

**DIVERSITY OF STYLOSTOME STRUCTURE AMONG PARASITIC LARVAL WATER MITES
(PROSTIGMATA: HYDRACHNIDA)**

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ABSTRACT - Stylostomes, or feeding tubes, result from secretions into hosts by parasitic larval water mites. This structure is generally destroyed when preserving and slide-mounting specimens and hence has largely been ignored by past researchers. I surveyed stylostome structure in species representing 15 genera, 12 families, and 5 superfamilies. Most early-derivative water mite superfamilies have multiply-branched stylostomes (Eylaoidea, Hydrachnoidea, Hydryphantoidea) whereas later-derived water mite superfamilies (Hygrobatoidea, Arrenuroidea) have unbranched, closed-ended stylostomes. Many genera of the latter group have long, thin stylostomes, presumably the plesiotypic condition within that clade, while some have shortened conical, disc-shaped or spherical structures. The total absence of stylostomes among sampled species of lebertioid genera is curious given that this superfamily is allied with Hygrobatoidea and Arrenuroidea based upon a multitude of morphological and life-history characteristics. Stylostomes were also absent from species of two genera of Hydryphantoidea, but have been recorded from other hydryphantoid species. There was considerable variability in stylostome morphology within *Arrenurus* and *Piona* and it appears that this structure could be valuable for identifying species and species groups in these genera. Immune responses by hosts to stylostomes were fairly common. Given the current interest in ecological immunity, insect /water mite relationships provide a convenient opportunity for population-level studies on immune responses.

Keywords - Hydrachnida, water mite, stylostome, parasitism, melanotic encapsulation.

INTRODUCTION

Stylostomes, or feeding tubes, are enigmatic acellular structures associated with larval parasitengone mites. There has been much speculation as to their function and origin: they stain with Alcian Blue which indicates presence of acid mucopolysaccharides, they lack chitin, and many stylostomes are without any external openings (Åbro, 1979, 1982; Lanciani, 1979; Redmond and Hochberg, 1981). Larval parasitengones are fluid-feeders, apparently feeding from liquified host tissue and haemolymph (Pflügfelder, 1970; Åbro, 1979; Voight, 1970). While stylostomes of trombiculid larvae are open-ended and could function much like a drinking straw, closed-ended stylostomes could only act by passive diffusion given that active transport would

require cells with mitochondria. There has been much debate as to whether stylostomes are organs of the mite, salivary secretions of the mite, reactions by the host, or a combination of the latter two, but current consensus is that they result from salivary secretions (Davids, 1973; Åbro, 1979; Redmond and Hochberg, 1981; Smith, 1988; Wohltmann, 2001).

There are a number of references to stylostomes in the literature. Many deal with chiggers (Trombiculidae), there are a few papers describing trombiculid stylostomes, while papers referring to stylostomes of water mites almost exclusively involve species of *Arrenurus* and *Hydrachna* (e.g., see reviews by Åbro, 1979; Davids, 1973; Smith, 1988; Wohltmann, 2001). Stylostomes of these taxa are significantly different in form: unbranched and open-ended with chiggers, unbranched closed-ended

sacs for *Arrenurus*, and multiply-branched root-like stylostomes for *Hydrachna* and trombidids. Given that these records represent only four families and three distantly related superfamilies of Parasitengona, there are conspicuous gaps in available knowledge.

The goal of this study was to conduct an extensive survey of stylostome form among species representing a diversity of genera, families, and superfamilies of water mites. While most genera and families of water mites are relatively stable and believed to be holophyletic, the relationships among superfamilies and within at least 5 of the superfamilies are questionable (Smith et al., 2001). Perhaps stylostome morphology can add useful information for resolving relationships among taxa. Further, a survey of stylostome form may illuminate differences among taxa in terms of host/parasite interactions.

MATERIALS AND METHODS

This survey was conducted at the Queens University Biological Station (QUBS), located ca. 2 km west of Chaffeys Lock, Ontario, Canada (44°34' N x 79°15' W). Chironomid midges and caddisflies were collected at the station itself, attracted to blacklights between 10:00 pm and midnight. A cordless car vacuum was used to sample insects from a white sheet located behind the light source, and the vacuum's collection chamber was then placed in a freezer until the insects were sorted. *Chaoborus* midges were collected by aerial net from evening mating swarms, vacuumed from the net, then also frozen. Collections were later thawed and a dissecting microscope was used to sort out parasitized hosts and to do preliminary identifications. *Aedes* spp. mosquitoes parasitized with *Thyas barbigera* were collected individually with a straight-barrel aspirator as they landed on the author. Parasitized odonates were collected by aerial net from various sites on the extensive QUBS property (location corresponding to each specimen is given in results). Wings, legs and heads were removed before clearing. To obtain stylostomes of *Arrenurus angustilimbatus*, *Aedes aegypti* mosquitoes were parasitized by mites in the laboratory. Adult *A. angustilimbatus* were collected in Algonquin Park, Ontario, Canada (45° 33' N 78° 37' W) at a boggy pond and seepage area located on the south side of Hwy 60 at km 22, just east of the Little Madawaska River. Adult mites were kept alive until they laid eggs. Pupal mosquitoes were exposed to resultant larval mites, and about 24 hrs after emergence, parasitized adult hosts were put in clearing solution.

All specimens were placed individually into glass

shell vials (4.5 cm tall X 1.5 cm diameter) and cleared in Andre's Solution (chloral hydrate, glacial acetic acid and water, 1:1:1 by weight), for 24 to 72 hours. Cleared host insects were transferred into a drop of glycerine on a microscope slide, dissected, transferred to a glycerine drop on new slide, and a coverslip was added. Images of specimens were taken from a video surveillance camera attached to a Wild M20 interference phase contrast microscope, via Snappy image capture hardware and software (Play Inc., 1996). Images of a slide micrometer were used for calibration. Measurements of stylostomes were made using SigmaScan™ v. 4.0 software (SPSS Inc., 1998).

RESULTS

Hosts parasitized by larvae representing at least 15 genera, 12 families, and 5 superfamilies were examined. When possible, multiple specimens of each taxon were examined. Results are presented in taxonomic order.

Hydryphantoidea - Species representing two genera and two families were encountered and in neither case were there any associated stylostomes. Larval *Hydrodroma* sp. (Hydrodromidae) were found parasitizing *Chaoborus* sp. (Diptera: Chaoboridae), typically attached to the anterior and lateral regions of the host's thorax. Twenty parasitized hosts representing different stages of larval engorgement were examined. Four *Aedes* spp. mosquitoes (Diptera: Culicidae) parasitized by *Thyas barbigera* (Hydryphantidae) were carefully cleared and dissected but no stylostomes were present. The larval mites were attached to the posterior surface of the thorax under the junction with the abdomen.

Eylaoidea - *Limnochares americana* (Limnocharidae) parasitizing the lateral and ventral thoracic surfaces of *Leucorrhinia frigida* (Odonata: Libellulidae) were collected from Hebert Bog. It was exceedingly difficult to prepare good mounts of stylostomes because of the thick cuticle and dense thoracic musculature of the host. Stylostomes were multiply-branched and the example illustrated in figure 1 is 81.5 µm long X 54.1 µm wide. *Limnochares aquatica* attached to the dorsal surface of 4th instar *Gerris comatus* (Hemiptera: Gerridae; Stonehouse Creek, July 22, 1998) were also dissected and similar stylostomes were examined. In this case, a black melanotic deposit had formed on the host's cuticle at the puncture wound. Stylostomes of *L. aquatica* were slightly smaller, the one example measured was 54.1 µm long X 42.9 µm wide, and the melanotic ring was 25.7 µm X 31.2 µm.

Lebertioidea - Waters of the region surveyed in Ontario were predominantly lentic, and relatively few species of Lebertioidea were encountered. About 12 specimens of midge parasitized by Oxidae were cleared and dissected but there were no stylostomes discovered. The mites involved were species of *Oxus* and/or *Frontipoda*: there is no reliable way to distinguish between genera for larvae of these species. The mites were attached to the anterolateral regions of the hosts' thoraxes. Four midges parasitized by larval *Limnesia* sp. (Limnesiidae) were also examined but again, no stylostomes were encountered.

Hygrobatoidae - Stylostomes of *Atractides* (Hygrobatidae) were reasonably commonly encountered in the thoraxes of midges (Figs. 2, 3). These were long, thin structures, frequently extending through several abdominal segments of the host. One representative stylostome was measured as 435.9 μm long and averaged 8.3 μm wide, with very little width variation along its length (range 6.7 - 10.2 μm). The surface of the feeding tube was not smooth, but textured, appearing at lower magnifications as if it had rings around its diameter. On several hosts there were black melanotic spots at the mite's attachment site and in one case the stylostome was encapsulated for much of its length (Fig. 3).

Species representing three genera of Unionicolidae were examined. *Neumania* spp. were the most common; the stylostomes were very long and thin (Fig. 4), with an elliptical widened tip (referred to in the stylostome literature as a tome, e.g., Lanciani and Smith 1989). Three stylostomes measured were 574.3, 677.9, and 694.6 μm long, with the tome representing 93.83, 130.6, and 41.2 μm of the length (respectively). For one stylostome, the tome was a maximum of 25.1 μm wide while the rest of the stylostome averaged 7.7 μm wide (6.7 - 8.6 μm). In some cases, the host's body wall was strongly melanized at the point of mite attachment (Fig. 4). The stylostome appeared to have a smooth texture with some wrinkling - presumably the feeding tube was collapsed in these preparations. Stylostomes of *Unionicola* sp. (Fig. 5) and *Koenikea* sp. (Fig. 6) were much smaller, much less than the length of a mite. In the former case, an example measured was 205.2 μm long and ranging from 8.8 - 40.7 μm wide, with a well defined bulb-like tome constituting 73.0 μm of the length. The stylostome of *Unionicola* sp. was quite smooth in appearance. The two *Koenikea* sp. stylostomes measured were 127.7 and 88.5 μm long, with one being 10.4 - 25.3 μm wide. These stylostomes were much more gradually tapered than those of *Unionicola* sp., and except for the specimen in figure 6, the stylostomes again appeared to

be smooth and unwrinkled.

Feeding tubes of *Albia* sp. (Aturidae) were recovered from parasitized *Tranodes* sp. caddisflies. They were among the longest stylostomes encountered, with total lengths of 1613.7 and 1423.9 μm (Fig. 7), but were not noticeably wider than other stylostomes, averaging 22.1 and 22.9 μm , respectively (ranges 10.7 - 35.5, 12.0 - 33.7 μm , respectively). The stylostomes tapered very gradually over their length, with no defined tome region, and the exterior surfaces had a lightly rippled appearance.

Among the Pionidae, stylostomes were found for species of the genera *Piona* and *Forelia*. Different species of *Piona* had stylostomes of different lengths (Figs. 8, 9) but similar overall appearance. The surface of the feeding tube was very smooth and even. While there was no well-defined tome region, the apical end was widened and spatulate. One *Piona* species had an extremely long stylostome, measuring 1576.4 μm (Fig. 9) whereas the feeding tube of the other species was 1022.5 and 886.5 μm for the two specimens measured (Fig. 8). Ranges of widths for these stylostomes were 14.3 - 64.0, 15.1 - 50.7, 19.7 - 68.2 μm respectively. In at least one case the feeding tube had been encapsulated by the host's immune response (Fig. 10). The stylostome of *Forelia* sp. (Fig. 11) was very different in shape from *Piona* spp.: it was a flattened, circular disk (diameter 109.8 - 140.9 μm) in contrast to the long, thin form associated with *Piona* species.

Arrenuroidea - The stylostomes of many Arrenuroidea were long and thin, with a wrinkled or folded appearance, looking reminiscent of the folds of an accordion. There was usually a well-defined apical tome. One parasitized orthoclad midge yielded two stylostomes of *Mideopsis* sp. (Mideopsidae, Fig. 12) which were 706.9 and 642.1 μm long and attached to the intersegmental membrane joining the host's head and thorax. Several specimens of *Krendowskia similis* (Krendowskiidae) were also discovered, parasitizing the ventral thorax region of *Procladius* spp. midges. Much shorter stylostomes were associated with *K. similis* than with *Mideopsis* sp., being 202.1 and 182.2 μm long (Fig. 13), with a well defined tome of 83.2 and 44.3 μm respectively. The width of the main tube of the stylostomes ranged from 39.1 - 46.4 and 30.4 - 36.5 μm for the two specimens measured, with tomes measuring 64.3 and 36.4 μm wide.

The greatest number of species and diversity of stylostome form were observed in the genus *Arremurus* (Arrenuridae). Many species had long, thin stylostomes with a well-defined tome, while feeding tubes of different

species or species groups within the subgenus *Arrenurus* differed morphologically. *Arrenurus (Truncaturus) angustilimbatus* (Fig. 14) from experimental infections of *Aedes aegypti* had stylostomes measuring 879.4 and 1000.1 μm long and ranging 8.4 - 30.5 and 11.0 - 30.2 μm wide, with the tomes being 88.4 and 65.1 μm long and ranging 24.3 - 30.5 and 25.6 - 28.2 μm wide. Feeding tubes of *Arrenurus (Megaluracarus) birgei* from *Ablebesmyia* sp. midges were similar, with the one measured example being 1155.3 μm long, ranging in width from 17.9 - 26.8 μm , with a poorly-defined tome (Fig. 15). *Arrenurus (Megaluracarus) cardiacus* had stylostomes of similar form and size. The variety seen within the subgenus *Arrenurus* was even evident within one host (Fig. 16): preparations from the abdomen of *Ischnura verticalis* damselflies (Telephone Bay, Lake Opinicon) often yielded both *A. (Arrenurus) pseudosuperior*, which had the standard linear stylostome form, and *A. (Arrenurus) major*, which had a cone-shaped stylostome that superficially looked like a light bulb. In dimensions, the stylostome of *A. pseudosuperior* was 364.0 μm long and ranged from 11.9 - 31.2 μm wide, whereas that of *A. major* was 131.4 μm long and from 24.0 - 72.5 μm wide. Note that there was an immune response around the base of the stylostome of *A. major* but none around that of *A. pseudosuperior*. *Arrenurus (Arrenurus) compactilis* collected from the damselfly *Enallagma ebrium* (Two Island Lake) is in the *americanus* species group as is *A. major*, and had a similarly-shaped feeding tube (Fig. 17): it was 293.7 μm long and varied from 19.7 - 103.6 μm wide, looking like an elongate and larger version of the *A. major* stylostome. Two species were found parasitizing *Libellula luctuosa* dragonflies (Lindsay Lake Road): *A. (Arrenurus) pinguisomus* (Fig. 18), which secreted a thick, short, tubular stylostome (371.6 μm long, 19.5 - 36.0 μm wide) into the lateral surfaces of the thorax, and *A. (Arrenurus) fissicornis* (Fig. 19) which secreted a spherical stylostome (135.6 - 161.4 μm and 128.0 - 173.0 μm for two examples measured) into the ventral surface of the abdomen. The feeding tube form seen with *A. fissicornis* was also associated with *A. reflexus* parasitic on the ventral abdominal surface of *Leucorrhinia intacta* (Barb's Marsh), except that the sphere was considerably larger (258.2 - 311.0 μm). Notable variation was encountered for stylostomes produced by *A. (Arrenurus) planus* (Fig. 20; Yezerinac's Pond): the feeding tube was a sessile sphere when formed in *Sympetrum obtusum* and *S. internum* dragonflies but a stalked sphere when formed in *S. vicinum* dragonflies and *Lestes* spp. damselflies. Further, two different types of immune response were

encountered: a melanotic deposit at the base and along the length of the stylostome in some *Lestes* spp. (previously reported in Yourth et al. 2001) and a clustering of haemocytes and collapsed stylostome in *S. internum* (previously reported in Forbes et al. 1999). There appeared to be a brownish cluster of haemocytes at the base of the stylostome in *S. internum*, the stylostome was collapsed, and the mite was dead. The attachment site of stylostomes in *S. vicinum* and *L. dryas* had a black melanotic spot and the mites were alive.

DISCUSSION

Previously published work suggested that there were at least 3 general forms of stylostomes among the water mites. Two types encountered in my survey were the multiply-branched dendritic systems and the unbranched, closed-ended structures. Gledhill (1985) presented a figure of an unidentified pionid larva with an unbranched stylostome that appeared to have an open, fan-shaped distal end. While he made reference to the presence of the stylostome, Gledhill did not describe its form. I did not encounter any similar stylostome; either there is nothing comparable among the pionid genera surveyed above or I was wrong in interpreting that the stylostome in Gledhill's figure was open-ended (see Smith, 1988; Smith et al., 2001).

Multiply-branched stylostomes have now been reported from *Limnochares americana* and *Limnochares aquatica*. Their stylostomes were very similar to those of *Hydrachna* (Davids 1973) and *Trombidium holosericeum* (Wohltmann, 2001) although smaller. This size difference could reflect longer duration of parasitic association or greater degree of larval engorgement in the case of *Hydrachna* spp. vs. *Limnochares* spp., but duration and engorgement are similar for larval trombidids and *Limnochares* spp. (e.g., see Wohltmann, 2001 for data on trombidids). The records of multiply-branched stylostomes associated with Hydrachnoidea, various trombidids (*Allothrombium*, *Trombidium*: Wohltmann, 2001), several hydrophantoidea genera (*Hydryphantes*, *Panisellus*: Wohltmann, 2001), and two genera of Eylaoidea (*Limnochares*: above; *Rhyncholimnochares*: Smith, 1988) suggests that this is the plesiotypic form for early-derivative water mites and their terrestrial relatives. The stylostome of Trombiculidae is quite different, being open-ended and unbranched (see Voight, 1970; reviews in Davids, 1973 and Wohltmann, 2001) but it is probable that this divergent structure is apotypic and related to trombiculids having shifted to parasitizing vertebrate hosts.

It is ambiguous whether these multiply-branched stylostomes are open- or closed-ended. Davids (1973) raised the controversy when reviewing the literature on both aquatic and terrestrial parasitengonines (including Trombiculidae). Apparently Pflügefelder (1950) had assumed that multiply-branched stylostomes of an unidentified trombidid were open-ended (Davids 1973). Davids (1973) did not clearly state an opinion: he reasoned that the stylostome could be dissolved and reformed at the margins, but he also qualified that the stylostome of *Hydrachna conjecta* may be closed over winter months when larval growth (and presumably, parasitic feeding) is minimal. My interpretation of the literature had been that multiply-branched stylostomes are open-ended (Smith, 1988; Smith et al., 2001; also see Redmond and Hochberg, 1981) but others have stated that they are not (e.g., Wohltmann, 2001). I could not resolve an opening at the end of the branches in stylostomes of *Limnochares* spp.: the openings are either too small to be seen with light microscopy or there are no openings.

Unbranched closed-ended stylostomes were associated with a diversity of species of Hygrobatoida and Arrenuroidea. Stylostome size varied greatly, from lengths of 1.5 mm (*Albia* sp., *Piona* sp.), much longer than the larval mite and representing a considerable proportion of the host's body length, to less than 90 µm, much shorter than the mite's length. Diameter varied from a maximum of over 300 µm in spherical stylostomes (*Arrenurus reflexus*) and over 60 µm in some linear stylostomes (*Piona* sp.) down to a maximum of about 10 µm (*Atractides* sp., *Unionicola* sp.). Larger stylostomes were found in larger host species (e.g., *Trianodes* sp. caddisflies parasitized by *Albia* sp., large Chironominae parasitized by *Piona* sp.) which leads to speculation that size is in part an adaptation to the size of the host. Hosts with reasonably short parasitic associations (e.g., *Unionicola* sp.) had very small stylostomes: possibly size in part reflects duration of association. However, there were enough examples where these patterns did not fit that it would be speculative to draw conclusions, other than host size and duration of association may potentially set maximal limits on stylostome size. Linear arrenuroid stylostomes typically had large numbers of cross-folds, appearing corrugated, usually with a well-defined bulb or tome, whereas *Piona* spp. had very smooth-textured stylostomes, gradually widened to a rounded apex. While species-specific patterns were quite clear, it would be difficult to characterize structure associated with genera in most cases. One exception is *Forelia* sp. in which these stylostomes were conspicuously disc-shaped and

unlike any others, however it remains to be seen whether this is consistent among congeneric species. Given that a large number of species in genera scattered throughout the Hygrobatoida + Arrenuroidea had reasonably long and thin closed-ended stylostomes, this is presumably the plesiotypic condition for these superfamilies.

Differences in stylostome structure among species within the genera *Arrenurus* and *Piona* indicate that these structures may be useful in distinguishing among species or species groups. This could be especially useful in parasitological ecology where stylostomes could be used to determine intensity of past parasitism and species involved even after the mites had departed (e.g., Lanciani, 1979). Species of the subgenera *Truncaturus* and *Megahuracarus* generally have the long, accordion-pleated tube which may have a bulblike tome on the apex, although there are exceptions (Lanciani and Smith, 1989). This form of stylostome was also found associated with some *Arrenurus* (*Arrenurus*) species in the *superior* species group (e.g., *A. pseudosuperior*), while the *reflexus* group has spherical stylostomes and many of the *americanus* group apparently have cone-shaped or short elliptical stylostomes. Generally, within a mite species there is reasonable constancy in stylostome form regardless of host species (Lanciani and Smith 1989). However, there was noteworthy variation in *A. planus*: stylostomes in *Sympetrum vicinum* and *Lestes* spp. consisted of a large spherical tome attached to the host's body wall with a long, thin, pleated tube, whereas stylostomes in *S. obtusum* and *S. internum* lacked the pleated tube. It is clear that for using stylostomes to identify past history of parasitism in ecological studies, consistency of form among host species would need to be confirmed.

It was fairly common to see some form of host's immune response to stylostomes. These ranged from blackened rings on the host's body wall around the puncture wound (e.g., *Neumania* sp., *Arrenurus major*) to partial or total encapsulation of the length of the stylostome (e.g., *Piona* sp., *Atractides* sp., *Arrenurus* spp.). This has been reported previously, characteristic among certain host/parasite combinations (e.g., Lanciani and Smith, 1989; Forbes et al., 1999; Yourth et al., 2001). Immune responses to stylostomes can occur in two forms: 1) melanotic encapsulation, which is quite conspicuous because of the black deposits (Åbro, 1982; Lanciani and Smith, 1989; Yourth et al., 2001) and 2) apparent haemocyte clusters at the base of the stylostome, apparently causing collapse of the stylostome (Forbes et al., 1999). Presumably the sheaths of densely black melanin attracted the attention of early researchers to

feeding tubes (e.g., Marshall and Staley, 1929; Brug, 1932; Feng and Hoeppli, 1933; Miyazaki, 1936; see discussion by Åbro, 1979). The recent flurry of research in the developing field of ecological immunology could rekindle interest in host responses to stylostomes. Water mite/insect systems have considerable potential for studies in this field because of several important factors: 1) large sample sizes needed in ecological studies are easily obtained (e.g., Forbes et al., 1999; Yourth et al., 2001, 2002), 2) some host species mount an immune response to a mite species while other host species do not (Lanciani and Smith, 1989; Yourth et al., 2001), 3) some host species react to one mite species but not to other mite species (Lanciani and Smith, 1989), 4) degree of response among individuals within a host/parasite species combination may vary greatly under different conditions (Yourth et al., 2002).

The absence of stylostomes in some host/parasite combinations is both perplexing and intriguing. While I did not see any stylostomes associated with *Hydrodroma* sp. and *Thyas barbiger*a, other authors have observed these structures with other hydrophantoid mites (mentioned above). I am confident that if stylostomes had been present they would not have been missed given the number of specimens dissected and intensity of effort. Mullen (1977) also looked for stylostomes in mosquitoes parasitized by *T. barbiger*a and concluded that they were not produced by this mite. The lack of stylostomes in midges parasitized by *Oxus/Fontipoda* spp. and *Limnesia* spp. suggests that possibly lebertioid species do not produce stylostomes but it would be premature to draw this conclusion before a greater diversity of genera have been sampled. If a stylostome plays an instrumental role in feeding then it raises the question, how do mites of these taxa feed without them - what is different? Lebertioidea includes the Sperchontidae, which are believed to be most similar to the hypothetical ancestor between early-derivative superfamilies that contain at least some species that produce a highly-branched, rootlike stylostome and the later-derived superfamilies containing species that produce a simple, blind-ended stylostome. This suggests that either an ancestor of the Lebertioidea lost the production of a stylostome, or that the stylostome production in two groups of water mites were separately evolved traits, possibly explaining why there are two distinct morphological forms (Smith et al., 2001).

Many genera and families need to be investigated for the structure of any associated stylostomes. While morphology does not appear to shed much light on relationships among genera and families, the presence or

absence and two general forms may be useful for inferring affinities among superfamilies. The physiological role of the stylostome has yet to be investigated; presumably they play some role in selective filtration or diffusion of compounds into the mite. Presently, the most promising avenue of study is the differential immune response among individuals and species of host to the presence of mite stylostomes and the ecological consequences of this variation.

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