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Structure and Function of the Basal Lamina and of the Cell Junctions in the Midgut Epithelium (Stomach) of Female *Aedes aegypti* L. (Insecta, Diptera)

C. Reinhardt and H. Hecker

Introduction

Vertebrate and invertebrate epithelia are separated from connective tissue or from the haemocoel by a basal lamina (BL). The BL consists of a matrix within which filamentous structures may be embedded (Fawcett 1966, Ashhurst 1968). Biochemical investigations of BL in various vertebrate tissues reveal filamentous tropocollagen-like macromolecules bound to antigenic matrix glycoproteins. The BL is composed of about 10% carbohydrate and 90% protein (Kupfer & Geyer 1968, Rambourg et al. 1969, Pierce 1970, Spiro 1970). In insect BL, fibrous collagen-like structure may be associated with the mucopolysaccharides of the matrix (Ashhurst 1968).

The following insect epithelia exhibit BL with regularly arrayed particles or grid-like structures in the amorphous matrix: ovarian follicular tubes (Bertram & Bird 1961), salivary glands (Ashhurst 1968), ovotestis (Coggeshall 1970), malpighian tubes (Reinhardt, unpublished observation on fleas). In addition, the following insect midguts contain grid-like structures in the BL matrix:

- **Heteroptera**
  - *Ranatra linearis*
  - *Nepa cinerea*  
  - *6 different species*
- **Coleoptera**
  - *Ctenophthalmus spec.*
  - *Xenopsylla cheopsis*
  - *Echidnophaga gallinacea*
- **Siphonaptera**
  - *Anopheles quadrimaculatus ♀*
  - *Aedes aegypti ♂*

Using light microscope histochemical techniques, Holter (1970) found protein structures in a carbohydrate containing matrix of the BL from coleopteran midguts. Ultrastructural, cytochemical and enzyme extraction studies on the cockroach midgut BL demonstrated a pattern of collagen-like particles embedded in a polysaccharide matrix (Gouranton 1970).

Membrane junctions control cell-to-cell relations such as the movement of ions along the longitudinal and transverse axes of an epithelium. They also play an important role in the mechanical maintenance of cell contact (Toner & Carr 1968, Smith et al. 1969).

*Gap junctions* (gj) or close junctions with a 20–40 Å gap, containing hexagonally arrayed particles with a center-to-center distance of 90–100 Å, have been

In some invertebrates, septate junctions (sj) or septate desmosomes were originally thought to be responsible for ion transport from cell to cell (Gilula et al. 1970, Satir & Gilula 1970, Rose 1971). More recent investigations confirm the coexistence of sj and gj in Chironomus and lamellibranch electron coupled tissues (Berger & Uhrik 1972, Gilula & Satir 1971). Based on our knowledge of vertebrate gj, these results suggest that invertebrate gj may be primarily responsible for ion transport. In support of this hypothesis Berger & Uhrik (1972) have shown that gj disappear in anisosmotic (= uncoupling) fixatives. Bullivant & Loewenstein (1968) have found that sj do not change in uncoupling media. Coexistence of gj and sj appears to be quite common in epithelia of other invertebrates (cockroach midgut, Hagopian 1970; sugar-mite proctodeum, Noirot & Noirot 1971, 1971a; mollusc egg capsule gland, Flower 1971; hydra gastrodermis, Hand & Gobel 1972; Periplaneta midgut caeca, Oschman & Wall 1972); however, these epithelia have not been tested for electrical coupling. It should be added that there are a few studies on invertebrate epithelia in which gj were not found in the junctional complex (Smith 1966, Leik & Kelly 1970, Priester de 1971).

Sj and gj both play an important role in cellular adhesion (Wood 1959, Goodenough & Revel 1970, 1971, Hudspeth & Revel 1971, Hand & Gobel 1972). While electrical coupling is thought to be correlated with gj, sealing function and barrier properties of the intercellular cleft (in the epithelial transverse axis) is correlated with sj (Flower 1971, Berger & Uhrik 1972).

In the apical half of the midgut epithelium of cockroaches and termites (Noirot & Noirot 1967, 1972) and of collembolans (Dallas 1970) an intercellular junction was found, the "zonula continua", filled with an electron dense, more or less homogeneous material. In addition, tight junctions have also been found in invertebrate epithelia (Anderson & Harvey 1966, Satir & Gilula 1970).

Maculae adhaerentes (ma) occur in a number of invertebrate tissues: the earthworm epidermis (Coggeshall 1966); tracheal cells, follicular epithelia and rectal papillae of cockroaches (Smith 1966); a sensillum of the termite leg (Stuart & Satir 1968); between the nerve cord and connective tissue (Ashhurst 1970), and midgut of a moth (Smith et al. 1969); the hypodermis of a cockroach nymph (Hagopian 1970); epithelia of cockroaches and termites (Noirot & Noirot 1972); and gut diverticula of leeches (Hammersten & Pokhar 1972).

In invertebrate midgut epithilum zonula adhaerentes or "intermediary junctions" (Anderson & Harvey 1966, Satir & Gilula 1970, Noirot & Noirot 1972) and hemidesmosomes (Smith et al. 1969, Priester de 1971) have been described.

The above three types of invertebrate desmosomes lack tonofilaments; their vertebrate counterparts (known to form attachment zones [Fawcett 1966, Armstrong 1970, Hagopian 1970, Sheffield 1970]) are larger and more complex.

In a study of imaginal midgut differentiation in Aedes aegypti by Hecker et al. (1971, 1971a), sj were found in both males and females whereas ma occurred only in females.

The present study was undertaken to obtain more detailed structural and cytochemical information on the BL and the various cell junction types found by Hecker et al. (1971) in the female A. aegypti stomach epithelium. During the course of this investigation further cell junctions were found; descriptions of these have been included in this paper.
Material and methods

Our strain of *Aedes aegypti* L. was originally derived from the Congo (Zaïre) and has been maintained for many years in our laboratory. The preparation of the female midguts for electron microscopy has been described by Hecker et al. (1971).

In order to best preserve its original form, mechanical stretching of the "stomach" (posterior part of the midgut) was carefully avoided during dissection. In addition to double fixation in glutaraldehyde followed by OsO₄, two other fixation procedures were used: a) a mixture of 3 or 5% glutaraldehyde and 2% acrolein in 0.1 M cacodylate buffer (pH 7.2–7.4) at 4°C/2 hrs, followed by OsO₄; b) the "triple fixation" technique (Hecker 1970). None of these three fixation procedures caused measurable differences in the preservation of junctional structures, such as the width of the intercellular cleft, and of the BL.

To determine if the first bloodmeal (BM) causes changes in the dimensions and structure of the stomach BL and cell junctions, 3-day-old females were examined immediately after BM and at the following other times: 12 hrs, 1, 2, 3, 5, and 7 days post BM. Control non-fed 3-day-old females were also studied. Measurements of investigated structures for the most important stages are shown in table 1.

To identify polysaccharides in junctions and in the BL the Thiéry (1967) periodic acid-TCH-silver-proteinate staining technique as modified by Jenni (1971) was applied to ultrathin sections. To demonstrate alkaline amino acid rich proteins in cell coats and in the BL, midguts from 3-day-old-non-fed females were fixed in glutaraldehyde and then incubated in 1% phosphotungstic acid solution (e-PTA) (Bloom & Aghajanian 1968, Meyer 1969, Pfenninger 1971).

Results

1. Stomach of unfed mosquitoes

1.1. Basal lamina (BL)

The heterogenous BL consists of 4–7 superimposed or stacked layers, which follow an undulating course along the base of the epithelial cell (Terzakis 1967). These layers are embedded in an amorphous matrix which is partly continuous with the BL of the muscle cells (Hecker et al. 1971). In cross sections of the BL (fig.1) the layers exhibit regularly arranged structures ("beads"). A grid-like substructure can be seen in a tangent section parallel to the base of a cell (fig. 3). Diagram 1 is a schematic representation of the grid-like substructures in one layer (mesh width 300 ± 5 Å, table 1). Grid lines generally intersect at right angles. Two different electron lucent "holes" can be distinguished, "hole" I (diameter ~ 200 Å) between the grid lines and "hole" II (diameter ~ 70 Å) in the annular shaped intersections of the grid lines. Cross and tangential sections of one BL layer exhibit a continuous grid. The direction of grid lines may differ from one layer to the other. In fig. 3 several subsequent layers are hit by the section plane with each layer showing another grid line orientation.