# REDESCRIPTION OF MALE *HATSCHEKIA HIPPOGLOSSI* (GUÉRIN-MÉNEVILLE, [1837]) (COPEPODA: SIPHONOSTOMATOIDA) AND ADDITIONAL INFORMATION ON THE FEMALE

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A description is based on 21 males and 20 females obtained from the gills of halibut *Hippoglossus hippoglossus* (L.), caught off East Greenland in 1994. Until now the type male has been unique and inadequately described. Both sexes were studied in light microscopy and SEM. The mean length of males and females was 1.18 and 7.36 mm, respectively. The antennule, legs and caudal rami of male are comparatively more prominent than those of the female, and the shapes of cephalothorax and trunk are different. The cephalothorax with cuticular ridges, constitutes about 1/4 of total length of the male. Second pedigerous somite is larger than the first one. The trunk is club-shaped with characteristic cuticular teeth ventrally and rounded posterior extremity, different from that of female. Abdomen is large, 1-segmented, and with long and slim caudal rami. Both sexes have frontal organ.

Males were compared with Scott's specimen and the six other known *Hatschekia* males. *Hatschekia reinhardtii* Wierzbicka is synonymous with *H. hippoglossi*. This is the first description of a male hatschekiid based on SEM.

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#### INTRODUCTION

The family Hatschekiidae Kabata, 1979 consists of parasitic species living on the gills of marine teleost fishes. Its diminutive members are most abundant in the lower latitudes, and become scarcer and fewer on host species in temperate zones of the oceans.

The genus *Hatschekia* Poche, 1902 was competently revised by J.B. Jones in 1985 who settled many taxonomic uncertainties, discussed interspecies variation, worked out a key and illustrated each species. The number of species was reduced from about 100 to 68. Males are rarely found, in fact they have only been described, more or less thoroughly, for seven species (Wilson 1913; Cressey 1968; Jones 1985). These include:

H. conifera Yamaguti, 1939

H. hippoglossi (Guérin-Méneville, [1837])

H. harkema Pearse, 1948

H. iridescens Wilson, 1913

H. petiti Nunes-Ruivo, 1954

H. pinguis Wilson, 1908

H. prionoti Pearse, 1947

In addition Brian (1906) described a male *Hatschekia* sp. with uncertain affinity. A further three species, with unknown males, were described by UMADEVI & SHYAMASUNDARI (1980). These were included in Jones' (1985) revision as a note added in proof.

Since 1985, 21 new species of *Hatschekia* have been described (VILLALBA 1986; CASTRO & BAEZA 1986; 1989; WIERZBICKA 1989; JONES & CABRAL 1990; KABATA 1991). Only in one of them, *Hatschekia reinhardtii*, the male was described. Thus 91 *Hatschekia* species have been described as females, but males are only known for eight species. Therefore males are rare or unknown in more than 90 percent of the described *Hatschekia* species.

The male *H. hippoglossi*, which is the type species of the genus, was described by T. Scott in 1901 (as *Clavella hippoglossi*, Kröyer). He found it among a considerable number of females taken from a halibut in the fish market at Aberdeen. A short description and a single drawing were given, the illustration was later reproduced in Scott & Scott (1913) and redrawn by Kabata (1979). The description given by Scott (1901) was not only short but insufficient, and the illustration was also imperfect, missing all

appendages except antennae and caudal rami. The need for redescription was obvious as soon as we compared our males with Scott's (1901) description. The present description is based on 20 females and 21 males, but altogether 333 females and 40 males have been found, all on halibut *Hippoglossus hippoglossus* (L.) caught in East Greenland waters.

The authorship of the name *Hatschekia hippoglossi* has been incorrectly assigned for a long time but was corrected by the The International Commission on Zoological Nomenclature in 1987 (ICZN 1987).

The lack of suitable morphological characters is one of the characteristics of Hatschekia, due to its reduction in both segmentation and appendages (Jones 1985). Jones used the general shape, and proportions and dimensions of the body, to describe H. hippoglossi and found that these are subject to fairly extensive variation, which may be due to fixation, age, host fish and condition of parasite. Although Kabata (1979) and Scott & Scott (1913) have given the best descriptions of the female (Jones 1985), they are at a loss when the male is to be compared with the female. An updated description is necessary also because of the general lack of suitable characters mentioned above. To be able to compare male and female characters, it was necessary to redescribe the female, using scanning electron microscopy. In the following text, female morphology is presented before the male is redescribed and compared with males described by Scott (1901), WIERZBICKA (1989), and other authors.

#### 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 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. Specimens for scanning electron microscopy were postfixed in 2.5 % glutaraldehyde, and thereafter treated as described in Schram (1991). Nomenclature follows that of Kabata (1979).

#### RESULTS

The *Hatschekia* material comes from 13 halibut, each carrying between 1 and 83 females and 0-12 males, the latter distributed on eight hosts. Within each host the mean total length of females varied between 5.5 and 7.8 mm. Mean length of females based on 129 measurements was 7.36 mm (SD 0.96) and range 2.6-9.3 mm. The mean

width of cephalothorax was 1.00 mm (N = 23, SD 0.06), total range 0.9-1.1 mm. The mean width of trunk within each host varied between 0.90 and 1.37 mm, and mean based on 80 measurements was 1.17 mm (SD 0.26) and range 0.7-1.5 mm. The mean length of egg sacs in samples from the different fishes varied between 1.86 and 10.9 mm, and the grand mean was 10.00 mm (SD 2.78), range 1.5-15.0 mm based on 103 measurements. Between 57-100 % of females on the different fishes carried egg sacs (mean 82%). Females measuring 2.6-5.0 mm do not carry egg sacs, whereas animals 5.5 mm long have sacs 1.5-2.6 mm long with 12-24 eggs. In such short strings the eggs are not as closely packed, egg height c. 90 µm, whereas in longer sacs the egg height is c. 70 µm. The width of the egg sacs is approximately the same in all females i.e. 300 um. The length of the egg sacs in relation to the length of body varies between 35 % (young specimens) to 195 % i.e. sacs up to the double length of body. Normally, the sacs are longer than the parasite, mean 133 % (N = 113)SD 34, range 26-202).

#### Female general morphology

Cephalothorax oval in dorsal aspect, width larger than length, tripartite or nearly straight anterior margin between the base of the antennule (Figs 1A-B, G; 2A-C). Dorsal shield bears a medial ridge, symmetrically bifid at both ends. On its side, one and sometimes two U-shaped rib-like cuticular ridges can be seen (Fig. 1G).

In lateral view the cephalothorax is curved ventrally. The first pedigerous somite, which is fused to the cephalothorax, is not visible or ill-defined, although a constriction may be seen (Fig. 1B). It may also be difficult to detect in dorsal view, especially in adult specimens. In younger parasites it appears as a narrow somite partly incorporated in cephalothorax, indistinctly delimited from the second pedigerous somite by constrictions (Figs 1A; 2A). Ventrally, the first pedigerous somite, the interpodal bar, and basipodites stand out and are seen in all females (Fig. 2A, C). The width of the first pedigerous somite is approximately half of that of the cephalothorax.

The second pedigerous somite is much larger than the first one due to expansion of sympods, its width is approximately 75 % of the cephalothorax (Figs 1A; 2A). In all specimens, this somite is clearly separated by constrictions from cephalothorax and the genital somite. The narrowest constriction is against the trunk where the width is approximately 40 % of that of the cephalothorax. From this neck the trunk expands gradually posteriorly until it reaches a width equal to approximately 80 % of cephalothorax width in younger specimens (Fig. 1A) and 150 % of cephalothorax width in adult females.

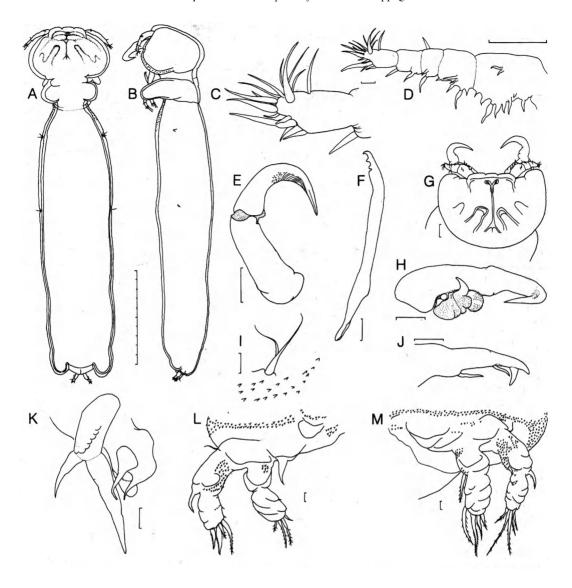
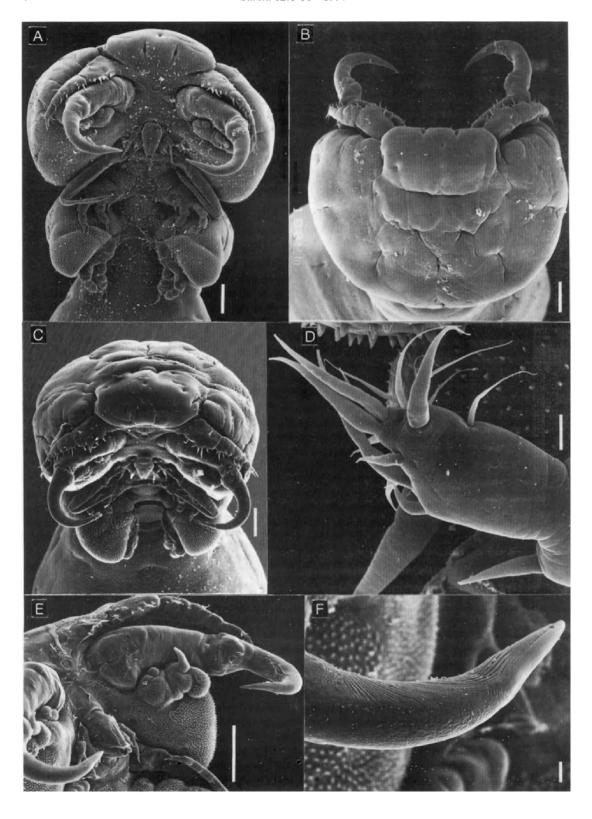


Fig. 1. Hatschekia hippoglossi, female. A. Young female, dorsal view. B. Same, lateral view. C. Tip of antennule, dorsal. D. Antennule, dorsal. E. Antenna, ventral. F. Mandible, lateral. G. Cephalothorax, anterodorsal view. H. Antenna and parabasal papillae, ventral. I. Third leg, lateral. J. Tip of maxilla, ventral. K. Right maxillule, ventral. L. First leg, ventral. M. Second leg, ventral. Scale bars 1 mm in A-B, 100 μm in D-E, H, L-M, and 10 μm in C, F-G, I-K.

Genital complex cylindrical, somewhat dorsoventrally flattened, five (young specimens) to seven (adult) times longer than cephalothorax with semispherical posterolateral processes. The posterolateral lobes, which protrude somewhat beyond the posterior margin of abdomen, give a trilobed appearance to the posterior (Figs 1A; 3C).

Abdomen small, 1-segmented, standing out clearly from the trunk both dorsally and ventrally, with well developed caudal rami attached below the posterior margin (Figs 1A; 3C-D). Caudal ramus cylindrical, length approximately 120  $\Box$ m, slightly constricted and tapering distally, ending in a slim setiform outgrowth with rows of hairlike setules



distally (Fig. 3F). Two processes equipped with setules are present on either side of the terminal part, that on the medial is side somewhat longer than the lateral one (Fig. 3F). On the dorsal side of the caudal ramus there is one long slender seta, whereas two unequal setae are situated laterally.

The anus is situated between caudal rami, gonopores dorsally on the posterolateral corners of abdomen, and copulatory pores ventrolaterally below the gonopores (Fig. 3D).

Pairs of spermatophores have been found on the ventral terminal edge of abdomen on some females, with crossing tubes to the orifices of receptaculum seminis. Spermatophores were 0.2 mm long and 0.08 mm broad (N = 9).

The ventral cuticle, anterior to the parabasal papillae and on the basipodites of the first and second legs, is covered with numerous cuticular denticles (Figs 2A, C, E; 4 A-B). Furthermore, spinules are present in patches on the medial area posterior to the base of maxilla, between the interpodal bars of the first and second leg, and on the ventrolateral sides of the genital trunk (Figs 2A; 3B). Here on the lateral sides the spinules form a distinct pattern of penta- to polygonal figures (Fig. 3B). The first half of ventral surface of trunk is also covered with small denticles, whereas they are more sparse or not present at all in the second half. All cuticular denticles which are situated posterior to the second legs, point backwards (Fig. 4F). The whole dorsal cuticle and lateral area dorsal to leg three and four are without ornamentation, although some few may be seen dorsally on the posterolateral lobes (Fig. 3C).

Antennule and antenna. Antennule uniramous. about 325 µm long, indistinctly six-segmented and tapered (Fig. 1D). Basal segment broadest and longest, comprising approximately 40 % of the total length of the appendage. It carries two subequal setae on the ventral wall and seven prominent broad setae on the anterior margin, plus a smaller one on the ventral surface. This second proximal seta is smaller than the others and difficult to detect. Second segment with six setae; four on anterior margin, one smaller on ventral surface and a last one somewhat more posteriorly on the ventral surface. Third segment with one seta on anterior margin, one smaller on ventral surface and one on posterior margin. Fourth segment, which could be interpreted as a double segment, with two setae on anterior margin. The terminal part i.e. the fifth and sixth segment, carries altogether 15 elements (Figs 1C; 2D). Lack of suture between the larger fifth and the smaller sixth segment makes is difficult to ascertain the setation of each segment. A prominent aesthetasc,  $50~\mu m$  long, which protrudes from the anterior margin approximately 1/4 distance from the apex of this fused segment, is believed to belong to the fifth segment. The aesthetasc, the largest element of the antennule, extends well beyond the tip of the appendage and nearly to the tip of the two large apical setae (c.  $40~\mu m$ ). In addition one long robust seta stands out on the posterior margin of the antennule. These four elements; the aesthetasc, the two large apical setae and the seta on the posterior margin, are the largest elements of antennule.

Antenna three-segmented, basal segment short and broad, second long, distally tapering, and third unciform claw long and sharply curved, distal half with delicate longitudinal ridges (Figs 1E; 2B, E-F).

Just posterior to antenna a well developed, broad (170  $\mu$ m), parabasal papilla is present (Figs 1H; 2E). The lateral third is a large swollen tubercle, the middle portion is equipped with a distal nude conical process and the medial part has two small tubercles anteriorly. The posterior portion of the parabasal papilla is denticulated, the lateral tubercle with larger denticles than the rest of the papilla (Fig. 2E).

In the middle, ventrally between the base of the antennae, is a frontal organ and somewhat more anteriorly a protuberance (Figs 2E; 3E). Lateral to the protuberance, a single sensory seta is present on each side.

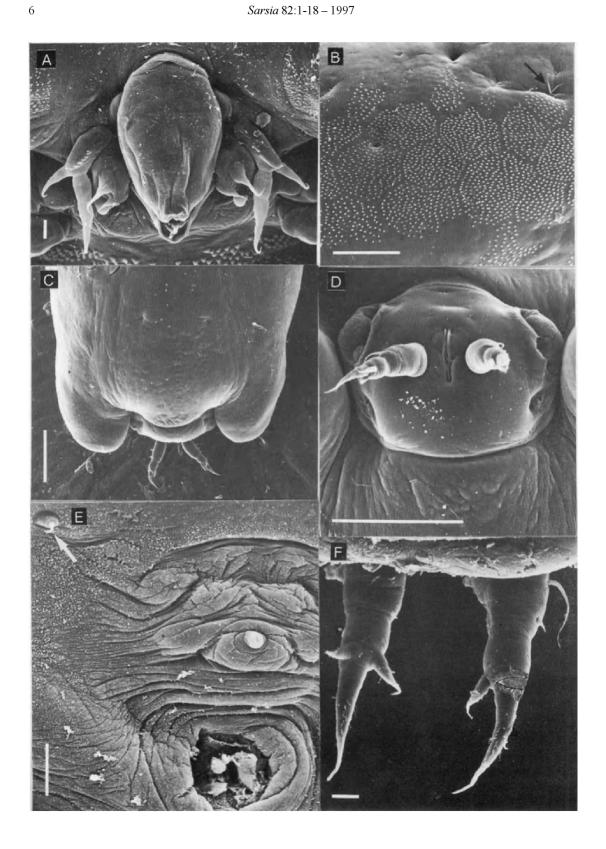
Other appendages. The siphonostome mouth cone is medial, somewhat posterior to the parabasal papillae (Fig. 2A). Mandible flat and unsegmented armed with three triangular teeth; the distance between the first and second distal ones is larger than between the second and third one (Fig. 1F).

Maxillule biramous, both rami bifid with subequal spines (Figs 1K; 3A). Endopod 20  $\mu$ m broad and c. 35  $\mu$ m long with a round outgrowth posteriorly and two cirri gradually tapering to fine points; one small (10  $\mu$ m) posteriorly, the other (30  $\mu$ m) situated more anteriorly. Exopod about equally long but more slender (14  $\mu$ m), its ventral surface equipped with a keel that may be subdivided into studs (Figs 1K & 3A); it has also short lateral (20  $\mu$ m) and long medial (50  $\mu$ m) processes.

Maxilla uniramous and 4-segmented; short basal segment, broad lacertus with short (10  $\mu m)$  setiform spine on inner margin near base. Brachium long and slender with short seta (9  $\mu m)$  at distal end of inner margin. Terminal claw short, curved, robust and bifid armed with a short seta (5-6  $\mu m)$  at about mid-length of inner margin (Figs 1J; 2A).



Fig. 2. Hatschekia hippoglossi, female. A. Cephalothorax, ventral. B. Same, anterodorsal. C. Same, anteroventral. D. Tip of antennule, dorsolateral view. E. Antennule, antenna, and parabasal papilla. F. Tip of claw of antenna. Scale bars 100 μm in A-C, E, and 10 μm in D & F.



L e g s. The first two pairs of thoracic legs are biramous with sympod inflated to form prominent ventrolateral swellings, second leg much larger than first. Armature of the rami is as follows:

|         | Endopod |   | Exopod |   |
|---------|---------|---|--------|---|
| Segment | 1       | 2 | 1      | 2 |
| Leg 1   | 0 - 0   | 4 | 0 - 1  | 4 |
| Leg 2   | 1 - 0   | 4 | 0 - 1  | 5 |

First leg situated at posterolateral corners of sympod, which has a width of c. 40 µm (Fig. 2A). Sympod with long stout process at medial side of endopod and a seta on the outer side near exopod (Fig. 1L). The two medial setae terminally on endopod are longer than the other two. Proximal segment of exopod with prominent outer seta. Two of the four setae terminally on the exopod pinnate, the other setae plumose (Fig. 4F). Cuticular crescent-shaped folds on sympod, endo- and exopods (Fig. 4B). Ventral surfaces of swollen base, interpodal bar, basal segments of endo- and exopods with prominent patches of denticulation (Figs 1L; 2A; 4B).

Second leg (Fig. 1M) situated posteromedial on the large swollen base of sympod which is much larger and more swollen than that of first leg (Fig. 2A). Width across the swollen base of sympod c. 65 µm. The rami of the second leg are larger than that of the first leg. One of the four terminal setae on the endopod pinnate, and the other setae plumose (Fig. 4D). Cuticular folds present as in first leg (Figs 1M, 4C). The rim of the fold pectinate. In addition to the prominent cuticular folds there are smaller bands of setules on the surface consisting of teeth only (Fig. 4E).

Third leg, about 0.3 mm from base of second leg, reduced to two setae protruding from a small common base situated in a depression of the cuticula (Figs 1A-B, I; 3B). Fourth leg, about 0.5 mm from the base of the third leg, reduced to a single seta protruding from the bottom of a depression (Fig. 1A-B).

#### Male general morphology

Males resemble females but are much smaller, mean length  $1.18 \, \text{mm}$  (N = 32, SD 0.04) with range 1.13-1.28 mm. The antennules, legs and caudal rami are comparatively more prominent than in the female, and the shapes of cephalothorax and trunk are different (Cf. Figs 1A & 5A).

Cephalothorax shield angular, longer than broad, with characteristic pattern of cuticular ridges. Dorsal surface subdivided at mid-dorsal line by a well-developed riblike suture flanked by two parallel curved bars connected to it posteriorly (Figs 5A; 6A-B). The mean length of the cephalothorax shield was 248  $\mu$ m (N = 12, SD 13) with range 230-280  $\mu$ m, and mean width 221  $\mu$ m (N = 21, SD 11, range 190-240). The shield, which constitutes about 1/4 of the total length of the animal, is clearly defined and separated from the rest of body by a broad, shallow, neck-like constriction. The neck is slightly bent upwards when seen in lateral view (Fig. 6B).

The first two pedigerous segments can be seen from all directions, but have no dorsal sutures. The second pedigerous segment is larger than the first, and is separated from the trunk by a slight constriction only seen in ventral view (Fig. 7A). Just behind this narrow part the genital complex expands gradually until the trunk gets its characteristic club-shaped appearance, with largest width somewhat before the posterior end (Figs 5A; 7A). Mean maximum width of the genital complex is 207 µm  $(N = 18, SD 12, range 177-228 \mu m)$ . Thus the male trunk is somewhat slimmer than the width of cephalothorax. The club-shape is also apparent in lateral view. The lateral margins of genital complex taper somewhat terminally with rounded posterior extremity (Fig. 5A). Laterally, evenly rounded posterior lobes are seen. These fuse dorsally to the trunk, and meet ventrally in a long sinus which marks the end of the genital segment (Fig. 7A). The genital openings are found underneath the posterior margin of the lobes (Fig. 7D).

The abdomen is well marked off and constitutes the posterior end of the animal. It is more narrow than the genital complex, 1-segmented, c. 60  $\mu$ m long and 35  $\mu$ m broad, and in part incorporated into genital complex. It is not as clearly delimited from trunk dorsally as it is ventrally (cf. Figs 5A; 7D). The caudal rami are long and slim, mean length 239  $\mu$ m (N = 16, SD 17). This is twice that of the female caudal rami, but they have the same morphology and armature. (Fig. 8E).

On the ventral and lateral surface characteristic cuticular teeth are present (Figs 5A; 7A). On cephalothorax the armature is seen posteriorly on the lateral sides, on the 'cheeks' as separate teeth grouped together. Medially, posterior to the base of maxilla, between first and second leg and posterior to the second leg, characteristic groups of teeth are seen (Fig. 6C). Anterior to the basipodites of the first leg a patch is present laterally, and denticles are present on basipodites of both legs. Rows of teeth are also present across the trunk ventrally and laterally (Fig. 7A). Posterior to the sinus of the trunk there are few teeth except for a short row on each side of the posterolateral corners (Fig. 7A, D).

 $\leftarrow$ 

Fig. 3. Hatschekia hippoglossi, female. A. Mouth cone and maxillules, ventral. B. Third leg (arrowed) and patches of denticulations below, lateral. C. Posterior end of female, dorsal. D. Terminal view of abdominal segment. E. Frontal organ, protuberance and sensory seta (arrowed), ventral. F. Caudal rami, ventral. Scale bars 100 μm in B-D and 10 μm in A, E-F.

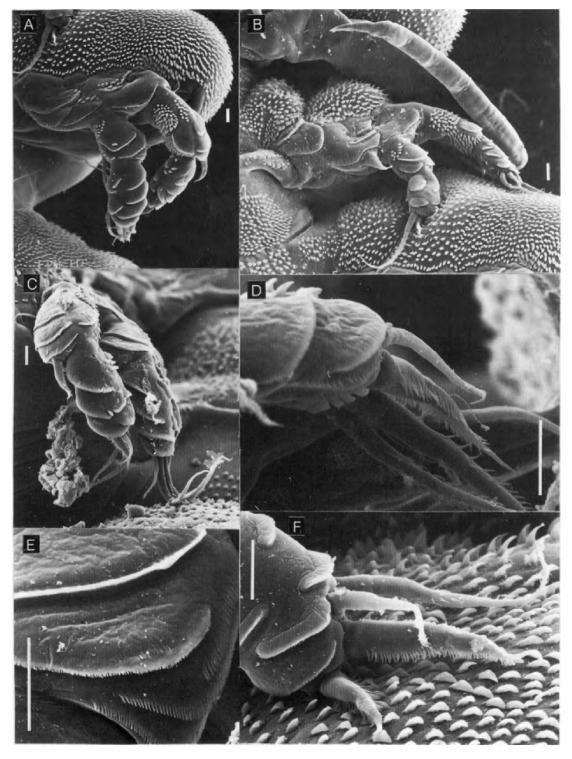


Fig. 4. *Hatschekia hippoglossi*, female. A. Second leg, ventral. B. Maxilla and first leg, ventral. C. Rami of second leg, endopod nearest. D. Terminal setae on endopod of first leg. E. Cuticular folds and teeth on proximal segment of endopod of leg 2. F. Terminal setae on exopod of first leg. Scale bars: 10 µm.

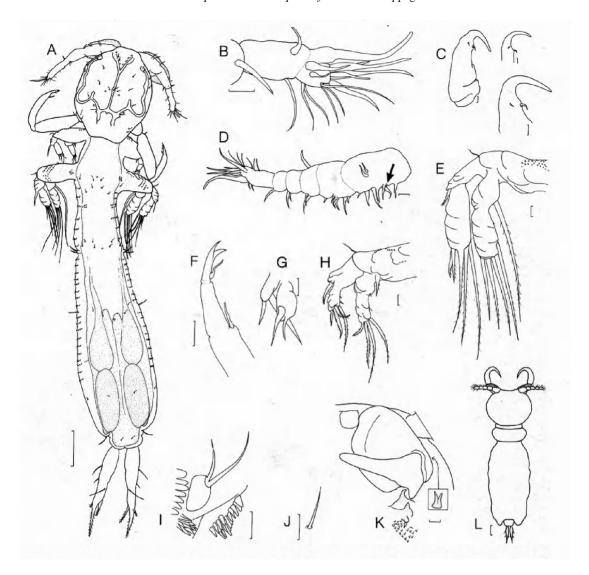


Fig. 5. Hatschekia hippoglossi, male. A. Male, dorsal. B. Tip of antennule, ventral. C. Antenna ventral, and terminal hooks from different points of view. D. Antennule, dorsolateral view. E. Second leg. F. Tip of maxilla, ventral. G. Right maxillule, ventral. H. First leg, ventral. I. Third leg. J. Vestige of fourth leg. K. Antenna and parabasal papillae, ventrolateral view. Inserted; two cirri hidden by antenna. L. Male, reproduced from Scott & Scott 1913. Scale bar 100 μm in A and 10 μm in the other illustrations.

Many paired pores and sensory setules are located symmetrically on the integument of the male (Fig. 5A). These structures are mostly seen on the dorsal surface, but they are also present on the cephalothorax, on the ventral/lateral cuticle. The cephalothorax has a characteristic pattern of sensory structures (Figs 5A; 6A). Medial on the dorsal surface between the right and left second leg, a group of eight setules and a hole is present. Identical set is found just anterior to the third

legs, and another group of four setae and a hole is found between the fourth legs. More posteriorly, four setae are present medially. On the posterolateral corner of the genital segment, one distinct seta is present on each side, and finally, two setules are found dorsally on the abdomen (Fig. 5A). These are the most prominent sensory structures of the male, but in addition single setules may be seen, especially laterally. Moreover, pores and setules may have been overlooked because of small size.

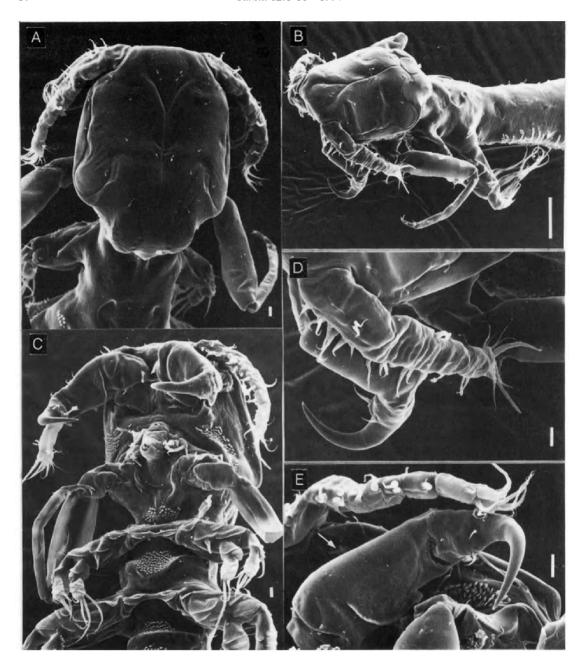


Fig. 6. *Hatschekia hippoglossi*, male. A. Cephalothorax, dorsal. B. Same, dorsolateral. C. Same, ventral. D. Antennule and antenna, dorsolateral. Processes on cephalothorax arrowed. E. Antennule and antenna, ventral. Scale bar 100 μm in B and 10 μm in A, C, D-E.

Antennule and antenna. Antennule uniramous, 180-200 µm long, slightly tapered and indistinctly six- (or seven) segmented (Figs 5D; 6D). It is similar to that of the female, but proportionally larger. Proximal segment large,

comprising approximately 30 % of the total length of the appendage. It is equipped with ten elements as in the female; eight marginal or submarginal setae and two subequal setae on the ventral wall. Second segment with six setae

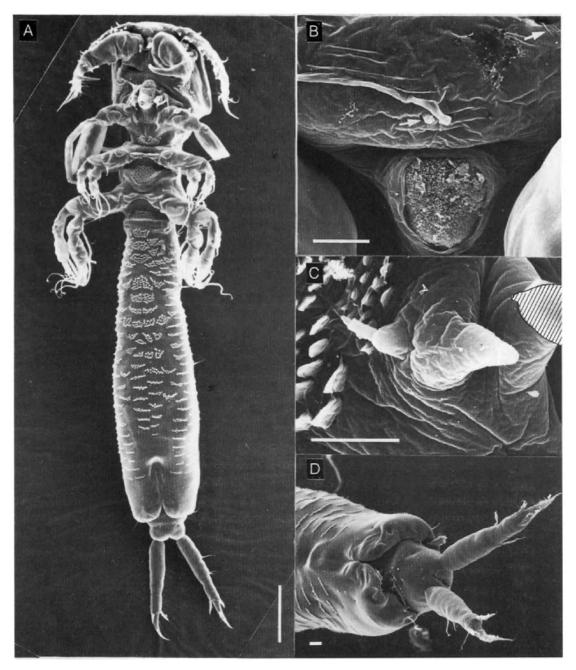


Fig. 7. Hatschekia hippoglossi, male. A. Male, ventral. B. Frontal organ, protuberance (arrowed), and seta (arrowed), ventral. C. Parabasal papillae. The third papilla hidden by flange on antenna (hatched). D. Posterior end of male, ventrolateral view. Scale bar is 100 μm in A and 10 μm in B-D.

situated as in the female, in groups of two, three, and one seta. Third segment with three setae, of which one prominent on the posterior margin. Fourth segment with two subequal setae close together on the anterior margin, which is one more than in female, and fifth segment with a single seta on the anterior margin. In the female the fourth segment is interpreted as a double segment, but they are similar in both sexes, except for an additional seta in males.

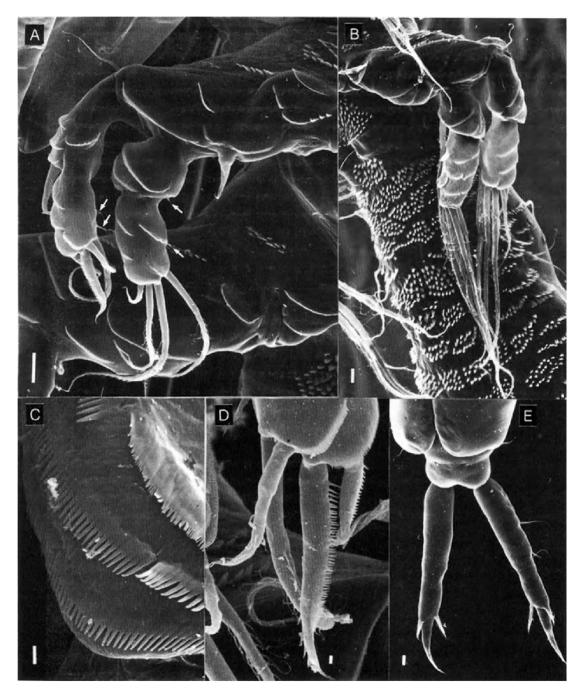


Fig. 8. Hatschekia hippoglossi, male. A. First leg, ventral. B. Second leg, ventrolateral view. C. Cuticular folds and teeth on proximal segment of endopod of second leg. D. Terminal setae on exopod of first leg. E. Posterior end with urosomes, ventral. Scale bars 10 μm in A-B, E and 1μm in C-D.

The terminal part, the fifth and sixth segments carry altogether 15 elements, as in the female, but the size is slightly different. In ventral view all elements may be seen (Fig.

5B),whereas the seta situated medial on the gibber (Kabata 1979, text fig. 66B), is hidden in dorsal/lateral view so that only 14 elements are illustrated in Fig. 5D.Aesthetasc more

prominent than in female, c.  $40 \, \mu m$  long, sausage-shaped with swollen base. It is somewhat shorter than in female, in spite of much larger size of female antennule (>  $100 \, \mu m$ ). All setae are grouped as described for the female.

Antenna indistinctly three-segmented, basal segment short, second long, broad at the base distally tapering, claw apparently not as curved and without the longitudinal striations found on distal half of claw in the female (Figs 5C; 6D-E). A prominent flange, pointing posteriorly, is present at the base of the terminal segment close to the articulation (Figs 5K; 6C). This projecting part is normally only seen in ventrolateral view. The curvature of the claw varies with the point of view as appears from Fig. 5C. The male antenna is armed with two small setae at the base of the terminal segment (Fig. 6D). The second segment is broad at the base and has a crenulate ridge going approximately halfway across it (Figs 5C; 6E).

Other appendages. Between the bases of the antennae there is a frontal organ apparently larger than in the female (Fig. 7B). A small protuberance with sensory seta on each side, anterior to the frontal organ, is also present. Ventrally on cephalothorax and lateral to the base of antenna, two small tapering processes protrude from a common base (Figs 5K; 6E). These outgrowths are normally hidden by the antenna. We were unable to find these papilla in the female specimens, but that does not preclude the possibility that they are present.

Posterior to the antenna and just anterior to the cuticular teeth on the 'cheek', two conical processes and a small three-segmented appendage are present (Figs 6C; 7C). The latter are situated just at the anterior border of the patch of cuticular teeth on the 'cheek'. These three parabasal structures are clearly different from those of female.

Mandible similar to that of the female but smaller.

Maxillule similar to that of female, but process on male endoped is relatively longer than that of the female (Figs 5G; 6C).

Maxilla similar to that of female, but stands out as the largest appendage of the male (Fig. 5A). The seta on the branchium (9  $\mu$ m) and on the terminal claw (9  $\mu$ m) of the male, are just as long as those in the female, although the male appendage is much shorter. The terminal claw of the male is relatively longer and more slender, and not so curved as in the female (cf. Figs 1J & 5F).

L e g s . The first two pairs of thoracic legs are biramous with prominent ventrolateral sympods, but without the powerful basal swellings characteristic of female. The sympod of first leg is smaller than of the second leg, but both legs stand out as large lateral extensions of body as seen in dorsal view (Fig. 5A). Male rami are, however, relatively longer and narrower, and setae are relatively longer than in female.

The setae on endopod of the first leg have fine hairlike setules on their distal half (Fig. 8A). The number of setae, their position, relative mutual length and equipment, are just as described for the female. Two small additional setules  $(c. 5 \square m)$  are, however, present on the medial side of exoand endopod (Figs 5H; 8A).

Second leg similar to that of the female (Figs 5E; 8B). The cuticular folds have fringes, and in-between these folds, crescent-shaped comblike borders of setules are present (Fig. 8C).

The third and fourth legs are found on ventrolateral wall of genital complex; represented by two subequal setae from a common convex base, and a single seta protruding from a very small base, respectively (Fig. 5I-J). These vestiges are seen both dorsally and laterally and are situated approximately  $200 \,\Box$ m posterior to base of second leg and c.  $200 \,\Box$ m from base of the third leg, respectively (Fig. 5A).

#### DISCUSSION

#### General morphology

Jones (1985) measured 112 female specimens of *H. hippoglossi*, from different American, Danish and British localities, and found that they ranged from 3.52-8.42 mm in length. Our smallest (2.6 mm), and largest (9.3 mm) both exceed his range. Scott (1900) has, however, reported two specimens 9.0 and 9.5 mm long, the latter being the longest *H. hippoglossi* known to date. Wilson (1932) gave a range of 6-8 mm and Ronald (1958) 7-9 mm in his material from the Gulf of St. Lawrence. Kabata's (1979) specimens range from 3.9-5.8 mm. We agree with Jones (1985) that this large variation makes size a poor character for identification of *H. hippoglossi*.

The mean length of our female parasites from different fishes varied less (5.5-7.8 mm) than in Jones' (1985) samples, which varied between 4.2 and 7.7 mm. The grand mean length of 7.4 mm, based on our total material, shows that the present female *Hatschekia* were generally longest, which is in accord with previous findings, where specimens from Greenland waters are the longest ones (Jones 1985). The mean width of the trunk, however, was approximately the same (1.2 mm) in our material and that of Jones (1985).

The egg string length is variable although it is mentioned as a distinctive feature by several authors (Jones 1985). The variation in the length of egg string in the present material, 1.5-15.0 mm, implies that an egg string may be up to the double of the length of the female. The longest egg string in our material was longer than those found by Krøyer (1837), Wilson (1932), Ronald (1958), and Scott (1900) reporting length of 8, 10, 10, and 13.5 mm, respectively. Generally, *Hatschekia* species have short egg

strings, rarely more than 10 eggs, usually 1-3 (Jones 1985). The type species *H. hippoglossi* is thus especial, being a large subarctic species with long egg strings.

Jones (1985:216) mentioned that *H. hippoglossi* has oviducts 'near the posterior margin merging into 1-segmented abdomen'. In contrast *H. pholas* (Wilson, 1906) has its oviducts on a separate small segment between genital complex and abdomen. Jones (1985) also states that it is unfortunate that there are so many intermediate examples, such as *H. quadrabdominalis* Yu, 1933, where the oviduct openings are on the abdominal segment, that no clear generic differences can be defined. We have shown that oviduct openings (and copulatory pores, sensu Huys & Boxshall 1991) in the type species are situated on the abdominal segment as in *H. quadrabdominalis*.

## Comparison with Kabata's (1979) description of the female

Kabata (1979) has illustrated the same female both in relaxed and contracted position and thus verified the large proportional differences which may be found among preserved specimens. The relative differences in length and width of females presented above must be interpreted as a guidance, but the body proportions are in accordance with that given by Kabata (1979).

According to Kabata (1979) the posterolateral corners of the trunk do not usually protrude beyond the posterior abdominal region, and the abdomen is not clearly delimited from the trunk. In our material the abdomen is clearly delimited from trunk, but extends shorter posteriorly than the posterolateral lobes. Kabata (1979) stated that the 'entire cuticle is covered with sparse denticulation'. Our SEM photos clearly show this is not correct, the larger part of skin is in fact without denticles at all.

Except for an extra seta on the basal segment of antennule and three extra setae on the terminal segment (se below), the segmentation and setation is in accordance with that described by Kabata (1979). The segment which in the present paper is described as number four in the antennule, may be interpreted as two segments; each with a single seta.

Kabata (1991) has described a 'standard' apical armature of hatschekiids with numbered elements, altogether 11 setae and an aesthetasc. His description of the terminal armature on the antennule of *H. hippoglossi* fits his generalised scheme (Kabata 1991). We have found the same numbered elements plus three extra setae: a relatively short one close to the two terminal ones, an additional long and thin one on the posterior margin, and somewhat more proximally; a slender seta on the posterior margin. The latter corresponds to the extra seta found in some species other than *H. hippoglossi*, ringed in his illustrations (Kabata 1991).

It should be remembered that a slight rotation of the antennule will often cause a profound change in the appearance of the apical structure, moving out of sight some of its components or displaying them more prominently (Kabata 1991). Moreover, the fragility of the setae makes them liable to damage during the process of dissection and mounting. We are well aware of these facts, but can assure that the description of the 15 elements of the antennule is based on studies of a large number of SEM photographs as well as light microscopy.

The antenna, parabasal papilla, mandible, and the typical branchiform maxilla are principally as described by Kabata (1979).

The frontal organ consists of uniform, closely packed papilla and is not unlike the filament gland of *Lepeophtheirus pectoralis* described by Anstensrud (1990). This may signify that hatschekiids too are attached to their hosts with a filament at some point in their development.

Kabata's (1979) description of the maxillule is defective, missing the most centrally situated outgrowth (cirrus) from the endopod ramous. The maxillule has the biramous form which appears to be the most common form (Kabata 1991).

The gross morphology of the legs is in accordance with Kabata's (1979) description, except the fourth leg which consists of a single seta only. As the present description is more detailed, we could show that both pinnate and plumose setae can be found on hatschekiid biramous legs, contrary to Kabata (1991). Furthermore, we give information on reproductive orifices, central organ, the central protuberance, and other morphological structures which were not mentioned by Kabata (1979).

Comparison with Scorr's (1901) description of the male The description of the male was, as mentioned, published with a short text and a single drawing (Scott 1901, pl. VII:11). The parasite was about 1.5 mm long, 0.2 mm longer than the longest male in the present material.

The antennule, like those of the female, is shown as five jointed, thus SCOTT failed to notice that the terminal segment is divided. The antenna resembled those of the female, but it was much more strongly hooked (SCOTT 1901). These hooks were large and strong, projecting well in front of cephalothorax. By comparing his figure of female hook (SCOTT 1900, pl. VII:3) with his male drawing (SCOTT 1901, pl. VII:11) one gets the impression that the curvature of the claws is the same. In our view his drawing of male antenna shows hooks with curvature more similar to that of female than to our males (cf. Figs 1E & 5C) but, as mentioned previously, the shape of the hook varies with visual angle.

In Scott's description the head was proportionally larger, the thorax more distinctly segmented, and the genital segment considerably shorter than in the female. The abdominal appendages were more prominent and elongated, as shown by the drawing (Scott 1901:126, pl. VII:11). By comparing Scott & Scott's illustration of the male (1913, here reproduced in Fig. 5L) with our representative (Fig. 5A), one must admit that the resemblance is not close. Both drawings show parasites of approximately the same size, where the shields of cephalothoraces are large, with laterally protruding antennules. Moreover, the relative length of genital complex is of the same order of magnitude, and the abdomen carries long appendages. In addition Scott (1901) illustrated the antennae as protruding anteriorly from cephalothorax, a position not seen by us. The antennae are, however, principally similar as commented previously. Other appendages are not mentioned nor illustrated by Scott (1901). The prominent maxilla and the two pairs of legs which contribute to the appearance of the male, are not included in the description. Furthermore, there are clear differences in the thorax. It is more distinctly segmented in Scott's male than in his female, whereas no sutures are seen in our male specimens. Furthermore, the shape of genital complex is different. In Scott's specimen the lateral sides are roughly parallel but wavy, and the posterolateral corners have short, rounded lobes protruding to the posterior margin of abdominal region, as in the female. Our males have a club-shaped trunk without posterolateral corners protruding posteriorly. The abdomen is narrow and clearly delineated dorsally in Scott's male, which is not in accordance with our findings. The general shape of trunk, its posterior border and the broad abdomen is clearly different in the parasites being compared.

All other characteristic morphological structures described in the present paper have not been depicted by Scott (1901).

#### Comparison with Hatschekia reinhardtii

Wierzbicka (1989) has described both sexes of a new Hatschekia species, H. reinhardtii from Greenland halibut Reinhardtius hippoglossoides (Walbaum, 1792), caught in eastern Bering Sea (North Pacific). This parasite is according to Arthur & Albert (1994) only known from the original findings of Wierzbicka (1988; 1989). Neither H. reinhardtii nor its near relative H. hippoglossi were found by Wierzbicka (1989) on a much larger fish material of Greenland halibut (261) caught off Labrador and in the Barents Sea, i.e. on locations connected to the Atlantic Ocean. These negative findings have been supported by ROKICKI (1982) and ARTHUR & ALBERT (1994), who did not find any Hatschekia species in a survey of parasites of Greenland halibut caught off Atlantic Canada. Zubchenko (1980) has, however, found H. hippoglossi on both Atlantic and Greenland halibut from the Northwest Atlantic, but he found only three specimens of H. hippoglossi on a

Greenland halibut, which is the sole report of this specimen on this host (Arthur & Albert 1994). In a recent book Kabata (1992) has added Greenland halibut to the host list of *H. hippoglossi*. This parasite has, however, only been reported from fishes caught in northern seas that have connection to the Atlantic ocean, and never in the northern Pacific. Halibut and Greenland halibut have overlapping distributions in the Northeast Atlantic (Wheeler 1978), but Greenland halibut is also distributed in the North Pacific (Masuda & al., 1984).

Wierzbicka's (1989) drawings of female *H. reinhardtii* show a general appearance similar to *H. hippoglossi*, but the former were longer (6.0-11.5 mm) and wider (1.5-2.1 mm), and bore egg sacs up to 22 mm, much longer than the longest *H. hippoglossi* strings in present material (15.0 mm). According to Wierzbicka (1989) the trunk is 6-9 times longer than cephalothorax, which is not in agreement with her drawings (4-5 x). The trunk of *H. reinhardtii* has rounded lobes which usually do not protrude beyond posterior margin and cuticular teeth covering the entire body except the dorsal shield (Wierzbicka 1989). This does not distinguish *H. reinhardtii* from *H. hippoglossi*, as described by Kabata (1979). The information above, on relative length of trunk and distribution of cuticular teeth in *H. reinhardtii*, is not in accordance with our findings.

Wierzbicka's (1989) illustrations of *H. reinhardtii* generally agree with ours. Thus its antennule carries 15 terminal elements and maxillule is a biramous appendage. The first two legs are biramous, generally similar to that of the present material, but only three terminal setae are present on the endopod of the first leg (one seta missing?). The material for the description of the female parasites is not given, but four of seven fishes were parasitized with intensity 1-36 crustaceans per fish.

The drawing of male *H. reinhardtii*, based on two specimens, shows a parasite with more rounded cephalothoracic shield, wider than long, and a broader thorax and trunk, than our *H. hippoglossi* male. The two measured 1.8-1.9 mm in length and 0.40-0.45 mm in width, i.e. they were 0.8-0.9 mm longer, and their trunk 0.22 mm broader than that of our *H. hippoglossi*. The cuticular ridges on the head are, however, generally similar to those of our males. The trunk of *H. reinhardtii* is broadest halfway down its length, tapers terminally, and its abdomen is different from *H. hippoglossi*«s. The caudal rami of *H. reinhardtii* are relatively shorter and thicker than those of *H. hippoglossi*. Numerous cuticular teeth were observed on the genital trunk, but their distribution pattern was not reported.

According to Wierzbicka (1989) the morphology of the antennule of male and female is almost identical. The fourth segment of the antennule of the male has one extra seta, as in present *H. hippoglossi*, and the antenna has a spine at the base of the terminal segment (present material: 2). The other appendages are morphologically identical in the two

sexes of *H. reinhardtii*. This implies that there are only three terminal setae on endopod of first leg (four in present material). The male setae are, however, longer and plumose, different from the female's. The caudal rami of *H. reinhardtii* are relatively short and thick, blunt apically as in the female. They differ from that of *H. hippoglossi* which is much longer and slimmer in the male. Furthermore, the terminal and lateral processes are longer and end in setiform outgrowths (both sexes) which are different from the short and thick processes of *H. reinhardtii*.

Wierzbicka (1989) writes that the female morphology of the parasites from Greenland halibut is close to that of *H. hippoglossi*, but points out 'certain very important differences', one of these is the number of elements on the terminal part of the antennule. *Hatschekia hippoglossi* as described by Kabata (1979) has 12 elements, whereas *H. reinhardtii* has 15. As shown, the parasites of our material all carry 15 elements.

Wierzbicka's (1989) second point relates to the maxillule. As stated, Kabata's (1979) description of this appendage is defective, the largest tapering process of the endopod was missing. We have found that the maxillule of *H. hippoglossi*, (both sexes) is principally similar to that of *H. reinhardtii* so in neither of these respects there are differences between the two species.

Wierzbicka (1989) has also discussed differences in armature terminally on the endopod of the first leg, three setae in *H. reinhardtii* and four in *H. hippoglossi* (Kabata 1979). We document the presence of four setae in *H. hippoglossi*. Possibly one seta, presumably the most medial one, was overlooked in Wierzbicka's (1989) study.

Wierzbicka's (1989) last point relates to difference in shape and ornamentation of caudal rami. As mentioned above, the caudal rami of *H. hippoglossi* seem to be slimmer than those of *H. reinhardtii*, but we are not convinced that the drawings of Wierzbicka give the correct impression of their morphology. One long and two unequal setae on the caudal ramus were found by Kabata (1979), Wierzbicka (1989) and the present authors. The presumed difference, however, relates to the armature on the two lateral processes and the terminal end of the caudal ramus, that of *H. reinhardtii* were said to be 'covered with thin hairs'. Although Kabata (1979) did not mentioned any terminal ornamentation, we have found setules on caudal rami of both sexes of *H. hippoglossi*.

Most of the differences between Wierzbicka's (1989) description of female *H. reinhardtii* and Kabata's (1979) description of *H. hippoglossi* could also be seen on material of *H. hippoglossi* from halibut borrowed from Berlin Museum. Wierzbicka's drawings of maxillule, first leg and caudal ramus (Wierzbicka 1989, fig. 13) 'conform to Kabata's descriptions and confirm the existence of the differences discussed' (Wierzbicka 1989). We do not share her opinion. The maxillule is just as inaccurately described

as that of Kabata's, and although the setae of first leg now are in agreement with Kabata's and our findings, we think that the first leg of his parasites missed one seta. Although her drawing of the caudal ramus, based on museum material, is more like our illustrations, but without terminal ornamentation, the small differences seen in caudal rami of *Hatschekia* cannot justify a description of a new species. We thus conclude that *H. reinhardtii*, Wierzbicka is a synonym of *H. hippoglossi* (Guérin-Méneville). This conclusion is also based on the fact that there is disagreement between her text and drawings, which do not show the necessary details.

#### Comparison with other hatschekiid males

Nunes-Ruivo (1954:488-489) described both sexes of Hatschekia petiti. She found a single male, 0.5 mm long, attached to the posterior part of the genital complex of a female. The male, measuring 1/3 of a female, bore a clear resemblance to that of H. hippoglossi. It had a cephalothorax shield longer than broad, a thorax without real constrictions, only indicated just posterior to the third leg. The trunk was subcylindrical, the abdomen with caudal rami more developed than in female. The antenna carried a claw-like prominent process on second segment not unlike the smaller flange found in the male H. hippoglossi, and a single seta on the base of the recurved terminal claw (two in H. hippoglossi). Hatschekia petiti carried long caudal rami, but with armature different from that of H. hippoglossi. There are also other differences between the males of the two species, but descriptions do not allow a closer comparison. However, the male of H. petiti shows many points of generic resemblance to the male of H. hippoglossi. These species have clear similarities in gross morphological features of body and appendages, which may be interpreted as general male morphology of a Hatschekia species.

Cressey (1968) redescribed Hatschekia conifera and described the male for the first time. He found 12 males, total length 1.12 mm which corresponds to approximately 40 % of the female length. The male of H. hippoglossi resembles that of H. conifera. It has a cephalothoracic shield as long as wide, comprising about one-fourth of total length. The first and second thoracic segments were separated. The trunk was barrelshaped, with ventral sinus near terminal end, as in H. hippoglossi, and 'ventral surface covered with delicate scales'. The abdomen was 1-segmented with relatively short caudal rami. In the male an armature was present on the antenna whereas that of the female was nude. The first and second legs were biramous with 'scale like processes' and with long plumose setae, longer than that of female. As the male of Hatschekia petiti, that of *H. conifera* shows many points of generic resemblance to the male of *H. hippoglossi*. Thus this drawing of the male of *H. conifera* (Cressey 1968: fig. 2C) is the published illustration which shows the greatest resemblance to the male of *H. hippoglossi*.

The male of *Hatschekia pinguis* which was described by Wilson (1908:456-458, pl. 75) is morphologically quite different from that of *Hatschekia hippoglossi*, but there are some similar features. It is 0.85 mm long, approximately half that of the female, and its cephalothorax is equipped with cuticular ridges. The abdomen is 1-segmented with caudal rami considerably longer than abdomen.

WILSON (1913) also described both sexes of *Hatschekia iridescens*. He found two males, 1 mm long, attached to the gill filaments of the host. The male (Wilson 1913: 249-250, pl. 44, fig. 247), which measured 1/3 of a female length, was similar to the female, but quite different from that of *H. hippoglossi*. The male appendages and caudal rami were longer and more slender than that of the female.

Pearse (1947) described *H. prionoti* where the male was clinging to the ventral posterior part of female trunk. Both sexes were redescribed by Jones (1985). The male (Pearse 1947:12) was 0.59 mm long, somewhat longer than half that of the female (1.0 mm), and had a cylindrical body much broader than that of male *H. hippoglossi*, although superficially similar to it. As in the male *H. hippoglossi*, the posterior end of the genital segment was bilobed, and the lobes met ventrally in a long sinus (Pearse 1947, fig. 43).

Pearse (1948) described both sexes of *Hatschekia harkema*. The male was minute, only 0.4 mm long, compared to the females measuring 1.8 to 2.4 mm (Pearse 1948:131). The head of male was slightly wider than long. Other thoracic segments and genital complex were fused, the former as broad as the head, the latter much thinner, only half as broad as the cephalothorax shield. The description is short and the single drawing highly stylised, but this male does not resemble the male of *H. hippoglossi* at all.

Brian (1906:70, pl.III, fig. 4) described a male (*Hatschekia* sp.) which could be *H. gerro* Leigh-Sharpe, 1936, *H. labracis* (VAN BENEDEN, 1871) (cf. Jones 1985:240) or *H. pygmaea* T. Scott, 1913 (cf. Jones 1985:262). Brian's description of the 0.5 mm long male and the highly stylised drawing cannot be used for comparison. The specimen shows a superficial similarity with the male *H. harkema* both having cephalothorax twice as broad as trunk. None of these males bear the slightest resemblance to the present male.

Generally, *Hatschekia* males have in common enlarged antennae, distinct segmentation of the thorax, genital complex and abdomen clearly visible and larger caudal rami than females. On several males the appendages are longer, more slender and setae on the legs longer than in the females. The antennae are equipped with armature not found

in the female. Finally, the male trunk has more pronounced, and different denticulations than that of the female.

Males of all species are much smaller than females. Their length constitutes between 16 % and 32 % of female H. reinhardtii, which is the longest Hatschekia that has been described (1.8-1.9 mm). The length of *H. hippoglossi* males constitute approximately 16 % of female, varying between 13% of long females and up to 39 % in younger (shorter) specimens. The other males are shorter than c. 1 mm. Except for the smallest male H. harkema (0.4 mm), which has a length 16-22 % of female, the other species have males with lengths constituting between 1/3 and 1/2 of female, i.e. the males of small-sized species are proportionally longer in relation to their females than are those of their larger relatives, such as H. hippoglossi and H. reinhardtii. The scarcity of male records may in part be due to their diminutive size; they are easily overlooked. Moreover, males are mobile and those few described have been found free in the samples or clinging to females.

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