The egg string attachment mechanism in *Hatschekia hippoglossi* (Guérin-Méneville, [1837]) (Copepoda, Hatschekiidae)

Thomas A. Schram

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The female *Hatschekia hippoglossi* carries two egg strings, which protrude from its abdominal segment. The anatomy of the genital complex and the hook apparatus that keeps the trailing egg strings in position is illustrated and described. The oviduct openings and the copulatory pores are, in contrast to other parasitic copepods, situated on the abdominal segment where also the relative large hooks are visible. Based on light and scanning electron microscopy, it is shown how the sacs are mechanically secured by the penetration of a pair of hooks through the proximal ends of the strings. The suspension structure and the muscles that move the hooks are described. The hook apparatus is compared with that of the salmon louse *Lepeophtheirus salmonis*, which is anatomically different but principally similar and described in a previous paper.

Thomas A. Schram, University of Oslo, Department of Biology, PO Box 1064 Blindern, N-0316 Oslo, Norway.
E-mail: t.a.schram@bio.uio.no

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INTRODUCTION

In a previous paper, it was shown that the egg string attachment apparatus of the well known salmon louse *Lepeophtheirus salmonis* (Krøyer, 1837), mechanically secured the trailing egg strings (Schram 2000). For most parasitic copepod groups very little is known about their functional morphology, especially the structure and organization of their reproductive organs. This paper describes the functional morphology of the female reproductive system of *Hatschekia hippoglossi*, with special attention being paid to the mechanism by which the egg strings are held on the body. Whereas salmon lice mainly are situated on the skin of its host, the Hatschekiids are diminutive species living on the gills of marine teleost fishes. It will be demonstrated that *Hatschekia hippoglossi* from the halibut has a locking device for its egg sacs, which is anatomically different but principally similar to that of salmon lice.

MATERIAL AND METHODS

The material was collected from halibut *Hippoglossus hippoglossus* (L.), caught on longlines 8 August 1994 at 90 m depth off East Greenland (65°41'65"N, 38°27'65"W). On landing, the fish were gutted and their gills were frozen separately. In the laboratory the gills were thawed and each arch inspected for parasites before they were rinsed in fresh water. Parasites were gently brushed off into the water, which was subsequently strained through a sieve with mesh size 0.25 mm. The material was preserved in alcohol, postfixed in 4 % formaldehyde and cleared in lactic acid for light microscopy. The parts of the parasite which were studied in detail, were transferred to polyvinyl lactophenol for permanent mounting. Specimens for scanning electron microscopy were postfixed in 2.5 % glutaraldehyde, and thereafter treated as described in Schram (1991). The terms being used are based on the publication by Huys & Boxshall (1991).

RESULTS

Anatomy of genital complex and abdomen

The abdomen of the mature female is small, 1-segmented, and stands out clearly from the trunk both dorsally and ventrally. Well developed caudal rami are attached below its posterior margin (Figs 1-2). The oviduct openings and copulatory pores are situated on the abdominal segment. Gonopores are present on the posterolateral corners and the copulatory pores ventrolaterally below the gonopores (Fig. 2A). The anus is situated between the caudal rami (Fig. 2A). The closed oviduct openings appear as c. 50 µm curved sloping cracks, and the copulatory pores as circular openings c. 8 µm in diameter in terminal view (Fig. 2A). A closer look reveals, however,

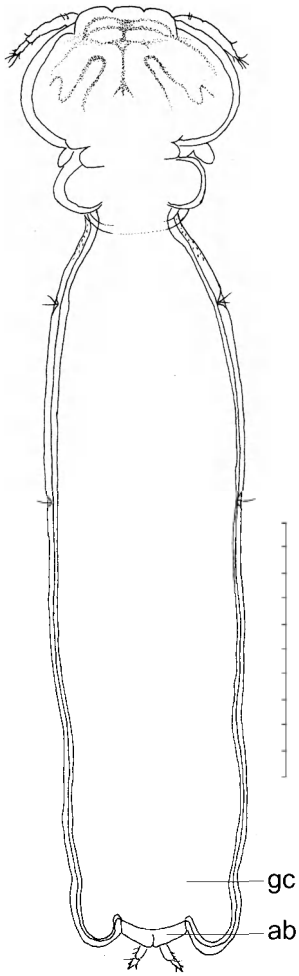

Fig. 1. *Hatschekia hippoglossi*. Young female in dorsal view. Abbreviations: ab, abdomen; gc genital complex. Scale bar 1 mm.

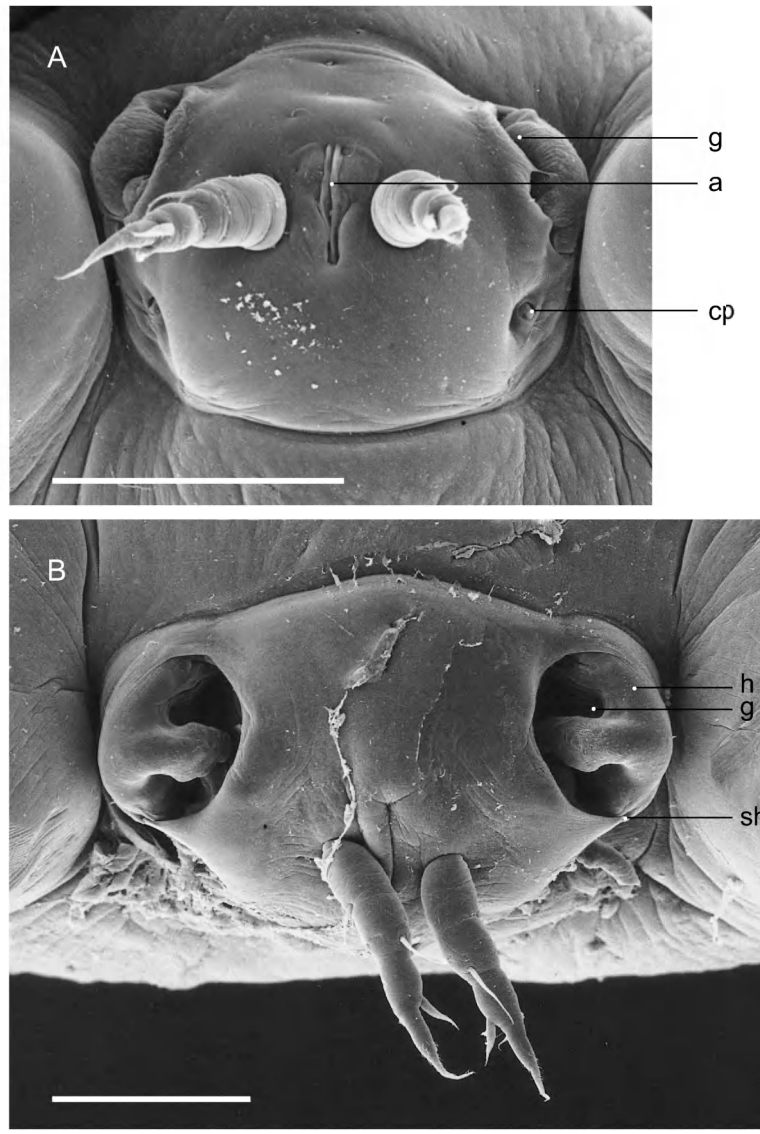

Fig. 2. *Hatschekia hippoglossi*, female. Terminal view of abdominal segment with closed gonopores (A) and partly opened ones (B). Abbreviations: a, anus; cp, copulatory pore; g, gonopore; h, hook; sh, simple hinge. Scale bars 0.1 mm.

that large hooks partly block the c. 90 µm long oval openings (Fig. 2). The hook consists of a large cupulate "support" with two "ears", and a strong curved hook pointing inwards (Figs 2; 4). The hook thus pierces the egg sac laterally (from the outside).

The ovaries are located anteriorly and the oviducts pass posteriorly, making two turns before they reach the genital antra, and proceed further backwards again and open to the exterior via the gonopores. The paired vitellaria (cement glands) are situated ventrally in the genital complex. These are sausage-shaped organs which are closed off anteriorly, and extend posteriorly turn dorsally and merge into the genital antra (Fig. 3). The seminal receptacles are ventrally located. They are fused in the middle and open dorsally on each side to the genital antrum (Fig. 3). From the spermatophores, which are attached below the caudal rami, the tubules cross to the copulatory pores on the opposite side. These are connected to the receptaculum seminis (Fig. 3). Spermatophores are 0.2 mm long and 0.08 mm wide (N = 9). The vitellaria, the

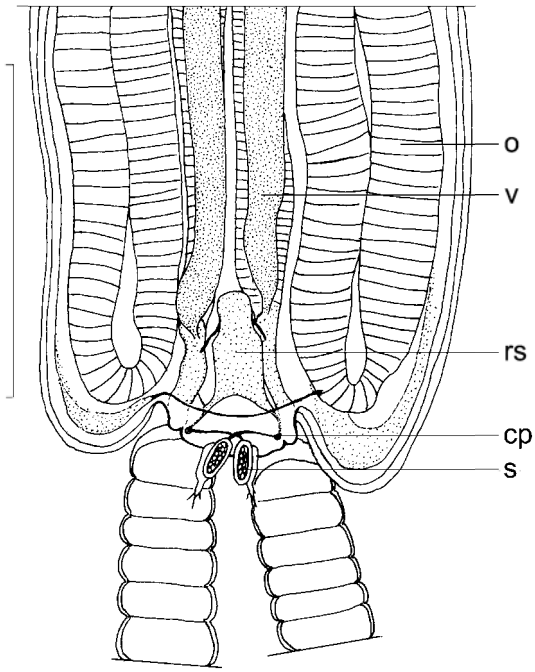

Fig. 3. *Hatschekia hippoglossi.* Posterior part of genital complex and abdomen with internal organs, spermatophores, and egg sacs, in ventral view. The hooks are omitted. Abbreviations: cp, copulatory pore; o, oviduct; rs, receptaculum seminis; s, spermatophore; v, vitellarium. Scale bar 1 mm.

oviducts, and the receptacle ducts from the receptaculum seminis all open into internal chambers, the paired genital antra, where fertilization takes place. The intestine is dorsally situated and not visible in ventral view (cf. Figs 3 & 5).

The hook apparatus

The cuticle covers the hook laterally. Medially it is flexing against a cupulate concave structure ("cup") which is visible in the gonopore (Fig. 4A). The hook seems to have a simple hinge against the abdomen, ventrally (Figs 2; 4). The hook is suspended in a frame with a dorsal and a ventral chitinized accessory structure in the genital complex that terminates posteriorly in the abdomen (Fig. 5). Fig. 6A shows that the shape of the dorsal and ventral parts of the frame and the ears of the hook, are different. The length of the frame is 300-350 µm. In lateral view, the hook is 75-95 µm broad and 90-100 µm high (Fig. 6A). In dorsal view the bend of the hook is c. 95 µm long and its dorsal ear and support 110 µm (Fig. 4A). Its shape appears from Figs 4 & 6, but it is not clearly visible that the bend of the hook rises from a broad cupulate support. The cross-sections of the hook vary from oval c. 30 x 18 µm to circular (13 µm) at its blunt apex. The point of the hook has furrows (Fig. 6B-C). As mentioned before, the point of the hook moves against a cup. The muscle bands that move the hook are inserted onto the hook centrally and to the anterior end of the frame (Fig. 6A).

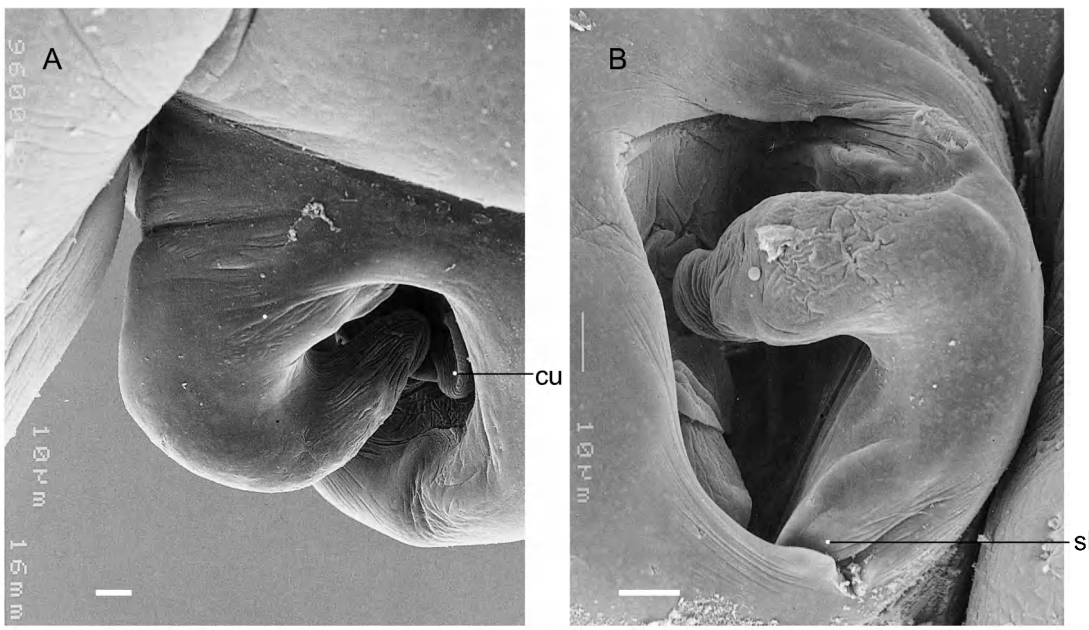

Fig. 4. *Hatschekia hippoglossi*, female. Dorsal view of left hook (A) and terminal view of the right one (B). Abbreviations: cu, cup; sh, simple hinge. Scale bars 10 µm.

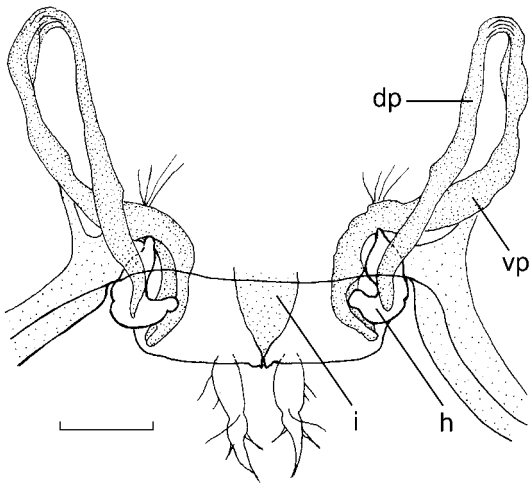

Fig. 5. *Hatschekia hippoglossi*. Posterior end of female without posterolateral lobes. The frames and hooks are shown in situ, dorsal view. Abbreviations: dp, dorsal part of frame; h, hook; i, intestine; vp, ventral part of frame. Scale bar 0.1 mm.

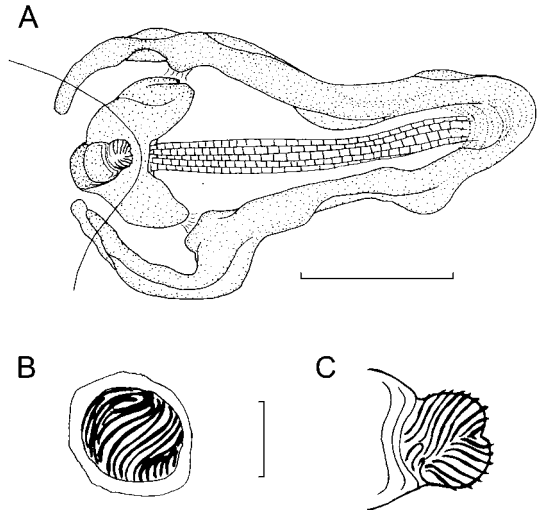

Fig. 6. *Hatschekia hippoglossi*, female. A. Medial view of the left hook. The hook with its cupulate support is suspended in a frame with dorsal and ventral parts. The connective tissue and muscle bands are indicated. B-C. Terminal and lateral view of the point of the hook. Scale bars 0.1 mm in A and 10 µm in B-C.

The egg strings

The two egg strings are locked dorsally in the abdomen and the posterolateral lobes of the genital complex are partly hidden by the sacs (Fig. 7A). String lengths vary between 1.5 and 15 mm (mean 10 mm) and usually they are longer than the parasite (Schram & Aspholm 1997). The proximal end of the egg sac is shown in Fig. 7B. The hook pierces the egg sac from outside making an oblique hole through the sides. The diameter of the hole is on the lateral and median side approximately 30 µm and 20 µm, respectively. Toward the point of attachment the egg sac has a strengthening border. The height of the eggs vary between 70 and 90 µm, depending on how closely they are packed, whereas the width of the sacs proper is approximately the same in all females, i.e. 0.3 mm.

DISCUSSION

Hatschekia hippoglossi is a large subarctic species which differs from other tropical Hatschekiids by having long eggstrings, normally longer than the parasite (Schram & Aspholm 1997). Normally, *Hatschekia* species have short strings, rarely more than 10 eggs, usually 1-3 (Jones 1985).

Both *H. hippoglossi* and its relative *H. quadrabdominalis* Yu, 1933, are different from other species within the genus in that their oviduct openings and copulatory pores are situated on the abdominal segment (Jones 1985; Schram & Aspholm 1997).

A comparison between the attachment mechanism in the salmon louse and that of *H. hippoglossi* reveals that in the latter species, the hooks are relatively larger and are visible in terminal view, where they partly block the oviduct openings. In the salmon louse, the egg string hooks are hidden, being located more anteriorly in the genital antra (Schram 2000). The tips of the egg string hooks of *H. hippoglossi* after piercing the egg strings make contact with a chitinized cup. In contrast, the tips of the egg string hooks of *L. salmonis* after penetrating the egg sac come to rest in a notch surrounding the tip of the hook (Schram 2000).

A conical hook from the side and sloping downward perforates the laterally compressed proximal end of the egg sac in salmon louse. The direction of motion of the hook of *H. hippoglossi,* however, is horizontal leaving only a hole, an imprint of the apex furrows (Fig. 6B).

Whereas the cupulate hook in *H. hippoglossi* is suspended in an attached frame, the hook of salmon louse is anteriorly and posteriorly inserted to the body wall and moved by muscle groups passing dorsally and ventrally toward and originate on the integument.

The hook apparatus of *H. hippoglossi* is found in the

genital complex and the abdomen. That of *L. salmonis* is restricted in its extent to the genital complex. The point of the hook in both species has furrows, or a fingerprint-like surface, which may assist in perforating the egg sac.

Although the shape, size, position, and help structures of the hooks in the species representing the two families Caligidae and Hatschekiidae are different, they both use similar mechanical methods to secure their egg strings. Ongoing studies on other copepods have shown that species belonging to the parasitic family Pennellidae also have hooks that mechanically holds on the egg strings of reproductive females, whereas *Acanthochondria cornuta* (Müller, 1776) in the parasitic family Chondracanthidae holds on its egg sacs by a clamp system.

Most calanoids release eggs continuously, but a few carry their eggs, including the freshwater family Diaptomidae, the marine family Euchaetidae, and the genera *Pseudocalanus* Boeck and *Eurytemora* Giesbrecht (Huys & Boxshall 1991). Examination of the egg mass on the urosome of a female *Eurytemora velox* (Lilljeborg) reveals that the eggs are not enclosed within a membranous sac (Huys & Boxshall 1991).

However, Ohman & Townsend (1998) described the egg strings of the calanoid *Euchirella pseudopulchra* (Aetideidae). Each membrane-bound; single-file row of eggs contained 11-14 relative large ova. The sticky egg string membrane was fixed to its site on the female genital segment (Ohman & Townsend 1998). Ohman (pers. commn) found no evidence of a hook or specialized attachment structure, other than what he loosely called a "coupler" in the paper, which smoothly follows the contours of the ventral surface of the genital segment. His presumption is that the egg string membrane attaches to the remains affixed to the genital segment by "some sort of adhesive".

The egg-carrying calanoid copepod *Eudiaptomus gracilis* has a membranous sac but it is not known how it is attached to the urosome. Svensson (1996) has reported clutch detachment in this species after capture by predators (*Chaoborus* spp.) which may be due to active removal by the female before she is eaten, or the result of accidental loss by the predator during handling.

Premature release of egg sacs is known from other Calanoids e.g. *Pareuchaeta norvegica* (Boeck).

Paired egg sacs are typical for Cyclopoida, but release/hooks systems as described for *Lepeophtheirus salmonis* and *Hatschekia hippoglossi* is to my knowledge not described from free-living copepods.

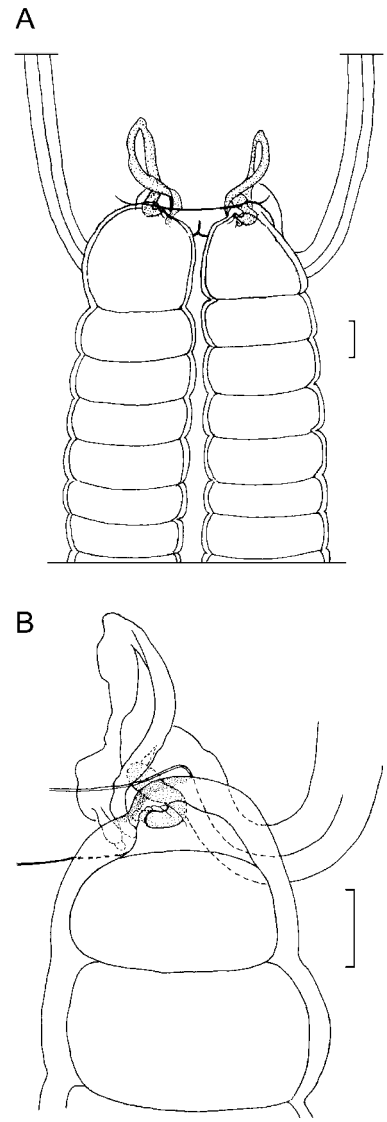

Fig. 7. *Hatschekia hippoglossi*, female. A. Posterior end of genital complex and abdomen with egg sacs in dorsal view. B. Right end of genital complex with hook, frames, and egg sac in situ, dorsal view. Scale bars 0.1 mm.

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