STUDIES ON THE FUNCTION OF THE MEMBRACID PRONOTUM (HOMOPTERA)

I. OCCURRENCE AND DISTRIBUTION OF ARTICULATED HAIRS

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Abstract

Articulated sensilla occur on the pronotum of 100 species in 65 genera of membracids. The abundance of the sensilla and their universal occurrence in this group suggests that sensory reception is a significant function of the membracid pronotum. Bizarre forms of the pronotum may be a result of selection pressure to increase surface area.

Can. Ent. 106: 143–148 (1974)

Introduction

The membracid pronotum is enlarged and often takes bizarre forms (Funkhouser 1951). Poulton (1903), after examining some museum specimens, suggested that the pronotum may cryptically resemble part of the host plant or serve as a warning signal to predators. Funkhouser (1951) suggested a camouflage function for it in some species, but emphasized that, in many of the more grotesque forms, the pronotum makes them *more* conspicuous. Our conclusions generally agree with those of Funkhouser. Mimicry, aposematic coloration, and display (visual signals exchanged with conspecifics) functions are all possible for the pronotum but experimental studies are lacking. Ekkens (1972) suggested that in some forms, shape and hardness of the pronotum may make grasping or swallowing of the insect more difficult for a vertebrate predator.

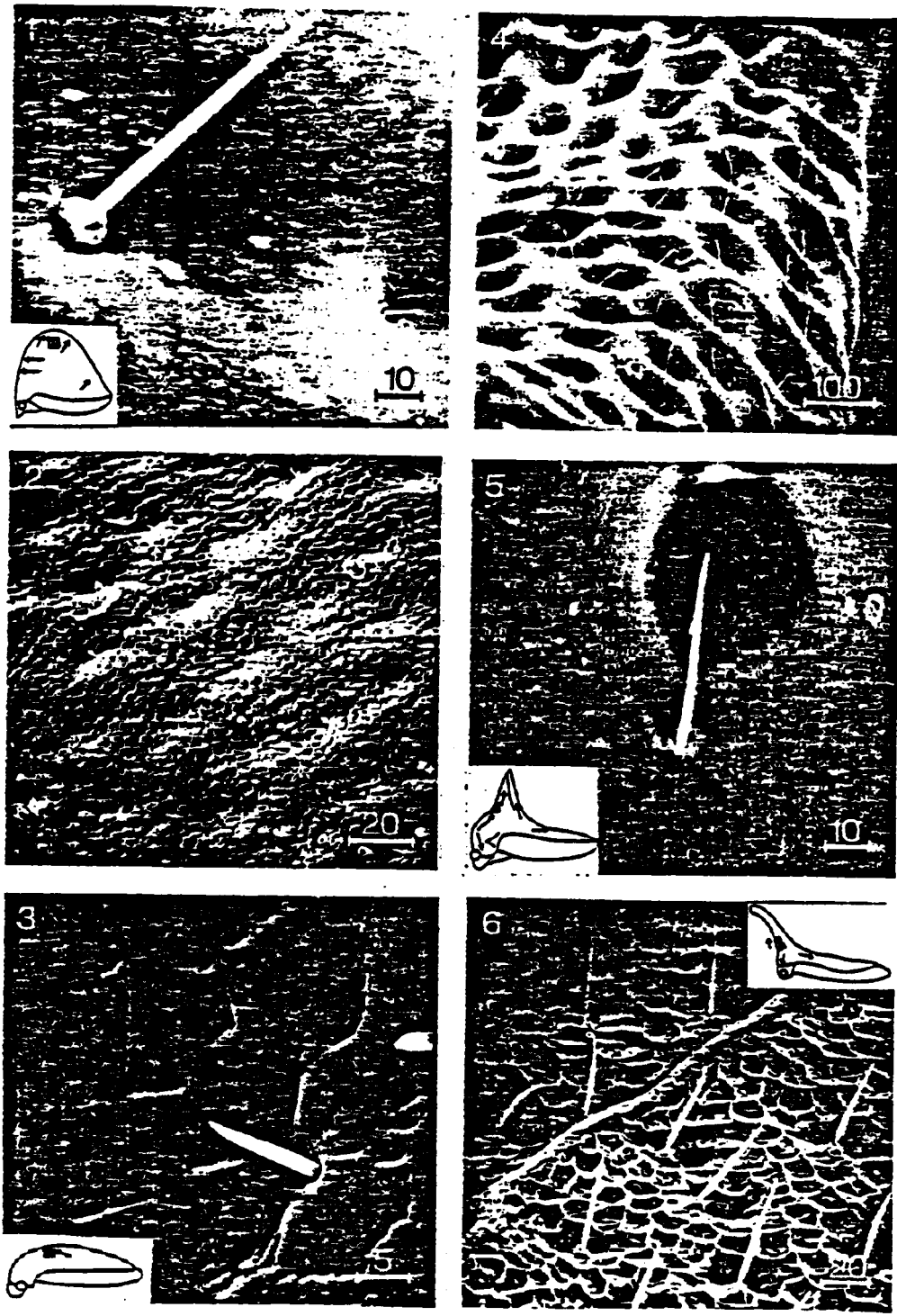
Funkhouser (1951) stated that the pronotal structures have no physiological function and concluded they are "merely hollow extensions of the chitinized body wall." He maintained that the pronotum has no connection with the tracheal system and no associated glandular system. Unpublished studies (Wood) demonstrate that the pronotum of *Umbonia crassicornis* Amyot and Serville is innervated and that the nerves are enlarged at the base of the pronotal hairs. These studies have also demonstrated the occurrence of abundant tracheae, indicating a high rate of metabolism.

Funkhouser (1951) mentioned the presence of many deep punctations (pits), each with a hair projecting over it but minimized the sensory significance of these since he could not see hairs in some punctate forms. The purpose of this study was to survey the occurrence of such sensory hairs and pits. Pinned specimens of 100 species in 65 genera were determined by T. K. Wood and examined with a dissecting microscope. Eleven of these species were selected for study with the scanning electron microscope (SEM).

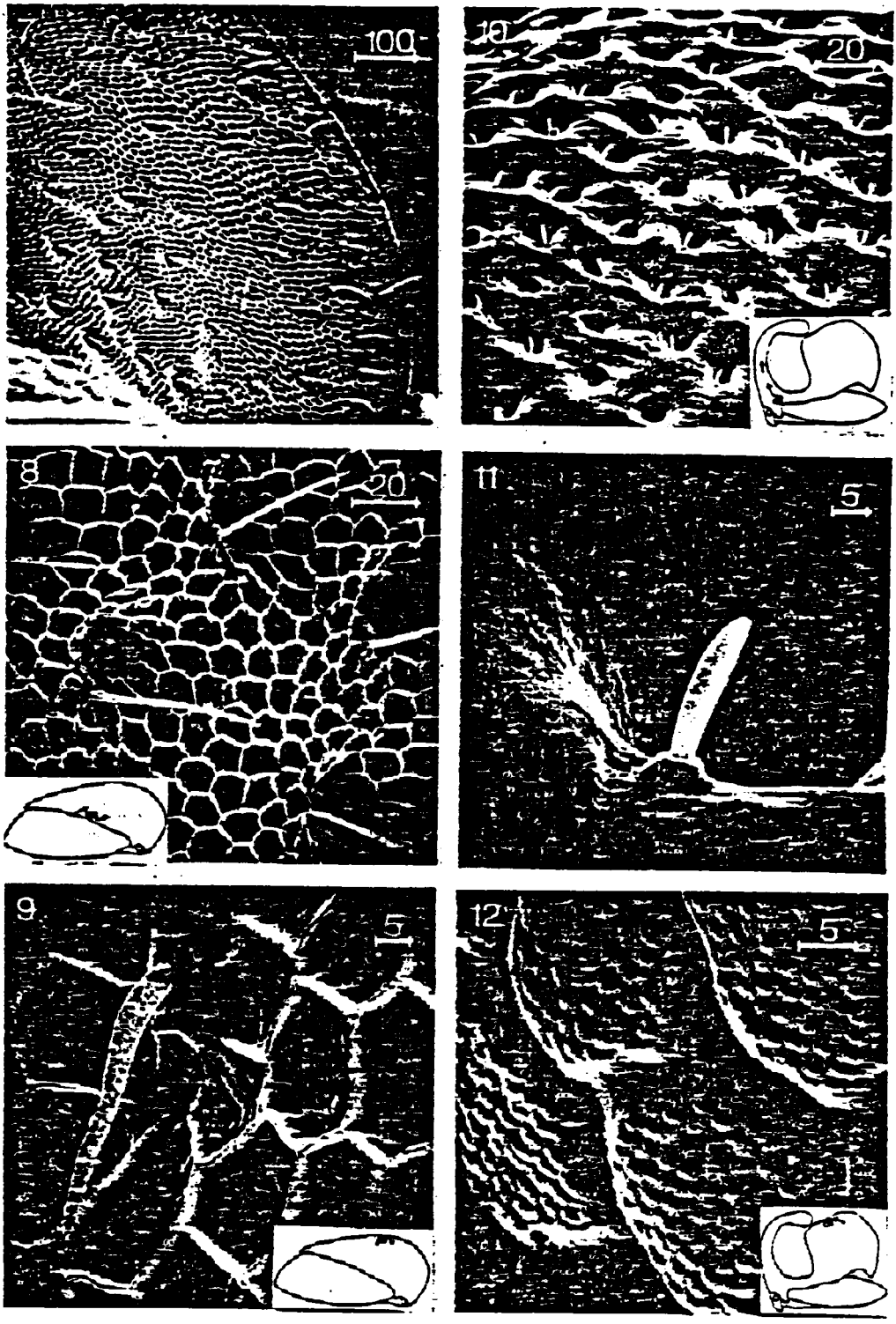
Results

All forms examined (Table I) have sensilla on the pronotum; the sensilla exhibit a characteristic distribution and density. The associated depressions vary in depth from shallow to deep. Many forms have sensilla which project over the pit, while in others there is a short sensillum in the bottom of each pit.

In the following genera, sensilla were not easily seen with the dissecting microscope and specimens were examined with the SEM: *Idioderma*, *Archasia*, *Cyrtolobus*, and *Stictopelta*. *Idioderma virescens* Van Duzee is a small species with an



FIGS. 1–6. Scanning electron micrographs, scale μm, of sensilla and associated punctations (pits or shallow depressions). · Shaded areas of lateral view line-drawings indicate the pronotal region micrographed; arrows indicate the orientation of hairs. 1, *Archasia belfragei*: shallow depressions and sensilla of two lengths; 2–3, *Stictopelta marmorata*: very shallow depression; 4–5, *Umbonia crassicornis*: pits extremely deep, hairs directed toward apex of horn; 6, *Enchenopa binotata*.



FIGS. 7–12. Scanning electron micrographs, scale μm, of sensilla and associated punctations (pits or shallow depressions). Shaded areas of lateral view line-drawings indicate the pronotal region micrographed; arrows indicate the orientation of hairs. 7–9, *Membracis mexicana*; 10–12, *Sphongophorus inflatus*.

Table I. List of subfamilies and genera examined for the presence of pits and hairs*,†

Subfamily Centrotinae		
Monobelus (1)	*Campylocentrus* (2)	*Microcentrus* (1)
Lycoderes (2)	*Tylocentrus* (1)	
Bocydium (1)	*Centrodontus* (1)	
Subfamily Hoplophorioninae		
Hoplophorion (1)	*Umbonia* (1)‡	
Platycotis (1)‡		
Subfamily Darninae		
Aconophora (1)	*Darnoides* (1)	*Cymbomorpha* (2)
Sundarion (1)	*Heteronotus* (2)	*Stictopelta* (2)‡
Subfamily Tragopinae		
Tragopa (1)		
Horiola (1)		
Subfamily Smiliinae		
Telonaca (1)	*Ennya* (1)	*Harmonides* (1)
Telamonanthe (1)	*Poppea* (1)	*Ophiderma* (3)
Acutalis (1)	*Amastris* (1)	*Glossonotus* (3)
Micrutalis (1)	*Atymna* (2)	*Carynota* (1)
Stictocephala (1)	*Heliria* (3)	*Thelia* (1)
Entylia (1)	*Evashmeadea* (1)	*Vanduzeea* (1)
Publilia (1)	*Helonica* (1)	*Polyglypta* (1)
Bryantopsis (1)	*Parantonae* (1)‡	*Grandolobus* (1)
Archasia (1)‡	*Idioderma* (1)‡	*Telamona* (3)
Xantholobus (1)	*Platycentrus* (1)‡	*Cyrtolobus* (3)‡
Bilimekia (2)	*Bajulata* (1)	*Antianthe* (1)
Cyphonia (3)	*Smilia* (2)	
Subfamily Membracinae		
Philya (1)	*Notocera* (2)	*Sphongophorus* (2)‡
Multareis (1)	*Guayaquila* (2)	*Tylopelta* (1)
Multareoides (1)	*Leiosycta* (1)	*Campylenchia* (1)
Belbonota (2)	*Enchenopa* (8)‡	*Membracis* (6)‡

*Numbers in parentheses indicate number of species examined in each genus.
†Classification of Metcalf and Wade (1965).
‡Examined with scanning electron microscope.

evenly rounded pronotum having shallow punctation. Located in the bottom of each depression is an articulated hair which is either long or short. A similar situation exists on the pronotum of *Archasia belfragei* Stål (Fig. 1). *Cyrtolobus dixianus* Woodruff has a very small articulated hair in the bottom of each depression, while, in *Stictopelta marmorata* Goding (Figs. 2, 3), each depression is less marked with the hair located near its edge.

In *U. crassicornis* the pronotum is densely punctate, each punctum a deep pit having a marginally inserted articulated hair projecting over it. Figures 4 and 5 show the arrangement of hairs and pits on the frontal surface of the horn. The pronotum of *Platycotis vittata* Fabricius is similar. In both of these species the orientation of the hairs on the horn is toward the horn apex.

Between the bulbous pronotal inflations of *Parantonae hispida* Fowler are pits with articulated sensilla. The overall pronotal surface is smooth with long articulated sensilla. *Cyphonia* and *Poppea* have the same type of arrangement. In *Platycentrus taurinas* Ball two suprahumeral horns project laterally from the humeri.

The outside of each horn bears dense mats of articulated sensilla; between the horns is a series of articulated hairs, each projecting over a pit.

Enchenopa binotata Say has a porrect horn, projecting anteriorly over the head. The horn (Fig. 6) has sensilla situated beside pits and oriented toward the apex of the horn. Sensilla over the pits in other areas of the pronotum are oriented either toward the head or the dorsal carina. In the eight species of *Enchenopa* examined, the orientation of sensilla is similar. Similar arrangements of sensilla and pits are found in other genera with anterior horns such as *Platycotis*, *Aconophora*, *Thelia*, *Guayaquila*, and *Campylenchia*.

The genus *Membracis* is characterized by an extremely high and foliaceous pronotum with very fine punctation. The distribution and orientation of the sensilla in *Membracis mexicana* Guérin-Menéville are characteristic. Sensilla over the head (Fig. 7) project downward toward the head while those on the portion of the pronotum covering the thorax and abdomen are very fine with a dorsal orientation (Fig. 8). Along the dorsal carina are found long articulated setae (Fig. 9).

In *Sphongophorus amyoti* Metcalf and Wade the hairs project over the pits and orient toward the apex of the horn. Figures 10–12 show the arrangement of pits and hairs in *Sphongophorus inflatus* Fowler.

Most pronotal sensilla are of the trichoid type. Other types of sensilla are present such as the appressed type in *M. mexicana* (Fig. 9) and *Stictopelta nova* Goding. Very small sensilla are found on the bulbous inflation of *S. inflatus*.

Discussion

It is clear that articulated sensilla are generally distributed on the membracid pronotum and that many species show a characteristic orientation of these hairs. In other insects such structures are considered to be sensory receptors usually mechanoreceptors (Chapman 1969; Dethier 1963).

It is not surprising that Funkhouser overlooked the sensilla in some species, where hairs can only be detected with the SEM. In discussing the position of the Membracidae within the Homoptera (1951) he argued that although the pronotum is highly specialized, it is purely ornamental and therefore has no phylogenetic significance. Our studies suggest otherwise.

Trichoid sensilla are certainly not unique to membracids; however, their association with pits is more unusual. Their presence on the unique membracid pronotum suggests that pronotal functions other than protection must be explored. In specific cases crypsis, mimicry, aposematic coloration, and display may prove to be functions of the pronotum but to these must be added a possible role in sensory reception: the detection of odor, air currents, or air-borne sound. The extreme modification of the pronotum may be a result of selective pressures to increase the surface area and the amount of directional sensory input.

Acknowledgments

Thanks to Miss Barbara Ramey and appreciation to Armco Steel of Middletown, Ohio, and Mr. Don Lentz for the use of the scanning electron microscope. Acknowledgment is also made of the use of the scanning electron microscope housed at the Royal Ontario Museum and provided for the University of Toronto, Department of Zoology, through a grant from the National Research Council of Canada.

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(Received 4 June 1973)