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The Scent Glands of Opiliones: A Review of Their Function

ABSTRACT

Opilionids are unique among the arachnids in that they possess a pair of glands that open dorsally near the lateral edge of the prosoma. These glands are variously called scent, odoriferous, repugnatory, or stink glands and generally have been considered as a defensive mechanism against predators. Theoretically, the glands may function in several ways such as in waste removal, protection from microorganisms, repulsion of predators and parasites, intraspecific recognition, and sexual, alarm, and aggregation behaviors. In actuality, only two functions have been proven—predator defense and aggregation formation. Many of the chemicals found in the secretions of scent glands effectively deter attacks by ants. Indeed some of these chemicals are ant alarm pheromones. Other evidence for predator repulsion is very fragmentary and often based on single observations. Though opilionids are typically solitary, some species form aggregations that may consist of thousands of individuals. In at least one species of *Leiobuninae*, scent-gland secretions promote aggregation behavior. As more work is done on opilionid scent glands, multiple use of the secretions are likely to be found.

A unique feature of opilionids, or harvestmen, is that they possess a pair of glands that open dorsally on the prosoma. In the 1800s the openings of these glands were mistaken to be spiracles or eyes (Hansen and Sørensen 1904). Once their glandular nature was determined, however, they have generally been considered a defensive mechanism against predators. This paper reviews evidence for this function and examines other possible interspecific and intraspecific uses.

The scent glands, as they are now generally called, are hollow sacs connected to the exterior by a canal. The walls of the sacs consist of three basic layers: a basement membrane, a middle layer of glandular epithelium, and an inner chitinous membrane. Members of the suborder Palpatores have the simplest structure; there is only a single layer of glandular cells and the opening of the gland is closed by two muscles. The glands are emptied by indirect pressure from adjacent muscles or organs. The Cyphophthalmi have the most complex structure; there is more than one layer of glandular cells, the wall of the sac is interlaced with muscle fibers, and the gland orifice is opened by one muscle and closed by another. Moreover, the canal is comparatively long and opens at the tip of a tubercle. The Laniatores are intermediate (Juberthie 1961a,b; 1976).

The chemistry of the scent gland secretions has been reviewed by Eisner et al. (1978) and added to by Duffield et al. (1981), Roach et al. (1980) and Wiemer et al. (1978). No secretions have been analyzed from the Cyphophthalmi. In the Laniatores, 3 quinones and 5 phenols have been found in 10 species within 3 families; in the Palpatores, 6 ketones, 3 alcohols, 1 aldehyde and 2 naphthoquinones in 10 species of the Phalangidae.

Usually the secretions ooze slowly out of the glands but, in a few species, they are forcibly sprayed. The secretions may spread over the prosoma by capillary action and, in several families of Laniatores, may reach the opisthosoma via lateral grooves. In the Laniatores the glandular secretion is diluted with enteric fluid that moves *up* from the mouth by way of the leg coxae (Eisner et al. 1971, Duffield et al. 1981). In the Cyphophthalmi and Laniatores the secretions may be transferred to an offending object by a leg (Juberthie 1961a; Eisner et al. 1971, 1977). This mechanism of secretion transfer raises two interesting questions: 1) Can those species that possess this behavior effectively use it against external parasites such as mites? and 2) Is this mechanism absent in those species, especially the Phalangidae, that can automatize their legs?

Though defense against predators is probably the main function of opilionid scent glands, confirmatory evidence

is rather meager. Direct repulsion has been shown best for ants (Blum and Edgar 1971; Duffield et al. 1981; Eisner et al. 1971; Weimer et al. 1978) and to a lesser extent for spiders (Bristowe 1941; Forster 1954; Juberthie 1976) and other opilionids (Juberthie 1961a). Limited evidence is available for opilionids repelling scorpions (Stahnke 1945), various other arthropods (Juberthie 1976), frogs (Edgar 1960) and lizards (Duffield et al. 1981). The evidence of ant repulsion is especially interesting as several of the chemicals are also ant alarm pheromones (Blum 1980).

Data on the effectiveness of the secretions against predators is probably best gained through direct observation of opilionid-predator encounters. This method is more advantageous than, say, stomach content analysis because complicating factors such as predator-prey sizes and densities, predator hunger levels and prior learning experiences, relative depletion of scent glands, and opilionid availability in time and space can be avoided, at least to some extent.

Estable et al. (1955) found that the secretion of a laniatorid was an effective antibiotic against various bacteria and protozoa. Whether this action is only incidental to predator defense has not been studied.

Bishop (1950) was the first to suggest that the scent gland secretions might be used for intraspecific communication. He observed that the secretions in a *Leiobunum* moved *down* the coxae and suggested that they could be deposited on the ground as a trail marker. It is also possible that scent gland secretions are used in sexual recognition or attraction behaviors. However, the probability of this is slight, because other glandular structures have been found that may serve this function (e.g., Martens 1979; Martens and Schawaller 1977) and there is no known difference between the secretions of males and females.

Most opilionids are solitary. However some members of the Leiobuninae, Gyantinae, and Gagrellinae of the Phalangidae form aggregations during aestivation and hibernation (Martens 1978; Wagner 1954). Wagner postulated that opilionids are attracted to the aggregation sites by the odor of the scent glands. It is also possible that the chemicals could be used in the opposite sense, that is as an alarm pheromone instead of an aggregation pheromone, when the aggregations are disturbed.

In conclusion, even though the evidence is fragmentary, the best postulate is that opilionid scent glands are used primarily for defense. Other uses are possible but if they exist, probably secondary.

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