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THE INITIAL STYLOSTOME FORMATION BY PARASITIC LARVAE OF THE WATER-MITE GENUS ARRENURUS ON ZYGOPTERAN IMAGINES

BY Arnold ÅBRO*

ABSTRACT: Arrenurid water-mite larvae, ectoparasitic on zygopteran imagines (Odonata), attach themselves to the host’s cuticle and pierce it with the cheliceral blades to obtain the host’s tissue fluids. Promptly after anchoring in feeding position, secretions of the larval mite are forced into the host beneath the attachment site, where a subcuticular vesicle, bounded by a delicate gelatinous membrane, appears in the epidermis layer. The vesicle constitutes a local space of thin fluid into which the larva ejects a liquid that rapidly gels and forms a slender resilient blind sac, the stylostome. The vesicle provides a buffer zone for the nascent stylostome, protecting it against vehement defence reaction on the part of the host. The early stylostome undergoes a phase of extreme inflation of the distal thin-walled portion, which is associated with expansion of the primary vesicle. Epidermal cells adjoining the primary vesicle undergo lysis and fuse with the vesicle, transforming it into an epidermal abscess, whose cell juice acts as a pool of nutrient to the larval mite. Initially short, wrinkled and thin-walled, the stylostome increases in size, elongating and remodelling as larval engorgement proceeds. Eventually the stylostome breaks the rim of the abscess, which becomes modified to a melanized sleeve around the origin of the stylostome. When fully formed, the stylostome is mostly lodged in a cleft in the epidermis separated from the haemocoele and deeper tissues by the sheet of epidermal basal lamina. The delicate meshwork of the basal lamina, closely applied to the outside of the stylostome, seems to prevent haemocytic reactions to the stylostome in later developmental stages.

RÉSUMÉ: Les larves d’Arrenurides, ectoparasites sur les imagos de Zygoptères (Odonata), s’attachent à la cuticule de leur hôte et la transpercent de leurs lames chélicériennes pour atteindre les fluides tissulaires. Aussitôt après ancrage en position de nutrition, la larve introduit de force des sécrétions au-dessous du site d’attache sur l’hôte où apparaît dans la couche épidermique une vésicule subcuticulaire fermée par une délicate membrane gelatineuse. La vésicule constitue un espace local de liquide fin dans lequel la larve expulse un liquide qui se prend rapidement en gelatine et rejaillit en formant un sac aveugle, élancé, le stylostome. La vésicule fournit une zone tampon au stylostome en formation, le protégeant des véhémentes réactions de défense de l’hôte. Le stylostome nouveau entreprend

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une phase de gonflement extrême de sa portion distale à fines parois, qui s'associe à l'expansion de la vésicule primaire. Les cellules épidérmiques attenantes à la vésicule primaire entrent en lyse et fusionnent avec la vésicule, la transformant en un abcès épidémique dont le jus cellulaire joue le rôle d'un réservoir alimentaire pour la larve. Initialement court, plissé et à parois fines, le stylostome augmente de taille, s'allongeant et se remodelant au fur et à mesure que se poursuit l'engorgement larvaire. Éventuellement le stylostome peut rompre les parois de l'abcès qui se trouve transformé en une manche mélanisée entourant le départ du stylostome. Une fois complètement formé, le stylostome est essentiellement logé dans une fente de l'épiderme, séparée de l'hémocele et des tissus profonds par le feuillet de la lamina basalis épidémique. Le délicat filet de la lamina basalis, étroitement appliqué à la paroi externe du stylostome, semble prévenir les réactions hémocytiques au stylostome dans les stades ultérieurs du développement.

**INTRODUCTION**

Water-mite larvae of the genus *Arrenurus* Dugès (Acari, Hydrachnellae), ectoparasitic on zygopteran imagines (Odonata), attach themselves to the host's cuticle and pierce it to obtain the host's tissue fluids. Within the host's epidermis, the larval mite produces a feeding device, the stylostome, a slender gelatinous resilient blind sac (ÅBRO 1979, 1982). During parasitization the larval mite undergoes considerable engorgement. Usually, the larvae remain anchored to the original attachment site throughout their parasitic phase. In the zygopteran species *Enallagma cyathigerum* Charp., the parasitic phase of arrenurids is preceded by a phase of phoresis, with the tiny larval mites resting without feeding on their host to be, then in the terminal naiad stage (ÅBRO 1982). When the naiad leaves the water for ecdysis, the arrenurids remain quietly on the host, but as ecdysis proceeds they become active and move from the naiad skin to the emerging imago to attach themselves to it. Promptly after anchoring in a feeding position, the arrenurid larva starts formation of a stylostome, which develops so quickly that its initial developmental stages were beyond the reach of earlier studies (ÅBRO 1979). The present report deals with the course of events taking place at the attachment site when the host's cuticle is punctured by the larval mite and immediately afterwards during early stylostome formation, and with accompanying reactive alterations in the host up to 24 hours.

**MATERIAL AND METHODS**

*Arrenurus* larvae on the zygopteran *Enallagma cyathigerum*, bred in a tarn near Bergen, Western Norway, were studied at the beginning of the zygopteran flying season.

Fixing fluid was gently injected with a fine hypodermic needle into the body of emerging or teneral zygopteran imagines; excised integumentary fragments with attached larval mites were immersed in larger volumes of the same fixative and kept under vacuum. Fixation was performed in 3 % glutaraldehyde in 0.2 M cacodylate buffer (pH 7.4) and post-fixation in 1 % osmium tetroxide in the same buffer. The specimens were rinsed in the buffer alone, dehydrated through a graded series of ethanol, cleared in propylene oxide, and infiltrated with and embedded in Spurr's medium. Ultrathin sections were cut with a diamond knife on a LKB ultramicrotome, mounted on Formvar and carbon-coated single-hole copper grids, and stained with lead citrate before examination in a Philips EM 300 electron microscope.

Attempts to capture the very early stages of stylostome formation by fixation in the field proved unsuccessful, because of the extreme sensitivity of the zygopterans to any motion or disturbance before and during emergence of the imagines. To facilitate fixation of specimens at the initial stages of stylostome development, terminal naiads of the phoretic phase were collected, brought to the laboratory, and allowed to accli-
matize to aquarium conditions in the dark at 10 ± 1°C before providing emergence/ecdysis through alternating periods of 12 hours of artificial illumination followed by 12 hours in darkness and raising the water temperature to 20 ± 1°C. In the laboratory, hatching of zygopteran imagines and attachment of the larval mites were viewed under a Zeiss surgical operating microscope.

Another difficulty concerns larval mites just anchored to the host’s cuticle, as they tend to detach themselves during the fixation procedure. The larval mites are not readily killed at fixation, since their cuticle seems to resist penetration of the fixing fluids for a fairly long time. With somewhat varying success, spontaneous detachment of mites during fixation could be prevented by rapidly cooling the specimens to 3-5°C and keeping them at that temperature. Ultrathin sectioning of the host’s body wall through areas of preceding attachment sites, without larval mites in feeding position or other landmarks to indicate the exact puncture, is a very troublesome task.

Per definition, emergence of the zygopteran imago is said to begin as ecdysis starts with the naiad arching its back and a split appearing in its skin along the mid-dorsal line of the thorax. In the present study, the age of the stylostome means the time elapsed between beginning of the ecdysis and fixation of the specimen.

Melanin tests were performed according to Åbro (1979).

RESULTS

The Attachment of the Larval Mite

During the phoretic phase, hexapod larval mites usually conceal themselves under the wing-sheaths of the zygopteran naiad; they transfer from the naiad skin to the emerging imago. With their gnathosoma stretched out in front, tiny larval mites could be seen crawling quickly over the ventral thoracic surface of the emerging imago, searching eagerly for a suitable site to which to attach themselves. On the gnathosomal apex, at the position of the larval mouth, a glistening liquid droplet could be recognized. With the pedipalp claws, the larval mite hooks on to the soft resilient host cuticle and then performs a rapid ventrad folding of its gnathosoma, thus securing the palpal grasp with the buccal aperture tightly appressed to the surface of the cuticle. With the cheliceral blades just protruding through the aperture, the mite can start penetrating the cuticle; when fully extended, the blades diverge, reaching the layer of the host’s epidermal cells (Figs. 3, 5, 11, 20). Thus inserted into an oblique narrowing perforating tear in the host’s resilient cuticle, the cheliceral apices point opposite to the palpal claws. Locked in that position the mouthparts constitute an anchor to the larval mite. Between themselves the two protracted cheliceral blades provide for an open passage from the larval pharynx through the perforation to the pool of nutrient. If disturbed soon after attachment, the larval mite detaches itself and searches for another site to hook on to. Normally, however, the larval mite remains attached to one and the same puncture site.

Mature naiads prevented from climbing above the water for ecdysis drown slowly. Larval mites then attach themselves to the soft naiad cuticle exposed at the proximal joints of the legs, at positions where they are normally accustomed to attach themselves to the emerging imago. In a few cases, larval mites have been found in small clusters attached to areas of thin cuticle on apparently sound naiads, certainly without undergoing engorgement.

The Early Development of the Stylostome

On electron micrographs, the earliest preserved stages preceding stylostome development (≤ 10
FIG. 1: Ventral aspect of an unengorged hexapod *Arrenurus* larva with a nascent stylostome adhering to its mouthparts, dissected free from a zygopteran host taken on the emergence site. Whole mount, fresh preparation submersed in insect Ringer's solution and viewed in transmitted light. Age 39 minutes.

FIG. 2: A piece of zygopteran body wall showing a developing stylostome within an intra-epidermal vesicle bounded by a thin melanized rim, here viewed through the cuticle in transmitted light after the larval mite has been dislodged. The arrow is situated between holes in the cuticle caused by the powerful palpal claws and points in the direction of the cheliceral sabres. Note dark melanin deposits at the puncture site. Whole mount, fresh preparation in Ringer's solution. Age 55 minutes. Scale lines: 100 μm (figs. 1, 2).

minutes) show a portion of dense substance discharged just beneath the perforating tear in the host's cuticle (Fig. 3); in the light microscope the substance is usually recognized as a hyaline mass. A less dense, fine granular material very soon replenishes the interior of the dense substance and appears to expand it into a vesicle with the dense substance stretched out to a thin bounding rim or membrane (Figs. 4, 5). Into the rather homogeneous interior of fine granular material appears to be ejected another liquid that becomes condensed just beneath the perforating tear into a distinct lamella at the border against surrounding granular material (Fig. 14). Proximally, at the chelicerae, the lamella becomes strongly plicated, distally smoothed. Thus is produced a slender unbranched thin-walled transversely plicated hose, the stylostome, slightly expanding distally, where it assumes the form of a sausage (Figs. 5; 7 A, B). The proximal plicated part of the tiny coiled stylostome is the oldest one and is laid down initially. Very early during its formation the hose may transitorily be found open at the distal tip, where new lamella is about to condense (Fig. 13). Soon the stylostome appears as an oblong blind-ending sac without any openings; on successive stages it remains closed without any detectable pores or canaliculi. The luminal contents of some such early stylostomes (at 10-15 minutes) may appear dense in the proximal parts and diluted flocculent distally (Fig. 8 A, B); other stylostomes at a similar developmental stage exhibit contents diluted or almost empty-looking proximally and most dense in the distal smooth part (Figs. 5; 7 A, B). The last specimens often exhibit the distal part of the stylostome considerably expanded with a very thin wall (Figs. 9, 10) almost to the distension of the vesicle (Fig. 6), in others it appears strongly compressed (Figs. 11, 12). Section profiles of compressed stylostomes were often associated with a radiating pattern in the
FIG. 3: Vertical section through the feeding site of an arrenurid larval mite. Beneath the puncture in the cuticle, dense substance has been discharged into the host. Age 8 minutes.

FIG. 4: Subcuticularly introduced substance expanded beneath the puncture site. The early traces of a coming stylostome are seen. The hole in the host's cuticle (asterisk) is caused by the large pedipalp claw. Age 9 minutes.

FIG. 5: In the host's epidermis beneath the puncture, a subcuticular vesicle has appeared within which a stylostome is formed. The proximal part of the stylostome exhibits an apparent empty lumen. Age 12 minutes.

FIG. 6: A subcuticular vesicle with a stylostome (expanded state) sectioned through the distal part. Age 15 minutes.

Scale lines: 10 μm (figs. 3-6).

The dense substance originally discharged into the wound also moulds itself around the larval mouthparts. Before this substance becomes solidified and cements the larval mouthparts to the host's body wall, it is possible to dissect the mite and its adhering bare stylostome free from the host tissues (Fig. 1). Excised fragments of the host's body wall with feeding larval mites often reveal the presence of a slender stylostome within a subcuticular vesicle after dislodging the mite (Fig. 2).
Host Reactions to the Developing Stylostome

Melanin is deposited at the bounding rim of the subcuticular vesicle, primarily and most prominently near the inserted chelicerae. On close-up, melanin could be recognized within the fine granular material of the vesicle as smaller or larger patches settled on a fibrillar matrix (Fig. 24); later stages show piles of lamellar melanin added to the interior of the vesicular membrane (Fig. 23). A delicate melanized margin appears in the perforating tear in the host’s cuticle. At the puncture site, the subcuticular epidermis layer with a vesicle will bulge somewhat toward the haemocoel (Fig. 9, 10, 11, 12). The vesicle is separated from the haemocoel or underlying tissues by the subepidermal sheet of connective tissue or base-
FIG. 9: A subcuticular vesicle with section profiles of the distal part of the stylostome (expanded state). The pedipalp claw, sectioned in the sagittal plane, is seen inserted in the host's cuticle (asterisk). Age 22 minutes.

FIG. 10: Sagittal section through a larval gnathosoma and the associated subcuticular vesicle with stylostome profiles (expanded state) and adjacent epidermal vacuities and cells in stages of lysis. Age 25 minutes.

FIG. 11: Frontal section through a larval gnathosoma and the associated subcuticular vesicle with several profiles of the stylostome (compressed state). Age 29 minutes.

FIG. 12: Section of a subcuticular vesicle with stylostome (compressed state) surrounded by a lysed area of the epidermis. Age 26 minutes.

Scale lines: 10 μm (figs. 9-12).
ment lamina. Occasionally, the piercing of the host's cuticle by a larval mite and incipient vesicle development cause local damage to the epidermis and also to its basement lamina, so that the injected substances immediately run into the circulating haemolymph plasma. Also in such cases a vesicle similar to those developing intra-epidermally is formed (Fig. 8 A, B), but now it becomes surrounded by granular precipitates in the haemolymph plasma. Usually, the further development of the stylostome takes place at the expense of the host's epidermis, which is more or less affected (Fig. 12). Close to the vesicle sooner or later appear vacuities and compartments with lysing epidermal cells (Fig. 10); these eventually fuse with the expanding vesicle, which gradually assumes the character of an epidermal abscess.

The development of an epidermal abscess and the stylostome within displays striking synchronism and conformity among larval mites settled on one and the same host. Eventually, the growing stylostome breaks the abscess, whose melanized bounding rim becomes modified to a melanin sleeve or funnel around the origin and proximal part of the stylostome. The thickness of this sleeve is most prominent near the inner orifice of the cuticular tear (Fig. 21). When fully formed, the sole stylostome is usually lodged in a subcuticular cleft or cavity in the epidermis and separated from the haemocoele by the sheet of subepidermal basal lamina, which might adhere closely to the exterior surface of the stylostome (Fig. 17). The basal lamina consists of a filamentous meshwork with an adhering amorphous substance (Fig. 18). In heavily mite-loaded hosts, epidermal cavities caused by functional stylostomes of close proximity fuse after considerable areas of the epidermis have been eroded, so that the subepidermal lamina splits off from the body wall. The stretched membranous basal lamina that envelops the stylostome will deteriorate, exposing stylostomes to reactive haemocytes. Soon after the stylostome becomes freely exposed to circulating haemolymph plasma, flocculent layers are deposited upon its outer surface (Fig. 19). At the wound, congregating haemocytes containing dense cytoplasmic granules leave a clear zone around the functional stylostome (Fig. 22). Next to the exposed stylostome a granular precipitate accumulates, together with decomposing haemocytes.

DISCUSSION

Knowledge of the nature and timing of early events in the process of modelling the arrenurid stylostome promotes a better understanding of its role. Although incomplete, the sequence of
FIG. 20: Sagittal section through a cheliceral sabre (broken off) inserted in the cuticular tear of the feeding site demonstrating the origin of the stylostome (here in expanded condition) together with parts of the melanized bounding membrane of the subcuticular vesicle. Note common origin (asterisks) of stylostome and bounding membrane. Age 24 minutes.

FIG. 21: The proximal portion of a stylostome with a cheliceral apex sectioned (arrow). The stylostome has broken the bounding rim of the vesicle, the rest of which here constitutes a melanized sleeve around the proximal stylostome. Disintegrating haemocytes appear to contribute to melanization of the sleeve. Age 19 hours.

FIG. 22: At the feeding site, haemocytes containing dense cytoplasmic granules will aggregate leaving a clear zone around the stylostome, here sectioned through the middle part. Age 21 hours.

FIG. 23: From a subcuticular vesicle with stylostome in contracted state. Lamellae of melanin add to the inner face of the vesicular bounding membrane (arrows). Age 28 minutes.

FIG. 24: Within the subcuticular vesicle melanin seems to be deposited on a fibrous matrix forming flakes (arrows). Age 15 minutes.

Scale lines: 10 μm (figs. 21, 22); 5 μm (fig. 20); 1 μm (figs. 23, 24).
selected images in the present study suggests certain stages in stylostome development and warrants a tentative explanation of its functioning.

Observations made in the laboratory with the surgical operating microscope on emerging zygop terans confirm that attachment of ectoparasitic *Arrenurus* larvae takes place in a manner previously predicted (Åbro 1979). Arrenurid larvae appear to secrete into the puncture a liquid that gels to the resilient substance of the stylostome and accessory structures. The host’s defensive apparatus seems ineffective in coping with functional stylostomes (Åbro 1979). The larva is presumed to inject venom into the wound thus producing a temporary local paralysis that affords the larva sufficient time for stylostome development without being subject to violent defensive reaction on the part of the host (Åbro 1982). In addition to the stylostome proper, its liquid precursor seems to contribute also to the bounding membrane of the primary vesicle of larval secretions discharged into the host tissue. The initial stage of a developing stylostome could be demonstrated 8-10 minutes after beginning the anchorage. The action of piercing the toughened host cuticle until the inserted cheliceral blades become fully extended takes up to 8 minutes. It lasts for several minutes until the liquid droplet visible on the gnathosomal apex just before larval attachment becomes sufficiently solidified to cement the gnathosoma to the host’s cuticle. The gnathosomal droplet appears to give rise to the dense gelatinous coat on the larval mouthparts, including the circumbuccal integumentary fold with sensilla, which contribute to establishing a continuous communication between the larval pharynx and the pool of nutrients in the host. The gelatinous substance seals any gaps, thus forming a functional juncture. Obviously, this represents a critical stage in the anchoring procedure of the larval mite, which at that time is particularly sensitive to disturbances. Before the formation of a stylostome can start, establishment of such a juncture appears crucial. Subsequently, the subcuticular vesicle with a developing stylostome appears very quickly.

The primary subcuticular vesicle is thought to result from a complex salivary secretion poured into the host along with a gelatinizing substance forming the delicate bounding rim against surrounding epidermal tissue. It could also be that owing to damage inflicted on the cuticle, adjoining epidermal cells become activated to form a resistant gelatinlike membrane trying to isolate the influx of foreign toxic materials. Bulging of the epidermal layer beneath the puncture site immediately after attachment takes place indicates that larval secretions are forced into the host. Initially only a few epidermal cells seem to be disrupted. That a similar vesicle also appears in cases where the epidermis and its accompanying basal lamina happen to be locally damaged already during the action of penetrating the cuticle, suggests that the primary vesicle does not result solely from an epidermal host reaction. In such cases local coagulation of haemolymph plasma, visible as coarse granular precipitates, seems to support the vesicle and contribute to walling it off from neighbouring tissues, thus preventing loss of body fluids. The narrowing of the perforating tear owing to the resiliency of the host’s cuticle interferes with bleeding from the wound (Åbro 1979).

Into the primary vesicle is ejected liquid that rapidly condenses and gels on the contacting border against the surrounding thin salivary solution, possibly by interaction with salivary components, thus coming to form walls of a tubule. Through the first established slender tubulous portion, which constitutes a prolongation of the cuticular perforation, is forced additional liquid that flows down the tubule and adds new segments distally. Gradually the flow becomes more steady, thus shaping a rather smooth-walled distal portion of the stylostome. This supports the opinion previously maintained that the arrenurid stylostome is in all essentials derived from the mite itself (Åbro 1979). The concept that the stylostome originates from an interaction of both mite secretion and host tissues (Aoki 1957) ought to be modified. The present study indicates that early stylostome formation takes place within salivary secretion while later developmental stages are surrounded mainly by the host’s tissue fluids or hae-
molymp plasma. The primary vesicle provides a humoral space within the host tissues necessary to develop a stylostome. Moreover, the vesicle serves as a buffer zone smoothing the way for the tiny nascent stylostome and protecting it from direct vehement defensive reactions on the part of the host. Secondarily, the vesicle develops into an abscess, which to the larva becomes a pool of nutrient juice from lysed cells. At least two different kinds of secretions appear to be discharged from the larval mite, a thin venomous saliva and a liquid that turns viscous and eventually attains a resilient gel-like consistence. This accords with two pairs of salivary glands recognized in larval trombiculid mites (Jones 1950). Others have postulated as many as seven pairs of digestive glands from trombiculid larvae (Aoki 1957). Unfortunately, very little is hitherto known about the digestive glands in arrenurid larvae.

As a humoral-mediated defence reaction, components in the host's tissue fluids seem to permeate the bounding membrane of the subcuticular vesicle from the surroundings and evoke melanogenesis: melanin becomes deposited in the gelatinized membrane of the vesicle and also on the margin of the cuticular tear. Before this process becomes recognizable very early after the vesicle has come into being, the stylostome wall and the rim of the vesicle appear very similar as to texture. Both have a common origin in the inner orifice of the cuticular tear near the inserted chelicerae (Åbro 1979). Judged on morphological features, the vesicular membrane and the stylostome might consist of the same or similar materials, although this becomes concealed very soon because of melanin deposition in the vesicular membrane. Affected cellular environments indicate that cytotoxins will leak across the bounding membrane of the vesicle, probably by simple diffusion.

Variability of the luminal width among section profiles of early stylostomes and changing density of their contents seem to reflect alternate extension and contraction as the stylostome is blown out or sucked in by the larval mite, as formerly stated (Åbro 1979, 1982). The early stylostome appears to undergo a phase of extreme expansion of the distal thin-walled part. Expansion of the primary vesicle could be due to extreme stylostome inflation, which is associated with lysis of adjoining epidermal cells. The appearance of a radiating pattern around the contracted thin-walled distal portion of the stylostome indicates that substances are sucked into it from the surrounding salivary tissue juice. Despite their dense appearances in ultrathin sections, both the vitreous stylostome wall and the bounding membrane of the vesicle give the impression of possessing considerable permeability, particularly so in the thin-walled distal portion of the stylostome. The early stylostome serves a dual function, partly conveying ejected materials for its own lengthening and remodelling, partly conveying digestive substances into the host and nutrient back to the larva. During feeding, the arrenurid larva alternates phases of suction of tissue juice extracts and ejection of salivary secretions through the stylostome. Most of the larval feeding might occur during formation of the stylostome; normally, the larva reaches repletion within two days (Åbro 1982).

The delicate meshwork of the sheet of epidermal basal lamina, closely applied outside the stylostome and separating it from the haemocoel, seems to prevent haemocytic reactions to the stylostome in later developmental stages. Gaps in the adhered basal lamina, exposing the stylostome to circulating haemolymph, allow irritants to stimulate a local haemocytic aggregation. When freely exposed to haemolymph, deposition of successive flocculent layers upon the outside of the stylostome might represent coagulated haemolymph plasma. Initially, aggregating haemocytes leave a clearing zone, often with some cell debris, around the stylostome, probably because salivary cytotoxins exude from it and host cells are unable to deactivate these substances.

The arrenurid stylostome functions as a closed sac of digestive fluids separated from the host's tissues but nevertheless in a condition to extract nutrients from the host (Redmond & Hochberg 1981). It differs from the stylostome of larval trombiculid mites that possess a true feeding tubule, opening at the tip into the host tissues.
previously liquefied (HASE et al. 1978). Acid polysaccharides appear to be included in the arrrenurid stylostome (ÅBRO 1979), but beyond that its composition and properties are not clearly defined. Subjected to alternate jerky extension and contraction as it is blown out or sucked in by the larval mite, an interchange of materials takes place across the stylostome wall, especially over the thin-walled distal portion, which becomes compressed during suction (ÅBRO 1982). Thus the functional arrrenurid stylostome serves to probe the host tissue. Presumably the larval pharyngeal pump provides most of the force for suction. Components of the liquefied tissues surrounding the stylostome are sucked through the opposing groves formed by the protracted cheliceral blades, which provide for an open passage through the oblique tear in the resilient cuticle. During feeding, the larva is presumed to dispose of substances preventing gelation of the stylostome content and the haemolymph plasma immediately surrounding it. The completely closed arrrenurid stylostome might be interpreted as an adaptation preventing hard melanized tissue fragments or chitinous pieces in the host from being imbibed by the larva where they could fasten and clog the narrow pharynx and oesophagus. This is in contrast to the open stylostome of trombiculid larvae, parasites on the skin of mammals and birds, in which the liquefied tissue does not comprise hard injurious particles to be sucked in.

**Abbreviations and symbols in the figures**

B lumen of the vesicle  
bl subepidermal basal lamina  
C host cuticle  
ch cheliceral sabre, distal part  
ep host epidermis (= hypodermis)  
G gnathosoma of larval mite  
H host haemocoel  
if integumentary fold with sensilla surrounding the larval mouth  
L stylostome lumen  
m melanized membrane of the subcuticular vesicle  
mu muscle  
p pedipalp  
s stylostome

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