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STUDIES ON THE FUNCTION OF THE MEMBRACID PRONOTUM (HOMOPTERA) II. HISTOLOGY

T. K. Wood
Box 1224, Wilmington College, Wilmington, Ohio 45177

ABSTRACT—The membracid pronotum historically has been considered an ornamental and protective structure with no physiological function. This paper demonstrates the pronotum of *Umbonia crassicornis* to be a complex cellular structure permeated with trachea suggesting a high metabolic rate. Two types of cells which may be secretory in function are present. Nerves in association with trichoid sensilla offer further evidence that the pronotum may have a sensory function.

Membracidae are characterized by an enlarged pronotum, which takes many bizarre forms. Poulton (1903) and Funkhouser (1951) discussed crypsis, mimicry, aposematic display and shape as possible functions of the pronotum, but these contentions lack experimental verification. Funkhouser (1951) stated that even the hairs and punctations (pits) on the pronotum were not functional since he found no evidence of nervous, tracheal or glandular connections. He concluded that pronotal structures were not involved in any physiological processes and were "merely hollow extensions of the chitinized wall." In contrast Wood and Morris (in press) demonstrated the general occurrence of trichoid sensilla and pits on the membracid pronotum, which implied a sensory function for the pronotum. These conflicting statements led me to reexamine the histology of the pronotum and demonstrate its cellular nature.

Methods

The pronotum with head attached was removed from live *Umbonia crassicornis* (Amyot and Serville) and fixed in a modified Carnoy's fixative (Salthouse, 1958). Tetrahydrofuran was used for dehydration, the pronotum was then double embedded with paraloidin and paraffin. Paraffin infiltration was done under vacuum. Serial longitudinal, horizontal, and cross sections were made and stained with Delafield's hematoxylin and eosin Y. The Ramon y Cajal's

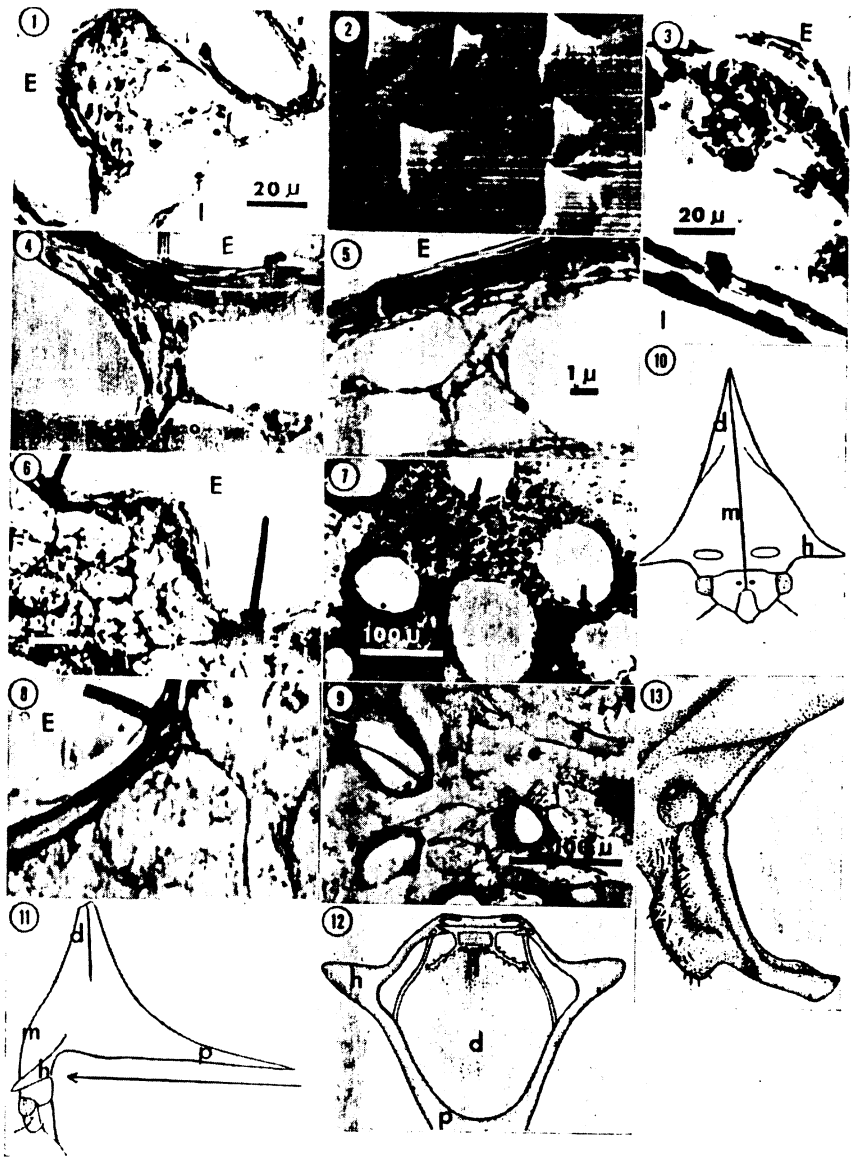

Fig. 1–13, illustrations and photomicrographs of the pronotum of *Umbonia crassicornis* Amyot and Serville. Symbols: E = exterior cuticle, I = interior cuticle, d = dorsal horn, m = metopidium, h = humeral horn, p = posterior process, c.s. = cross section, l.s. = longitudinal section. 1, relationship between (c.s.) cuticular layers and pits. 2, scanning electron micrograph of conical projections on interior cuticular surface. 3, secretory cells (c.s.) below exterior and interior cuticle. 4, trichoid sensilla with elongate cells (c.s.) at base of hair. 5, squamous epithelial cells (c.s.) lining exterior cuticle. 6, two adjacent pits (c.s.) demonstrating secretory cells below exterior cuticle. The relationship between trichoid sensilla and the nerve at base of hair is also shown. 7, dorsal horn (l.s.) with exterior cuticle removed. 8, nerve along pit (c.s) with a peripheral fiber to interior cuticular surface. 9, humeral horn (c.s.) demonstrating trachea. 10, frontal view of head and pronotum. 11, lateral view of head and pronotum, the arrow indicates view of Fig. 12. 12, a posterior-ventral view of metopidial surface showing the transverse and lateral ridges. 13, frontal view of eye fossa showing position of exterior opening to transverse and lateral ridges.

pyridine silver method (Humason, 1962) was used for silver impregnation then double embedded and sectioned (15 to 20μ). The detached pronotum was examined for main tracheal trunks under 70% ethyl alcohol with the dissecting microscope. Glycerin mounts were made by spreading the pronota of adults (3 to 4 days old) out on microscope slides. Glycerin mounts were studied with a bright field microscope.

Results

A matrix of cells between two cuticular layers characterize the wall of the expanded pronotum. The exterior[1] surface is marked by punctures (pits) and associated trichoid sensilla (Wood and Morris, in press). Surface punctures are invaginations which terminate above the interior cuticular wall (Fig. 1). On the interior cuticular layer are conical projections (Fig. 2) uniformly distributed and not associated with the pits.

Large cuboidal cells (Fig. 1) surround the pits. Adjacent to these cells are large elongate cells (Fig. 4) which extend from the base of the trichoid sensilla to the interior cuticular layer. A layer of squamous epithelial cells with elongate nuclei (Fig. 5) are found below the exterior cuticula. Hematoxylin stains these cells in a similar fashion as the neurosecretory cells of the brain. The large cuboidal cells lining the pits also have similar staining properties indicating a probable secretory function.

The silver nitrate procedure stains neurofibrils black; nerve cells stain yellow-brown. At the bottom of the pit and running along the clear cuticula is a single layer of yellow-brown cells (Fig. 3). Between and surrounding the pits below the exterior cuticula are clusters of large cuboidal cells which stain yellow with black nuclei. The relationship of these cells to the pits are shown in cross section (Fig. 6) and longitudinal section (Fig. 7). The stain affinities of these cells suggest a secretory function. A large nerve fiber which runs from these secretory cells to the base of the trichoid sensilla can be seen in cross sections through adjacent pits and sensilla (Fig. 6). Below the base of the trichoid sensilla the nerve fiber is enlarged (Fig. 8) with a peripheral fiber running toward the interior cuticular surface. Sections through the dorsal horn show nerve fibers run parallel to the trachea with peripheral fibers to the cells surrounding the pits. The interior contents of some trichoid sensilla stain black.

The relationship between the head and pronotum is shown in Fig. 10, 11. The pronotum is an enlargement of the prothoracic tergum which is expanded dorsally into the humeral and dorsal horns (Fig. 10, 11) and into a posterior process (Fig. 11).

[1] Exterior and interior refer to the cuticular layers of the pronotum and not to the relationship of the pronotum with the thorax.

The interior surface of the metopidial wall (Fig. 12) has two chitinized lateral ridges and one transverse ridge which contain tracheae. Branches from the tracheae in the lateral ridges permeate both dorsal and humeral horns, and the posterior process. Two tracheal trunks from the transverse ridge supply the metopidium. Silver nitrate sections through the humeral (Fig. 9) and dorsal horns substantiate the general presence of trachea.

The large numbers of anastomosing tracheae in the expanded pronotum suggest either a tracheal connection with the mesothorax or an external opening. The only spiracles mentioned by Funkhouser (1917) were on the mesothorax and metathorax. I found no tracheal connection to the mesothorax but did find an external opening. Examination of the eye fossa reveals a lateral depression with an external opening at the bottom (Fig. 13). The lateral and transverse ridges with their tracheae originate at this opening.

Discussion

The pronotum has been considered an ornamental structure and discussion of its function has centered on possible protective roles. Probable secretory and/or neurosecretory cells between and surrounding the pits suggests the possibility the pits function as chemoreceptors or perhaps as dispersal sites for pheromones. Behavioral studies (Wood, in press) indicate that pheromones may be involved in mating and aggregation in *U. crassicornis*. The function of the conical projections on the cuticle below the pit is unknown.

The presence of nerves and their association with trichoid sensilla gives credence to the suggestion by Wood and Morris (in press) that the pronotum has a significant sensory function. The trichoid sensilla may act as mechano- or chemoreceptors. The pronotum's complex tracheal system supplying the cellular matrix indicates it has a high oxygen requirement and metabolism.

The demonstration of the complex nature of the pronotum demands that functional roles in addition to possible protection be further investigated.

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AN INVALID LECTOTYPE DESIGNATION FOR GREENOIDEA PHYLLANTHI (GREEN) IS DISCUSSED AND CORRECTED

Gerson and Davidson (1974, Proc. Entomol. Soc. Wash. 76(2):156–162) designated a lectotype and 3 paralectotypes for *Greenoidea phyllanthi* (Green) from 2 slides deposited in the U.S. National Museum. These designations are invalid according to rule 74 (A) (i) of the International Code of Zoological Nomenclature because the specimens are apparently not part of the syntypical series used by Green (1905, J. Bombay Nat. Hist. Soc. 16:344–345) in the original description of *Aspidiotus* (*Targionia*) *phyllanthi*. The type-data in the original description reads "On *Phyllanthus myrtifolius*. Peradeniya. February." The slide designated by Gerson and Davidson as lectotype reads "*Aspidiotus phyllanthi* Green n.s. *Phyllanthus myrtifolius* Peradenija [misspelled] Ceylon E. E. Green Coll. June 1900." Thus Green's (type) material was apparently collected 5 months earlier than the U.S.N.M. material cited by Gerson and Davidson.

I thank Dr. D. J. Williams for calling attention to this error and for providing a slide from the British Museum (Nat. Hist.) for the following lectotype designation.

Type-data: The adult female left hand specimen (nearest locality label) of 3 specimens is here designated as the lectotype. The slide bears a label on the left side reading "*Aspidiotus phyllanthi* Green from *Phyllanthus myrtifolius* Peradeniya, Ceylon E. E. G. coll. Feb. 1900." A label on the right side bears the word "TYPE" in red. I placed a label on the back mapping the lectotype's position. The other 2 specimens are paralectotypes. The lectotype can be recognized by having normally developed pygidial lobes. Both paralectotypes have broken or malformed lobes.

JOHN A. DAVIDSON, *Department of Entomology, University of Maryland, College Park, Maryland 20742.* Scientific Article No. A2705, Contribution No. 5028, of the Maryland Agricultural Experiment Station.

DESCRIPTION OF HISTIOSTOMA CONJUNCTA (NEW COMB.) (ACARI: ANOETIDAE), AN ASSOCIATE OF CENTRAL AMERICAN BARK BEETLES

J. P. WOODRING
Department of Zoology, Louisiana State University, Baton Rouge, La. 70803
and
J. C. MOSER
Southern Forest Experiment Station, Pineville, La. 71360

ABSTRACT—The adult female and male plus the tritonymph of *Histiostoma conjuncta* (Woodring and Moser, 1970) (new comb.) are described. The species is known to be associated with various pine bark beetles from Honduras, Guatemala, and Louisiana.

Woodring and Moser (1970) described 5 new species of *Anoetus* associated with North American Scolytidae. One of these was *A. conjuncta*, which was based however only on the deutonymph. Fresh material has revealed the adult stages of *conjuncta*, which are herein described. The species is placed in the genus *Histiostoma*, a new combination, based on a redefinition of the genera *Histiostoma* and *Anoetus* by Woodring (1973).

Histiostoma conjuncta Woodring & Moser, (1970) new combination

FEMALE (Fig. 1, 4, 6, 7): Length of single female 256 μ; probably a young female (based on the short opisthosoma and length being in range of male). Cuticular surface smooth with minute, dark conical projections as in retangular inset of Fig. 1. Propodosomal shield not heavily sclerotized, but boundaries clearly distinguishable. Anterior margin of histerosoma indistinct. All dorsal setae gently curved, evenly tapered, and of approximate equal length. Dorsal opisthosomal setae (do1–do7) arise from small mounds. Opening of opisthosomal gland (gl) heavily sclerotized, large, and cup shaped. All ventral leg apodemes except a8 present, thick and dark in color. Cuticular area around anterior ring (r1) dark. Apodemes A1 join in midline to form short sternum (St1). Seta vm1 minute. Leg I largest and thickest, legs II and IV near equal length (II slightly thicker), and legs III shortest and thinnest. Outer, anterior edge of each coxa with distinct, thickened lip. Tarsal I setae e and f short, thick and blunt (Fig. 4). Distal cheliceral digit flattened, strongly curved at tip with 2 subapical teeth (Fig. 7).

MALE (Fig. 2, 5, 6, 7): Length of 2 specimens 242 and 260 μ. Entire dorsum thick and heavily sclerotized. Irregular areas of slightly thinner cuticle forms an uneven, irregular pattern over entire dorsum except propodosomal shield (Fig. 2). Dorsal hysterosomal shield curves over posterior end of body and extends onto ventrum. Anterior edge of hysterosoma distinct. All dorsal setae slightly curved, evenly tapered, and all of approximate equal length. Only median areas of ventor with thin cuticle. All leg apodemes thick and very dark. Edges of all coxal cavities and of camerostome with very thick, dark cuticle; most of coxal