drop (Jones, 1962). Thus, variation in the hemocyte count depends on the technical method of studying haemocytes and the characters adopted by other researchers (Giulianini *et al*., 2003; George and Ambrose, 2004; Ribeiro and Brehelin, 2006).

3.3. Hemocyte Population and Endocrine Control in Insects:

Growth and development in insects are regulated by a number of hormones, such as the steroid 20-hydroxyecdysone (20E; molting hormone; ecdysone or ecdysterone), the sesquiterpenoid JHs, eclosion hormone and other neurohormones (Dhadialla *et al*., 1998). The cyclical changes in the haemocyte population have been frequently demonstrated by many researchers during growth and development of insects but their studies did not provide any information on the role of hormone(s) in the quantitative (THC) or qualitative (DHC) variations of haemogram (Yeager**,** 1945; Jones, 1965). Nappi (1974**)** suggested the involvement of brain endocrine complex in the haemocyte accumulation following some initial stimulus.

However, the endocrine regulation of the hemocyte population dynamics will be briefly reviewed on the following pages. Some of the classical experiments of extirpation and implantation of endocrines had been carried out. Hoffmann (1970) extirpated and implanted certain endocrine glands into the locust *L. migratoria*. He reported that the electro-coagulation of pars intercerebralis in the females affected the THC which abruptly increased. He surgically removed the corpora allata (CA) and recorded a decrease in the THC. After the implantation of corpora cardiaca (CC), the THC increased but extirpation of CC affected the rate of haemocyte differentiation. Some years later, Pathak (1983) performed the extirpation and implantation of endocrine glands into the bug *H. dentata*. Depending on his extirpation experiments, it was obvious that the hormonal secretion of CA influences the THC. He assumed that the haemocyte population is not entirely under the influence of CA throughout the life span, and/or physiological conditions of an insect. This assumption is further strengthened by other extirpation experiments. After removal of both CC and CA from the insects, the THC remained significantly low throughout the life span, while removal of only CA led to a significant increase of THC after the 6^{th} day. With regard to the adults, the transplantation of both CA and CC into 1-day old adults, no change in the THC throughout the adult longevity

was observed. In the other case, when CC of 6-day-old adult insects had been transplanted into I-day-old adults, the THC increased for only the first 3 days. He concluded that the CA influenced the THC during the early part of adult life, and secretion of neurosecretory cells of the brain and the CC influenced the THC during the late half of adult life.

Some authors (Akai and Sato, 1973; Arnold, 1974; Crossley, 1975) showed that the presence of ecdysteroids in haemolymph would be responsible for the increase of THC and release of hemocytes from the hematopoietic organs. In addition, Hinks and Arnold (1977) demonstrated that ecdysone enhances the rate of mitosis in hemocytes. In lepidopterous insects, some authors (Rao *et al*., 1984; Lanot *et al*., 2001) suggested that the appearance of hemocytes at the prepupal state is regulated by the ecdysone titer. Since the ecdysone titer is high towards the latter part of each larval instar (Nishikawa and Natori, 2001; Xu and Kawasaki, 2001), the sudden rise in THC in the prepupal state of the butterfly *P. demoleus* and the steep decline in THC in the pupae could be due to the role of ecdysone (Jalali and Salehi (2008). During the adult life of honey bee *A. mellifera*, as the worker transition (typically at around 2-3 weeks of the adult life) to tasks, such as foraging that take them outside of the hive, the THC declines. This THC decline can be reversed if workers are forced to revert for performing tasks inside the hive (Amdam *et al*., 2004). On the other hand, Trawinski (2016) found that the queen mandibular pheromone exposure resulted in increased titer of ecdysone and an increase in THC in 12-day old bees.

Although Han *et al*. (1995) reported that both 20E and JH activate the release of hemocytes from hemopoietic organs in *B. mori*, the literature sources show that 20E induces the proliferation of hemocytes (increasing THC), while JH shows adverse effect (James and Xu, 2012). In this context, it may be important to report that the JH acts as a factor affecting the number of immunocytes (Gelbič *et al*., 2006; Franssens *et al*., 2006; Zibaee *et al*., 2012; Rahimi *et al*., 2013). It seemed, also, plausible that light may be the main signal to trigger the neurosecretory cells, releasing specific hormones that bring about chemical changes in the haemolymph which in turn determine the appearance and disappearance of hemocytes in and from the circulation (Islam and Roy, 1982).

4. Haemolymph Volume as A Quantitative Haemogram Parameter in Insects:

The estimation of total haemogram in insects includes, also, the determination of blood volume, BV (haemolymph volume, HV) because the population of circulating hemocytes depends upon BV or is affected by it (Chapman, 1982; Bardoloi *et al*., 2016; Khosravi *et al*., 2016). In other words, BV determination is essential in many cases for an accurate evaluation of the THC. Early, Mellanby (1939) reported that the blood in insects is the means by which pressure is transferred from one part of the body to another, and thus assists in hatching and moulting. The reduction of BV may interfere with these processes. The BV, also, serves to maintain the body size, and if the BV is decreased during development, an undersized adult may result.

Some authors have preferred the 'absolute haemocyte count (AHC), beside the THC in insects. Gupta (1985) considered AHC as an estimate of both the THC and DHC in relation to the blood volume (BV). It can be estimated by multiplying the THC by the BV. Experimentally, two or more different methods had been described for determining the BV in different insects, such as the cockroach *Periplaneta fuliginosa* (Yeager and Tauber, 1932), the locust *S. gregaria* (Lee, 1961) and the coleopteran *T. molitor* (Ahmed and Kloft, 1985). In his comprehensive

review, Jones (1962) discussed several methods for determining the BV in insects. Shapiro (1979b) calculated the blood volume in Galleria by the following formula:

$$V= d(c' - c'')l /c''$$

where V = BV in µl; d = volume of amaranth dye (1% aqueous solution) injected in µl; c' = original concentration of dye (percentage); c'' = concentration of the dye after circulation (percentage). To obtain the BV, divide the V value by the body weight of the insect. In the present section, we will give an insight into the relationship between BV and THC in insects and review the major factors influencing the BV.

4.1. Relationship between BV and Hemocyte Population:

Jones (1967b) found that BV increased in *Rhodnius* after feeding and the proportion of GRs and OEs also increased while the PLs decreased. As reported by Feir and O'Connor (1969), the hemocyte adhesiveness and BV are considered as important factors influencing THC of circulating haemocytes, so the increase or decrease in BV can lead to changes in THC. Webley (1951) observed the interrelationship between THC and BV in the locust *L. migratoria migratorioides* and concluded that in older adults a decrease in BV is related to an increase in THC. In a study on the aggressive cricket *S. monstrosus*, Islam and Roy (1984) determined an increase of BV accompanying by increased THC during the early periods of fighting, compared to the later periods. The same authors attributed this increase to a higher rate of release of sessile hemocytes into the circulation.

An inverse relationship between the THC and BV in larvae of *B. mori* was advocated by Nittono (1960). Also, an inverse relationship exists between the THC and the BV after incubation of *E. kuehniella* larvae at 40°C (Ghasemi *et al*., 2013b). In his early study on changes of THC in relation to BV during the moulting cycle of the cockroach *P. americana*, Wheeler (1963) found that the increase of THC prior to ecdysis was not significant and the decrease of THC at ecdysis itself results from a sudden but brief increase of BV. He concluded that as the BV goes up the THC falls. In *H. dentate*, it had been found that there is a significant decrease in THC after ecdysis. A possible explanation for this would be that after ecdysis the BV falls suddenly so that a good number of haemocytes may attach themselves to the tissues and may not come into circulation. Probably, they return to the circulating blood again when the BV becomes normal after feeding, usually during the middle period of a stadium (Bahadur and Pathak, 1971). In *H. dentata* and *B. mori* some studies were performed to establish the interrelationship between BV, endocrine glands and THC (Pathak, 1984). Essawy *et al*. (1984) studied the THC and BV in order to estimate the changes which occur in the haemocyte picture in the last larval instar of *H. armigera*. They recorded that with the increase of BV at 96 hr the absolute number of haemocytes increased but at this time the THC is decreased. The observed changes in BV may also be assigned to the same explanation as that of changes in THC. However, the difference in BV might have influenced the THC. This relationship had been reported by Bardoloi and Hazarika (1992) in *A. assama*.

4.2. Factors Influencing the Variable BV Value:

Insects regulate their BV by a variety of mechanisms including hormonal and metabolic factors. In any given insect species, the BV, at any particular time during the life cycle, will tend to be fairly constant. However, BV per unit mass is not always constant (Shapiro, 1979; Pathak, 1986). Stressing the insect, for example by exposure to very high temperatures or by starvation, will result in changes in the BV (Smith, 1994). In the present review, special attention should be paid to some factors influencing the BV, such as the developmental stage, age, sex, physical and nutritive conditions.

4.2.1. BV variation Due to the Developmental Stage:

The changeable BV was studied during the different developmental periods of some insects. For examples, BV rises during the latter half of an instar on *S. gregaria*, and attains its highest level just prior to ecdysis and then falls sharply to a mid-instar (Lee, 1961). In each of the latter two nymphal instars of *L. m. migratorioides*, Loughton and Tobe (1969) recorded that the BV was low at first, increased sharply at the mid stage, and remained high until after ecdysis, then it suddenly decreased. In the young adults, the BV was low until the 8th day. Thereafter, the sexually mature adults possessed higher BV. The BV/unit weight of female adults of the cricket *G. bimaculatus* decreases sharply immediately after ecdysis (Ehler *et al*., 1986). In *S. hospes*, there was no difference between BV in the last (5th) instar larvae and mated adult females. Whereas BV decreased upon the adult eclosion after which it gradually increased (Sanjayan *et al*., 1996). In the *B mori* larvae, BV gradually increased until the end of the obligatory feeding period, BV reached its peak value at 10th day, but it decreased during the prepupal period and pupation (Essawy, 1997). In *A. assama*, BV continuously increased from 1st to 5th instar larvae but sharply declined in the pupal stage (Bardoloi *et al*., 2016). BV of *A. ochropus* changed from the 2nd larval instar to pupal stage. In contrast, BV reached its maximum on the 1st day of prepupal and pupal stage (Khosravi *et al*., 2016).

4.2.2. BV Variation Due to the Age and Sex:

The changes in BV during the same larval instar, depending on the age, had been reported in some insects. For examples, BV rises during the second half of a nymphal instar in *S. gregaria*, and attains its highest level just prior to ecdysis. This high BV is maintained for about 24 hr after ecdysis and then falls sharply to a mid-instar (Lee, 1961). During the 5th larval instar of the castor semi-looper *Achaea janata*, Ramdev and Rao (1984) observed increasing BV with the age but a slight reduction was observed at the 96 hr-old larvae. The BV/unit weight of female adults of the cricket *G. bimaculatus* did not alter greatly with age (Ehler *et al*., 1986). Abozenadah (2010) determined the BV during the 2nd larval instar of *M. domestica* as 2.14±0.159, 2.71±0.111, 7.38±0.331 and 13.44±0.197 µl /larva, at 6, 12, 24 and 48hr, respectively. Thus, the BV increased with age. Increasing BV with larval age was also reported in *A. ochropus* (Khosravi *et al*., 2016). In the last instar larvae of *B. mori*, Essawy and Saad (2013) recorded a gradual increase in BV, starting from the 1st day which continued to reach its peak at the 9th day (the end of feeding period), then a decrease was recorded after the 9th day until the end of the last instar.

With regard to the sex, as a factor influencing the BV, mean BV of the newly emerged adult males of *T. molitor* remained constant between day 2 and day 3 after emergence. In comparison, the newly emerged females had increasing BV at these days (Ahmed and Kloft, 1985).

4.2.3. BV Variation Due to the Physical Conditions:

To the best of our knowledge, the earliest study concerning the effects of physical factors on the BV was conducted by Mellanby (1939). Depending on this study, the higher moisture content in the insect larvae influences higher BV; since BV serves as a reservoir of water. Holdich and Mayes (1976) investigated the changes in the BV and total water content of the woodlouse *Oniscus asellus*. They found that the rates of reduction of BV, total water content and body weight were different in the humidities of 0% RH and 62% RH. As recorded by Cohen et al. (1986), the desiccation and rehydration had significant effects on the BV in the

blister beetle *Cysteodemus armatus*. When *Periplaneta* adult males were dehydrated, the BV was markedly reduced (Edney, 1968; Wall, 1970). When *D. melanogaster* was subjected to desiccation, the BV was reduced to less than 25% of its initial value (Albers and Bradley, 2004). Dehydration of the Namib Desert tenebrionid *Onymacris unguicularis* for 10 days at 27°C resulted in a 37% decrease in BV. Rehydration resulted in increases in BV (sub-normal at the end of rehydration) (Naidu, 2008). The difference in BV between the two sets of larvae of *A. assama* reared on the host plants *Machilus bombycina* and *Litsea polyantha* had been reported by Hazarika *et al*. (1994) owing to the leaf moisture content of these host plants.

If *R. prolixus* larvae were given a sufficiently long heat-treatment prior to feeding, moulting is delayed in association with an enormous increase in the BV (Okasha, 1968 a, b). The impact of cold stress on the BV in *E. kuehniella* was studied by Somme (1966) who found that the cold stress induced an increase in the BV. More than four decades later, Ghasemi *et al.* (2013b) studied the responses of larval instars of the same lepidopterous insect to the thermal stress, heat (40°C) and chill (4°C) stresses. Among their results, the high temperature caused a drastic reduction in BV.

4.2.4. BV Variation Due to the Nutritive Factors:

Depending on the available literature, nutrition appeared to act as a factor influencing the BV, since the changes in BV could be related to the transport of nutrients from one part of the body to another. In addition, the BV was reported to be decreased during starvation (Arvy *et al*., 1948; Rosenberger and Jones, 1960; Wharton *et al*., 1965). According to Chen (1989), the BV increased in *S. calcitrans* to approximately three times the pre-feeding level 3-6 hr after a blood meal and gradually returned to normal 18 hr after the blood meal. Depending on the study of Essawy and Saad (2013), the last instar larvae of *B. mori* were fed on salt-treated mulberry leaves (two mineral salts: potassium sulphate and sodium sulphate) at the first day. Feeding of larvae on leaves treated with potassium sulphate or salt mixture enhanced the BV to reach its peak at 10^{th} day of the feeding period. Feeding of larvae on leaves treated with sodium sulphate enhanced the BV during the feeding period from the 4^{th} day until 8^{th} day. The *A. assama* larvae were reared by Bardoloi *et al*. (2016) on two host plants: *Machilus bombycina* and *Litsea polyantha*. In the 5^{th} instar larvae, they recorded higher BV in those larvae reared on *L. polyantha* than that of larvae reared on *M. bombycina*. They could tentatively assume that the observed differences in BV were due to the dietary water more than due to any other nutrient in these host plants.

4.2.5. BV Variation with some Behavioral Activities:

Beenakkers (1973) found no effect of flight on BV in *L. migratoria*. In the long-winged cricket *Gryllus texensis*, flying for 5 min had no significant effect on the cricket BV (Adamo *et al*., 2008). On the other hand, the same authors recorded an average BV of 162±12.8 μlg^{-1} wet mass in flying crickets whereas control crickets had an average BV of 156±16.5 μlg^{-1} wet mass.

4.3. An Endocrine Insight into the BV Status:

On the basis of the available literature, few research works focused on the aspects of hormonal regulation of BV in insects. To explore the role of endocrine or neuroendocrine organs in the regulation of BV, Girardie (1964) and Goldsworthy (1971) surgically removed the cerebral neurosecretory cells from the brain of *L. migratoria*. They observed an increase of BV. After the electro-coagulation of pars

intercerebralis in the males of *L. migratoria,* Hoffmann (1970) recorded 235.5% BV more than the intact insects. Mandal *et al*. (1984) found that only allatectomy (surgical extirpation of corpora allata CA, organs producing JH) or only brain cauterization in *Gryllotalba gryllotalba,* BV slightly increased. But simultaneous removal of CA and brain produced a significant fall of BV which is enigmatic. Results of these studies can be considered as an informative for the neuroendocrine control of BV in insects.

The diuretic and antidiuretic hormones may participate in the endocrine control of BV in insects; since the pupal-adult ecdysis of the cabbage white butterfly *Pieris brassicae* was followed by a short but fast diuresis which drastically reduced the BV (Nicolson, 1976a). The level of diuretic hormone might tend to rise continuously as the BV was lowered during diuresis (Nicolson, 1976b). As reported by Pathak (1984), some studies were performed to investigate the interrelationship between BV and endocrine glands in *H. dentata* and *B. mori*. In *H. dentata,* Pathak (1983) surmised that in 6-day-old, well-fed adults, neurosecretory cells of brain secrete diuretic hormone which reduces the BV. In the spinning larvae of *B. mori* It was noted that due to the influence of the diuretic hormone secreted from either neurosecretory cells of the brain or from corpora cardiaca the fluid from the haemolymph is excreted which affects BV (Pathak, 1986). On the other hand, increasing BV may be caused by the release of antidiuretic hormone from the neurosecretory cells of the thoraco-abdominal ganglionic mass in *H. dentata*. This hormone decelerates the rate of excretion leading to the increase of the BV (Pathak, 1991).

4.4. Interrelationship between BV and Osmotic Pressure:

Haemolymph is considered as a water reservoir which is influenced by numerous factors, such as age, development stage, diet and hydration (Edney, 1968). Regulation of the osmotic pressure of the haemolymph had been studied in some insects, such as the cockroach *Leucophaea maderae* (Laird *et al*., 1972), the locusts *Chortoicetes termimfera* (Djajakusumah and Miles, 1966), and *S. gregaria* (Shaw and Stobbart, 1972). In the dipteran *C. erythrocephala*, haemolymph osmotic pressure increased during dehydration by 25% after two days of water deprivation (Phillips (1969). Wall (1970) recorded a similar trend in the cockroach *P. americana* during dehydration. In his review on water balance in land arthropods, Edney (1977) concluded that the insects are able to regulate osmotic potential of haemolymph under different stressed conditions and ions play very important role in regulating osmotic potential. By rearing *B. mori* larvae on certain artificial diet, the osmotic pressure of haemolymph increased rapidly from day 0 to day 5, then declined until day 8. These results suggested that the change in the osmotic pressure may play a role in the transformation from larvae to pupae (Nakayama, 1990). For some detail of osmotic strategies in insects, see Garrett and Bradley (1984), Hyatt and Marshall (1985), Hadley (1994), Patrick and Bradley (2000).

To our knowledge, very little information exists in the available literature concerning the interrelationship between BV and osmotic pressure in insects. As reported by Chen (1989), the osmotic pressure of haemolymph in *S. calcitrans* decreased approximately 10% following a blood meal and gradually returned to normal with a pattern that was a mirror-image of that of the BV. However, the interrelationship between BV and osmotic pressure is affected by different stressors. Locusts are able to drink only under certain conditions, and the stimulus to drink may well be initiated by a reduced BV, which may be a sensitive indicator of the extent of water reserves (Dethier and Evans, 1961). When the cockroach *P. americana* is

dehydrated, the BV was remarkably decreased, but its osmotic pressure slightly increased, indicating that during dehydration solutes are removed from the haemolymph (Edney, 1968; Wall, 1970). Cohen and Patana (1982) studied the impact of heat and cold in the beet army worms. The cold-stressed larvae showed a significant increase in the BV and osmotic potential but the reverse was observed in heat-stressed larvae. The effect of starvation on the osmotic pressure of the haemolymph is very different according to the species of insects. In larvae of *Aeshna cyanea* there was no change in haemolymph osmotic pressure after starvation for 240 h in tap water (Moens, 1973). Albers and Bradley (2004) found that *D. melanogaster* displayed strict osmotic regulation under conditions of dehydration, being able to regulate osmotic concentration when over two-thirds of the BV has been lost. Similarly, recovery of BV could be achieved with a variety of recovery fluids, including distilled water.

5. Mitotic Index as a Parameter of Haemogram Profile in Insects:

Many authors (Gardiner and Strand, 2000; Tu *et al*., 2002; Saito and Iwabuchi, 2003; Okazaki *et al*., 2006) reported that the maintenance of hemocyte populations is thought to be regulated by the mitotic division of circulating hemocytes and by production and release of hemocytes in the hematopoietic organs. Mitotic index (MI) is a measure for the proliferation status of a hemocyte population and can be defined as "the ratio between the number of cells, in a population undergoing mitosis, to THC in a population". The MI is employed as the criterion of response to various treatments involving factors which might affect this activity.

The MI in circulating hemocytes rarely exceeds 1% in almost all cases (Jones, 1967a, b; Jones and Liu, 1968). On the other hand, the mitotic activity varies with developmental stages of the same insect. For examples, Feir and McClain (1968) found that the MI in the bug *Oncopeltus fasciatus* was very low immediately after ecdysis into the 5^{th} instar. They noted that mitotic activity began to rise at 23 hr post-ecdysis, reaching its peak (4.06 %) in the 30-hr group, remained high until 74 hr, and then declined during the remainder of the larval stage. Sanjayan *et al*. (1996) observed different values of the MI in the last instar and adults of *Spilostethus hospes*. In a similar trend, Ghasemi *et al*. (2013b) revealed that the mitotic activity varies with developmental stages of *E. kuehniella*; since the MI of hemocytes was found to be high in the early part of each larval stage than in the later larval stage and in prepupa.

Depending on the currently available literature, scarce studies have examined the interrelationship between MI and THC, but some studies have searched the interrelationship between MI and DHCs of some hemocyte types in few insect species. For some detail, the mitotic activity has been most consistently reported in the PRs and hemocyte differentiation studies in some insect species revealed that PRs are the stem cells from which the other cells arise (Gupta, 1991). In the case of *B. mori*, it was proved that approximately 43% of PRs differentiate into PLs, GRs and SPs (Yamashita and Iwabuchi, 2001). The population of PRs in 1^{st} and 3^{rd} instars was significantly higher than that in 2^{nd} and 4^{th} instars and prepupa. The rapid decline in their counts coinciding with the increase in PLs and partially OEs in the later part of larval instar suggested that their differentiation is probably toward the formation of PLs and OEs at that time. Mitotic activity in the rose sawfly *Arge ochropus* had been reported for most hemocyte classes despite it is usually considered to be primarily a property of the PRs (Khosravi *et al*., 2016). Other types of hemocytes have rarely been reported with higher MI than PRs. Mitotic cells were found among SPs of *B. mori* (Siddiqui and Al-Khalifa, 2014).

6. Is the Heartbeat Rate Related to the Hemocyte Population or BV in Insects?

In this section, we would like to shed some light on the interrelationship between the heartbeat rate and hemocyte population and/or BV in insects. Insect haemolymph is circulated in the body cavity by a heart, which is simply a long muscular dorsal vessel (Wigglesworth, 1965; Jones, 1977; Woodring, 1985). Although the gaseous transport is not important to the heart (Fox, 1982), the primary function of the heart in insects is to transport nutrients from the absorptive sites to the tissues of the body, waste products to excretory organs, and hormones from glands to target cells (Tsai *et al*., 2004). Proper functioning of the heart is one of the major physiological processes essential for the normal functioning of an insect (Feliciano *et al*., 2011). Even slight alterations in the heart functioning may interrupt the homeostasis and cause severe changes in insects (Piazza and Wessells, 2011).

Changes in the heart contraction patterns have been described in *D. melanogaster*. Although the contraction rate and its relation to contraction direction were being debated (Wasserthal, 2007), Dulcis and Levine (2005) argued that systole and diastole are synonymous with anterograde and retrograde contractions, respectively (Glenn *et al*., 2010). Marciniak *et al*. (2010) studied the heart contractile activity in three beetle species: the giant mealworm beetle *Zophobas atratus*, *T. molitor* and *L. decemlineata*. An example of typical heartbeat was recorded where the retrograde phase of peristaltic waves of the heart pulsations was clearly distinguished by the lower frequency of the systolic contractions (12–14 beats/min) and a fast anterograde phase of contractile activity (23–25 beats/min) was observed.

Heartbeat rate (the number of beats per minute) was reported to depend on the development stage of an insect. As for example, Slama and Farkas (2005) investigated the heartbeat rate during the postembryonic development of *D. melanogaster*. They found that the 1st instar larvae exhibited the fastest rate. During the larval growth, the frequency of anterograde pulsations successively decreased during and after puparium formation, with progressively prolonged periods of cardiac rest. Heartbeat reversal was first noticed during metamorphosis, in a 2-day old puparium, coincident with the formation of the conical heart chamber. Similarly, as in other insect species and stages, the anterograde heartbeat of pupal or pharate adults of *D. melanogaster* occurred in localized bouts of systolic contractions.

With regard to the endocrine control of heartbeat in insects, many authors (Hinks, 1966; Wigglesworth, 1984; Miller, 1985) cited the internal control on the heartbeat rate in a number of insect species. Early Orser and Brown (1951) suggested a neuroendocrine control of heartbeat in *P. americana*, since the heart of decapitated individuals showed a gradual decrease in pulsation rate. Some years later, some authors (Miller, 1979; Miller, 1985) reported that the dorsal vessel receives direct innervations which may also control the rate of heartbeat in many insects. Chiang *et al*. (1992) investigated the effects of certain drugs on the heartbeat of the bug *R. prolixus* and concluded that this vital function is neurally controlled. However, control mechanisms for the insect heart are not fully elucidated but several works indicated that aminergic and peptidergic hormones have effects on the heart function in insects (Fox, 1982; Tsai *et al*., 2001). In fact, the control factors of the cardiac output in arthropods are complex. In addition, the heart rate and stroke volume can be controlled independently (McMahon, 2001).

Depending on the currently available literature, scarce studies have examined the interrelationship between the heartbeat and BV. There are many methods for recording the cardiac potential and the mechanical force of heart in insects. It is easy to analyze the heartbeat rate and cardiac cycle of the insects (Miller, 1985; Johnson

et al., 1997). However, during the heart contracting in the cockroach *P. americana*, it could not easily measure the BV changes, called the stroke volume (the BV ejected by each ventricle with each beat). Therefore, the cardiac output (the total BV ejected by each ventricle per minute) of an insect was also difficult to be calculated (Tsai *et al*., 2004). On the other hand, our search of the available literature regarding the interrelationship between heartbeat and hemocyte population revealed no reliable information exists.

7. Summary Points:

***** The worldwide research on the circulating haemocytes has received much attention because these cells perform different physiological functions in the insects.

***** Circulating hemocytes are initially produced from the median mesoderm during embryogenesis. Maintenance of these hemocytes during the postembryonic development has been attributed to both the mitosis of hemocytes already in circulation as well as to the release of hemocytes from hematopoietic organs.

***** Identification and categorization of hemocyte types are important for understanding their functions in insects. The numbers and types of the circulating hemocytes vary among insect species and depend on several factors, such as the developmental stage of the same insect.

***** There are some controversial terminology and technical difficulties of the hemocyte identification. Thus, none of the individual methods was entirely satisfactory for all cell types within a given insect.

***** The major quantitative parameters of haemogram in insects are the total haemocyte count (THC), blood volume (BV) and mitotic index.

***** THC varies not only according to the insect species but also depending on different biological, physiological and environmental factors. These influencing factors include: the developmental stage, sex, age, reproductive status, circadian rhythm, physical and topographic conditions, diet and nutrition, as well as the measuring technical method.

***** With regard to the endocrine control of hemocyte population, both ecdysone (20E) and juvenile hormone (JH) were reported to influence the release of hemocytes from hemopoietic organs in some insects.

***** The estimation of total haemogram in insects includes, also, the determination of blood volume (BV**)** because the population of circulating hemocytes depends upon BV or is affected by it. Therefore, BV determination is essential in many cases for an accurate evaluation of the THC. An inverse relationship exists between the THC and the BV in many insects.

***** With regard to endocrine control of BV, the neurosecretory cells, corpora allata and corpora cardiaca were found to be involved in this respect. Also, the diuretic hormone reduces the BV, while antidiuretic hormone decelerates the rate of excretion leading to increasing of the BV.

***** There is very little information concerning the interrelationship between BV and osmotic pressure in insects. This interrelationship is affected by different stressors, such as dehydration, starvation, and thermal stress.

***** Mitotic index (the ratio between the cell number in a population undergoing mitosis to the THC in a population) is employed as the criterion of response to various treatments involving factors which might affect this activity. The mitotic activity, or MI, varies with developmental stages in some insects. Scarce studies have examined the interrelationship between MI and THC, but some studies have searched the interrelationship between MI and some types of hemocytes in few insect species.

***** Heartbeat rate (the number of beats per minute) was reported to depend on the

development stage of an insect. Control mechanisms for the insect heart are not fully elucidated. Only scarce studies have examined the interrelationship between the heartbeat and BV. No reliable information on the interrelationship between heartbeat and hemocyte population exists in the available literature.

8. Conclusions and Prospects for Future Work:

As shown the present review, the circulating haemocytes perform different physiological functions in the insects. Identification and categorization of hemocyte types are important for understanding their various functions in insects. There are some controversial terminology and technical difficulties of the hemocyte identification. Thus, none of the individual methods was satisfactory for all cell types within a given insect, but a combination of different techniques should be used. Also, the hemocyte classification in an insect species should be revised several times. In addition, there is a need to develop a more uniform terminology for naming hemocytes in different insect species. For determining the total hemocyte count (THC), it should be taken several influencing factors into account. Determination of the blood volume (BV) is essential in many cases for an accurate evaluation of the THC. Thus, special attention should be paid to factors influencing the BV, such as the developmental stage, age and sex, as well as stressing factors, such as physical conditions and nutritive materials. The interrelationship between BV and osmotic pressure and the different stressors on this interrelationship is not well understood. Therefore, this aspect needs further investigation in the future. Mitotic index (MI) is employed as the criterion of response to various treatments involving factors which may affect the mitotic activity. The interrelationship between MI and THC was poorly examined and needs more studies in different insects. Heartbeat rate was reported to depend on the development stage of an insect. Control mechanisms for the insect heart are not fully elucidated. Also, the interrelationship between the heartbeat rate, BV and THC should be thoroughly investigated in the target insect.

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