Fine structure of the axillary organs of *Hericia janehenleyi* Fashing (Algophagidae: Astigmatina : Sarcoptiformes) and the potential correlation of axillary organ size with habitat

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**ABSTRACT**

Members of the astigmatine family Algophagidae occur in a wide variety of habitats. Many are aquatic and live fully submerged, whereas others are semi-aquatic and wade in liquid, and yet others are alleged to be completely terrestrial. One of the major characteristics of the family Algophagidae is the presence of axillary organs, which are sclerotized bands of cuticle located on each side of the propodosoma between legs I and II. To date, the fine structure of the axillary organs has been described for only two species, *Algophagus pennsylvanicus* Fashing and Wiseman, a fully aquatic species in the subfamily Algophaginae that inhabits water-filled treeholes, and *Fusohericia lawrencei* Baker and Crossley, a semi-aquatic member of the subfamily Hericiinae that inhabits the sap flux areas of trees. The present study describes the fine structure of the axillary organs of *Hericia janehenleyi* Fashing, a member of the subfamily Hericiinae that inhabits fermenting sap flux on oak trees (*Quercus* spp.). In addition, the sizes of axillary organs of species from differing habitats are compared to determine whether these two variables are correlated.

**Key words:** genital papillae, acetabula, Claparède organs, osmoregulation, sap flux, slime flux

**INTRODUCTION**

With the exception of some terrestrial and semi-terrestrial species, members of the astigmatine family Algophagidae are aquatic, living fully submerged, or are semi-aquatic, wading in liquid (Fashing et al. 2000). Known species derive from the Palearctic, Nearctic, and Oriental regions as well as from islands in the sub-Antarctic (Marshall et al. 2001). One of the major characteristics of the family Algophagidae is the presence of axillary organs, the sclerotized bands of cuticle located on each side of the propodosoma between legs I and II; axillary organs are found...
on all instars with the exception of the deutonymph (Fashing 1984). Although Fain and Johnston (1975) speculated that the axillary organs might function as air chambers serving for both respiration and flotation, fine structural studies have implicated a probable role in osmoregulation (Alberti and Coons 1999; Fashing 1984; Fashing and Marcuson 1996). To date, the fine structure of axillary organs has been described for only two species, *Algophagus pennsylvanicus* Fashing and Wiseman, a fully aquatic species in the subfamily Algophaginae that inhabits water-filled treeholes (Fashing 1984), and *Fusohericia lawrencei* Baker and Crossley, a semi-aquatic member of the subfamily Hericiinae that inhabits sap fluxes (also known as slime fluxes) and the wet subcortical habitats of trees (Fashing and Marcuson 1996). The present study describes the fine structure of the axillary organs of *Hericia janehenleyi* Fashing, a second member of the subfamily Hericiinae which inhabits fermenting sap fluxes on oak trees (*Quercus* spp.) (Fashing 2008; Fashing and Okabe 2006). The size or number (or both) of osmoregulatory organs of acarine species has been suggested to be correlated with habitat (Alberti and Bader 1990; Barr 1982; Fashing 2004; Goldschmidt et al. 1999). Here the size of axillary organs is compared across genera and species of Algophagidae in an attempt to correlate size with habitat.

**METHODS AND MATERIALS**

Bark samples from areas with fermenting sap flux were collected from oak trees (*Quercus* spp.) in the Williamsburg, Virginia, area and examined in the lab for *H. janehenleyi*. Adult male and female specimens obtained from the samples were used for investigation.

For observation using phase-contrast and Hoffman modulation-contrast microscopy, specimens were cleared in Nesbitt’s solution and mounted in Hoyer’s medium on microscope slides (Krantz and Walter 2009).

For transmission electron microscopy (TEM), the integument of the idiosoma was first ruptured with a minuten pin to facilitate fixation and specimens then placed in a fixative of 3.5% gluteraldehyde, 2.5% paraformaldehyde, and 2% acrolein in cacodylate buffer (pH 7.4) for 12 h at 4°C. After several brief rinses in cacodylate buffer, specimens were post-fixed for 1.5 h at 4°C and an additional 1.5 h at room temperature in 1% OsO4 in cacodylate buffer. Specimens were then briefly rinsed in 50% acetone and soaked overnight in a 2% uranyl acetate, 70% acetone solution at 4°C. Dehydration was completed in acetone, and Spurr’s medium was used for infiltration and embedding. Thin sections were stained in lead citrate, and microscopy was performed on a Zeiss EM 109 (Carl Zeiss Microscopy GmbH, Carl Zeiss Promenade 10, 07745 Jena, Germany).

For observation under scanning electron microscopy (SEM), live mites were first vigorously rinsed in several baths of distilled water to cleanse them of debris and then briefly submerged in near-boiling distilled water, to force protraction of appendages. The samples were then dehydrated in baths of ethyl alcohol, dried in a Tousimis Samdri-PVT-3B critical-point drier (Tousimis Research Corporation, P. O. Box 2189, Rockville, MD 20852, USA), individually affixed to stubs by using double-sided tape, and coated with gold–palladium in an Anatech LTD Hummer VII sputter coater (Anatech Ltd, 2817 Whipple Road, Union City, CA 94587, USA). Microscopy was performed on an AMR 1810 (Amray Inc., 160 Middlesex Turnpike, Bedford,
MA 01730, USA).

To compare axillary organ size and associate it with habitat, slide-mounted specimens of *Algophagus pennsylvanicus*; *Algophagopsis* n. sp.; *Algophagopsis pneumatica* Fain and Johnston; *Lamingtonacarus oreillyorum* Fashing, OConnor, and Kitching; *L. posidonis* Fashing, OConnor and Kitching; *Hericia* n. sp.; *H. janehenleyi*; *H. sanukiensis* Fashing and Okabe; *Fusohericia heliconiae* Fashing and Glist; and *F. lawrencei* were examined under the compound microscope. Species descriptions in the literature were used for determination of axillary organ size and habitat for all other species (Clark and Adrews 2012; Hughes and Goodman 1969; Marshall et al. 2001, 2003).

**RESULTS AND DISCUSSION**

The axillary organs of *H. janehenleyi* are paired structures that originate dorsally between legs I and II, extend laterally between the legs, and extend ventrally onto the coxae (Figs. 1, 2). These structures are broader throughout as well as more rounded on the dorsal margin in females than in males. Observation via SEM indicates that each organ is covered by a cuticular plate containing numerous small pores and surrounded by a ridge of thickened cuticle (Figs. 3, 4). The ridge projects across the cuticular plate approximately midway of its length, thereby forming a bridge-like structure. Observations under a TEM reveal that each organ is covered by a non-

**Figs. 1 and 2.** *Hericia janehenleyi*, shape and location of axillary organ (in red). 1, male; 2, female.
laminate cuticular plate that is thinner than normal cuticle and contains numerous pores (Figs. 5-9). The thickened ridge surrounding the thin cuticular plate likely provides structural support for the thin plate. The narrow cavity between the cuticular plate and the underlying epidermal cells contains a thin layer of electron-dense, extracellular material (Figs. 5-9). The epicuticle lines the inside of the pores as well as the roof of the cavity (Fig. 7). The underlying epidermal cells are quite large and characterized by the presence of numerous mitochondria in close association with plasma membrane plications (“mitochondrial pump”) (Figs. 5, 6, 8, 9). Near the apical surface of the cells, the plasma membranes proliferate into a network of numerous membranous vesicular tubules (Figs. 8, 9). The number of specialized cells in an axillary organ was not determined.

The presence of numerous mitochondria in close association with plasma membrane plications is characteristic of cells with an active transport function (Alberti 1977; Alberti and Dabert 2012; Komnick 1997; Witaliński and Liana 2010). Such ultrastructural characteristics are found in the chloride cells of aquatic insects, and a great deal of evidence has been amassed to support the hypothesis that the chloride cells play an important role in osmoregulation and ion regulation (see Alberti 1977; Komnick 1977). Similar ultrastructural features are found in the supracoxal glands of *Falculifer rostratus* (Buchholz) (Alberti and Dabert 2012) as well as the acetabula of water mites (Alberti 1977; Goldschmidt et al. 1999), and several physiological and ultrastructural studies have proven these structures to be sites of osmoregulation (Alberti 1977; Goldschmidt et
Because the genital papillae of astigmatine mites are homologous to the acetabula of water mites (Grandjean 1938; Alberti 1979; Van der Hammen 1989) and have a similar ultrastructure, they too are considered to function in osmoregulation (Fashing 1988, 2004). Furthermore, given that the axillary organs of *A. pennsylvanicus* and *F. lawrencei*, and now a third species, *H. janehenleyi* (current study) are similar ultrastructurally to acetabulae and genital papillae, it is reasonable to conclude that axillary organs also function in osmoregulation (Alberti and Coons 1999; Fashing 1984; Fashing and Marcuson 1996).

The presence of axillary organs is coupled with vestigial genital papillae and the lack of Claparède organs—the larval homologs of genital papillae that are located between legs I and II—thus implying that axillary organs have taken over the osmoregulatory role in mites of the family Algophagidae (Fashing 1984; Fashing and Marcuson 1996). The facts that the location of axillary organs is similar to that of the Claparède organs of other actinotrichid mites and that these organs are similar ultrastructurally have led to the hypothesis that they are homologous.

Figs. 5 and 6. *Hericia janehenleyi*, TEM images of axillary organ. 5, extent of organ, illustrating numerous mitochondria throughout; 6, section through porous plate. Note the layer of electron-dense substance below the porous plate and the large number of mitochondria in close association with plasma membrane plications (Scale bars: Fig. 5=5μm, Fig. 6=2μm).
structures retained in post-larval instars (Alberti and Coons 1999; Alberti and Dabert 2012; Witaliński et al. 2002). Although Alberti and Coons (1999) note that retention of vestigial genital papillae coupled with the presence of axillary organs in post-larval instars is an exception to the typical ontogenetic pattern, such exceptions are not unknown. Claparède organs are retained in the post-larval instars of a few species in the prostigmatic family Halacaridae (Bartsch 1974) and the prostigmatic superfamily Tydeoidea (Andre 1991). In these cases, however, the Claparède organs are easily recognized by their normal shape and size, whereas the axillary organs of algophagids differ considerably from the typical astigmatine Claparède organs of related taxa. Consequently, a second hypothesis—that axillary organs are independently evolved structures—should be considered.

Regarding the possible independent evolution of axillary organs, Alberti and Coons (1999) acknowledge that some ultrastructural features of axillary organs differ strikingly from the genital papillae of hyrachnid and halacarid mites. The observed ultrastructural similarities can easily be
attributed to a common function, osmoregulation. In addition, consider that the larval instars of the family Carpoglyphidae, the sister group of the Algophagidae (O'Connor 1981, O'Connor and Moser 1985), lack Claparède organs as well as axillary organs and have normal rather than vestigial genital papillae (Clark 2010; Hubard and Fashing 1996). Finally, the post-larval retention of Claparède organs has never been recorded for a member of the Astigmatina. It therefore appears probable that the axillary organs of the Algophagidae are independently evolved structures.

Questions concerning the evolution of similarities and differences in the axillary organs of algophagid species are more difficult to decipher. Although minor differences in fine structure occur among the three species thus far investigated, the basic characteristics of active transport cells that function in osmoregulation are shared by all three (Fashing 1984; Fashing and Marcuson 1996). The observed minor differences might reflect variation in tissue fixation but are more likely due to adaptations to the osmoregulatory demands imposed by the habitats in which the organisms reside. However, information regarding axillary organ ultrastructure is available for too few species and from too few habitats to explore that hypothesis in detail. As an alternative, comparing the size of axillary organs among algophagid mite species from diverse habitats (see Appendix 1) might provide insight into this issue. For example, species have been located in brackish water, freshwater rivers, ponds, and lakes, sap fluxes and subcortical areas of trees, fluid-filled flower bracts, water-filled treeholes, and even terrestrial habitats. The osmotic pressure of the medium surrounding the idiosoma is characteristic of the habitat and likely determines the demands for osmoregulation, in that this medium might be isosmotic, hyperosmotic, or hypoosmotic to the mite's internal tissues. By extension, the amount of tissue devoted to osmoregulation (i.e., size of the axillary organ) might differ according to and thus be correlated with habitat.

In this regard, Goldschmidt et al. (1999) found that freshwater mites in the subcohort Hydrachnidae respond to their hypoosmotic environment by increasing the number of acetabula present on the idiosoma. In the case of the genus Neotyrrellia, an acetabula-like structure evolved on the coxae to supplement the osmoregulatory function of the existing acetabula.

Unlike acetabulae, axillary organs do not vary in number, but they do vary considerably in size. Species inhabiting freshwater, such as pools (e.g., A. antarcticus Hughes, A. laticollaris Fain) and rivers (Algophagopsis pneumatica), have well developed axillary organs that wrap around the idiosoma between legs I and II, extending dorsally, laterally, and ventrally (Fig. 10). Like freshwater algophagids, hydrachnidian water mites are in a hypoosmotic medium. The axillary organs of species inhabiting the phytotelm habitat of water-filled treeholes are similar to but slightly smaller than those of freshwater algophagid species (Fig. 10). The water in treeholes is the result of rainfall, the amount of which can vary by season. In addition, the decomposing leaves and detritus that accumulate in the rather small volume of a treehole adds solutes to the water it contains, thus likely creating a less hypoosmotic environment than that of fresh water. A decreasing osmoregulatory demand would result in smaller axillary organs.

Fusocericia heliconiae, another phytotelm inhabitant, resides in the fluid-filled flower bracts of Heliconia imbricata (Kuntze) Baker. Interestingly, it has rather large axillary organs (Fig. 10) that imply a greater osmoregulatory demand than those of species found in fresh water or water-
filled treeholes. Large osmoregulatory organs in the form of genital papillae also occur in an as-yet undescribed species of Histio stomatidae that shares the Heliconia bract habitat with *F. heliconiae* (Fashing 2004). The chemical composition of *Heliconia* bract fluid has not been studied but likely is quite different from that of fresh water or treehole water since it is produced...
by the plant and not the result of rain water (Bronstein 1986). Alternatively, the large axillary organs of *F. heliconiae* might simply reflect its evolutionary past, given that it is in the same genus as *F. lawrencei*, a species with extremely large axillary organs that inhabits sap fluxes and the moist subcortical areas of trees (Fig. 11).

Several authors (Hayashi et al. 2010, 2011) consider sap flux to be a phytotelm habitat, albeit very different from other phytotelmata. Sap flux is a viscous medium that contains high concentrations of sugar and other chemicals, and it is present for only a limited time during the year (Fashing 2008). During times with little or no sap flux, *F. lawrencei* adults, tritonymphs, and protonymphs can still be found in areas of the tree bark that are extremely wet due to rain or that simply are moist with no free water (personal observation). *Fusohericia lawrencei* is therefore adapted for a variety of osmoregulatory demands, perhaps explaining their extremely large axillary organs. Members of the genus *Hericia* inhabit sap flux also but have less extensive axillary organs than do *F. lawrencei* (Figs. 1, 2, 11). This difference may be reflect the response of *Hericia* spp. to lack of sap flux flow or drying, given that non-deutonymphal stages are found only in active sap flux. Periods with no sap flux flow yield only non-phoretic *Hericia* deutonymphs, an instar that is adapted to withstand adversity (Fashing 1991, 2008; Hayashi et al. 2010). The axillary organs of *Hericia* spp. vary in shape and size (Figs. 1, 2, 11), again potentially mirroring habitat differences. Species of *Hericia* are often specialists on a single species or genus of tree, and osmoregulatory demand is dependent on fluid chemistry, which in turn is dependent on tree species.

The smallest axillary organs are found on species that are considered to be terrestrial rather than aquatic, such as *Terraphagus antipodus* Clark and Andrews (collected from soil in petrel burrows) and members of the genus *Neohyadesia* (e.g., *N. microtricha* Marshall, O'Connor, and Pugh, which resides under beach boulders; *N. signyi* Hughes and Goodman, which dwells in flowering halophiles; *N. minor* Clark and Andrews, which is collected from algal wrack). The axillary organs in these species are restricted to the dorsum and are extremely reduced in size (Figs. 11, 12). In fact, Clarke and Andrews (2012) have suggested that the axillary organs of *T. antipodus* are vestigial.

Our present knowledge of algophagid biology and morphology reveals that exceptions to expected relationships between axillary organ size and habitat do occur. *Neohyadesia signyi* appears to have terrestrial-type axillary organs (Fig. 12) but has been collected from fresh to brackish pools (Hughes and Goodman 1969). Two species with axillary organs similar to those of aquatic species are described by Marshall et al. (2003) to be terrestrial according to morphometric analyses and the habitat from which they were collected: *A. brachytarsus* Marshall, O’Connor, and Pugh (collected from soil and decaying leaves) and *A. macrolithus* Marshall, O’Connor, and Pugh (collected under sublittoral boulders) (Fig. 11). According to the results of their analysis, the same authors (Marshall et al. 2003) consider *A. laticollaris* Fain, a species with freshwater-type axillary organs (Fig. 12), to be aquatic (see discussion of aquatic species above) despite its collection from flowering plants on eroded soil (Fain 1974). In addition, axillary organ size suggests that both *A. brachytarsus* and *A. macrolithus* utilize aquatic as well as terrestrial habitats. Furthermore, Marshall et al. (2003) reported a presumed new subspecies of *A. semicollaris* Fain collected from rocky shore supralittoral pools to be semi-terrestrial but then
included it in their “aquatic” category. Their specimens of *A. semicollaris* have axillary organs similar to those of aquatic species (i.e., extending both dorsally and ventrally), whereas the mites in the original species description have axillary organs only dorsally (Fig. 12) and were collected...
from freshwater, flowering plants from eroded dry soil, from moss on both eroded dry and moist soil, and from animal burrows, nests, and guano (Fain 1974). Therefore *A. semicollaris* is another species that utilizes both terrestrial and aquatic habits.

In summary, the results of a literature survey clearly indicate that some algophagid species are not habitat-specific and therefore have evolved axillary organs capable of functioning in terrestrial, semi-aquatic, and aquatic habitats or a combination thereof. Such species likely would require extensive axillary organs that can cope with a freshwater, hypoosmotic environment as well as adaptations that can meet the demands of brackish water and a terrestrial habitat.

A major adaptive radiation of algophagid species is evident in the sub-Antarctic, but representative species have not been collected extensively, especially when one considers the diversity of habitats. To a lesser extent, this is also true for many algophagid species from other parts of the world. A more thorough knowledge of algophagid ecology as well as fine-structural studies of the axillary organs of species from different habitats are necessary to establish a firm correlation between habitat and axillary organ size. However, our present knowledge supports at least a weak to moderate correlation between the two: species that inhabit fresh water have large axillary organs, whereas the axillary organs of those that are completely terrestrial are small.

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Appendix 1. List of species in the Algophagidae including habitat and collection locality, as well as method for determining size of axillary organ (literature, slide-mounted specimens, or both).

*Algophagopsis pneumatica* Fain and Johnston. Recorded from the Kings River in central California, USA (Fain and Johnston 1975). Both.

*Algophagopsis near pneumatica* (undescribed species). Recorded from deep in Crater Lake, Oregon, USA. Slide-mounted specimens.

*Algophagus antarcticus* Hughes. Recorded from sub-Antarctic freshwater pools at Heard Island (Hughes 1955) and Prince Edward Islands (Marshall et al. 2003). Also recorded from flowering plants, moss and vegetation debris on eroded dry and moist soil on sub-Antarctic islands (Fain 1974). Literature.

*Algophagus brachytarsus* Marshall, O'Connor and Pugh. Recorded from soil and decaying leaves in the sub-Antarctic on the Prince Edward Islands (Marshall et al. 2003). Literature.

*Algophagus laticollaris* Fain. Recorded from a sub-Antarctic man-made freshwater reservoir in the Prince Edward Islands (Marshall et al. 2003) and from flowering plants on eroded soil on islands in the sub-Antarctic (Fain 1974). Literature.

*Algophagus macrolithus* Marshall, O'Connor and Pugh. Recorded from supralittoral boulders on the Prince Edward Islands in the sub-Antarctic (Marshall et al. 2003). Literature.

*Algophagus pennsylvanicus* Fashing and Wiseman. Recorded from water-filled treeholes in eastern USA (Fashing and Wiseman 1980). Both. (Note - Marshall et al. (2003) consider this species to be a new genus).

*Algophagus semicollaris* Fain. Recorded from freshwater and terrestrial algae, vegetation debris and halophile humus. Flowering plants on eroded dry soil and eroded humid soil, moss on dry eroded soil and moist eroded soil, animal burrows and nests and guano from sub-Antarctic islands (Fain 1974). Also recorded from rocky shore supralittoral pools in the sub-Antarctic on the Prince Edward Islands (Marshall et al. 2003). Literature. (Note - Marshall et al. (2003) consider their specimens to be a new subspecies).

*Fusohericia heliconiae* Fashing and Glist. Recorded from the fluid-filled bracts of *Heliconia imbricata* (Kuntze) Baker in Costa Rica (Fashing and Glist 2012). Both.

*Fusohericia incredibilis* Vitzthum. Recorded from strongly fermenting fluid in a cut-off bamboo cane in Sumatra (Vitzthum 1931). Literature. (Note - The axillary organs are not included in the illustrations).

*Fusohericia lawrencii* Baker and Crosley. Recorded from sap flux and the moist subcortical areas of trees (personal observation) and from an artificial treehole (Baker and Crosley 1964) in the eastern USA. Both.

*Hericia fermentationis* Vitzthum. Recorded from strongly fermenting fluid in a cut-off bamboo cane in Sumatra (Vitzthum 1931). (Note - The axillary organs are not included in the illustrations).

*Hericia georgei* Michael (1903). Recorded from sap flux on trees in England, Finland, France, Russia and Sweden (Michael
1903, Samšiňák 1972). Literature.

Hericia hericia (Robin). Recorded from sap flux on trees in France (Robin, M. C. 1868). Literature.

Hericia janehenleyi Fashing. Recorded from sap flux on oak trees (Quercus sp.) in eastern USA (Fashing 2008). Both.

Hericia paradoxa Türk and Türk. Known only from the phoretic deutonymph (Türk, E. & F. Türk 1957).

Hericia sanukiensis Fashing and Ocabe. Recorded from sap flux on oak trees in Japan (Fashing and Ocabe 2006). Both.

Hericia undescribed species. Recorded from sap flux in England. Slide mounted specimens.

Lamingtonacarus oreillyorum Fashing, O'Connor and Kitching. Recorded from water-filled treeholes in Lamington National Park, Queensland, Australia (Fashing et al. 2000). Both.

Lamingtonacarus posidonis Fashing, O'Connor and Kitching Recorded from water-filled treeholes in Lamington National Park, Queensland, Australia (Fashing et al. 2000). Both.

Neohyadesia microtricha Marshall, O'Connor and Pugh. Recorded from sediments under beach boulders on Marion Island, sub-Antarctic (Marshall et al. 2001). Literature.

Neohyadesia minor Clark and Andrews. Recorded from algal wrack on a sub-Antarctic island (Clark and Andrews 2012). Literature.

Neohyadesia signyi Hughes and Goodman. Recorded from fresh to brackish pools on Signy Island, sub-Antarctic (Hughes and Goodman 1969) and from flowering halophiles on Kerguelen Island, sub-Antarctic (Fain 1974.). Literature.

Neohyadesia undescribed species – Recorded from mud in a penguin rookery on sub-Antarctic islands (Clark and Andrews 2012). (Note – illustrations not provided).

Prohericia longipes O'Connor and Moser. Known only from the phoretic deutonymph (O'Connor and Moser 1985).

Terraphagus antipodus Clark and Andrews. Recorded from soil in seabird burrows on Antipodes Islands, New Zealand (Clark and Andrews 2012). Literature.

Thalassophagacarus faime de la Cruz and Socarras. Recorded from the remains of semi-submerged turtle grass deposited by the waves on the beach in Cuba (de la Cruz and Socarras 1992). Although placed in the Algophagidae by the authors, this species is actually in the family Winterschmidtiidae and a member of the genus Neocalvolia (Reviewer comment).