ARTIGO DE REVISÃO

MORPHOLOGY AND FUNCTION OF INSECT FAT BODY CELLS: A REVIEW

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INTRODUCTION

The tissue that occupy the spaces among the insect organs, is generally named fat body and is compose by cells of mesodermal origin, sometimes containing, also, ectodermic cells. The mesodermal cells are the trophocytes and its derivates, and the ectodermal, the oenocytes. The proportion of the two cells in this tissue varies according to the phase of the life of the insect. During most of the life of the insect the cells of mesodermal origin, the trophocytes, are predominant and the oenocytes frequently are met disperse among them. In many cases the trophocytes acquire specialized functions and receive specific designations as: urocytes, chromatocytes or mycetocytes.

The designation adipocyte is sometimes found in the literature for the main fat body cell. This name is improper since this cell is not a simple deposit of fat but have a much more complex metabolism and storage also proteins and sugars. The term trophocyte, indicative of nutrients storage cell is also restrictive in relation to their effective functions, because beyond the storage function it has others variable functions along the life of the insects, secreting substances for exportation, besides detoxification and excretory functions (KILBY, 1963; ISAC; BOWENS, 1982). The denomination adopted in this work is trophocyte, however, it should be pointed out that other cells receive from some authors the same denomination, as the nurse cells present in the insect meroistic ovaries.

LOCATION AND ANATOMY

The trophocyte is a big cell containing a central nucleus of very irregular shape and different types of storage structures, variable with the insect type or life phase (Figure 1A and B). The lipids are deposited as small drops or in large vacuoles that may occupy most of the cytoplasm. The proteins form electron dense granules of variable sizes and shapes, in some cases appearing christallized. The carbohydrates appear as glycogen, distributed in the cytosol islands free of lipids and proteins (WIGGLESWORTH, 1942; PRICE, 1973; THOMSEN; THOMSEN, 1978; TADBOWSKI; JONES, 1979; WYATT, 1980; KEELEY, 1985; ROSELL; WHEELER, 1995).

The nucleus is generally surrounded by a ring of cytoplasm where the regular cell organelles are found, as mitochondria, Golgi, endoplasmatic reticulum, lysosomes etc. This cell tend to be spherical and the stored reserves are, also, absent of the peripheral cytoplasm, where the cell organelles are again present. A peripheric labyrinth of canals limited by membranes, of variable extension is frequently found (LOCKE, 1984).

The main ultrastructural characteristic of trophocytes are: surface covered by a thin basal sheath; abundant amount of rough endoplasmic reticulum and Golgi in some phases; round or elongated mitochondria; presence of peroxisomes and lysosomes; presence of multivesicular bodies storaged lipids, proteins, glycogen and urate (BABTHAN; GILBERT, 1972; HAN; BORDEREAU, 1982; LOCKE, 1984; CRUZ-LANDIM, 1985b; DEAN et al., 1985; KEELEY, 1985; CAETANO et al., 1993) (Figure 2A and B). In spite of the ultrastructural features allow to attribute to these cells ability for synthetic activity, it seems that most of the constituent reserves are absorbed directly from the haemolymph and just stored in the trophocytes (LOCKE; COLLINS, 1966; PRICE, 1973; THOMSEN; THOMSEN, 1978; WYATT, 1980).

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The fat body appears in the insects as a slack aggregated or a compact mass of cells, with whitish coloration (SNODGRASS, 1935), organized in thin layers with one or two cells thickness. It can also appear as small nodules suspended in the haemocel by insect components of connective tissue and tracheoles.

The fat body can be found irregularly distributed in the perivisceral space of the abdomen and the thorax, surrounding the organs or in the abdomen dorsal and ventral sinus, closed to the tegument, in the head and even in the body appendixes. The cells of the fat body always appear in contact with the haemolymph, facilitating the metabolic changes (CHAPMAN, 1998). The anatomy of the tissue can vary a lot in the different orders of the insects, however, in a same specie, the arrangement of their cells are constant (DEAN et al., 1985).

The cells of the fat body are usually faintly adhered one to the another being the consistence of the tissue given by the tracheoles that link a cell to other and the amorphous components of the connective tissue. In some rare cases, they present adhesive and communication junctions between them (CHAPMAN, 1998).

PHYSIOLOGY AND FUNCTION OF THE CELLS OF THE FAT BODY

The main ultrastructural characteristic of the trophocytes is it well developed vacuolar system (LOCKE, 1984). The sequence of structural alterations in the vacuolar system, during the development, can distinguish a fat body developmental phase from other and can be compared with the physiological processes in course. Studies involving the correspondence between physiological and ultrastructural alterations was made in *Galleria mellonella* (Linaeus, 1978) (Lepidoptera: Galleridae) during the metamorphosis, and demonstrated the existence of differences in the type of material present in the reserves (DUTKWOSKI, 1974). Even the excising of the ovaries from larvae of fruit flies moth (GAUDECKER, 1963) and of silkworm, provoked morphologic alterations in the cells of the fat body (ISHIZAKI, 1965).

The vesicles transporting substances can be characterized as pre or post-transcriptional, by the thickness of their membrane and by their content that has not yet passed (pre) or has already passed (post) through for the Golgi complex. In the fat body of the insects, are found several types of vesicular structures that are framed in two fundamental classes: digestive vacuoles (autophagic and heterophagic vacuoles and multivesicular bodies) and storage vacuoles (containing tyrosine, urates, proteins or symbionts, associated with glycogen deposits and the lipid droplets) (LOCKE, 1984).

Locke (1984), suggested the origin of the superficial small vacuoles from the fusion of vesicles (provacuoles) derivated from invaginations of the plasmic membrane, based upon measures of the membrane thickness of the vacuoles in the different cellular compartments. Large vacuoles usually have aqueous content and lipofucsin deposits in the inner surface of their membrane (WIGGLESWORTH, 1982). McDermid and Locke (1983) related the presence of large vacuoles in larvae of *Calpodes ethlius* (Stoll, 1782) (Lepidoptera: Hesperiidae) to the cycle of cuticular molt. The vacuoles enlarge as the larvae approach the end of the intermolt and enter in the molt. According to Larsen (1976), the tyrosine vacuoles are not found in the pupal stages or during the molt of pupa to adult.

The vacuoles associated to the glycogen deposits, contain membranous structures inside the glycogen masses. The presence of these vacuoles suggests a mechanism that allows the mobilization of carbohydrates to assist a sudden and large demand of energy. The origin of these vacuoles is not still well explained, and their presence is not the rule in the insects. The autophagic vacuoles, contains organelles being digested. There are several morphologic characteristics that indicate when an organelle is to enter in this process: vesicles juxtaposed to their surfaces, fusion, and formation of membranes around it. A lysosome may fuse to vacuoles of this type or it can firstly fuse to others autophagic vesicles, becoming larger before fusing with the lysosome (LOCKE, 1984).

The multivesicular bodies are of two origins: from pinocytic vesicles formed in the surface of the plasmic membrane and lysosomes from Golgi. Depending upon the stage of development of the fat body, the multivesicular bodies can be involved mainly in the turnover of membranes, in the digestion of received extracellular materials, or in both. In *Calpodes ethlius*, in the beginning of the fifth larval stage, when the protein titers in the haemolymph is low, there are few multivesicular bodies and these have poor content. After the metamorphosis the multivesicular bodies increase in size and in content. In the pupae, when the titer of protein in the haemolymph is again low, the multivesicular bodies return to the appearance of the intermolt (LOCKE; COLLINS, 1967; 1968).

The lamellar bodies, are also involved in the turnover of membranes. They appear in the fat body when a large amount of membranes is liberated by the passage of the content of the tyrosine vacuoles to the haemolymph (MCDERMID; LOCKE, 1983).

Besides the vacuoles, the fat body cells contain proteic granules, glycogen deposits and others components less frequent. The proteic granules, in general have origin from coated vesicles formed by pinocytosis. This cells absorb proteins from haemolymph selectively and, frequently, only those that they store. According to Locke (1984), the selective absorption results from a specific protein link to the plasmic membrane surface, in the covered pits that precede the pinocytosis. Therefore, they only bind the proteins for which the cell has membrane receptors. The fat body cells also store the proteins that they synthesize. These proteins are thrown to the haemolymph, in certain occasions, and eventually may be thus retaken later for storage (LOCKE, 1984).

Several different types of proteic granules have been described, which contain several types of proteins already biochemically identified, some of them, species-specific (TOJO et al., 1978; MILLER; SILHACEK, 1982; RIDDIFORD; LAW, 1983; RYAN et al., 1985; HAUNERLAND; BOWERS, 1986a; 1986b; JONES et al., 1988). The presence of one of those proteins only in the visceral compartment of the fat body of corn earworm, made Haunerland et al., (1990) conclude that in this specie the parietal and visceral compartments of the fat body are structural and functionally different. Ultrastructural imunocytochemistry confirmed this datum (WANG; HAUNERLAND, 1993).

The granules containing secretion resultant from cellular synthesis, are distinguishable those that storaged materials by their proximity to the Golgi, and morphological clues of Golgian origin. According to Locke and Huie (1976), Locke (1980), in the larvae of *Calpodes ethlius* the Golgi is formed by vesicles that spring from the smooth face of the rough granular reticulum and their content crosses the Golgi as the cistern formed while they migrate. In the area of the Golgi condensation vacuoles, secretory vesicles and lysosomes are observed (MCCLINTOCK; LOCKE, 1982). The vacuoles coming from the Golgi, contain proteins, with a loose membrane involving them. With the condensation of the content the membrane is adjusted and the structure become more spherical, characterizing a secretion granule. Later the content of the granule may crystallize.

The trophocytes present polimorphic characteristics according to the function that is being carried out. The pinocytosis intensity in the cells of the fat body is variable in amount and quality, with the developmental phase of the insect (LOCKE; COLLINS, 1968; LOCKE et al., 1982; DEAN et al., 1985). In the males there is not great variation in the cell morphology and their main role is the proteic synthesis. In the females, the variations are larger due to the vitellogenin production (LOCKE, 1984). In the social insects there are also differences related to the castes.

By the end of larval phase the synthesis in the trophocytes cease. However, in the pre-pupal phase, a small synthetic activity of some components, may still occurs, but in the pupa the main occurrence is the lise of the cells of the fat body liberating the storaged nourishment (CRUZ-LANDIM, 1975).

In the immature insects, in a general way, in the intermolt the fat body is synthesizing or mobilizing reserves, while in the molt mainly in mobilization phase (HAUNERLAND; SHIRK, 1995). Eventually an increase in the number of the cells occurs during the molt, by differentiation of resting mesodermal cells.

The size of the fat body cells increases during the larval phase becoming the largest cells of the body of the insects. Therefore, it is during the larval stage that happens the main accumulation of substances almost occupying the whole cytoplasm of the cell. During the immature phase the fat body pass through phases of storage and mobilization reserves, and during the metamorphosis to adult, the reserves are intensely mobilized. In the early pupae of holometabolous insects, the lysosomic activity mobilizes the reserves accumulated during the larval phase in order to sustain the supply of energy for this transformation phase (CRUZ-LANDIM, 1983; MARX, 1987). The larval fat body alternates two different phases: a phase of proteic synthesis, during which the cell seems unable of absorption of elaborated products from haemolymph and the resting phase when the cellular synthesis is low and the absorption and storage of proteins from haemolymph is higher.

When the insects get ready for the pupation, the synthesis of proteins in the fat body is interrupted. The proteins, originally synthesized and secreted by those cells, now are reabsorbed from the haemolymph and storaged in cellular granules (HAUNERLAND et al., 1990). Some intake of proteins may happens during the phase of proteic synthesis, but this intake is not

selective and the proteins won't be stored, instead of that they are digested inside of the cell. The intracellular digestion of the intake materials is interrupted at the end of the synthesis period and the one then selectively intaked starts to be stored.

During the preparation for the molt the trophocyte carries out synthetic activity and occurs an extensive replication of nuclear DNA, without nuclear division. Therefore, the cells become polyploid. At the same time there is synthesis of RNA with an increase of the ribosome numbers, proliferation of the rough endoplasmatic reticulum and mitochondria. After this the trophocyte is ready to begin the synthetic phase. Besides the cellular changes, preparative for the synthesis, it is also observed a series of infolds of the plasmatic membrane that form a peripheral reticular system or labyrinth which, increases the surface of exchanges with the haemolymph (LOCKE, 1986). The surface membrane folds are negatively charged, condition that controls the access of some loaded large molecules to the lumen of the reticular system. These membranous channels can be involved with the reception and discharge of the lipophorins, therefore, with the metabolism of lipid (LOCKE; HUIE, 1983). Such folds according to Locke and Collins (1968), Locke (1984) and Dean et al. (1985) are very prominent in the fat body cells of larvae of *Calpodes ethlius*. In this specie, Locke (1969) also described this kind of structure in the oenocytes. Close to the molt the organelles involved in the proteic synthesis decrease (LOCKE, 1984). The protein absorption is directly associated with the increased volume of those cells (WANG; HAUNERLAND, 1993).

Another function attributed to the fat body is the storage of carbohydrates, mainly in the glycogen form. The glycogen is an important reserve of energy for insect as for other animals. The primary deposits of this carbohydrate are in the fat body (CHAPMAN, 1998).

The glycogen stock in the adult insects tissues not is susceptible to changes related to seasonal and physiological conditions (SINGH; SIDHU, 1979). Among the social insects castes there are differences too. In some insects, the glycogen appears in the tissue during the feeding periods. A hyperglycemic hormone, is responsible for the regulation of sugar concentration in the haemolymph. It is produced in the *corpora allata*, and activates the glycogen-fosforilase elevating the trehalose production, and its liberation into the haemolymph (RÖSELER; RÖSELER, 1986).

Some roles are attribute to the trophocytes as the function of storage hydrocarbons during the formation of the cuticle, but in earlier phases of the development, the hydrocarbons are synthesized by the oenocytes, delivered to the haemolymph and transported to the cells of the fat body (YOUNG, et al., 1999).

The insect fat body is the principal tissue storing lipids. More than 70% of the dry weight of the tissue are lipids, and most of the lipids are triglicerides. The amount of lipid stored varies depending on the developmental and nutritional state of the insect. The stockes increases during the feeding period and decay when the feeding stops or when the lipids are used during the oogenesis or flight. The amount of lipids

can appear in all the types of the fat body cells, in certain phases of the life, but only when they constitute almost the unique cellular deposit, the cell is characterized as an urocyte. Urate granules were observed in Lepidoptera (TOJO et al., 1978), particularly in silkmoth (MORI et al., 1970) and in *Calpodes ethlius* (LOCKE, 1984; DEAN et al., 1985). The origin these granules is mainly from the degradation of proteins absorbed from the haemolymph to the interior of a special type of the multivesicular body (TOJO et al., 1978) or from the metabolism of nucleic acids, resulting from autofagy of the rough endoplasmatic reticulum, due to the waste let by the intense proteic synthesis.

There are two convergent hypotheses in relation to the function carried out by the urate cells. One of them suggests that they are substitutes of the Malpighian tubules during the metamorphosis, while the larval tubules are being reabsorbed and the adult tubules are still being formed. This happens mainly in the larvae of Apocrita himenopterans and Lepidoptera. The other hypothesis says that the urate cells store urate granules that are produced inside of the cells of the fat body, corresponding to the metabolism and transformation of the proteic inclusions resulting of the activity of the trophocytes. Then, some cells of the fat body, that absorb these products from the haemolymph would differ in urocyte types. The urate granules appear during the pupal stage and they are also found in young imagoes. The urate cells would be, then, excretory organs without ducts, present in the fat body. Their function would be the one of reducing the amount of toxicant products in the haemolymph by their absorption and accumulation in the cytoplasm until that it could be excreted by the Malpighian tubules (SNODGRASS, 1935).

Those two hypotheses are not excluding. In bees larger incidence of urate cells is verified from the end of larval phase to the beginning of the imago life, when the Malpighian tubules are not functional (CRUZ-LANDIM, 2000). On the other hand, it is also verified the presence of cells with intermediate characteristics between trophocytes and urate cells in all phases of the bee life. In this case they contains some urate granules that represent protein residues absorbed from haemolymph and neutralized into the trophocyte. The protein wastes are not always noxious, in the cockroaches the uric acid resulting from protein degradation provides stores of nitrogen that can be recycled (CHAPMAN, 1998).

The mycetocytes are also derived from the trophocytes. They are cells which posses symbionts non-pathogenic microorganisms in the cytoplasm. The cytoplasm of those cells is usually reduced, however, it can present lipid inclusions and glycogen deposits as the normal trophocyte.

A rare type of modified trophocyte, is the chromatocyte. This cell is flat and possess salient nucleus in the center and are arranged in layers of a single cell thickness, surrounded by the characteristic trophocytes, however it stays separate from them by the basal lamina. These cells are present in larvae of some aquatic insects (Simullidae and Thaumaleidae), that possess transparent tegument (CHAPMANN, 1998).

The Table 1 shows a relation of the occurrence and differentiation of the cells of the fat body in the principal and more studied orders of insects.

HORMONAL ACTION AND RELATIONSHIP WITH OOGENESIS

The development of the fat body in the adult is also controlled by hormones that can be liberated due to external influences (LOCKE, 1980). Its lyse during the pupation is hormonally controlled, being the hormone, the ecdysteroids (LOCKE, 1970; SASS; KOVACS, 1977; DEAN, 1978, POSTLETHWAIT; JONES, 1978, PELT-VERKUIL, 1979; KEELEY, 1985).

Some studies have demonstrated the importance of the hormone 20-hydroxy-ecdysone and juvenile hormone (JH) in the ultrastructural organization of these cells (COLLINS, 1969; 1974), since they are target cells, where these hormones act in an intense way. Studies on the hormonal action in the fat body cells were made **in vivo** by Dean (1978), in *Calpodes ethlius*; Thomasson and Mitchell (1972), Tysell and Butterworth (1978), Postlethwait and Jones (1978), in fruit flies moth; Pelt-Verkuil (1979), in blowfly; Cotton and Anstee (1991), in *Locusta migratoria* (Linnaeus, 1758) (Orthoptera: Acrididae), and **in vitro** with Lepidoptera by Sass and Kovacs (1977).

It is attributed to JH the control of the presence of proteic granules in the trophocytes. During metamorphosis the absence of JH promote cytolysis of the larval fat body and the formation of the corresponding adult's tissue. The JH, and their analogues, the JH-I causes vacuolization of the trophocytes and acceleration of the metamorphosis (ENGELMANN, 1976; COUBLE et al., 1979; COTTON; ANSTEE, 1991; SAYAH et al., 1994; BARBOSA-HETEM et al., 1998).

The influence of the JH on the adult's fat body is mainly in the production of the proteins for the haemolymph, and in it participation in the vitellogenesis (ADAMCZYK et al., 1996).

In *Apis mellifera* (Linaeus, 1758) (Hymenoptera: Apidae), studies of the hormonal influence were accomplished by Bishop (1958) and Marx (1987). Barbosa-Hetem et al., (1998) studied the effect of JH and of the 20-hidroxy-ecdysone on the ultrastructure of the trophocytes observing that the increase in the JH titer propitiated an increase in the number of mitochondria in the cells and a decrease of the Golgi areas. The 20-hydroxy-ecdysone, differently avoid the nuclear volume decrease, induced the increase of the proteic granules, pro-vacuoles and vacuoles in the cytoplasm and the precocious emergence of autophagic structures.

Cotton; Anstee (1991), using a analogous of JH, showed alterations as the increase in the nuclear size and in the concentration of RNA and of rough endoplasmatic reticulum in the trophocytes of *Locusta migratoria*. The treatment also caused the precocious appearance of the specific female proteins, probably the vitellogenin, that are part of a glicolipoprotein family. They are proteins of high molecular WEIGHT (KUNKEL; NORDIN, 1985).

According to Fescemyer et al. (1992), the decline in the titer of JH causes the initiation of the synthesis of vitellogenin in European gypsy moth larvae. The content of JH induces directly the vitellogenin synthesis in several species (ISAAC; BOWNES, 1982). In most of the orders of the insects, in the adult, the synthesis of vitellogenin is stimulated by JH.

The oocytes of the superior insects, acquire their nourishment reserves by taking the soluble precursor of the yolk, the vitellogenin, from the haemolymph. The vitellogenin titer in the haemolymph is determined by the balance among the synthesis rate in the fat body and the intake by the oocytes (GIORGI; MAZZINI, 1986). Confirming the participation of the fat body in the vitellogenesis, it has been observed the presence of a pick in the production of proteins, by its cells in close relationship with the reproductive cycle of the females, coincident with the phase in that happens the yolk deposition in the oocytes (ENGELMANN, 1971; BEHAN; HAGEDORN, 1978; TADBOWSKI; JONES, 1979; HAN; BORDEREAU, 1982; STAURENGO DA CUNHA; CRUZ-LANDIM, 1983, PAES DE OLIVEIRA; CRUZ-LANDIM, 2003).

Dutkowski (1974), was pioneer in demonstrate differences in the accumulation of reserves in the trophocytes with the excision of the ovaries of females of *Galleria mellonella*. A total regression of the machinery of proteic synthesis was observed after the pick of vitellogenin synthesis in yellow fever mosquito (BEHAN; HAGEDORN, 1978). Chen et al. (1976) linked the changed rates in vitellogenin synthesis with the degree of development of the rough endoplasmatic reticulum in the fat body of *Locusta migratoria*. They also related the presence of the lysosomic inclusions to the cellular remodeling in the end of the reproductive period. Tadkowski and Jones (1979), noticed that the nurse cells of the yellow fever mosquito ovaries are not linked to the oocyte by cytoplasmatic bridges, therefore those cells add little or none material to the oocytes. Them, the fat body cells have the function, as had already been told for other species as: silkmoth (SHIGEMATSU, 1958); cockroach (BROOKS, 1969); yellow fever mosquito (HAGEDORN; JUDSON, 1972) of produce vitellogenin.

Wuest (1978) in his studies with cockroach, noticed that during the vitellogenesis, the fat body pass by considerable alterations, as significant increase of the amount of rough endoplasmatic reticulum in the beginning of the reproductive cycle. Approximately five days later, the cell enters in high proteic synthetic activity, accumulating great amounts of protein granules and lipid droplets. In the end of the reproductive cycle, the synthetic apparatus become inactive and disappears. In screw-worm fly, there is a fall of 70% in the weight of the body passed the period of vitellogenesis (SPRADBERY; SANDS, 1981).

In queens of *Apis mellifera*, during the oviposition, very large and healthy trophocytes, with irregular nuclei, basophilic granular cytoplasm, disperse chromatin, besides a characteristic synthetic apparatus for protein production may be observed (CRUZ-LANDIM, 1985a).

Focusing the polimorphic differences among the castes, Han and Bordereau (1982) described different ultrastructural characteristics for the trophocytes of queens and males of three Termitidae species. In the queens the fat body presents every machinery and cell characteristics for protein synthesis, while in the males these cells just have the function of store products.

In studies on the vitellogenesis in insects, Giorgi and Mazzini, (1986), reached to the conclusion that the secretion granules present in fat body cells, located in the cellular periphery are vitellogenin and are thrown to the extracelular compartment through continuity between the part electrondense of the gra-

nule and the plasmic membrane, a characteristic process of exocytosis.

In *Locusta migratoria* and other insects, JH showed to have as much a promoter effect and a direct stimulant effect over the transcription of the genes of vitellogenin in the fat body. The JH is also involved in the regulation of the intake of vitellogenin by the ovaries through the interaction with membrane receptors in the follicle cells (BOWNES, 1986).

Quantitative analyses of JH, vitellogenesis and vitellogenin mRNA in lubber grasshopper showed that those components present similar profiles during the first oviposition cycle, that is, the three are low after the appearance, increase during the second week of the cycle and fall after the oviposition. That simultaneity of these products was also described for other insects. The level relatively low of vitellogenin in the haemolymph during the oviposition indicates that the persistent fraction of vitellogenin mRNA is not translated efficiently in this period, suggesting that the production of vitellogenin in this insect can be controlled through gene transcription and mRNA translation (BORST et al., 2000).

The factors regulating the proteic synthesis, are still not known with certainty, but it is already known that the JH and the ecdysteroids can be involved. The electric discharge of the fat body proteins is unchained by the 20-hydroxyecdysone in several insects. Perhaps this hormone acts through regulation or activation of the receptors in the trophocytes membrane.

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TABLE 1 – Ocurrence and differentiation of the fat body cells in several Orders of Insects.

Order	Studied Species	Cells and differentiation
Ephemeroptera	*Chirotonetes* sp.; *Heptagenia* sp.	(T)
Dictyoptera	*Blaberus* sp.; *Blatella germanica*; *Blatta orientais*; *Cryptocerus punctulatus*; *Diploptera punctata*; *Leucophaea maderae*; *Nauphoeta cinerea*; *Periplaneta americana*	(T) (M)
Isoptera	*Cornitermes cumulans*; *Cubitermes fungifaber*; *Kalotermes flavicollis*; *Macrotermes bellicosus*; *Macrotermes subhyalinus*; *Mastotermes* sp.[1]	(T) ([1]M)
Phasmida	*Carausius morosus*	(T) with tirosine vacuoles
Orthoptera	*Gryllus abbreviatus*; *Gryllus bimaculatus*; *Locusta migratoria*; *Melanoplus femur-rubrum*; *Orchelimun* sp.; *Schistocerca gregaria*; *Romalea microptera*	(T) (OE)
Hemiptera	*Acythosiphon pisum*[1]; *Aleyrodes* sp.; *Anisops* sp.[2], *Laodelphax striatellus*[1]; *Rhodnius prolixus*[3]	(T) ([1]M) ([2]HC) ([3]T) with tirosine vacuoles
Trichoptera	*Hydropsyche* sp.	(T)
Lepidoptera	*Achaea jonata*; *Antheraea pernyi*; *Bombyx mori*; *Calpodes ethlius*; *Camponotus festinatus*; *Diatraea grandiosella*; *Diatraea saccharalis*; *Ephestia kuehniella*; *Galleria mellonella*; *Heliothis zea*; *Hyalophora cecropia*; *Malacossoma americanum*; *Mamestra brassicae*; *Manduca sexta*; *Melitta satyriniformis*; *Philosamia cynthia*; *Phlegethontius quinquemaculata*; *Pieris brassicae*; *Pontia rapae*; *Protoparce quinquemaculata*; *Sitotroga cerealella*; *Trichoplusia ni*	(T) (U) all the cells of the fat body have storage of urate
Diptera	*Aedes aegypti*[1]; *Calliphora erythrocephala*[1]; *Calliphora stygia*[1]; *Calliphora vicina*[1]; *Chironomus* sp.[1,2]; *Chrysomya bezziana*; *Culex* sp.; *Dacus tryoni*; *Drosophila* sp.; *Gasterophilus intestinalis*[2]; *Glossina austeni*; *Musca domestica*; *Sarcophaga argyrostoma*; *Sarcophaga bullata*; *Simulium* sp.[3]	(T) (O) ([1]T) with tirosine storage, ([2]HC) ([3]CHR) in larvae
Coleoptera	*Leptinotarsa decemlineata*[1]; *Tenebrio molitor*	(T) (O) ([1]T) with tirosine
Hymenoptera	*Apis mellifera*; *Atta sexdens rubropilosa*[1]; *Bombus terrestris*; *Formica rufa*; *Melipona quadrifasciata*; *Neoponera villosa*; *Pachycondyla villosa*; *P. striata*; *Zacryptocerus pusillus*	(T) (U) (O) ([1]T) only

(T) trophocytes; (OE) oenocytes; (U) urocytes; (HC) hemoglobin cell; (CHR) chromatocytes; (M) micetocytes.

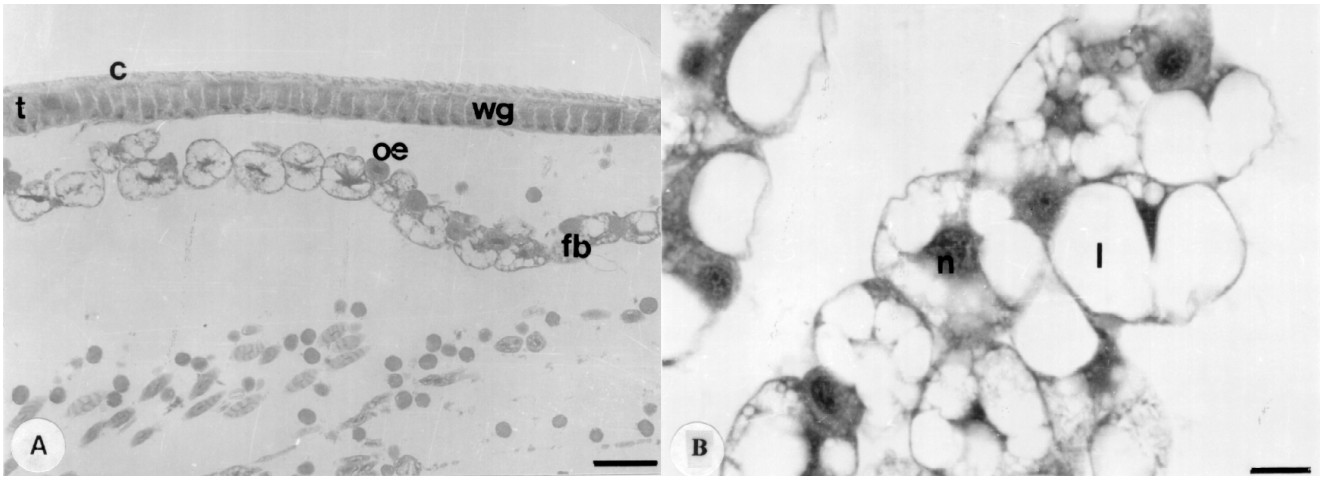

Fig. 1. (A) Longitudinal sections of abdomen worker of *Melipona quadrifasciata anthidioides* (Hymenoptera) showing the location of the trophocytes in relation to the tegument (t) in the parietal fat body (fb) by light microscopy. Note that the tissue is formed by a single layer of cells, in the which also oenocytes (oe) are interspersed. (c) = cuticle; (wg) = wax gland. Bar = 50µm. **(B)** Detail of the trophocytes showing the large nucleus (n) and the cytoplasm replete of lipid drops (l). Note that these drops occupy a most of the cytoplasm. Bar = 15µm.

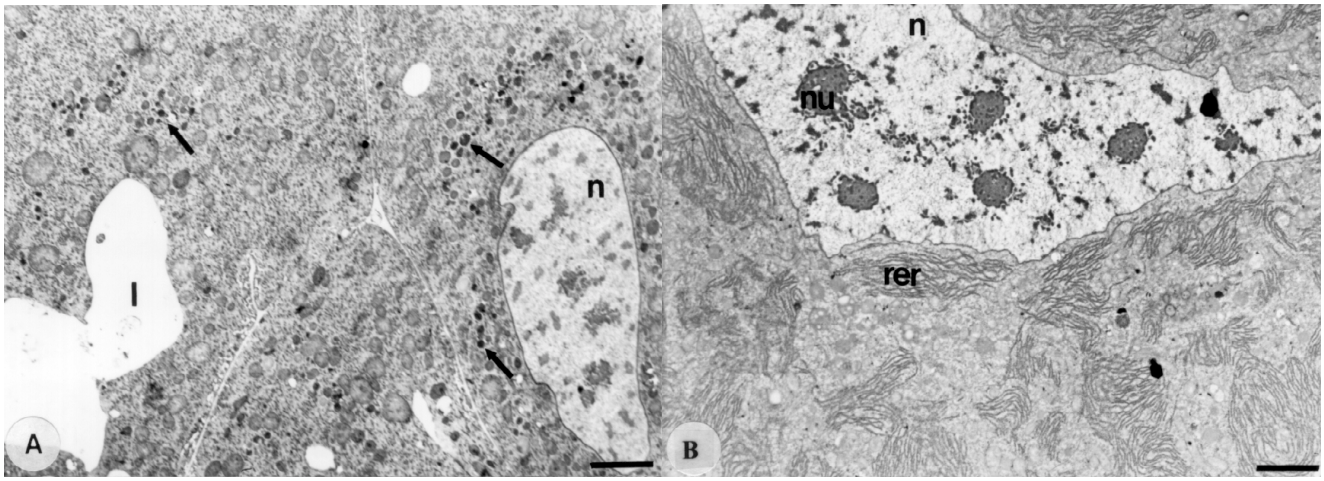

Fig. 2. (A) Trophocyte of a newly-emerged worker of *M. quadrifasciata anthidioides* showing the large nucleus (n) and the cytoplasm replete of inclusions of several natures: lipid (l) and protein (arrows) by transmission electron microscopy. Bar = 5µm. **(B)** Trophocyte of phisogastric queen of *Melipona bicolor* showing the large nucleus (n), with great nucleolus (nu) and a portion of the cytoplasm filled up by packages of rough endoplasmatic reticulum (rer). Note that in the cytoplasm of this cell are present other rare types of inclusions. Bar = 1µm.