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A scanning electron microscopic study of mechanoreceptors in the walking legs of the water strider, *Gerris remigis*

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INTRODUCTION

The water strider, *Gerris remigis* (Gerridae) locates prey by orienting toward and striking at the source of ripples produced by a struggling insect trapped in the surface film of ponds and streams (Liche, 1936; Rensing, 1961). Murphy (1971) found that tethered gerrids responded by turning towards a source of 5 μm ripples on the surface film at frequencies of 20–30 Hz, and that the angular components of the motor response correlated well with the angular deviation of a target from the longitudinal axis of the body. Murphy assumed the receptors mediating this response were associated with the legs, but he did not identify them.

The present paper reports the results of a scanning electron micrographic study of the walking legs of *Gerris remigis*, and suggests that the receptors mediating the orientation response to a vibration of the surface film are mechanosensory hairs of the distal trochanters and tarsal appendages of the walking legs.

METHODS

Wingless female specimens of *Gerris remigis* were taken from a stream on the campus of Stanford University at Palo Alto, California, in September and October of 1972, and washed in distilled water. Specimens were killed by immersion in 3 % glutaraldehyde (Ladd Industries) solution in 0·1 sodium cacodylate buffer at pH 7·4. Whole walking appendages were severed at the coxal-femoral joints and were placed for 24 hours at 4 °C in fresh glutaraldehyde fixative. Some appendages were trimmed to shorter lengths after 24 hours of fixation, and were then placed in new fixative for longer periods (up to 48 hours). Tissues were washed in buffer, dehydrated through 35 %, 50 %, 70 % and 95 % ethanol, and left in a second change of 100 % ethanol overnight at 4 °C. Material in 100 % ethanol was warmed gradually to room temperature, passed through a gradient of amyl acetate in absolute ethanol, left for 15 minutes in absolute amyl acetate and critically point dried. Specimens were mounted with glue on metal holders, coated with gold by vacuum evaporation, and examined in a Cambridge Stereoscan microscope, model S4.

Portions of some appendages fixed by the above technique were embedded in Epon and sectioned at 1·5 to 2 μm. These were stained with toluidine blue for studies of the intra- and sub-cuticular portions of the sensory hairs.

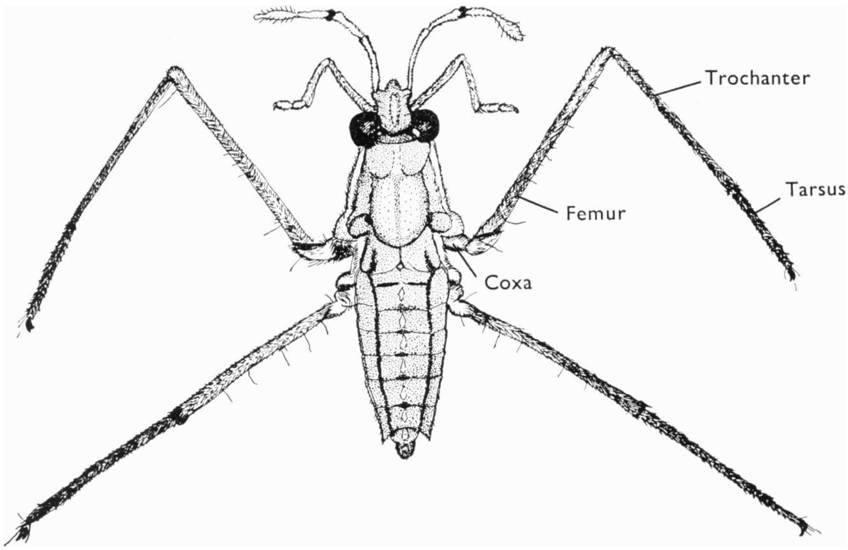


Fig. 1. 15 mm wingless female specimen of *Gerris remigis* depicting the segmentation of the thoracic appendages.

RESULTS

Thoracic appendages

Gerris has 3 pairs of thoracic limbs; one pair of raptorial forelimbs used in feeding and support but not in locomotion, and 2 pairs of walking appendages (Fig. 1). Each appendage consists of a proximal coxa, femur, trochanter, and two tarsal segments. The tips of the distal segments of the tarsi of the walking legs and the grasping appendages bear a pair of claws on their subapical surfaces (Fig. 2). These claws are used when the insect is climbing submerged vegetation and when walking on land. They can be retracted into sheaths when not in use.

Mechanoreceptive hairs on the thoracic appendages

Each appendage has its own typical array of hairs. The raptorial forelimbs and the walking legs are covered by fine investing unspecialized hairs. The proximal segments, coxae, femora and trochanters of the walking legs have shorter hairs than the distal segments, and stiffer conical hairs are also found at intervals on the trochanters and tarsi (Fig. 3).

During the locomotory power stroke, and while the insect is resting on the surface film, the tarsal segments and sometimes the trochanters of the walking appendages adjoin the meniscus. The extent of contact depends upon the surface tension and the posture of the animal. If the surface tension is low the distal segments of the tarsi sink below the meniscus. The surfaces of the portions of the appendages that make contact with the surface of the water are covered with long compliant hairs, which are of two kinds. At intervals along the ventral and lateral aspects of the femora, trochanters and tarsi of the walking appendages, 10–20 hairs about 2 μm in diameter and 125–150 μm long arise at right angles from regions of cuticle devoid of other

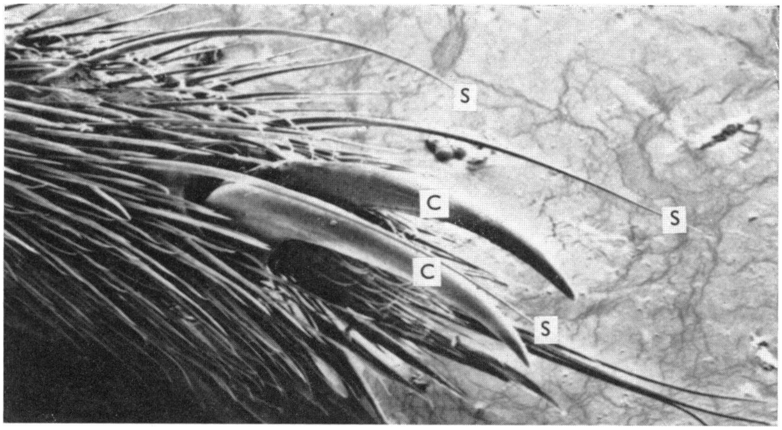


Fig. 2. Tarsal claws (C) and sensory hairs (S) on the distal tip of a walking leg of *Gerris remigis*. The claws can be retracted when not in use. The oblique orientation of the organs permits the convex surfaces of the hairs to rest upon the surface film.

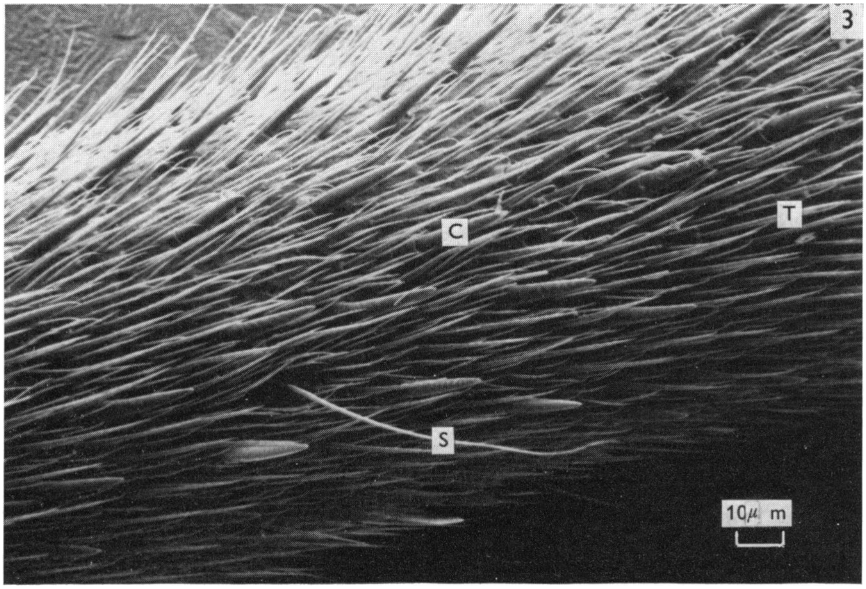
hairs (Figs. 3, 4, 5, 6). These organs have hollow central lumina and originate from enlarged spherical bases contained within depressions in the cuticle. Unlike the shorter investing hairs, which are composed of entwined cylindrical subunits, and whose bases show no elaboration, the longer hairs are smooth (Fig. 7). Each springs from a rounded, flattened base, elevated from the adjacent cuticle. The junction of the base plate and hair is marked by an annulus.

On the distal ends of the tarsal segments of the walking legs, 3 similar hairs arise from cuticular regions devoid of other hairs. These hairs are directed laterally, and form acute angles with the cuticle (Fig. 2). They are positioned on the ventral surface of the tarsi so that their convex ventral margins rest against the surface meniscus whenever the tarsi are in contact with the surface of the water.

Both groups of hairs are very compliant and the cuticular bases are associated with 20 μm cell bodies subjacent to the cuticle; these stain deeply with methylene blue (Fig. 8), suggesting that they may be the somata of neurons (Bullock & Horridge, 1965). When these hairs are stroked with a thin glass capillary, they bend easily at the base which adjoins the cuticle, and an unrestrained gerrid often turns and strikes in the direction of the stimulus. If the hairs are ablated or coated with thinned nail lacquer, the responses of such animals to a vibrating stimulus on the surface of the water are very much reduced. The behaviour of untethered gerrids with lacquered hairs to vibrational stimuli is reported elsewhere (Lawry, 1974).

DISCUSSION

Liche (1936) described the long hairs on the femora and trochanters of *Gerris*, calling them *Trichobothrien*. He was able to elicit prey-grasping when these hairs were stroked, and inferred that they responded to vibrations of the water surface. However, Liche was unable to ablate the hairs without damaging the insects, and was thus unable to test his hypothesis.



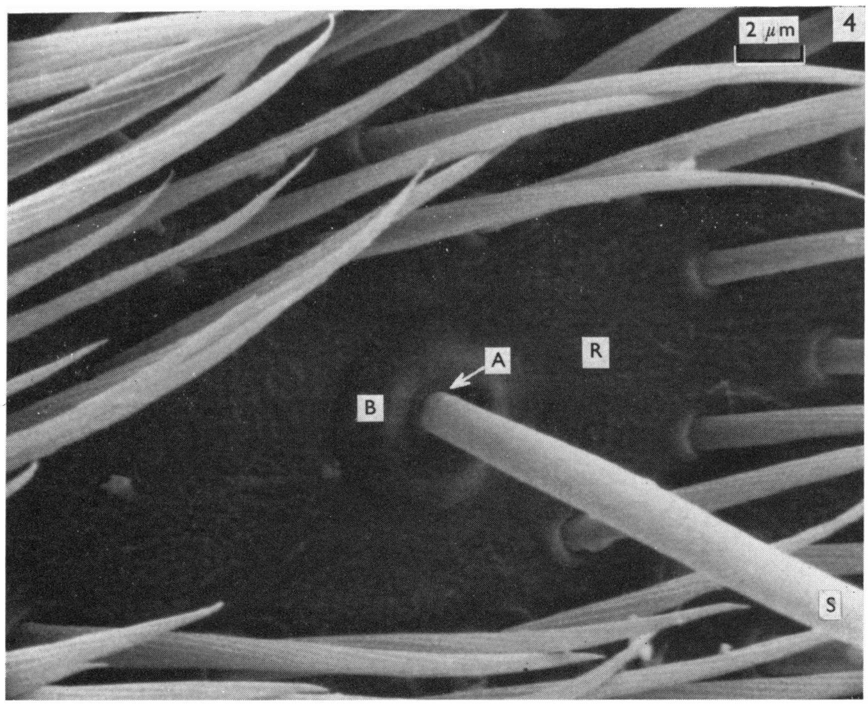
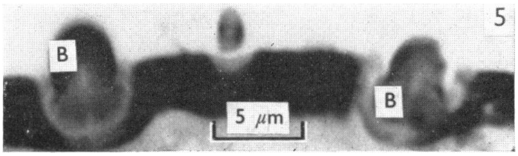
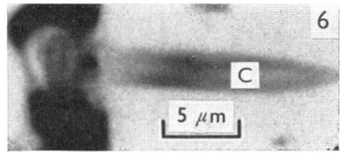


Fig. 3. A portion of the trochanter of *Gerris remigis* showing the thin investing hairs (T) which are found on all segments of the appendages, the stiff conical hairs (C) which are restricted to tarsal and trochanteric segments, and a specialized sensory hair (S).

Fig. 4. Detail of the base of a sensory hair from the trochanter of *Gerris remigis*. (B) base; (R) region of cuticle devoid of investing hairs; (A) annulus. Note the smooth surface of the hair (S) and its orientation normal to the cuticular surface.





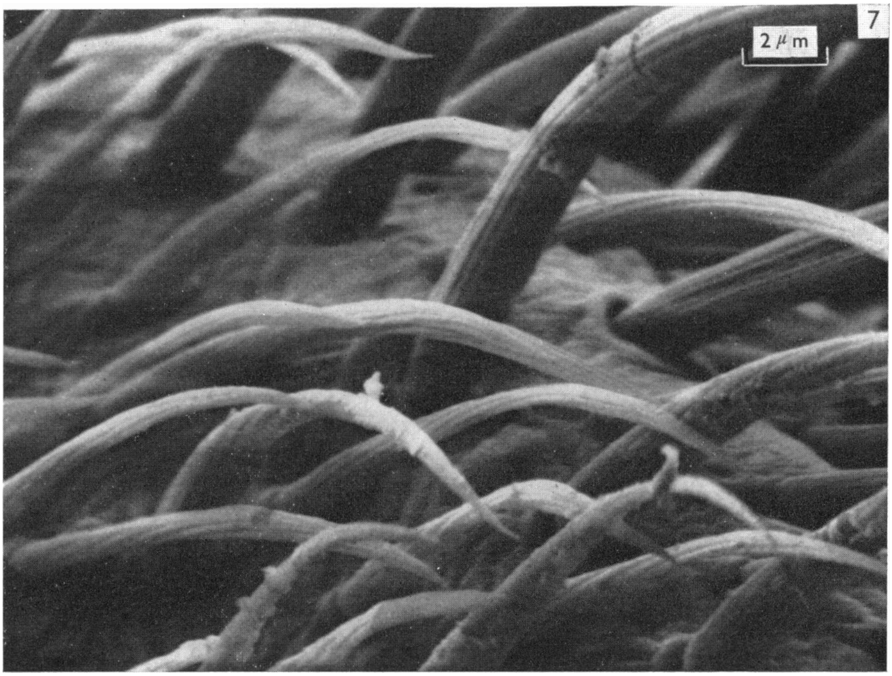


Fig. 5. A transverse vertical Epon section of the bases (B) of two sensory hairs from the tarsus of *Gerris remigis*.

Fig. 6. A transverse vertical Epon section through the longitudinal axis of a sensory hair from the tarsus of *Gerris remigis*, showing the hollow centre of the hair (C).

Fig. 7. Surface of the cuticle of the trochanter of *Gerris remigis* showing the investing hairs composed of entwined cord-like subunits.

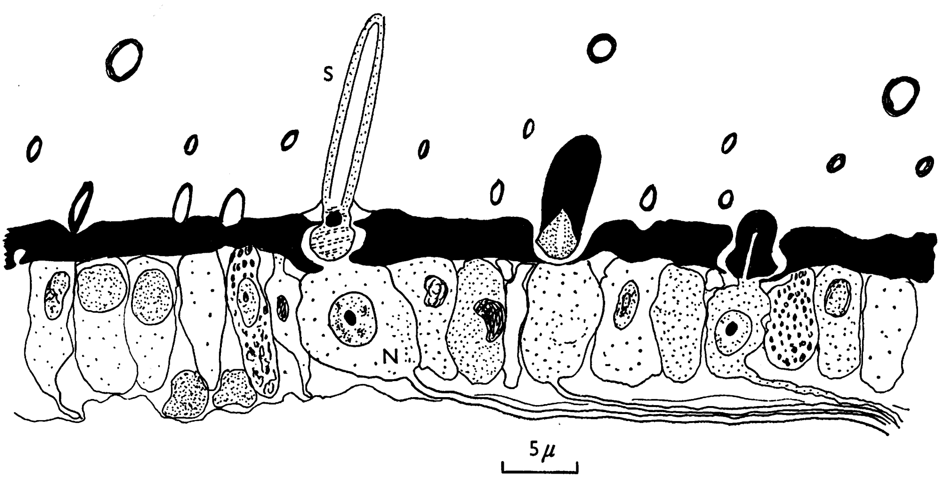


Fig. 8. Drawing of a photomicrograph of a vertical section through the cuticle of the tarsus of *Gerris remigis* showing the subjacent cells and the neuron somata (N) associated with the sensory hairs (S).

The long compliant hairs on the trochanters and tarsi of *Gerris* appear to be mechanoreceptors for the following reasons. (1) They arise from regions of cuticle devoid of investing hairs, suggesting that they can be moved, so forming oblique angles with the cuticle without interference from neighbouring hairs. (2) The long hairs are compliant, bending readily at their bases when probed with a fine capillary. (3) The bases of the long hairs appear specialized, while those of the investing hairs are unspecialized. (4) The long hairs are positioned at right angles to the surface of the cuticle and are found predominantly on the ventral and lateral aspects of the trochanters and tarsi, which are in contact with the surface during locomotion and when the insect is at rest on the meniscus. (5) The bases of the long hairs adjoin somata of cells which stain with methylene blue, suggesting that these cells are sensory neurons. Reports elsewhere corroborate these anatomical findings, because gerrids that have the distal tips of their walking legs coated with a thin layer of lacquer respond less readily and with reduced accuracy to a vibrational stimulus applied to the surface meniscus. It is also possible to record increased neural activity in the stumps of peripheral nerves attached to isolated legs of *Gerris* when long hairs are stroked (Lawry, in preparation).

SUMMARY

Sensory hairs occur on the walking appendages of the water strider, *Gerris remigis*. Each organ consists of a smooth compliant hair, 150 μm long and 2 μm in diameter, which arises from a circular base situated in a region of cuticle devoid of other hairs. Each sensory hair is hollow and is related to a 20 μm cell body subjacent to the 5 μm cuticle. Ten to twenty of these receptors are found along the posteroventral margins of the coxa, femur, trochanter and tarsal segments of each leg. Three hairs are positioned on the distal tarsal segments so that the compliant convex ventral margin of the hair rests on the surface film. These tarsal mechanoreceptors appear to mediate the orientation response to a vibratory stimulus, since the response is diminished or does not occur when the hairs are sectioned.

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