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Morphological characteristics of sensilla on the female ovipositor of *Lype phaeopa* (Psychomyiidae; Trichoptera)

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Abstract

An important aspect of the association of *Lype phaeopa* (Stephens) with submerged wood is the oviposition behavior of adult females, which preferably oviposit their eggs on moist emergent or submerged parts of woody debris with a structured surface. The eggs are commonly deposited in cracks and crevices using the elongated ovipositor. Ovipositor morphology and various sensilla on the tip and along the ovipositor were studied by scanning electron microscopy and their possible function discussed. Structure of these sensilla and pre-oviposition behavior of the females point to a preference for certain oviposition sites on woody debris. This may be a key factor for the distribution and development of the larvae.

Keywords: specialization, woody debris, ovipositor sensilla, underwater oviposition

Introduction

Adult female insects can predetermine larval habitat by their choice of oviposition places. There is an important interplay between choice of oviposition sites where eggs are protected against predators, where environmental conditions are suitable for egg development, and larvae can use the chosen substrate as life habitat (van Loon, 1996). For the dipteran *Liriomyzea sativae* (Agromyzidae) a genetic covariance between oviposition and larval performance has been shown (Via, 1986). The female choice of oviposition site is especially decisive for larval development in herbivorous species adapted to a limited number of host-plants (van Loon, 1996).

Adult female insects with aquatic larvae face a special problem of detecting suitable oviposition sites within the aquatic environment. Many species avoid this problem by releasing their eggs into the water by penetrating the water surface with the abdominal tip, on which the oviduct opening is located. Several dipteran families, such as Chironomidae (Armitage *et al.*, 1995) and Tipulidae (Hofsvang, 1997), and most ephemeropterans (Bauernfeind and Humpesch 2001) use this oviposition strategy. Other species lay their eggs on structures located outside the water (or in temporary stream areas) and the larvae enter the water after hatching by falling or crawling into it. This mechanism was reported for Limnephilidae (e.g. Hanna, 1961) and some Diptera, such as *Atherix ibis* (Dziock *et al.*, 1997) and Simuliidae (Jensen, 1997). These mechanisms of oviposition often result in a non-specific larval habitat predetermination and larvae of most of these species are forced to actively search for suitable habitats.

In contrast some species deposit their eggs on submerged substrates and therefore may influence larval development by predetermination of the nursery habitat. Underwater oviposition is reported for a few exceptional Plecoptera and for several Trichoptera (Malicky, 1973). Egg laying on specific substrates requires adaptations such as ovipositors with mechano- and chemoreceptors for exploring suitable sites. However, no information on mechanisms for detection of suitable egg laying sites under water are available.

Adult females of several psychomyiid caddisfly species have elongated ovipositors (Fisher, 1977, Alecke 1998) that support the oviposition into holes and openings of suitable substrates. A close association of oviposition and larval habitat was reported for *Tinodes unicolor* on tufa habitats in chalk streams (Alecke, 1998). The same is supposed for *Lype* species associated with submerged wood (Alderson, 1969, Wiberg-Larsen, 1995, Spänhoff *et al.*, 1999), but detailed information is still missing. Nevertheless, it is known that females of *L. phaeopa* oviposit their eggs on wood surfaces and occasionally on submerged wood (Alderson, 1969, Spänhoff *et al.*, 2000), where larvae are specialized for exploitation of wood by retreat-making and feeding behavior (Spänhoff et al., in press). The evolutionary trend of this substrate association might be founded on the oviposition behavior of adult females, and on the morphological characteristics of their elongated ovipositor, enabling the oviposition of eggs into cracks and crevices on wood surfaces. Our study tries to link the oviposition behavior of *L. phaeopa* females

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to the distribution and possible function of sensilla located on their ovipositor.

Material and Methods

Investigations of oviposition morphology were carried out with females reared under laboratory conditions. Therefore, branches obviously colonized by larvae of *Lype phaeopa* were collected randomly from lowland streams in the northern Muensterland (Northrhine-Westphalia, Germany). These branches were reared in glass aquaria (80x80x30cm) filled with stream water and held in a computer controlled climate chamber with a dark-light rhythm and temperature regime corresponding to outdoor conditions. Aquaria were covered by a screen with small mesh size and controlled every day for emerged adults.

Morphology of the female ovipositor was investigated by scanning electron microscopy. Specimens used for SEM investigations were taken from the rearing aquaria and immediately frozen at –18°C. Female abdominal segments were identified using the nomenclature of Nielsen (1980), and sensilla were classified mainly using Altner and Prillinger (1980), but in some cases the nomenclature was adapted from Faucheux (1995) and Keil (1997).

Results

Morphology of the female ovipositor and distribution of sensilla

The ovipositor (815 ± 40µm (n = 8) in length) consists of two body segments (IX and X). Segment IX is sclerotized but still flexible, slender and elongated compared to the other body segments. It is characterised by a longitudinal cleft on its ventral side reaching from the proximally located external gonopodit (eGon) to the tip of segment X (Fig. 1A). The dorsal view of the ovipositor shows a vaulted proximal part of segment IX accompanied by several long sensilla trichoidea (Fig. 1B). The integument of the ovipositor could be interpreted as apically raised and pointed epidermal plates (Fig. 1C). A row of long hairs along the lateral sides of segment IX are trichoid sensilla with inflexible sockets arising from the integument (Fig 1C).The distal part is somewhat dorso-ventrally flattened and bears laterally some shorter trichoid sensilla. Segment IX and X are connected by a joint-like structure (Fig. 1B, 2A). Segment X is slender like segment IX but much shorter. It also shows a longitudinal cleft that divides the segments distally on its half length into two lobes. Some obviously long trichoid sensilla reach from the distal end of segments to segment X (Fig. 2A). Beside several short bristles two sensilla chaetica with knob-like socket structures are located on the dorsal and two on the lateral side of the two lobes (Fig. 2A, B).

The opening of the oviductus is located distally on the ventral side of the ovipositor (Fig. 3A). Figure 3A shows that the oviduct consists of two skinny membranes that are folded into the longitudinal cleft of the ovipositior, and which are turned outside when an egg is transported through the ovipositor. Eggs are released at the end of the longitudinal cleft where the two lobes of segment X could be spread apart. An important function of the joint-like transition between segment IX and X is the flexibility to dorsally push up segment X when the egg is released from the oviductus (Fig. 3B). This is necessary because of the size of the ovally shaped

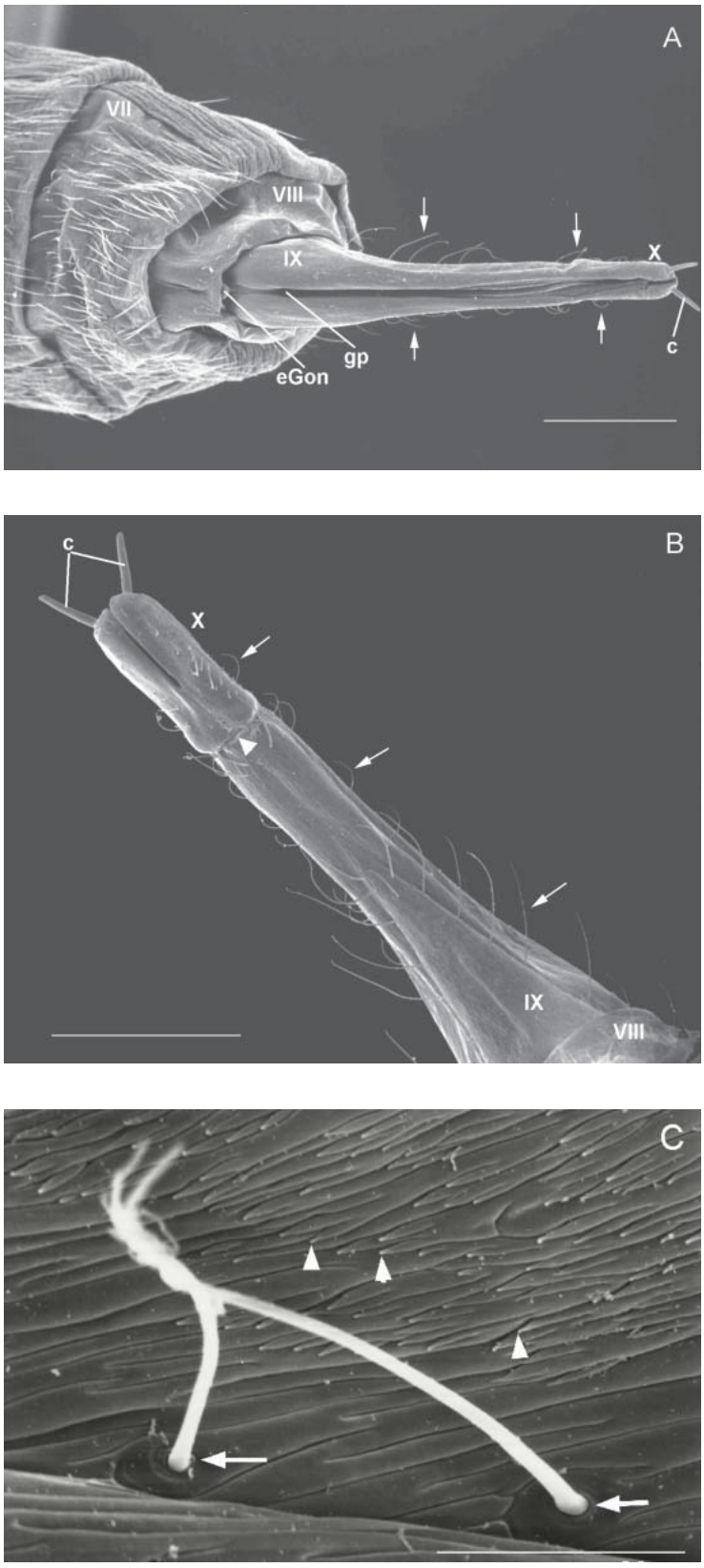

Figure 1A. Ventral view of the female ovipositor with several lateral trichoid sensilla and bristles (white arrows). VII-X = abdominal segments, eGon = external gonopod of segment VIII, gp = gonopore, c = cercus (scale bar = 250µm). **B.** Dorsal view of female ovipositor with dorso-lateral trichoid sensilla and bristles (white arrows) on segment IX and segment X. The joint-like transition between IX and X is indicated by the white arrowhead. (c = cerci, scale bar = 200µm). **C.** Dorso-lateral trichoid sensilla alongside segment IX (see also Fig. 1B) without sockets (arrows). The integument surface is structured by raised epidermal plates with pointed tips (arrowheads) (scale bar = 20µm).

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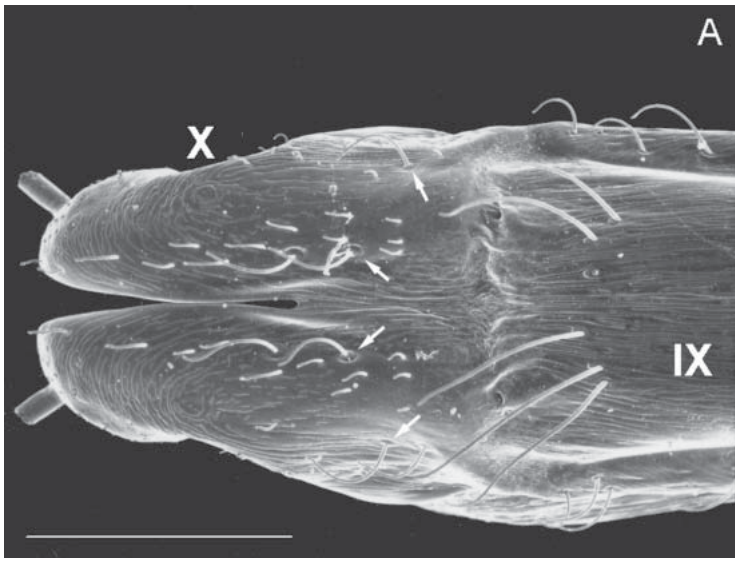


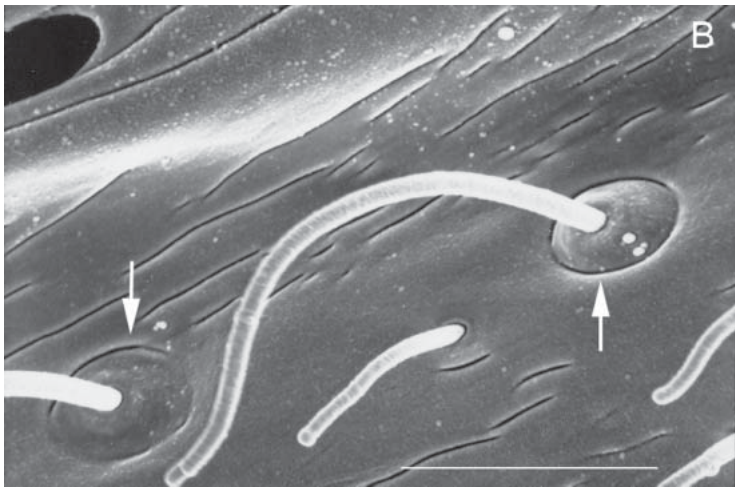
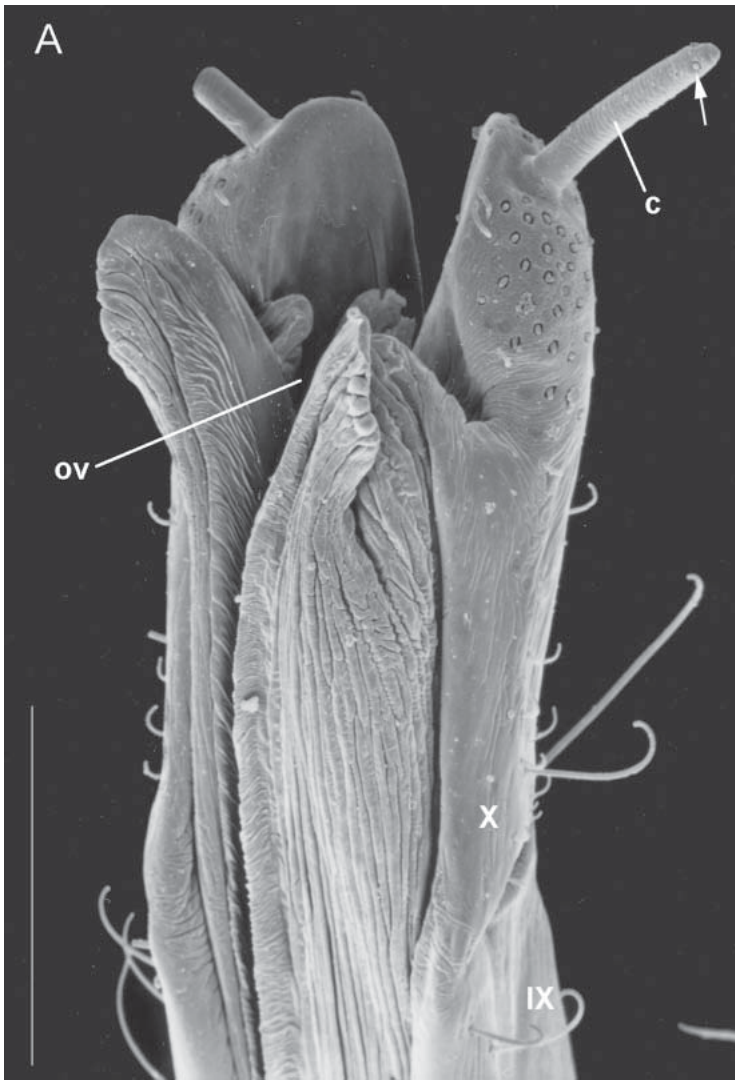


Figure 2A (Above). Tip of female ovipositor showing two lobes each with one cercus (broken off during preparation). Arrows = sensilla chaetica with basal socket structures (scale bar = 100µm). **B (Above).** Detail view of two sensilla chaetica with sockets (arrows) and a shorter bristle on the dorsal surface of segment X (scale bar = 10µm).

eggs which are ca. 215µm in length and 186µm in width (n = 40), whereas the ovipositor in neutral position is almost 100µm in width.

The surface of the ventral integument on the tip of segment X is much more structured than the smooth dorsal side, which is lined by several grooves (Fig. 4A). The apex of both lobes of segment X carry fields of two types of sensilla coeloconica with few campaniform sensilla, and some short bristles, as well as some rounded depressions in the integument surface (Fig. 4B). The campaniform sensilla are characterised by their knob-shaped central structure that is encircled by a collar-like, unstructured integument. In contrast, the peg-shaped sensilla coeloconica are surrounded by a multiple folded integument (Fig. 4C). Beside the deeply hollowed peg-like coeloconical sensilla, there is a second type of sensilla coeloconica, which represent an intermediate type of sensillum between sensilla coeloconica and basiconica. They are hollowed only very slightly into the ovipositior integument, but they are not peg-shaped. They showed a rounded, conical shape with an indistinct tip, but pores could not be detected on any studied specimen (Fig. 4D). Overall, we counted 3 sensilla campaniforma, 19 sensilla



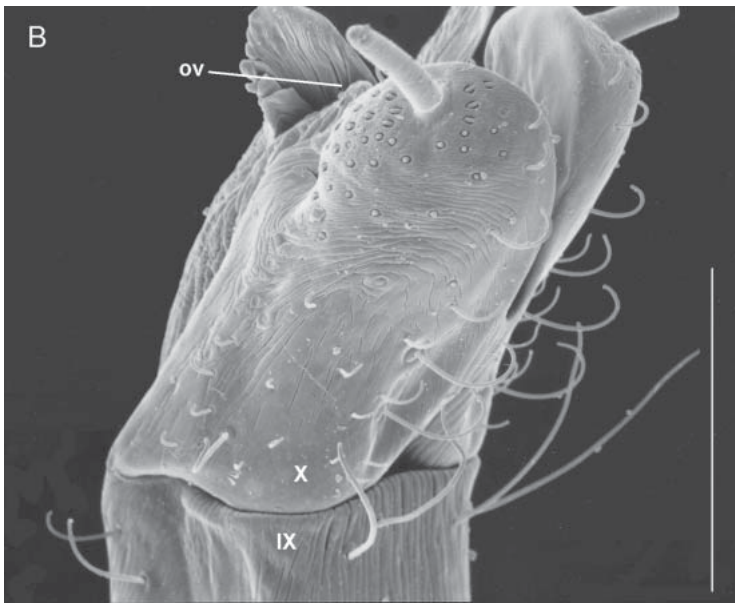


Figure 3A (Above). View of the ventral side of the ovipositor with an outfolded membrane characterising the oviduct . It is clearly visible that the membranes are part of each ovipositor side and separated from each other, not forming a close oviduct channel. ov = ending of the oviduct where the eggs were released, c = cercus, arrow = sensilla on the cercus tip (scale bar = 100µm). **B (Above).** Lateral view of segment X which is slightly bend dorsally (scale bar = 100µm).

Figure 3C on following page

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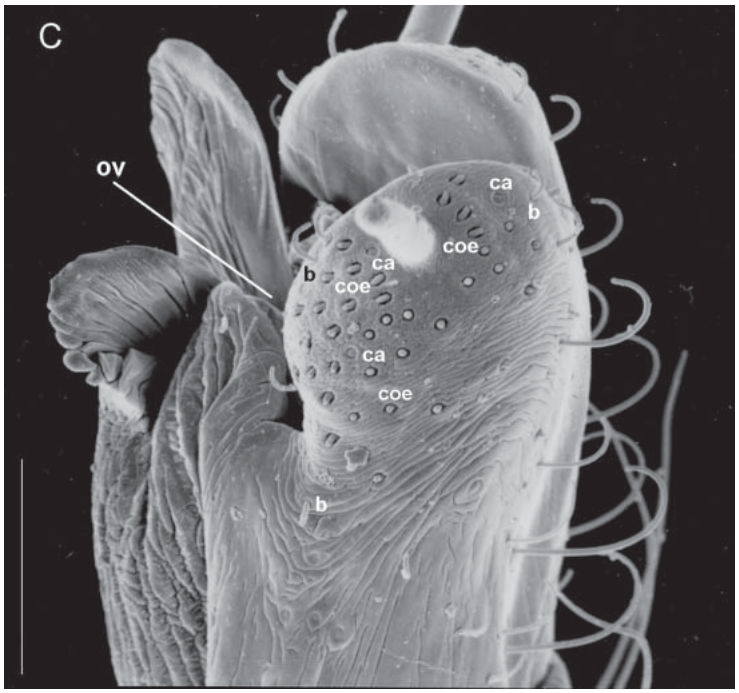
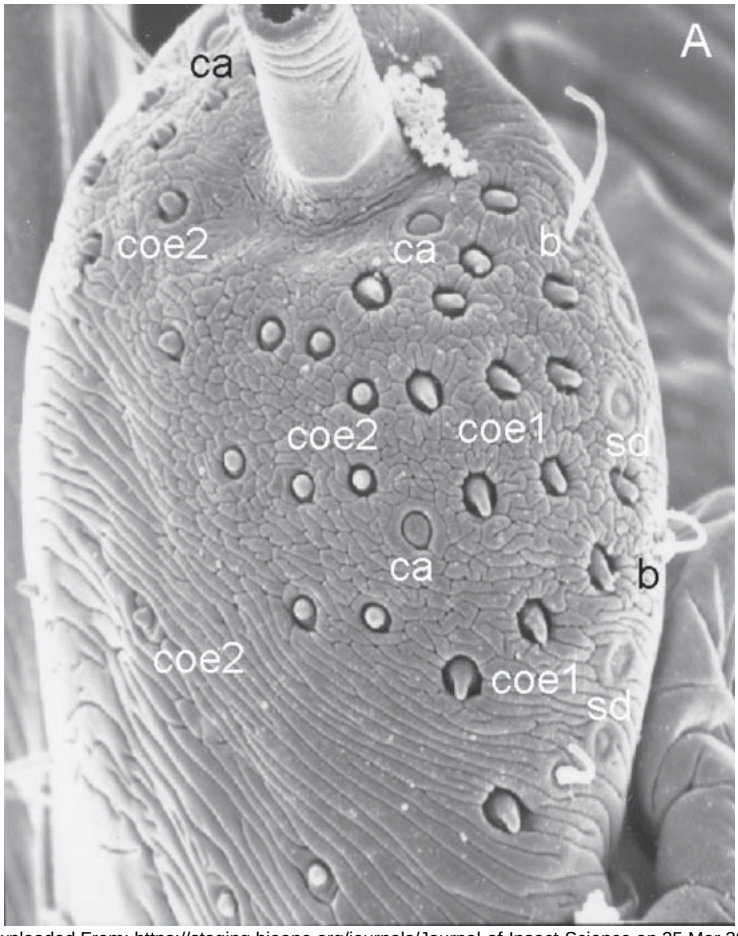
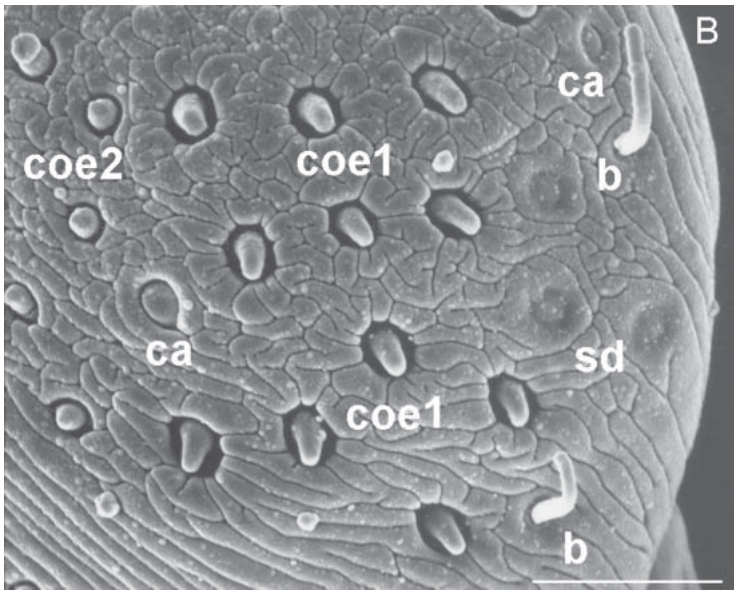
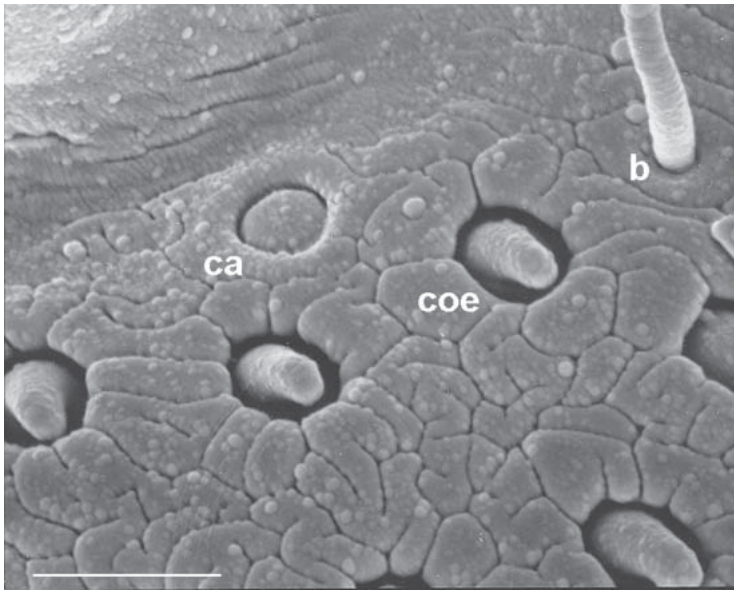


Figure 3C (Above). Sensilla distributed on the lobe tip. b = bristles, ca = sensilla campaniforma, coe = sensilla coeloconica (scale bar = 50µm).

coeloconica with peg-like shape, 18 sensilla coeloconica with spherical shape, 10 short bristles, and 10 slight depressions in the integument surface (Fig. 4A). The different distribution of the two types of sensilla coeloconica is remarkable. The peg-like shaped







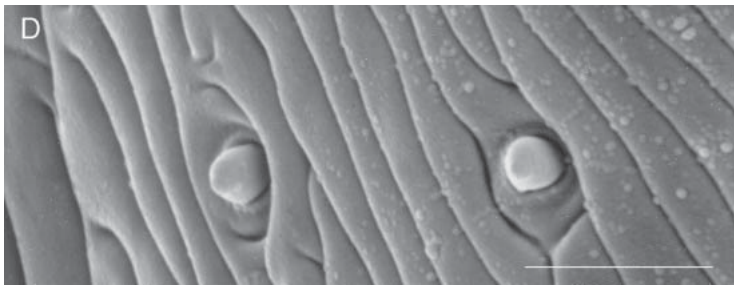


Figure 4A (Left). Lateral view of the ovipositor apex with the field of different types of sensilla: campaniforma (ca), peg-shaped (coe1) and spherical coeloconica (coe2), bristles (b), and slight surface depressions (sd) (scale bar = 20µm). **B (Above).** Detail view of the different sensilla types. Right side of the photo is the ventral side of the ovipositor. Note the different distribution of the sensilla (scale bar = 10µm). **C (Above).** Detail view of the campaniform and peg-shaped coeloconical sensilla near the cercus base. Note the different integument structure surrounding the sensilla (scale bar = 5µm). **D (Above).** Detail view of the spherical-shaped sensilla of segment X (scale bar = 5µm).

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sensilla coeloconica are distributed from the lateral towards the ventral side, whereas the spherical shaped ones are located more dorsally. The short bristles and the slight integumental depressions could be mainly found towards the margins of the ventral cleft (Fig. 3B).

From each of the lobes arises a cercus (60µm) with an annulated surface structure and apical sensilla coeloconica and one sensillum campaniformum (Fig. 5). The tip of the cercus bears two types of sensilla, subapically sensilla coeloconica and on the tip of the cercus a single sensillum coeloconicum dorsally and a campanifom sensillum ventrally (Fig. 5).

Females preferred moist emergent parts of branches for oviposition, but underwater oviposition was occasionally observed, as well. The females used their ovipositor to search for cavities in the wood surface where they inserted their ovipositors and deposited the eggs. The number of eggs deposited each time apparently depended on the size of these cracks and crevices. In most observations the majority of eggs were laid singly.

Discussion

Oviposition

As previously reported for *L. reducta* by Wiberg-Larsen (1995), female *L. phaeopa* use their elongated ovipositor to detect cracks and crevices in wood in which the eggs are deposited. This behavior is also reported in *T. unicolor* on tufa habitats in chalk streams (Alecke, 1998), and is primarily a protection mechanism against potential predators of eggs, such as leeches, water mites, or other egg suckers.

Adults were often observed at the streambanks, flying and crawling around tree roots or emergent parts of in-stream wood. Sode and Wiberg-Larsen (1993) showed that *Lype reducta* adults did not disperse away from their breeding stream, so it is very probable that they oviposit close to the habitat where they spent their juvenile life. The laboratory studies showed that females did not oviposit randomly. On the contrary, they searched very carefully for suitable oviposition sites, both on emergent moist wood, and on fully submerged wood by crawling into the stream along emergent wood pieces and often swimming to nearby submerged wood, as formerly described by Wiberg-Larsen (1995).

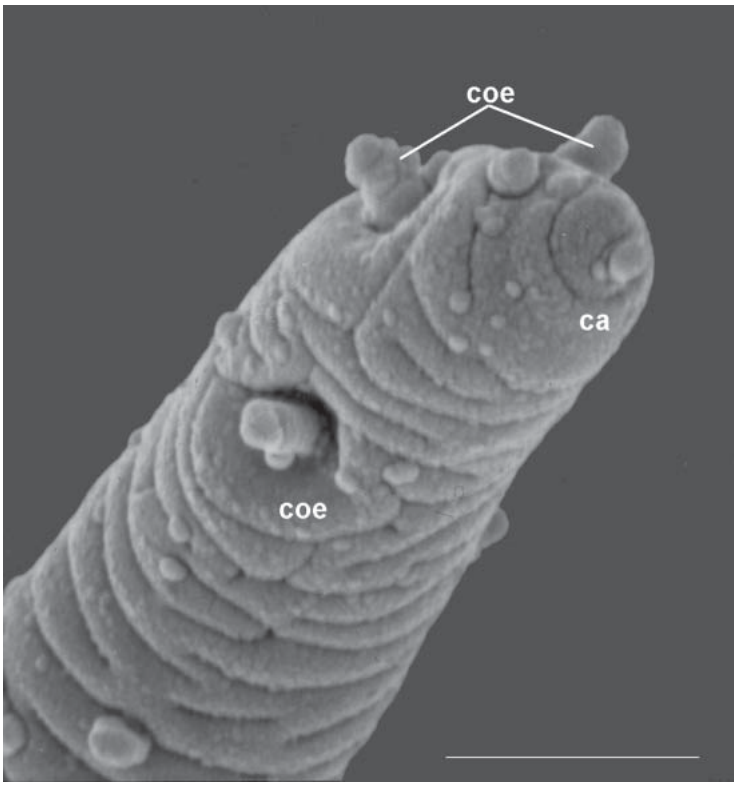

Figure 5. Tip of the cercus bearing one campaniform and three coeloconical sensilla. Note the folded integument structure of the cercus (scale bar = 5µm).

Anderson and Hallberg (1990) described the presence of oviposition-deterring pheromones (ODPs) released by larvae as one of the most important stimuli for ovipositon of the pyralid *Ephestia kuehniella* (Lepidoptera). This pattern of oviposition would require larval glands producing such ODPs and specialized chemoreceptors on the female ovipositor. The use of pheromones in aquatic insect larvae is unlikely due to the rapid dilution of chemical substances in an aquatic environment. Faucheux (1988) detected multiporous sensilla on the ovipositor of the tineid *Monopis crocicapitella* (Lepidoptera) and supposed that they play an olfactive role in detecting larval food volatiles, which would guarantee food resources for the hatching larvae. Such multiporous sensilla basiconica (sensu Faucheux, 1988) could not be found on the ovipositor of *Lype*-females.

Underwater oviposition has been already described for Hydropsychidae with preferences of species for distinct water depths and currents (Deutsch, 1984). Preference for water currents could enhance the survivability of hatched larvae when they expose their nets into this current to obtain a food supply. Although oviposition of *L. phaeopa* was not observed under natural conditions it is likely that the much smaller females, compared to the often larger Hydropsychidae, prefer slow moving stream sections, where the risk of downstream drifting is reduced. Advantages of underwater oviposition are obvious, because females can choose suitable substrates where eggs are hidden against predators and hatching larvae will find nutrient resources for their development. By placing the eggs on submerged woods the risk of drying, especially during the summer months, is reduced. The risk to the females by fish predation or other aquatic carnivorous invertebrates during oviposition may be balanced by the risk arising from ovipositing in a terrestrial environment from predators like birds, spiders or others.

Distribution and possible function of sensilla on the ovipositor of Lype phaeopa

The nomenclature of sensilla types is still inconsistent (Hallberg and Hansson, 1999), because the external structure of sensilla does not clearly indicate their physiological function (Altner and Prillinger 1980, Steinbrecht, pers. comm.). Nevertheless, there are several studies available on sensilla of adult lepidopterans (e.g. Faucheux, 1988, Anderson and Hallberg, 1990, Faucheux, 1991, Faucheux, 1995) and some general reviews on insect sensilla (Altner and Prillinger 1980, Altner *et al.*, 1983, Keil, 1997, Steinbrecht, 1997, Hallberg and Hansson, 1999), allowing us to discuss the possible function of the sensilla found on *L. phaeopa* ovipositors. The elongated ovipositor allows probing of the wood surface for suitable cracks and crevices by touching the wood surface with the foreward bent ovipositor. Detailed mechanisms of oviposition are

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unknown for Trichoptera, but studies on the sister group Lepidoptera have reported a complex system of sensilla located on the antennae, mouthparts, tarsi and ovipositor of females (Anderson and Hallberg, 1990, Faucheux, 1991, Faucheux, 1995). The only studies on trichopteran ovipositors using SEM were done by Spinelli Batta and Moretti (1997) and Alecke (1998), but they only described the location and shape of the sensilla on the ovipositors without discussing their possible function.

The coeloconical, campaniform, chaetic, and bristle or trichoid sensilla at the apex of the ovipositor of *Lype* may be interpreted as receptors for tactile stimuli. They may help the females in finding suitable oviposition sites as already suggested by Wiberg-Larsen (1995). The long trichoid sensilla along the side margins of the ovipositor are tactile sensors as well, perhaps signaling to the female how deep the ovipositor is inserted into a cavity. These sensors may support the female in finding suitable egg laying places without visual observations. This is supported by the study of Faucheux (1995) who reported hair-like sensilla (sensilla trichodea) as important mechanoreceptors in the oviposition of *Homoeosoma* species (Lepidoptera, Pyralidae), laying their eggs mostly on the internal wall of anthers from flowering sunflower heads. The short sensilla of the bristle type subapically on the lobe tip on the ventral side of segment X might have tactile functions in controlling the position of the oviposited egg. When an egg is released from the oviduct, the tip of the ovipositor is pushed up through the joint-like transition between segments IX and X. This would place segment X in such a way that an egg slips into contact with the bristles on the ventral segment surface during oviposition. The female could check the position of the deposited egg by touching it with these sensilla.

In crickets, hair-like sensilla with flattened sockets at the lateral side of segments are described as receptors of air current or as receptors warning against approaching predators ('filiform' sensilla in Keil, 1997). In *L. phaeopa* these sensilla chaetica (according to Altner and Prillinger 1980) might be water current receptors estimating whether the oviposition site is permanently supplied with flowing water aerating the eggs. Oviposition into gaps on rotten wood surfaces with a high microbial activity and lacking water exchange could expose the eggs to low oxygen concentrations, which results in low survival of eggs and newly hatched larvae. This fact is very important in lakes where *L. phaeopa* is distributed as well. There is low water movement and, as a result, the risk of anoxic conditions is higher. Therefore, the water current on the micro-scale might be more important for the choice of oviposition sites.

The tip of the cerci bears two different shaped sensilla. Nielsen (1980) described the structure on the cercus tip as an "intermediate between a sensillum basiconicum and sensillum styloconicum". In our opinion the two sensilla located directly on the apex of the cerci resemble a campaniform sensillum ventrally, with mechanoreceptorial function, and a coeloconical sensillum dorsally. If the coeloconical sensilla function as hygroreceptors (Faucheux 1995), they are especially useful during oviposition on emergent branches to probe the degree of water saturation of the wood. Additional coeloconical sensilla are located subapically around the cercal tip. The bases of these sensilla are slightly depressed into the surrounding integument and might act as hygro- and/or mechanoreceptors, as well.

The annulated structure of the cerci on the tip of the ovipositors clearly leads to an increasing surface area, which supports the uptake of olfactive stimuli during oviposition on wood. Nielsen (1980) described the cerci as structures with very thin walls and ring-like thickenings that cause the 'annulated' appearance. A very thin wall could support the exchange of chemical substances or tactile stimuli with the environment, so they might function as hygroreceptors (Altner *et al.*, 1983) to estimate the water content of wood as well, but much more studies on this topic are necessary.

Spinelli Batta and Moretti (1997) investigated Trichoptera species from different families and revealed some similarities between the sensilla on the ovipositors. Sensilla types and their distribution on ovipositors of *T. unicolor* (Psychomyiidae) are very similar to *L. phaeopa*, whereas *T. waeneri* showed a much shorter, stout ovipositor, but the tip of the apical cerci bears three coeloconical and one basiconical sensilla, which was also shown by Alecke (1998). Other species investigated by Spinelli Batta and Moretti (1997) bear mostly sensilla coeloconica and, additionally, campaniform or basiconical sensilla, on their apical cerci. We did not investigate other body parts than the ovipositor for sensilla that might play a role in oviposition, but sensilla on palps or tarsi might be involved in the choice of egg-laying places as well (Faucheux, 1991).

Both larvae and adults of *L. phaeopa* showed strong preferences for wood substrates. The evolutionary trend in this habitat specialization might be a result of the oviposition by females, which leads to a niche separation within the Psychomyiidae. Several species of Psychomyiidae have females with elongated ovipositors but they have exploited other substrates, such as stones (e.g. *Tinodes pallidulus*) or tufa habitats in chalk streams (*T. unicolor*), or they show a wider range of colonization substrates, e.g. *Tinodes waeneri* (Alecke, 1998).

Larvae of *L. phaeopa* are not exclusively restricted to wooden surfaces. Their digestive enzyme inventory is not specialized for wood digestion (unpublished data) and larval retreat-making is possible on other solid substrates than wood as well (unpublished data). The main reason for wood as larval habitat could be the preference of females to oviposit their eggs on these substrates, and a subsequent co-development leads to larval specialization of wood exploitation (Spänhoff et al., in press)

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References

Alderson R. 1969. *Studies on the larval biology of caddis flies of the family Psychomyiidae*. PhD thesis, University of Wales.

Alecke C. 1998. *Ökologie und Habitatbindung von Tinodes unicolor und T. pallidulus (Trichoptera; Insecta)*. Schüling Verlag,

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Münster: 1-184.

Altner H, Prillinger L. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *International Review of Cytology* 67: 69-139.

Altner H, Schaller-Selzer L, Stetter H, Wohlrab I. 1983. Poreless sensilla with inflexible sockets. *Cell and Tissue Research* 234: 279-307.

Anderson P, Hallberg E. 1990. Structure and distribution of tactile and bimodal taste/tactile sensilla on the ovipositor, tarsi and antennae of the flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae). *International Journal of Insect Morphology & Embryology* 19: 13-23.

Armitage P, Cranston PS, Pinder LCV. 1995. *The Chironomidae*. Chapman & Hall, London.

Bauernfeind E, Humpesch UH. 2001. *Die Eintagsfliegen Zentraleuropas (Insecta: Ephemeroptera): Bestimmung und Ökologie*. Verlag des Naturhistorischen Museums Wien: 239 pp.

Deutsch WG. 1984. Oviposition of Hydropsychidae (Trichoptera) in a large river. *Canadian Journal of Zoology* 62: 1988-1994.

Dziock F, Kaschek N, Meyer EI. 1997. Freiland- und Laboruntersuchungen zur Lebensweise von *Atherix ibis* (Fabricius, 1798) (Diptera, Athericidae). *Verhandlungen des Westdeutschen Entomologentages 1996,* Düsseldorf 1997: 101-113.

Faucheux MJ. 1988. Multiporous sensilla on the ovipositor of *Monopis crocicapitella* Clem. (Lepidoptera: Tineidae). *International Journal of Insect Morphology & Embryology* 17: 473-475.

Faucheux MJ. 1991. Morphology and distribution of sensilla on the cephalic appendages, tarsi and ovipositor of the European sunflower moth, *Homoeosoma nebulella* Den. & Schiff. (Lepidoptera: Pyralidae). *International Journal of Insect Morphology & Embryology* 20: 291-307.

Faucheux MJ. 1995. Sensilla on the antennae, mouthparts, tarsi and ovipositor of the sunflower moth, *Homoeosoma electellum* (Hulster) (Lepidoptera, Pyralidae): a scanning electron microscopic study. *Annales des Sciences naturelles, Zoologie, Paris 13e Série,* 16: 121-136.

Fisher D. 1977. Identification of adult females of *Tinodes* in Britain (Trichoptera: Psychomyiidae). *Systematic Entomology* 2: 105-110.

Hanna HM. 1961. Observations on the egg-laying of some British caddis flies and on case-building by newly hatched larvae. *Proceedings of the Royal Entomological Society of London (A)* 36: 57-62.

Hallberg E, Hansson BS. 1999. Arthropod sensilla: morphology and phylogenetic considerations. *Microscopy research and Technique* 47: 428-439.

Hofsvang T. 1997. Diptera Tipulidae, crane flies. In: Nilsson A, editor. *Aquatic Insects of North Europe*. 93-98, Volume 2. Stenstrup: Apollo Books.

Jensen F. 1997. Diptera Simuliiade, black flies. In: Nilsson A, editor. *Aquatic Insects of North Europe*. 209-241, Volume 2. Stenstrup: Apollo Books.

Keil T. 1997. Functional morphology of insect mechanoreceptors. *Microscopy research and Technique* 39: 506-531.

Malicky H. 1973. Trichoptera (Köcherfliegen). In: Helmcke JG, Starck D, Wermuth H, editors. *Handbuch der Zoologie*. IV. Band, 29. Berlin: Walter de Gruyter.

Nielsen A. 1980. A comparative study of the genital segments and the genital chamber in female Trichoptera. *Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* 23 (1): 1-200.

Sode A, Wiberg-Larsen P. 1993. Dispersal of adult Trichoptera at a Danish forest brook. *Freshwater Biology* 30: 439-446.

Spänhoff B, Alecke C, Meyer EI. 1999. The colonization of aquatic woody debris by Trichoptera, with special reference to the genus *Lype* (Psychomyiidae). *Proceedings of the 9th International Symposium on Trichoptera*: 349-358.

Spänhoff B, Alecke C, Kaschek N, Meyer EI. 2000. Ökologie holzbesiedelnder aquatischer Makroinvertebraten am Beispiel der Trichopterengattung *Lype* (Psychomyiidae). *Verhandlungen des Westdeutschen Entomologentages 1999,* Düsseldorf 2000: 209-224.

Spänhoff B, Schulte U, Alecke C, Kaschek N, Meyer EI. in press. Mouthparts morphology, gut content, and retreat making of the wood-dwelling larvae of *Lype phaeopa* (Trichoptera, Psychomyiidae). *European Journal of Entomology*

Spinelli Batta G, Moretti G. 1997. Morphology and distribution of sensilla on the ovipositor of the females of some Italian Trichoptera. *Proceedings of the 8th International Symposium on Trichoptera*: 435-440.

Steinbrecht RA. 1997. Pore structures in insect olfactory sensilla: a review of data and concepts. *International Journal of Insect Morphology & Embryology* 26: 229-245.

van Loon JJA. 1996. Chemosensory basis of feeding and oviposition behavior in herbivorous insects: a glance at the periphery. *Entomologia Experimentalis et Applicata* 80: 7-13.

Via S. 1986. Genetic covariance between oviposition preference and larval performance in an insect herbivore. *Evolution* 40: 778-785.

Wiberg-Larsen P. 1995. Identification of Danish adult females of *Lype* (Trichoptera; Psychomyiidae), with notes on reproduction. *Aquatic Insects* 17: 65-70.

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