Sense Organs on the Antennal Flagellum of the Human Louse, *Pediculus humanus* (Anoplura)

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ABSTRACT Tactile hairs are present on all three subsegments of the antennal flagellum of the human louse. They are, in addition, a single chemoreceptor (tuft organ) on subsegment 2 and 12 or 13 chemoreceptors (tuft organ, two pore organs and nine or ten pegs) on subsegment 3. The cuticle surrounding the bases of the pegs at the tip of the antenna is unusual in that parts of it are perforated by many fine pores. This cuticle is underlain by a thin layer of dendrites. This region may also have a chemoreceptor function.

The classic paper on the sensory physiology of the human louse is that of Wigglesworth ('41). He included in it a description of the antennal sense organs. Miller ('09) was the first to study the human louse with the scanning electron microscope. He added new details to Wigglesworth's account and also found that two of the structures that had been described earlier as tuft organs were actually different and had no tufts. Miller called them dome organs.

MATERIALS AND METHODS

Human body lice, *Pediculus humanus*, were obtained from a biological supply house in Baltimore, Maryland. These had been fixed in Bouin's fluid. Whole insects were immersed in a 0.5% solution of crystal violet in order to identify sense organs with pores in their cuticle (Miller, '09). The heads of others, with the antennae attached, were removed and stained with barium carmine. Sections were also made of material embedded in Paraplast and then stained with Mallory's connective tissue stain.

Some specimens were washed, dehydrated slowly in alcohol, cleared in xylol, and dried before being mounted and coated for study with the scanning electron microscope. It was found that details of the antenna were often obscured by debris. Treatment with a 5.25% solution of sodium hypochlorite (Clorox) for a few minutes during the washing period eliminated some of this. Specimens for study with the transmission electron microscope were fixed in a 2% solution of glutaraldehyde and treated as described elsewhere (Miller and Sekhon, '69).

RESULTS AND DISCUSSION

The antenna of *Pediculus humanus* consists of a scape, a pedicel, and a flagellum that is divided into three subsegments. The entire antenna is about 400 µm long and the flagellum about 220 µm. The three subsegments are, respectively, 50, 60, and 50 µm in length. The first two subsegments are cylindrical while subsegment three is slightly convex on its lateral surface and concave on its medial surface (Fig. 1). The cuticle on the inner side is much thicker than that on the outer side. A nerve and trachea traverse the antennal lumen and a blood vessel may be present although it could not be identified with certainty. No differences were found between antennal sense organs from males and those from females. This agrees with Miller’s conclusion in 1969.

Tactile hairs

Counts were made of the total number of tactile hairs that are present on each of the flagellar subsegments of 20 antennae. The first subsegment had from five to seven hairs, the second subsegment either four or five hairs, and the third subsegment had three hairs. This agrees well with the results of Wigglesworth ('41), who found five to seven.

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2 *Pediculus humanus* is a subspecies that has separate sexes. *Pediculus capitis* is the beetle and *P. humanus* the louse.

3 It should be pointed out that the material should be cultured with the aid of acetabularia, since these may be a cause of the results, which elsewhere and then present only a few or not at all.
proximal one, is a tuft organ and that the other two are pore organs, as he named them. The external parts of a tuft organ consist of a raised circular ring in the cuticle that is surrounded by a shallow groove (Fig. 1). A group of small hair-like structures, each about 5 μm long, emerges from an opening in the middle of the ring. This opening extends inward in a circular tube. The hair-like structures that are attached within its outer end are usually six in number, although from four to seven may occur. This agrees with Miller's results in 1969. The hairs stain bright red with aniline violet, and this strongly suggests that they are chemoreceptors. The tube that extends inward from the point of attachment of the tuft stains red with Mallory's stain. A typical cuticular sheath, which stains blue with Mallory's technique, extends inward from the lower end of the tube. The sheath passes through a fluid-filled vacuole and then turns proximally. A small group of sensory neurons lies beneath the inner end of the cuticular sheath. The number of neurons is close to five or six. The axons from these neurons extend inward together and join the antennal nerve. No conspicuous differences were noted between the tuft organ of subsegment two and that of subsegment three.

**Pore organs**

These two structures are situated close to the tuft organ on subsegment three and just distal to it (Fig. 1). Each consists of a shallow circular depression from 6 to 7 μm across and with a small opening in its center. Shallow grooves in the cuticle radiate from the opening and are visible in Miller's micrographs (Miller, '69, Figs. 1, 6, 7). In whole mounts and sections studied with the light microscope, a cuticular tube can be seen extending inward from the central pore. It closely resembles the tubular structure below the tuft organ and is likewise, surrounded by a fluid-filled space. From its inner end a cuticular sheath extends proximally. A small group of neurons and their sheath cells lie below its inner end and their axons combine to form a nerve that joins the antennal nerve. It would be interesting to know where the dendrites end distally, but we were unable to determine this. Recently, a product of the sense organ itself or debris originating from the surface of the host is present in the lumen of thin-walled chemoreceptors (Figs. 3-6). Then, larger dendrites were found to be leading to this layer from the region of the sensory neuron cell bodies (Fig. 7). Thus, the perforated area apparently has a chemoreceptor function. Since the house is a small insect and lives in a warm environment, water conservation must be a major problem. Compared to other insects, the house has very few chemoreceptors and this area may supplement the usual chemoreceptors without greatly increasing the surface where evaporation may occur. In some ways, these perforated regions are suggestive of the plate organs seen in some species of Homoptera, Trichoptera, Strepsiptera and Hymenoptera. It would be interesting to have a more detailed study of this specialized cuticle in the Anoplura.

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**LITERATURE CITED**


Fig. 2. Scanning electron micrograph of tip of subsegment of antenna of louse. Ten pegs present, one with sharp tip. Part of the outer end of a seta is visible at the back. × 2000.

Fig. 3. Electron micrograph of cross-section through tip of subsegment 3 close to peg bases. Note thin cuticular membrane with extremely fine pores traversing it at top of section. This is the medial surface of one of the curved ridges shown in Figure 2. A layer of dendrites is present below the cuticle and this is underlain by a cavity, filled with fluid, into which extend microvilli from the epidermal cells that contain it. × 24,000.

Fig. 4. Electron micrograph of a section through a ridge such as that shown in Fig. 2 to show transition from skin cuticle underneath by dendrites (above) to normal cuticle (right edge). Note presence of fine pores in cuticle above and dendrites below it and the absence of both in the normal cuticle at right. × 33,000.
The Auditory Region of Dermoptera: Morphology and Function Relative to Other Living Mammals

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ABSTRACT The dermopteran basi-cranium combines a primitively constructed and oriented auditory bulla formed by ectotympanic, rostral entotympanic, and tubal cartilage with derived features of the middle ear transformer and internal carotid circulation. Living dermopterans possess a primitive eutherian auditory region that has been structurally modified to receive a lower frequency sound spectrum than probably was utilized by ancestral Mesozoic therians. Perception of the low to mid-frequency range is enhanced in Dermoptera by reducing stiffness in the mechanical transformer while maintaining low mass of the component parts. Stiffness has been reduced by (1) development of an epitympanic sinus about four times the volume of the middle ear cavity proper, (2) detachment of the anterior process of the malleus from the entotympanic, and (3) by deliberate suspension of the ear ossicles within the middle ear.

We apply to dermopterans a measure of hearing efficiency derived from recent functional studies of the mammalian middle ear that regards the middle ear mechanism as an impedance matching transformer. Calculation of the impedance transformer ratio for Dermoptera suggests that these mammals are relatively efficient in comparison to other eutherians in their ability to match the impedance of cochlear fluids to that of air at the eardrum. Dermopterans theoretically are capable of using over 90% of incident sound energy striking the eardrum at the resonant or natural frequency. Mechanical impedance of the middle ear transformer exerts a minimal influence on hearing efficiency due to low mass, little stiffness, and little frictional resistance.

Analysis of measurements of the middle ear transformer published by Gerald Fliescher and integration of these data with current theory on the peripheral hearing mechanism in mammals allow us to propose a model that describes the structural and functional evolution of the mammalian middle ear transformer. Structural changes appear to be correlated with alteration in function from primitive small mammals with stiff middle ear transformers and high frequency dominated hearing to mammals with a wider range in body size with more mobile middle ear transformers and a greater range of frequency perception, after including improved sensitivity to lower frequencies.

Mammals employ different anatomical strategies in attainment of increased hearing efficiency and sensitivity. Efficiency is improved by adjustment of lever and area ratios of the middle ear transformer to achieve an optimum impedance match of external air and cochlear fluids. Sensitivity over a broad frequency spectrum is attained by minimizing mass, stiffness, and frictional resistance of the transformer. The morphology of the auditory region of both living and fossil mammals seems explicable in terms of selection pressure directed toward these ends.

The relationship of the southeast Asian colugos, or "flying lemurs," (class Mammalia, Order Dermoptera Gill 1811, Cynocephalus Boddaert 1768) to other living and fossil mammals has long been in question. Hypothesized relationships have been based on many different morphological features. Gregory (1907) reviewed proposed relationships of the colugos.