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BULLETIN OF THE FISHERIES  
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## Nearctic and Palaearctic *Heterotrissocladius* (Diptera:Chironomidae)



Ole A. Sæther


 Fisheries and Environment Canada  
 SH 223  
 B8213  
 no. 193  
 JC

BULLETIN 193  
1975

Fisheries and Environment  
 Service des pêches  
 et des sciences de la mer



Nearctic and Palearctic

*Heterotrissocladius*

(Diptera: Chironomidae)

Bulletins are designed to interpret current knowledge in scientific fields pertinent to Canadian fisheries and aquatic environments. Recent numbers in this series are listed at the back of this Bulletin.

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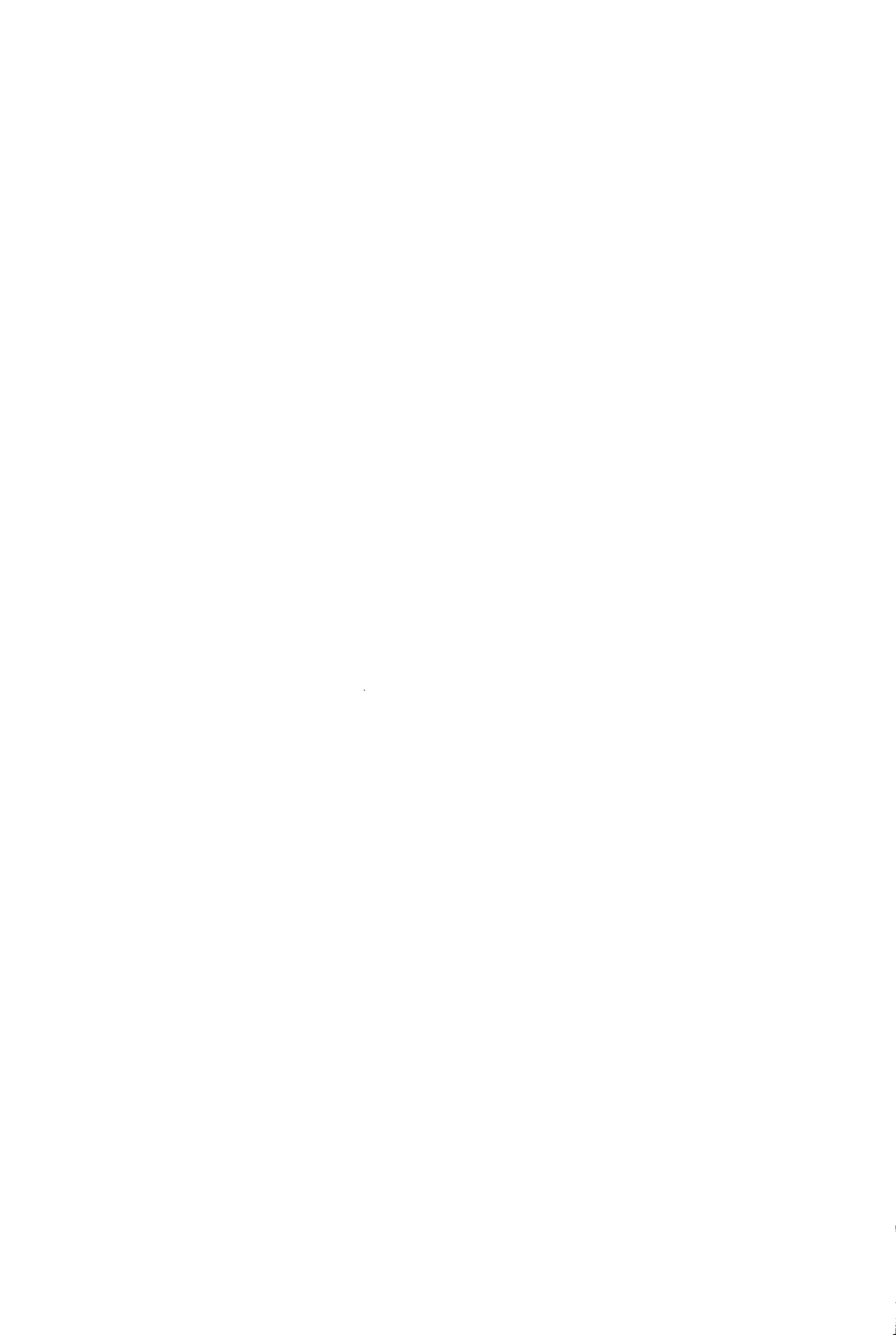
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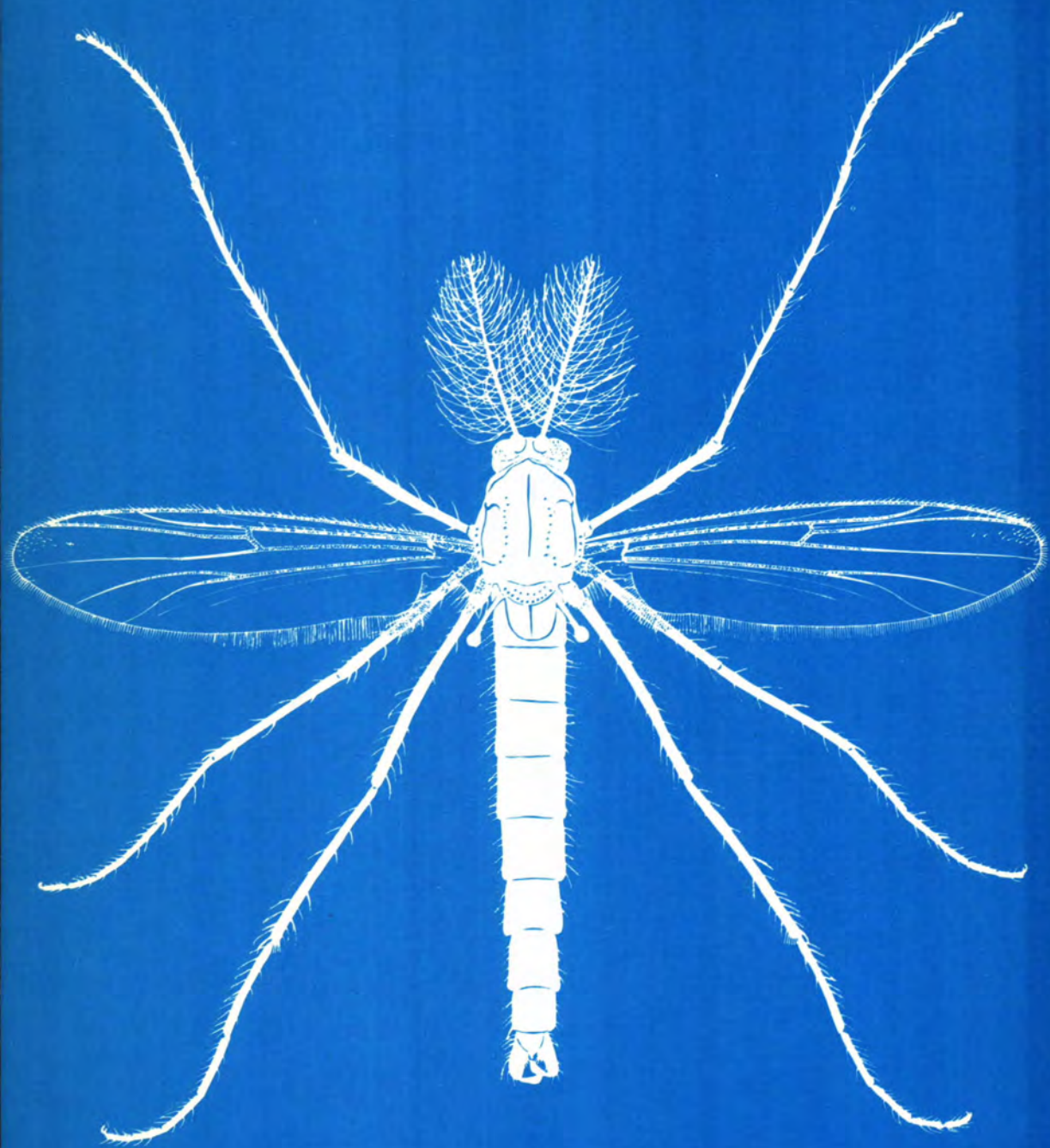
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K1A 0H3





*Heterotrissocladius oliveri* sp.n., male

Nearctic and Palaeartic  
*Heterotrissocladius*  
(Diptera: Chironomidae)

OLE A. SÆTHER

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DEPARTMENT OF THE ENVIRONMENT  
FISHERIES AND MARINE SERVICE

*Ottawa 1975*

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Canada: \$3.50

N° de catalogue Fs 94-193

Autres pays: \$4.20

*Prix sujet à changement sans avis préalable*  
Information Canada  
Ottawa 1975

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## Abstract

SÆTHER, O. A. 1975. Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 193: 67 p.

New descriptions, redescrptions, taxonomical and ecological comments, and distribution records are given for 15 species of *Heterotrissocladius* Spärck. Four new species are described in all stages: *Heterotrissocladius oliveri*, *Heterotrissocladius latilaminus*, *Heterotrissocladius hirtapex*, and *Heterotrissocladius changi*. The male of one new species, *Heterotrissocladius cooki*, is described. Two other species, *Heterotrissocladius grimshawi* (Edw.) and *Heterotrissocladius scutellatus* (Goetgh.), are redefined. Altogether eight species are completely described. Descriptions of the male, pupa, and larva of one species; the male of one species; the pupa and larva of two species; and the larva only of three species, are also provided.

Keys are given for male and female imagines, pupae, and larvae of the known Nearctic and Palaearctic species of the genus.

The phylogeny of the genus and of three related genera, *Paratrissocladius* Zavř., *Parametrioctenus* Goetgh., and *Paraphaenocladius* Thien., is discussed. Sixty-one trends have been deduced and a kladogenetic diagram erected showing *Paratrissocladius* as the sister group of *Heterotrissocladius*, and *Parametrioctenus* plus *Paraphaenocladius* as the sister group of the two first genera combined. *Heterotrissocladius* can be divided into three species groups with the *subpilosus* group being the sister group of the *maeaeri* and *marcidus* group combined.

The ecology of the species is discussed pointing out their important position as members of ultraoligotrophic and/or moderately oligotrophic lakes.

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## Résumé

SÆTHER, O. A. 1975. Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 193: 67 p.

L'auteur donne des descriptions nouvelles, des redescrptions, des commentaires taxonomiques et écologiques, et des signalements touchant 15 espèces d'*Heterotrissocladius* Spärck. Il décrit quatre nouvelles espèces à tous les stades: *Heterotrissocladius oliveri*, *Heterotrissocladius latilaminus*, *Heterotrissocladius hirtapex* et *Heterotrissocladius changi*. Il décrit le mâle d'une espèce nouvelle, *Heterotrissocladius cooki*. Il redéfinit deux autres espèces, *Heterotrissocladius grimshawi* (Edw.) et *Heterotrissocladius scutellatus* (Goetgh.).

Il donne des clés pour l'identification des imagos, pupes et larves mâles et femelles des espèces néarctiques et paléarctiques connues du genre.

Il analyse la phylogénie du genre et celle de trois genres apparentés, *Paratrissocladius* Zavř., *Parametrioctenus* Goetgh. et *Paraphaenocladius* Thien. Il en déduit 61 tendances et construit un diagramme kladogénétique montrant *Paratrissocladius* comme groupe-sœur d'*Heterotrissocladius* et de *Parametrioctenus*, et *Paraphaenocladius* comme groupe-sœur des deux premiers genres combinés. *Heterotrissocladius* peut se diviser en trois groupes d'espèces, le groupe *subpilosus* étant le groupe-sœur des groupes *maeaeri* et *marcidus* combinés.

Il examine l'écologie des espèces, faisant ressortir leur importante position comme membres de lacs ultra- ou modérément oligotrophes ou les deux.

## Introduction

The validity of chironomids as indicators of trophic levels in areas outside Europe is treated by Brundin (1956b). He demonstrated that the typology founded on chironomids probably has a world-wide validity, not only with regard to causal ecological principles, but also with regard to most of the different types of indicator communities chosen. The species may not be the same, but they are replaced by species within the same species groups or at least by species within the same genus or closely related genera. One major shortcoming, as mentioned by Sæther (1973) in an analysis of Nearctic benthic chironomid samples, is the lack of knowledge of the specific identities of the typologically more important animals. This has prevented the development of valid lists of indicator communities with the exception of the ultraoligotrophic communities described by Oliver (1963, 1964, 1968). The paucity of information on the zoogeographic distribution and general ecology of these species has further limited their prospective usefulness.

Sæther (1973, 1975a, b) has described several species of genera containing important members of ultraoligotrophic, moderately oligotrophic, and mesotrophic communities and has been able to develop preliminary lists of indicator communities for North America (Sæther 1975c). Whereas the other papers and a paper in press treat genera such as *Monodiamesa* Kieff., *Protanypus* Kieff., *Heterotanytarsus* Spärck, *Hydrobaenus* Fries, *Zalutschia* Lip., *Trissocladius* Kieff., and *Paratrissocladius* Zavř., the present paper compares the Nearctic and Palaearctic species of the genus *Heterotrissocladius* Spärck.

Although many records of *Heterotrissocladius* from North America can be found (Edwards 1935a, p. 472; Oliver 1963, p. 177; 1964, p. 79; 1968, p. 112; Hamilton 1965, part 2, p. 58; 1971, p. 259; Henson 1966, p. 47; Frantz and Cordone 1966, p. 10 [as *Metriocnemus* near *lundbecki* Joh.]; Sæther 1967b, p. 200; 1969, p. 45; 1970a, p. 12; Brinkhurst et al., 1968, p. 17; Schneider et al., 1969, p. 83 [as *Metriocnemus*]; Hiltunen 1969a, p. 48; 1969b, p. 129; 1971, p. 21; Johnson and Brinkhurst 1971, p. 1691; Sæther and McLean 1972, p. 9; Kinney 1972, p. 58; Mozley and Garcia 1972, p. 104; Welch 1973, p. 1115), none of these have been correctly identified to species. However, in most cases this was due to a lack of comparative European material of *H. subpilosus* (Kieff.); most records concern *H. oliveri* sp.n., a closely related sister species of *H. subpilosus*. Several others are also closely related sister species of European taxa and it was, therefore, necessary to examine the European members of the genus.

The male, female, pupa, and larva of four and the male, pupa, and larva of a fifth Palaearctic species, one of them Holarctic, have been redescribed. The male, female, pupa, and larva of four, the male of one, the pupa and larva only of two, and the larva only of three additional, exclusively Nearctic species are described. Altogether 15 species are described. If the apparent zoogeographic distribution is taken into account the larvae can be separated although not as readily as, for instance, in *Monodiamesa* Kieff. As the genus *Heterotrissocladius* contains some of the most important members of ultraoligotrophic and moderately oligotrophic lake communities the value of being able to distinguish the immatures is obvious.

## Methods and Morphology

The mounting procedure used is outlined by Sæther (1969, p. 1). In general the terminology follows Sæther (1971, 1974). Characters not mentioned there, and measurements and ratios, follow Schlee (1966) with the additions and modifications given by Sæther (1969). The terminology of sensillae follows Serra-Tosio (1970).

Although Hirvenoja (1973) to a large extent followed the same lines of reasoning as Sæther (1971) their conclusions concerning the terminology are often different. Some of these differences deserve further discussion and will be treated elsewhere. Some terms used by Hirvenoja are adopted here: brachiolum instead of basal vein or stem vein, laterosternite IX instead of laterotergite IX as used by Wensler and Rempel (1962, p. 201) and Sæther (1971, p. 1249), proctiger for the caudal lobe of tergite IX, and crista dorsalis is used for the preapical dorsal tooth or projection of gonostylus. The tarsal "Sinneszapfen" (SZ) of Hirvenoja is called sensilla chaetica here; although these are present in at least the females of many genera of Tanypodinae, Diamesinae, Orthocladinae, and Chironominae their taxonomical and phylogenetic importance were not noticed until pointed out by Hirvenoja (1973).

Hansen (1973) suggested that the cardo has been lost in most chironomids and that the dorsal-most projecting region of the maxilla is still part of the stipes. This is in contrast with Sæther (1971, p. 1245) who regarded the cardo as completely fused with the stipes. There seems to be reason to accept Hansen's argument and adopt the term stipes instead of cardostipes. The "vein" marked as  $Cu_2$  in Sæther (1969, figure 2B) is not really a vein but the vannal fold or plica vannalis as defined by Snodgrass (1935, p. 225, 244) and pointed out by Hansen (1973). Hansen also called the brachiolum (stem vein, basal vein) the remigium. Snodgrass (1935, p. 225, 244), however, defined the remigium as the wing area anterior to the vannal fold, and to avoid any ambiguities it seems better to use the term brachiolum.

The larvae of *Heterotrissocladius* have two lamellae between SI and pecten epipharyngis. These lamellae are called labral lamellae here.

A few new abbreviations are adopted here: T/A is the ratio of the length of the thoracic horn in the pupa to the length of the anal macrosetae; V/M is the ratio of the width of the larval ventromental plate measured as shown in Fig. 4H (VW) to the width of one median tooth including any remaining lateral notch; Sa/An is the length of the larval supraanal setae to the length of the anal setae.

It is important to remember that the legs are measured as outlined by Schlee (1966) and not as maximum lengths. The proximal elongation of the femur for instance is not included in the leg measurement. Particularly the length of the femur, the tibia, and the fifth tarsomere will be quite different from a straight maximum length measurement. Unfortunately, many authors fail to mention how their measurements were taken and a comparison is often impossible. The wing length is measured from the arculus. The total length of the imago is measured as the length of the thorax plus the length of the abdomen from the anteriomedian margin of the first tergite to the apex of the gonocoxite or the cercus (Sæther 1969, p. 2). In many cases, however, the abdominal segments are either telescoped into each other or stretched apart. In such cases the abdomen is measured as the sum of the lengths of the segments not including the conjunctives.

In the following description the measurements are given as ranges followed by a mean value when four or more measurements have been taken, followed by a number in parentheses giving the number measured (n).

Holotypes, allotypes, and if sufficient material is available, some paratypes have been deposited in the Canadian National Collection (CNC) in Ottawa. Remaining paratypes have been returned to lender or are retained in the collection of the Freshwater Institute, Winnipeg, Manitoba.

## *Heterotrissocladius* Spärck 1922

Type species: *H. cubitalis* Kieffer 1911 (? *marcidus* Walker 1856)

### IMAGO

**Diagnosis:** Eyes naked, dorsally elongated. Temporal setae well developed, inner verticals shorter than outer verticals but not set off from these, postorbitals more or less set off from outer verticals. Antep pronotum normally developed, median lobes not joined anterior to scutal projection. Dorsocentrals and prealars numerous. Acrostichals very long and strong and starting at scutal projection (*marcidus* group), longer than normal starting some distance from scutal projection (*maeeri* group), or weak or absent in the centre of scutum (*subpilosus* group). Wing membrane fully haired to void of setae in male, fully haired to a few apical setae in female. Anal lobe well developed, slightly protruding to obtusely rounded. Costa and  $R_{4+5}$  ends exactly at same place distal of  $M_{3+4}$  forming a weak notch in wing margin.  $R_{2+3}$  ends in the middle between  $R_1$  and  $R_{4+5}$ . FCu clearly distal of RM.  $Cu_1$  distinctly curved. An ends far distal of FCu. Squama fully fringed. Pulvilli absent. Tarsal pseudospurs absent. Hind leg with a beard. Sensilla chaetica absent or only 1 or 2 on  $ta_1$  of  $p_3$  in male, present on  $ta_1$  of  $p_2$  and  $p_3$  in female. Anal point long, strong, and conical, without microtrichia at apex and with setae of anal point and tergite IX numerous, but short and reduced. Phallapodeme normal. Sternapodeme normal with normal oral projections. Gonocoxite with more or less rounded triangular basal lobe. Gonostylus with crista dorsalis. Tergite IX of female divided into two setigerous protrusions. Gonapophysis VIII with very well developed dorsomesal and ventrolateral lobes and relatively distinct apodeme lobe. Gonocoxite normal, with several setae. Spermathecal ducts with strong angle or loop and with small bulbs before common opening. Labia relatively well-developed with indication of microtrichia. Cerci normal.

**Description:** Coloration uniformly brown to black. AR = 1.0–2.1 (1.0–1.2 in the *maeeri* group, 1.2–1.8 in the *marcidus* group, 1.4–2.1 in the *subpilosus* group). Thirteen flagellomeres in male, 5 or 6 (nearly always 5) in female, antennal groove reaching flagellomere 3–5; flagellomeres 2–4 with sensilla chaetica. Tentorium with microtrichia in anterior half. Palp 5 segmented, normal, with 2 or 3 sensilla chaetica at apical sensillum coeloconicum. Temporals 10–27. Clypeus with 2–4 setae. Antep pronotum with 6–16 setae. Dorsocentrals 18–35, prealars 5–14. The *subpilosus* group with or without 2–8 weak acrostichals in the center of scutum, i.e. as in *Hydrobaenus* Fries and *Zalutschia* Lip. (*Trissocladius* Brund. nec Kieff. pro parte); *maeeri* group with 5–10 strong acrostichals (about as strong as in *Bryophaenocladus* Thien.) starting some distance from scutal projection; *marcidus* group with 6–35 very long and strong acrostichals (as strong as in *Metriocnemus* v.d. Wulp and *Parametriocnemus* Goetgh.) starting at scutal projection (Fig. 6A). Scutellum with 8–24 setae in single to double transverse row (most numerous in *H. scutellatus* (Goetgh.) and *H. cooki* sp.n. with 22 or 23 setae and 13–24 setae respectively). Wing length 1.9–3.3 mm. Wing with only a few setae on the membrane, usually none on media and its branches, or cubitus and branch in the *subpilosus* and *maeeri* groups. The *marcidus* group with chaetotaxy ranging from that of *H. grimshawi* (Edw.) (generally with the smallest number of setae without setae on subcosta, M, Cu, An, and sometimes  $M_{3+4}$ , Cu, and vannal fold) to that of *H. marcidus* Kieff. with numerous setae on all the above-mentioned veins. Second most hairy wings

found in *H. scutellatus* Goetgh. followed by *H. cooki* sp.n. *Heterotrissocladius latilaminus* sp.n. and *H. hirtapex* sp.n. have wing chaetotaxy closest to that of *H. grimshawi*, whereas *H. changi* sp.n. intermediate between these and *H. cooki* sp.n. Sensilla campaniformes about 9–14 at base of brachiolum, 3 below setae of brachiolum, about 8–10 at apex of brachiolum, 1 at base of subcosta, 1 at base of  $R_1$ , and 1 on FR or on base of  $R_{4+5}$ . VR = 1.10–1.24. Squama with 10–48 setae in male, 21–49 setae in female. Sensilla chaetica absent in males of the *subpilosus* group; usually absent, but occasionally 1 or 2 on  $ta_1$  of  $p_2$  in *maeaeri* and *marcidus* groups. Females with 2–21 sensilla chaetica on  $ta_1$  of  $p_2$ , 8–25 on  $ta_1$  of  $p_3$ . LR<sub>1</sub> = 0.72–0.92, lowest in *H. maeaeri* Brund. and *H. subpilosus* (Kieff.). Bristle ratio 4.4–7.3 on hind leg of male, 2.9–5.2 on hind leg of female. Setae of tergites scattered without any obvious pattern. Setae of sternites in median and lateral rows. Tergite IX with 16–44 setae in male, 22–48 setae in female. Hypopygium as well as female genitalia very similar in all species. Differences in the hypopygium primarily consist of the shape of gonostylus (with or without outer corner) and its crista dorsalis (large and rounded or small and pointed).

## PUPA

**Diagnosis:** Frontal setae present. Three precorneal setae in one regular or irregular row. Thoracic horn long, covered with spinules, with apical point. Thorax more or less rugulose. Wing sheath with “pearls” (rows of small, rounded tubercles along margin, e.g. Sæther 1969, figure 59B) (*subpilosus* group) or only with fine marginal lines (*maeaeri* and *marcidus* groups). Shagreen medially on tergites II–VIII and occasionally a few posterior spinules on I, shagreen weak on VII and VIII. Tergite II with weak, orally curved hooks. Pedes spurii B vestigial (*subpilosus* group), or well developed, as high as wide (*maeaeri* group) to much wider than high (*marcidus* group) (Fig. 5F). Pedes spurii A present on IV–VI (*maeaeri* group), IV–VII (*marcidus* group), or IV–VIII (*subpilosus* group). Segments I–VI with 3 or 4 (usually 3) hairlike L-setae. Segment VII with 3 or 4 filamentous L-setae, segment VIII with 3–5 filamentous L-setae (5 in the *subpilosus* group). Sternite VIII with posterior spines in males, with two triangular projections with imbedded spines in females. Genital sac of male overreaching anal lobe, with conical (*subpilosus* group) or long fingerlike (*maeaeri* and *marcidus* groups) apicolateral projection. Setae present (*subpilosus* group) or absent (*maeaeri* and *marcidus* groups) dorsad of genital sac on sternite IX. Anal lobe fully fringed with long setae. Three equally long anal macrosetae.

**Description:** Length 3.6–6.4 mm (smallest in *H. maeaeri* and *H. changi* sp.n.). T/A = 1.2–2.2 (highest in *H. maeaeri*). Thoracic horn 0.30–0.48 mm long, 4.1–8.3 times as long as wide. Posterior spines on sternite VIII of male 9–56, 4–50 of them longer than 10  $\mu$ . Anal lobe with 17–36 setae.

## LARVA

**Diagnosis:** Antenna 7-segmented, segment 3 much smaller than segment 4; segment 7 very inconspicuous, hairlike. Lauterborn organs absent or vestigial. Blade of basal segment as long as, longer (*subpilosus* group), or shorter (*maeaeri* and *marcidus* groups) than segments 2–7 combined. Subapical style of second segment distinct. SI plumose, other S-setae simple. Labral lamella divided into two rounded, pointed, or triangular lamellae. Pecten epipharyngis weakly sclerotized, consisting of three serrated scalelike spines. Chaetulae laterales simple. Chaetulae basales with apical serration. Premandible with two indistinct teeth. Apical tooth of mandible shorter than combined width of remaining teeth. Seta subdentalis normal. Seta interna present. Mentum with 1 (*maeaeri* group) or 2 median, and 5 pairs of lateral teeth. Median mental teeth with or without lateral notch. Ventromental plates relatively conspicuous, without setae underneath. Parapods, procerci, and anal tubules well developed.

**Description:** Length of fourth instar 4.2–9.5 mm. Head capsule 0.29–0.54 mm long. Postmentum 130–246  $\mu$  long. AR 0.9–1.3 in *marcidus* group, 1.1–1.4 in *maeaeri* group, 1.5–2.1 in *subpilosus* group. Basal antennal segment 58–96  $\mu$  long, 3.0–4.7 times as long as wide. Premandible 60–107  $\mu$  long. Mandible 118–208  $\mu$  long. V/M in species with one median tooth 0.39–0.96, in species with two median teeth 0.44–1.56. Submentum brown to black in *maeaeri* group, *H. marcidus*, *H. latilaminus* sp.n., and *H. hirtapex* sp.n.

**Key to males of Nearctic and Palearctic species of *Heterotrissocladius*<sup>1</sup>**

- 1 Clypeus swollen, wider than width of pedicel; cibarial pump constricted at base, conspicuously widened posteriorly, cornua strong, divergent (Fig. 1D, H); 0–8 acrostichals less than 35  $\mu$  long starting some distance from scutal projection; wing dark greyish brown, membrane with 0–114, often less than 20, setae in cells  $r_{4+5}$  and  $m_{1+2}$ ; media, cubitus, and their branches without setae..... *subpilosus* group 2
- Clypeus and cibarial pump normal; 5–25 long acrostichals, the longest at least 40  $\mu$ ; wing membrane with more than 20 setae; media, cubitus, and their branches usually with setae..... 3
- 2 HV = 2.8–3.1; gonostylus (Fig. 1E) rounded at apex or with indication of a weak outer corner, crista dorsalis usually only slightly protruding; anal lobe of wing not or only slightly protruding; cibarial pump (Fig. 1H) strongly constricted at base, minimum width 41–58  $\mu$  or 0.6–0.8 times the distance between apices of cornua; clypeus 1.32–1.64 times as wide as pedicel; acrostichals sometimes present;  $LR_1 = 0.79–0.86$ ..... *H. oliveri* sp.n. (Nearctic) (p. 19)
- ..... *H. subpilosus* (Kieff.) (Palearctic) (p. 11)
- 3 HV = 3.2–3.5; gonostylus (Fig. 1A) with distinct outer corner and protruding crista dorsalis; anal lobe of wing slightly protruding; cibarial pump (Fig. 1D) less strongly constricted, minimum width 54–64  $\mu$  or 0.8–0.9 times the distance between apices of cornua; clypeus 1.28–1.35 times as wide as pedicel; acrostichals absent;  $LR_1 = 0.77–0.80$ ..... *H. subpilosus* (Kieff.) (Palearctic) (p. 11)
- 3 Wing light, membrane with about 25–80 distal setae; acrostichals about 30–40  $\mu$  long, starting some distance from scutal projection; AR = 1.1–1.3;  $LR_1 = 0.72–0.76$ ; widened portion of stipes nearly meeting at midline (Fig. 5B); basal lobe of gonocoxite with long setae only on distal side (Fig. 5A)..... *maeaeeri* group: *H. maeaeeri* Brund. (Palearctic) (p. 22)
- ..... *marcidus* group 4
- 4 Wing darker, light grey to brownish grey, membrane with a few hundred setae; acrostichals about 45–90  $\mu$  long starting at scutal projection (Fig. 6A); AR = 1.2–1.8;  $LR_1 = 0.76–0.92$ ; widened portion of stipes less projecting (Fig. 6C, F, G, I); basal lobe of gonocoxite at least with some medium long setae on basal side..... *marcidus* group 4
- 4 Wing membrane with setae on whole wing, with more than 450 setae in anal cell; gonostylus usually evenly rounded at outer margin (Fig. 7A–D); AR = 1.2–1.3..... *H. marcidus* (Walk.) (Holarctic) (p. 27)
- ..... *H. marcidus* (Walk.) (Holarctic) (p. 27)
- 5 Wing membrane with setae on apical half, with 0–162 setae in anal cell; gonostylus with or without outer corner; AR = 1.3–1.8..... 5

<sup>1</sup>In the following keys overlapping and continuous characters have sometimes been regarded as valuable. For instance the LR will not separate all males of *H. oliveri* from all of *H. subpilosus*, however, 9 out of 10 specimens can be separated, and in combination with another overlapping character such as the width of the clypeus to the width of the pedicel at least all specimens examined can easily be separated.

5	Prealars 9-14; dorsocentrals 17-35, when less than 23 subcosta with 17-54 setae, R <sub>1</sub> with 36-49 setae, and R <sub>4+5</sub> with 81-120 setae.....	6
	Prealars 5-9; dorsocentrals 7-19, when more than 16 subcosta with 0-4 setae, R <sub>1</sub> with 2-26 setae, and R <sub>4+5</sub> with 7-68 setae.....	7
6	Subcosta with 17-54 setae; dorsocentrals 17-18, acrostichals about 12; AR about 1.4-1.5; HV about 3.6-3.7; gonostylus (Fig. 12E, F) with small, sharply pointed crista dorsalis.....	<i>H. scutellatus</i> (Goetgh.) (Palearctic) (p. 43)
	Subcosta with 0-2 setae; dorsocentrals 23-35, acrostichals 18-33; AR 1.6-1.8; HV about 3.0-3.4; gonostylus (Fig. 11D) with large bluntly triangular crista dorsalis.....	<i>H. cooki</i> sp.n. (Nearctic) (p. 41)
7	Dorsal margin of cibarial pump not deepened (Fig. 6I); about 6 acrostichals; subcosta, M, Cu, An, cell an, and cell m basad of RM without setae; BR <sub>3</sub> about 7.3; gonostylus (Fig. 7E) with indication of an outer corner and with triangular crista dorsalis.....	<i>H. latilaminus</i> sp.n. (Nearctic) (p. 36)
	Dorsal margin of cibarial pump deepened (except in some specimens of <i>H. changi</i> ); 11-23 acrostichals; BR <sub>3</sub> 5.3-7.0; subcosta, M, Cu, An, cell an, and cell m basad of RM with or without setae; gonostylus with or without outer corner.....	8
8	Gonostylus (Fig. 7F) without outer corner, crista dorsalis rounded; wing conspicuously dark brownish grey; 18-23 acrostichals; subcosta, Cu, An, cell an, and cell m basad of RM without setae.....	<i>H. hirtapex</i> sp.n. (Nearctic) (p. 39)
	Gonostylus with outer corner, crista dorsalis triangular or rounded; wing usually lighter; 11-26 acrostichals; subcosta Cu, An, cell an, and cell m basad of RM with or without setae.....	9
9	Crista dorsalis (Fig. 12D) large, rounded; cell an with 0-4 setae; anal lobe of wing small, not protruding; BV <sub>2</sub> 3.2-3.5; LR <sub>1</sub> 0.76-0.82.....	<i>H. grimshawi</i> (Edw.) (Palearctic) (p. 53)
	Crista dorsalis (Fig. 12A-C) smaller, bluntly triangular; cell an with 0-95 setae (nearly always more than 10); anal lobe of wing slightly protruding BV <sub>2</sub> 2.9-3.3; LR <sub>1</sub> 0.81-0.92.....	<i>H. changi</i> sp.n. (Nearctic) (p. 47)

**Key to examined females of Nearctic and Palearctic species of *Heterotrissocladius***

(See footnote p. 5.)

1	Clypeus swollen, wider than width of pedicel; cibarial pump constricted at base, conspicuously widened posteriorly, cornua strong, divergent (Fig. 1G); 0-8 acrostichals less than 35 μ long starting some distance from scutal projection; wing dark greyish brown, membrane with a few setae, media, cubitus, and their branches without setae....	2
	..... <i>subpilosus</i> group	
	Clypeus not as wide as pedicel; cibarial pump not constricted; 5-25 long acrostichals the longest at least 40 μ; when wing membrane with only a few setae wing light.....	3

- 2 Tergite IX with 24–32 setae; seminal capsule mostly pearshaped (Fig. 2E); spermathecal duct usually with loop; cibarial pump (Fig. 1G) strongly constricted at base; acrostichals sometimes present; anal cell often without setae, squama with 21–40 setae.....  
..... *H. oliveri* sp.n. (Nearctic) (p. 19)
- Tergite IX with 38–47 setae; seminal capsule ovoid (SCa in Fig. 2A); spermathecal duct with 90° angle; cibarial pump less strongly constricted; acrostichals absent; anal cell with a single row of setae along margin and a number of setae on anal lobe; squama with 33–49 setae..... *H. subpilosus* (Kieff.) (Palaeartic) (p. 11)
- 3 Wing light, membrane with only a few setae; anal cell with single row of setae along margin; about 5–10 acrostichals starting about  $\frac{1}{3}$  the length of scutum from scutal projection..... *maeaeri* group: *H. maeaeri* Brund. (Palaeartic) (p. 22)
- Wing usually darker, membrane with setae practically on whole surface, 5–25 acrostichals starting anteriorly at scutal projection..... *marcidus* group 4
- 4 Cell m basad of RM with about 140 setae; brachiolum with 5–6 setae; subcosta with about 75–78 setae; R<sub>1</sub> with about 93–113 setae; M<sub>1+2</sub> with about 170 setae; vannal fold with about 142 setae; An<sub>1</sub> with about 120 setae; tergite IX with 35–58 setae; labia Fig. 9K) small with distinct microtrichia..... *H. marcidus* (Walk.) (Holarctic) (p. 27)
- Cell m basad of RM with 20–88 setae; brachiolum with 2–3 setae; subcosta with 23–69 setae; R<sub>1</sub> with 43–75 setae; M<sub>1+2</sub> with 70–140 setae; vannal fold with 37–93 setae; An<sub>1</sub> with 26–71 setae; tergite IX with 22–36 setae; microtrichia of labia very indistinct, but apparently longer than above..... 5
- 5 Dorsal margin of cibarial pump not deepened; about 5 acrostichals; wing 3.02–3.16 times as long as profemur; spermathecal duct with loop; ventrolateral lobe of gonapophysis VIII only slightly thicker and longer than dorsomesal lobe (Fig. 9D)....  
..... *H. latilaminus* sp.n. (Nearctic) (p. 36)
- Dorsal margin of cibarial pump deepened; 12–25 acrostichals; wing 2.64–2.96 times as long as profemur; spermathecal duct with or without loop; ventrolateral lobe of gonapophysis VIII clearly thicker and longer than dorsomesal lobe (Fig. 9A, F, J)..... 6
- 6 Spermathecal duct with loop (Fig. 9A); wing conspicuously dark brownish grey; dorsal margin of cibarial pump strongly deepened; scutellum with 24–28 setae; setigerous protrusions of tergite IX separated (Fig. 9B)..... *H. hirtapex* sp.n. (Nearctic) (p. 39)
- Spermathecal duct without loop, but with strong angle (Fig. 9F, 12A), wing not conspicuously dark; dorsal margin of cibarial pump less strongly deepened; scutellum with 14–22 setae; setigerous protrusions of tergite IX separate or in contact..... 7
- 7 Ventrolateral lobe of gonapophysis VIII about three times as wide as dorsomesal lobe (Fig. 9F), setigerous protrusions of tergite IX in contact (Fig. 9G), labium triangular, but rounded at apex (Fig. 9F, H)..... *H. changi* sp.n. (Nearctic) (p. 47)
- Ventrolateral lobe of gonapophysis VIII less than twice as wide as dorsomesal lobe (Fig. 12A), setigerous protrusions of tergite IX separated (Fig. 12B); labium triangular and pointed (Fig. 12C)..... *H. scutellatus* (Palaeartic) (p. 43)
- (*Heterotrissocladius grimshawi* (Edw.) from Ireland, Scotland, Belgium, and Fennoscandia is likely to key to couplet 7 and have lower numbers of setae on the wings than any other species of the *marcidus* group. *Heterotrissocladius cooki* sp.n. is likely to key to couplet 6 or 7 and to be recognizable by means of the high number of dorsocentrals, prealars, and acrostichals.)

Key to known pupae of Nearctic and Palearctic species of *Heterotrissocladius*

(See footnote p. 5.)

- 1 Segment VIII with 5 broad, filamentous L-setae; pedes spurii B small or vestigial; pedes spurii A present on IV–VIII (indistinct on VIII); genital sac of male (Fig. 3B, D, G) broad nearly to apex, with a conical point; two setae present (often lost) dorsad of genital sac on sternite IX; wing sheaths with a dorsal and a ventral row of irregular “pearls”..... *subpilosus* group 2
- Segment VIII at most with 4 filamentous L-setae and 1 hairlike L-seta; pedes spurii B well developed; pedes spurii A on IV–VI or VII; genital sac of male with long apicolateral fingerlike extension, seta apparently absent on sternite IX dorsad of genital sac; wing sheaths without “pearls,” but with fine lines..... 4
- 2 Setae dorsad of genital sac on sternite IX (when present) about 160–220  $\mu$  long, strong, dark, and conspicuous (Fig. 3D); abdominal segments of exuvia pale to greyish; T/A = 1.3–1.6..... *H. oliveri* sp.n. (Nearctic) (p. 19)
- Setae dorsad of genital sac on sternite IX (when present) about 50–70  $\mu$  long, lighter, and inconspicuous (Fig. 3B, G); abdominal segments of exuvia pale or dark..... 3
- 3 Abdominal segments of exuvia conspicuously dark, brownish grey; T/A = 1.1–1.4.....  
..... *H. sp. A.* (Nearctic) (p. 17)
- Abdominal segments of exuvia pale; T/A = 1.6–2.1.....  
..... *H. subpilosus* (Kieff.) (Palearctic) (p. 11)
- 4 Pedes spurii B narrow, about as high as wide (Fig. 5Fa); pedes spurii A present on IV–VI; segment VII with 3, and VIII with 3–4 filamentous L-setae.....  
..... *maeaeeri* group: *H. maeaeeri* Brund. (Palearctic) (p. 22)
- Pedes spurii B much wider than high (Fig. 5Fb); pedes spurii A present on IV–VII; segments VII and VIII each with 4 filamentous L-setae (except some specimens of *H. changi* sp.n.)..... *marcidus* group 5
- 5 Abdominal segments of exuvia conspicuously dark, brownish grey; tergite I occasionally with a few posterior spinules; length to width of thoracic horn 5.2–7.0.....  
..... *H. hirtapex* sp.n. (Nearctic) (p. 39)
- At most thorax of exuvia dark colored; abdomen transparent or very faintly greyish brown; tergite I either without or with about 15 spinules; length to width of thoracic horn 4.0–6.8 or 7.0–8.1..... 6
- 6 Tergite I with about 15 posterior spinules; length to width of thoracic horn 7.0–8.1.....  
..... *H. sp. D.* (Nearctic) (p. 52)
- Tergite I without spinules; length to width of thoracic horn 4.0–6.8..... 7
- 7 Thorax of exuvia yellowish brown; thoracic horn 0.44–0.50 mm long, 4.2–5.5 times as long as wide; 26–36 setae in fringe of anal lobe.....  
..... *H. marcidus* (Walk.) (Holarctic) (p. 27)
- Thorax of exuvia lighter; thoracic horn shorter than 0.42 mm (except in some specimens of *H. scutellatus*); 19–31 setae in fringe of anal lobe..... 8

8	Palaeartic species; T/A = 1.7-1.8.....	9
	Nearctic species; T/A = 1.3-1.7.....	
	..... <i>H. changi</i> sp.n. (probably only east of and in the Rocky Mountains) (p. 47)	
	..... <i>H. latilaminus</i> sp.n. (probably only west of the Rocky Mountains) (p. 36)	
9	24 ( <i>n</i> = 1) setae in fringe of anal lobe, Boreal species.....	<i>H. grimshawi</i> Edw. (p. 53)
	27-31 setae in fringe of anal lobe, species from the Alps and Schwarzwald.....	
	..... <i>H. scutellatus</i> (Goetgh.) (p. 43)	

**Key to known larvae of Nearctic and Palaeartic species of *Heterotrissocladius***

(See footnote p. 5.)

1	Blade at apex of basal antennal segment longer than segments 2-7 combined (Fig. 4F, G); AR = 1.5-2.1; mentum with 2 median teeth.....	<i>subpilosus</i> group	2
	Blade at apex of basal antennal segment shorter than segments 2-7 combined; AR = 0.9-1.4; mentum with 1 or 2 median teeth.....		4
2	Median spine in pecten epipharyngis as long as and nearly as strong as lateral spines (Fig. 4C); labral lamellae often apically pointed (Fig. 4C); SI long, but relatively narrow; basal antennal segment 3.0-3.9 times as long as wide; AR = 1.4-1.9.....	<i>H. oliveri</i> sp.n. (Nearctic)	(p. 19)
	Median spine in pecten epipharyngis shorter and weaker than lateral spines (at least in <i>H. subpilosus</i> ); labral lamellae apically rounded or truncate (Fig. 4B, D); SI relatively short (Fig. 4A, D); basal antennal segment 3.7-4.5 times as long as wide; AR = 1.8-2.1.....		3
3	SI broad and finely plumose; labral lamellae apically rounded (Fig. 4A, B); head capsule 0.49-0.54 mm long.....	<i>H. subpilosus</i> (Kieff.) (Palaeartic)	(p. 11)
	SI with relatively few lateral serrations; labral lamellae apically truncate (Fig. 4D); head capsule about 0.41 mm long.....	<i>H. sp. A</i> (Nearctic)	(p. 17)
4	Mentum with one median tooth.....	<i>maeaeri</i> group	5
	Mentum with two median teeth.....	<i>marcidus</i> group	7
5	First lateral tooth of mentum much lower than second lateral tooth (Fig. 5L); SII conspicuously broadened (Fig. 5J); postmentum 130-139 $\mu$ long; second mark of setae on basal antennal segment 58-68 $\mu$ from base (Fig. 5I).....	<i>H. sp. C</i> (Florida)	(p. 26)
	First lateral tooth of mentum clearly higher than second lateral tooth (Fig. 5D, H); SII not conspicuously broadened; postmentum 196-226 $\mu$ long; second mark of setae on basal antennal segment 26-34 $\mu$ from base.....		6
6	First lateral tooth of mentum broader and stronger than second lateral tooth (Fig. 5D), space between median and first lateral tooth usually approximately U-shaped.....	<i>H. maeaeri</i> Brund. (Palaeartic)	(p. 22)
	First lateral tooth of mentum about same size as second lateral tooth (Fig. 5H), space between median and first lateral tooth approximately V-shaped.....	<i>H. sp. B</i> (Nearctic)	(p. 26)

- 7 First lateral teeth of mentum as high as median teeth and much larger than second lateral teeth; median teeth with lateral notches or accessory teeth (Fig. 13F); submentum light;  $V/M = 1.20-1.42$ ;  $AR = 1.20-1.43$ ..... *H. sp. E.* (Nearctic) (p. 55)
- 8 First lateral teeth of mentum lower than median teeth and only slightly larger than second lateral teeth;  $V/M$  greater or smaller than 1.0;  $AR = 0.95-1.26$ ..... 8
- 8  $V/M = 0.67-0.78$  and submentum brownish black, distinctly darker than surrounding areas of head capsule; spines of pecten epipharyngis somewhat triangular and equal in size (Fig. 11N)..... *H. hirtapex* sp.n. (Nearctic) (p. 39)
- 9  $V/M$  greater than 1.0 when submentum is dark; median spine of pecten epipharyngis usually shorter and weaker than lateral spines..... 9
- 9 Submentum brownish black to brown, distinctly darker than surrounding areas of head capsule;  $V/M = 1.1-1.6$ ; basal antennal segment 78-95  $\mu$  long, 4.0-4.6 times as long as wide..... 10
- 10 Submentum not darker to moderately darker than surrounding areas;  $V/M = 0.8-1.1$  or when 1.0-1.6 basal antennal segment 58-86, mean 69  $\mu$  long, and 3.0-4.2, mean 3.6 times as long as wide..... 11
- 10 Submentum always brownish black; setae at base of mentum 2-3  $\mu$  wide at base.....  
..... *H. marcidus* (Walk.) (Holarctic) (p. 27)
- 10 Submentum usually lighter; setae at base of mentum 1-2  $\mu$  wide at base.....  
..... *H. latilaminus* sp.n. (Nearctic) (p. 36)
- 11 Nearctic species..... 12
- 11 Palaearctic species..... 13
- 12  $V/M = 0.77-0.91$ ; median mental tooth without distinct lateral notch; basal antennal segment 77-92, mean 85  $\mu$  long, and 22-25  $\mu$  wide; segment four 19-28, mean 23  $\mu$  long.  
..... *H. sp. D.* (probably only west of the Rocky Mountains) (p. 52)
- 12  $V/M = 1.03-1.57$ , median mental tooth usually with lateral notch; basal antennal segment 58-86, mean 69  $\mu$  long, and 16.5-23  $\mu$  wide; segment four 14-23, mean 18  $\mu$  long  
..... *H. changi* sp.n. (probably only east of and in the Rocky Mountains) (p. 47)
- 13 Submentum usually slightly darker than surrounding area;  $Sa/An = 0.22-0.30$ , basal antennal segment 75-86, mean 81  $\mu$  long; segment four 2.9-3.8 times as long as segment three..... *H. scutellatus* (Goetgh.) (the Alps) (p. 43)
- 13 Submentum usually of same color as surrounding area;  $Sa/An = 0.16-0.22$ ; basal antennal segment 68-78, mean 74  $\mu$  long; segment four 4.0-4.6 times as long as segment three in normal specimens, but may be less in some abnormal specimens.....  
..... *H. grimshawi* (Edw.) (Northern Europe) (p. 53)

## *subpilosus* group

Imagines with greatly enlarged clypeus; cibarial pump with strongly converging sides posteriorly and strong cornua; acrostichals absent or weak and few in number, starting some distance from anterior scutal projection; wing membrane at most with apical setae only in male and with central and proximal parts bare in female. Pupa with pedes spurii B absent or vestigial; pedes spurii A present on segments II–VIII in male, minute on VIII; wing sheaths with “pearls”; genital sac broad nearly to apex, then abruptly narrowed with a conical extension; strong or weak setae present on anal lobe dorsad of genital sac; segment VIII with 5 broad, filamentous L-setae. Larvae with antennal blade longer than segments 2–7 combined, AR of 1.5–2.1, two median mental teeth, mentum darker than submentum, and submentum not or only very slightly darker than surrounding areas of head capsule.

### *Heterotrissocladius subpilosus* (Kieffer)

(Fig. 1A–D, 2A–D, 3E–H, 4A, B, E, F, H, I)

*Dactylocladius subpilosus* Kieffer in Kieffer and Lundbeck 1911:273 (male, female), Kieffer 1919:114 (male, female).

*Spaniotoma (Orthocladius) subpilosus* (Kieff.), Edwards 1935b:537 (male, female).

*Metriocnemus (Heterotrissocladius) subpilosus* (Kieff.), Goetghebuer 1940–50:27 (male, female).

*Heterotrissocladius subpilosus* (Kieff.), Edwards 1937:142 (male, female), Thienemann 1941:215 (pupae), Brundin 1949:814 (male, female, larva), 1956a:80 (male), Oliver 1962:8 (male), Pankratova 1970:148 (larva).

?nec *Spaniotoma (Orthocladius) subpilosus* var?, Edwards 1935a:472.

nec *Heterotrissocladius subpilosus*, Oliver 1962:177; 1964:69; 1968:112; Henson 1966:47; Johnson and Brinkhurst 1971:1691.

nec *Heterotrissocladius* cf. *subpilosus*, Brinkhurst et al.; 1968:17, Sæther 1970a:6.

Imago characterized by moderately converging sides of cibarial pump, and moderately strong cornua; acrostichals absent; LR<sub>1</sub> of 0.77–0.80. Male with about 26–31 weak setae on tergite IX and anal point, gonostylus with an outer sharp angle and a prominent crista dorsalis. Female with about 38–47 setae on tergite IX, ovoid seminal capsule, and spermathecal duct with a 90° angle or with a very small loop.

Pupa with pale abdominal segments, T/A of 1.6–2.1 and weak setae dorsad of genital sac on sternite IX.

Larva with SI broad and finely plumose, apically rounded labial lamellae, and median spines in pecten epipharyngis shorter and weaker than lateral spines.

MALE IMAGO (N = 4, EXCEPT WHEN OTHERWISE STATED)

Length 4.49–5.09, 4.71 mm. Wing length 2.96–3.27, 3.11 mm. Total length/wing length: 1.45–1.55, 1.52. Wing length/length of profemur: 2.91–3.03, 2.98.

*Head* — AR = 1.70–1.91, 1.81(6). Temporal setae 18–23, 21. Postorbitals 3–4, 3; outer verticals 8–11, 10; inner verticals 6–9, 8. Clypeus 210–230, 220  $\mu$  wide, with 7–12, 10(6) setae. Ratio of width of clypeus to width of pedicel 1.28–1.35, 1.33(4). Cibarial pump, tentorium, and stipes as in Fig. 1D. Minimum width of cibarial pump 54–64, 57  $\mu$ (6). Distance between apices of cornuae 64–74, 70  $\mu$ (6). Ratio of minimum width to distance between cornuae 0.76–0.86, 0.82(6). Tentorium 190–200  $\mu$ (2) long, maximum width 36–53  $\mu$ (2), width anterior of posterior tentorial pit 12–13  $\mu$ (2), distance from apex to posterior tentorial pit 28–30  $\mu$ (2). Stipes 200–210  $\mu$ (2) long. Palp lengths in microns: 40–50, 43; 61–64, 62; 158–174, 169; 114–140, 126; 162–180, 170.

*Thorax* — Anteprenotum with 6 or 7 setae. Dorsocentrals 13–17, 15(6); prealars 7–10, 9(6); acrostichals absent (6). Scutellum with 15–20, 18 (6) setae.

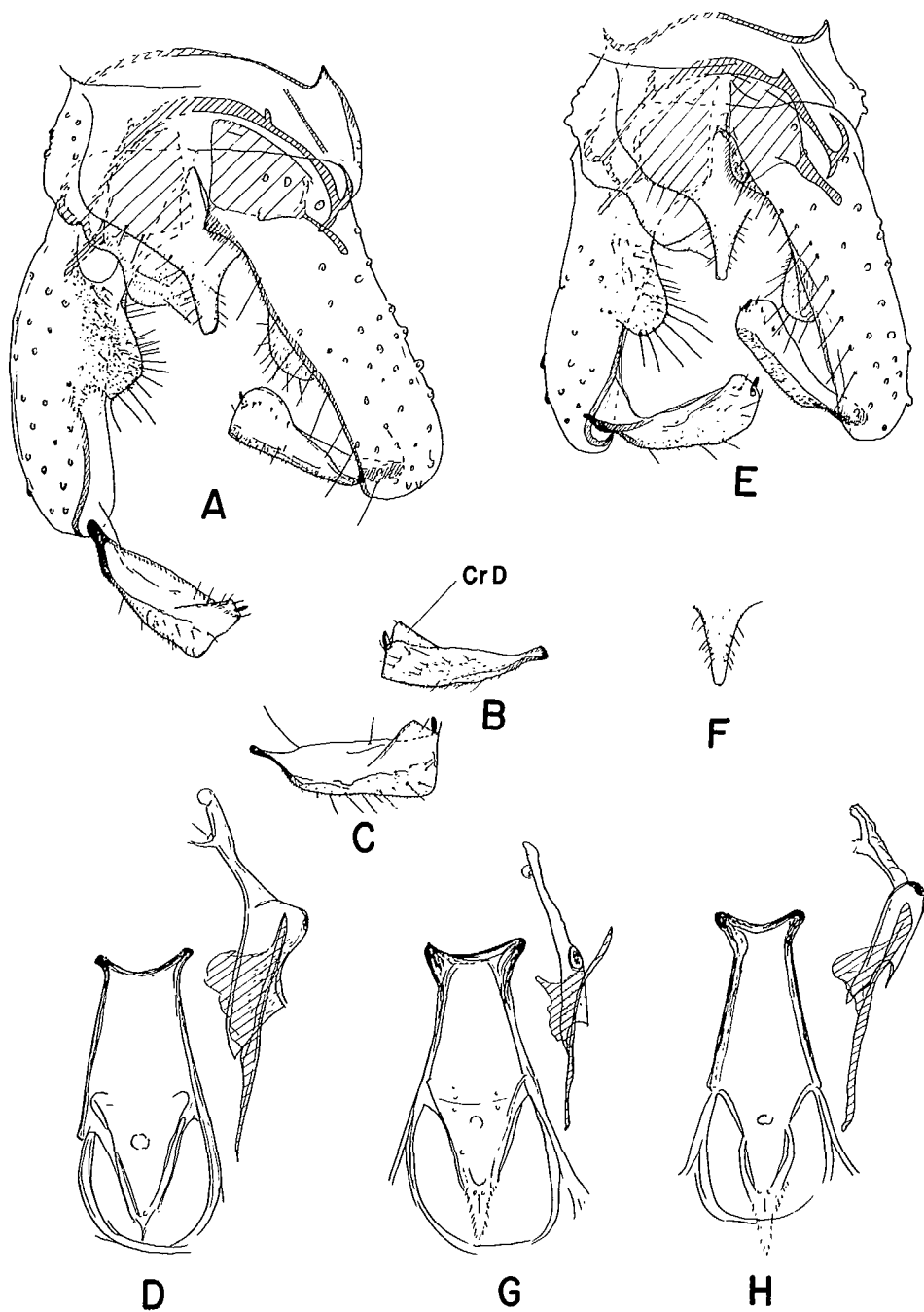


FIG. 1. *Heterotrissocladius subpilosus* — group, A-D, *H. subpilosus* (Kieff.): A) hypopygium of male from Norddalsfjell, Sweden, B) gonostylus of male from Lake Kilpisjärvi, Finland, C) gonostylus of male from Lake Vannakvatn, Norway, D) cibarial pump, tentorium, and stipes of male. E-H, *H. oliveri* sp.n.: E) hypopygium, F) variation of anal point, G, H) cibarial pump, tentorium, and stipes of female (G) and male (H).

*Wing* — Anal lobe well developed, somewhat protruding. VR = 1.11–1.18, 1.15. Brachiolum with 2(3) setae; R with 8–12, 10; R<sub>1</sub> with 3–5, 4; R<sub>4+5</sub> with 2–5, 4. Squama with 25–38, 30 setae. Cell Γ<sub>4+5</sub> with 0–40, 13(6) setae at apex.

*Legs* (*n* = 3) — Spur of front tibia 70–74 μ long; spurs of middle tibia 39–42 μ and 26–34 μ, of hind tibia 80–83 μ and 28–29 μ. Width at apex of front tibia 51–54 μ, of middle tibia 52–56 μ, of hind tibia 63–65 μ. Comb with 12 or 13 setae. Shortest seta 26 μ long, longest 50–52 μ. Sensilla chaetica absent. Lengths (in microns) and proportions of legs (*n* = 3):

	fc	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	1018–1055	1141–1184	902–932	429–460	325–331	215–227
p <sub>2</sub>	1018–1079	1043–1116	540–558	288–307	209–227	141–165
p <sub>3</sub>	1141–1202	1288–1343	736–761	393–423	331–356	196–215
	ta <sub>5</sub>	LR	BV	SV	BR	
p <sub>1</sub>	129	0.77–0.80	2.74–2.82	2.36–2.47	3.14–4.29	
p <sub>2</sub>	123	0.49–0.53	3.34–3.42	3.75–4.02	4.00–4.07	
p <sub>3</sub>	129–147	0.57–0.58	2.90–3.02	3.27–3.98	6.25–6.66	

*Hypopygium* (Fig. 1A, B, C) — Ninth tergite with 26–31, 30(6) weak setae including 19–26, 22(6) on anal point; laterosternites IX each with 8–13, 10 setae. Transverse sternapodeme 100–112, 104 μ(6) long. Phallapodeme 106–142, 122 μ(6) long. Anal point 5–12, 8 μ(6) wide at apex. Gonocoxite 290–350, 315 μ(6) long; gonostylus 137–147, 143 μ(6) long. Crista dorsalis prominent, triangular (Fig. 1B, C) to rounded (Fig. 1A). Gonostylus with an outer angle. HR = 2.07–2.41, 2.21(6); HV = 3.24–3.46, 3.30.

FEMALE IMAGO (DISSECTED FROM MATURE PUPAE, N = 4, EXCEPT WHEN OTHERWISE STATED)

*Head* — AR = 0.48–0.59, 0.55. Pedicel length/width (microns): 60–62/80. Flagellomeres length/width (microns): 94–110, 102/36–48, 44; 68–80, 73/34–36, 36; 74–86, 80/30–34, 32; 84–100, 92/29–34, 32; 170–196, 182/30–34, 32. Temporal setae 15–18, 16. Postorbitals 1–5, 3; outer verticals 4–9, 7; inner verticals 6–7, 6. Clypeus with 7–13, 10 setae. Minimum width of cibarial pump 52–68, 60 μ. Distance between apices of cornua 62–78, 72 μ. Ratio of minimum width to distance between cornua 0.73–0.87, 0.83. Palp lengths in microns: 38–44, 41; 50–52, 51; 90–122, 106; 90–121, 105; 120–160, 139.

*Thorax* — Anteprenotum with 7 or 8(2) setae. Dorsocentrals 19–21, 20; prealars 8 or 9, 9; acrostichals absent. Scutellum with 16–24, 21 setae.

*Wing* — Squama with 33–49(3) setae.

*Legs* (*n* = 2) — Spur of front tibia 58–60 μ long; spurs of middle tibia 36–42 μ and 32 μ, of hind tibia 64–72 μ and 28 μ. Width at apex of front tibia 49–58 μ, of middle tibia 52–61 μ, of hind tibia 56–64 μ. Comb with 10 setae, shortest seta 30 μ long, longest 40–54 μ. Sensilla chaetica 5 on ta<sub>1</sub> of p<sub>2</sub>, and 10–12 on ta<sub>1</sub> of p<sub>3</sub>. BR<sub>1</sub> = 2.42–2.53; BR<sub>2</sub> = 2.19–2.23; BR<sub>3</sub> = 4.71–5.16.

*Genitalia* (Fig. 2A–D) — Gonocoxite with 16–19, 18 setae. Tergite IX with 38–47, 41 setae. Cercus 140–160, 151 μ long, 32–34 μ(2) wide at apex. Notum 142–174, 157 μ long. Seminal capsule ovoid, slightly more than half darkly sclerotized; 85–91, 89 μ long; 64–68 μ (3) wide; with a 14–22 μ (3) long neck. Spermathecal duct with a sharp angle or a small loop.

#### PUPA

Length 4.53–6.40, 5.82 mm (15). T/A = 1.55–2.01, 1.79(28). Abdomen pale brownish gray.

*Cephalothorax* — Thoracic horn (Fig. 3H) 343–454, 423 μ(28) long; 59–60, 60 μ(4) wide; length/width 5.8–7.3, 6.6(4). Anterior precorneal seta 110 μ(1) long, located 28 μ(1) from median seta and 32 μ(1) from posterior seta. Median seta 110 μ(1) long, located 4 μ(1) from posterior seta. Posterior seta 80 μ(1) long, located 68 μ(1) from horn. Frontal seta 55–65, 60 μ(5) long.

*Abdomen* (Fig. 3E, F, G) — Pedes spurii B vestigial. Pedes spurii A present on sternites IV–VIII (very weak on VIII), longest spinules on IV–VI about 10 μ long, on VII about 6 μ, on VIII about 4.5 μ. Segments I–V with 3 hairlike L-setae; segment VI with 4 hairlike L-setae (L<sub>4</sub> minute); segment VII with 3 filamentous and 1 hairlike L-setae in 26 of 27 specimens and 4 filamentous L-setae in

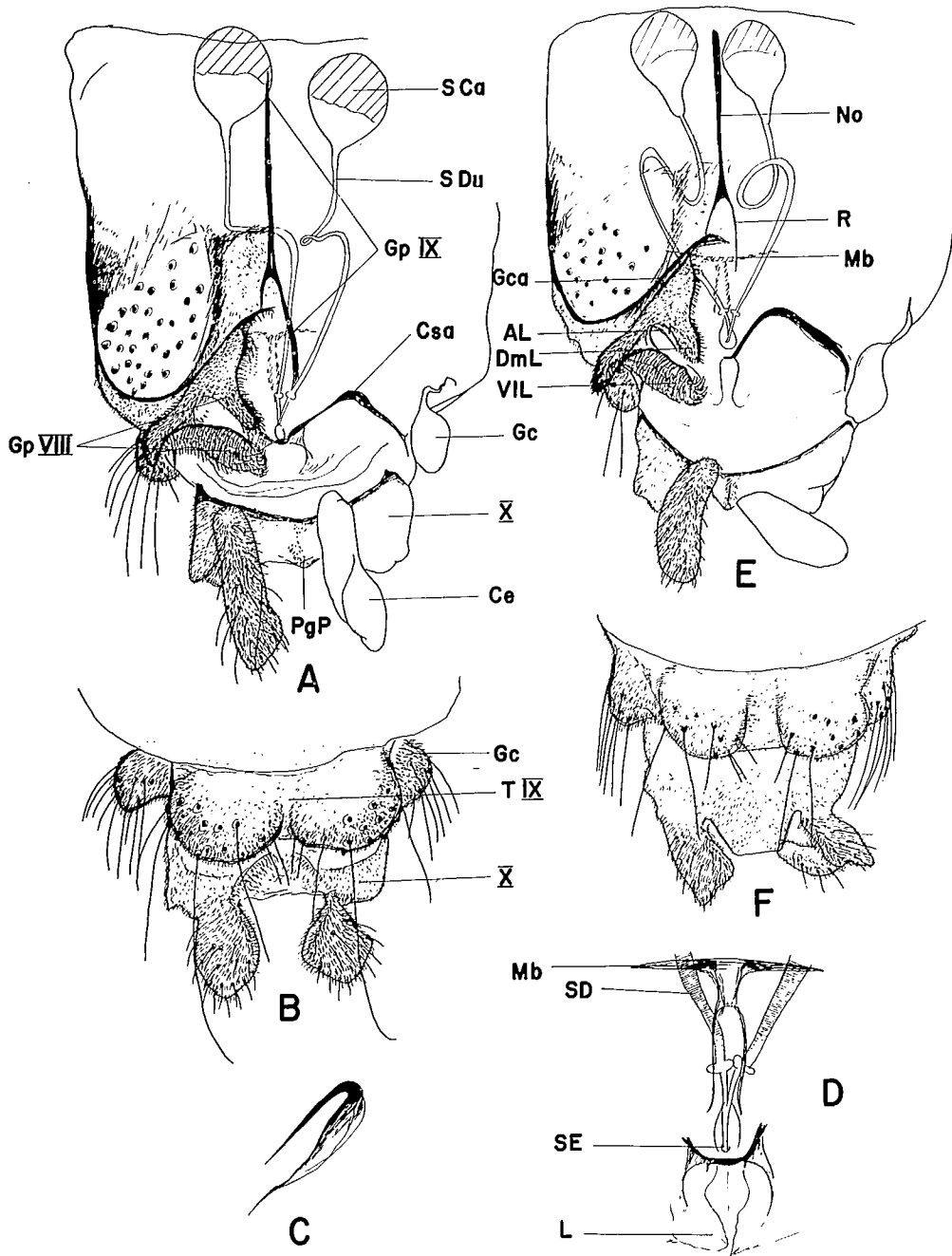


FIG. 2. *Heterotrissocladius subpilosus* — group, female genitalia. A–D, *H. subpilosus* (Kieff.): A) ventral view, B) dorsal view, C) apodeme lobe, D) spermathecal eminence, membrane, and labia. E–F, *H. oliveri* sp.n.: E) ventral view, F) dorsal view. (AL: apodeme lobe of gonapophysis VIII; Ce: cercus; Csa: coxosternapodeme; DmL: dorsomesal lobe of gonapophysis VIII; Gc: gonocoxite (IX); Gca: gonocoxapodeme (VIII); Gp VIII: gonapophysis VIII; L: labium; Mb: membrane or sclerotized hinge connecting gonapophyses VIII to each other; No: notum; PgP: postgenital plate; R: ramus; S Ca: seminal capsule; S Du: spermathecal duct; SE: spermathecal eminence; T IX: tergite IX; VIL: ventrolateral lobe of gonapophysis VIII; X: segment X.)

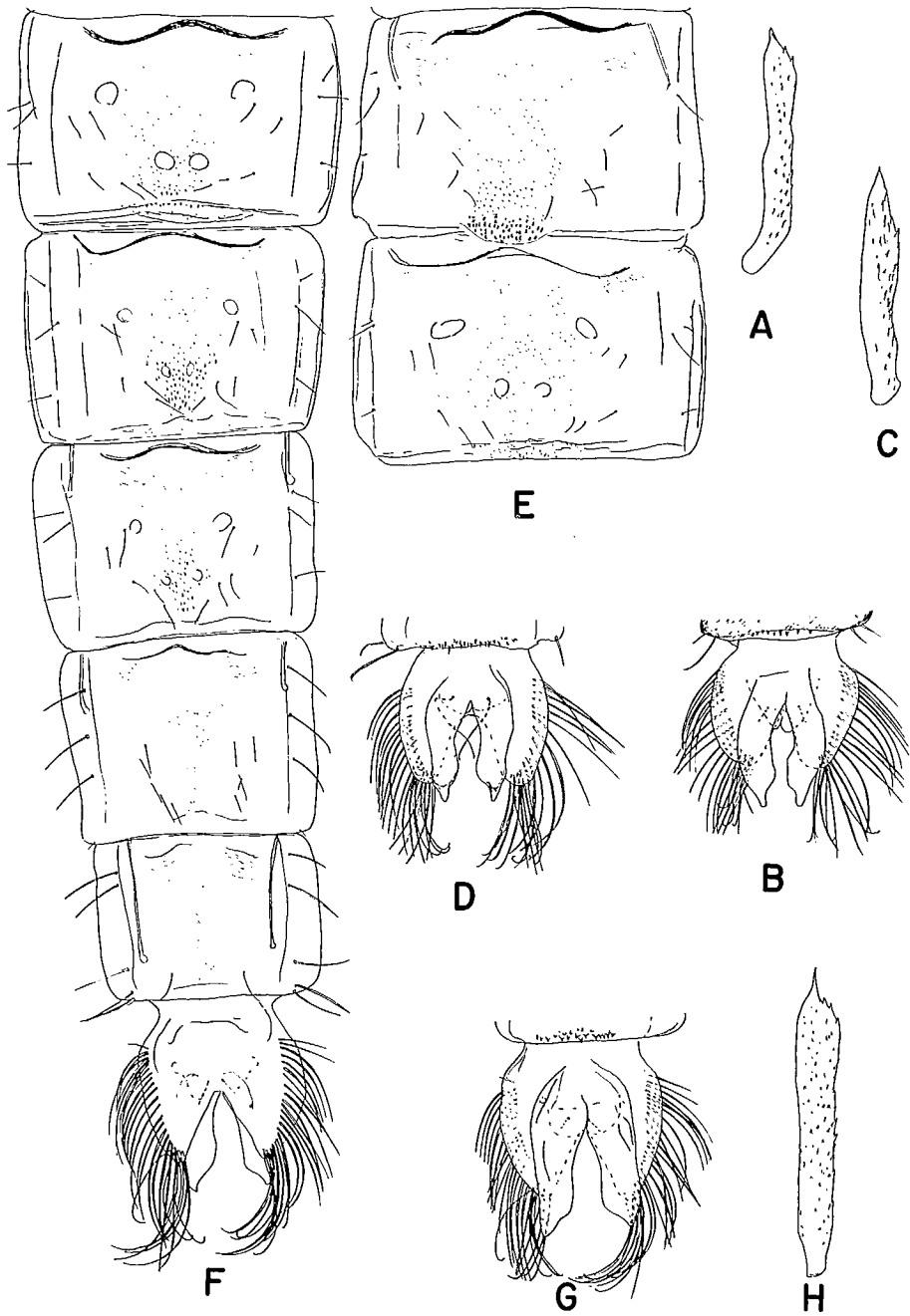


FIG. 3. *Heterotrissocladus subpilosus* — group, pupae. A–B, *H. sp. A*: A) thoracic horn, B) anal lobe, ventral view. C–D, *H. oliveri* sp.n.: C) thoracic horn, D) anal lobe, ventral view. E–H, *H. subpilosus* (Kieff.): E) segments II–III, dorsal view, F) segments IV–IX, dorsal view, G) anal lobe, ventral view, H) thoracic horn.

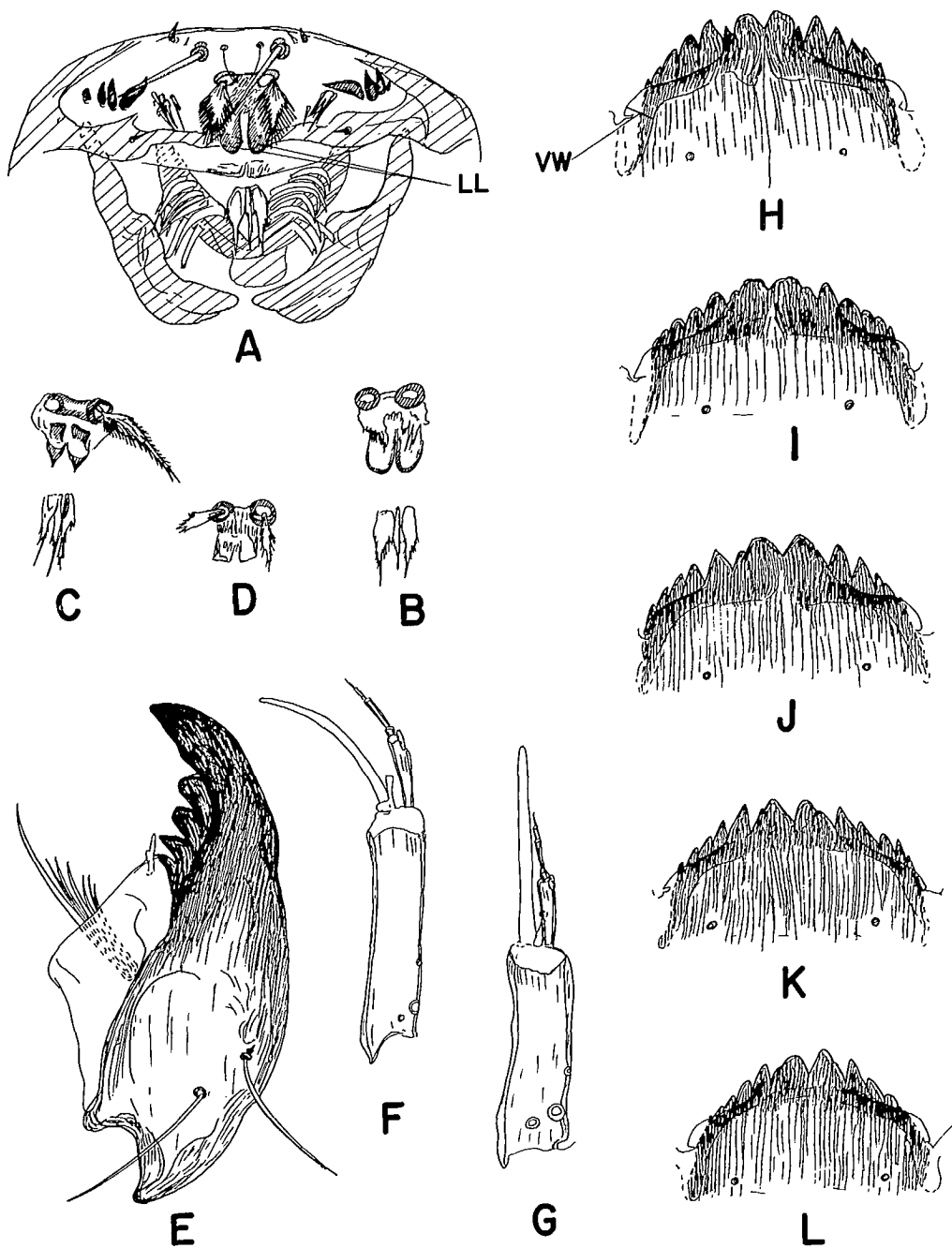


FIG. 4. *Heterotrissocladius subpilosus* — group, larvae. A–D, labrum and palatum with details of SI and labral lamellae (LL): A, B) *H. subpilosus* (Kieff.), C) *H. oliveri* sp.n., D) *H. sp. A*. E, *H. subpilosus* (Kieff.), mandible. F, *H. subpilosus* (Kieff.) antenna. G, *H. oliveri* sp. n., antenna. H–L, mentum: H–I) *H. subpilosus* (Kieff.), J–K) *H. oliveri* sp.n., L) *H. sp. A*. (VW: measuring line of width of ventromental plate.)

1 specimen; segment VIII with 5 filamentous L-setae (29). Sternite VIII of male with 14–46, 30(14) posterior spines; 5–35, 17(14) of which are longer than 10  $\mu$ . Anal macrosetae 209–260, 237  $\mu$ (29) long; 2.0–3.0, 2.5  $\mu$ (5) wide at base. Fringe of anal lobe with 19–30, 24(28) setae. Setae dorsad of genital sac on sternite IX 20–71, 58  $\mu$ (9) long, often lost. Genital sac as in Fig. 3G.

#### FOURTH INSTAR LARVA

Length 6.11–9.07, 8.11 mm (7). Head capsule length 0.49–0.54, 0.50 mm (10).

*Head* — Antenna as in Fig. 4F. Lengths of antennal segments in microns ( $n = 7$ –9): 86–96, 90; 26–30, 28; 4; 10–13, 11; 3–5, 3.7; 2–3, 2.6; 1–2, 1.1. AR = 1.76–2.09, 1.92(7). Basal antennal segment 20–23.5, 22  $\mu$ (9) wide; 3.66–4.50, 4.10(9) times as long as wide; distance from base to annular organ 10–17, 13.6  $\mu$ (7); to basal mark of seta 10–14, 12  $\mu$ (6); to distal mark of seta 24–38, 30  $\mu$ (7); blade at apex 60–76, 69  $\mu$ (6) long; accessory blade 13–17, 14  $\mu$ (8) long. Subapical style of second segment 5–7, 6  $\mu$ (7) long. Labrum and palatum as in Fig. 4A. SI broad, finely plumose. Labral lamellae rounded apically. Median spines of pecten epipharyngis shorter and much weaker than lateral spines (Fig. 4B). Premandible 90–107, 100  $\mu$ (10) long. Mandible (Fig. 4E) 182–208, 195  $\mu$ (9) long. Mentum as in Fig. 4H, I; width of one median tooth including lateral notch 25–32, 29  $\mu$ (10); width of ventromental plate 14–18, 16  $\mu$ (10); V/M = 0.44–0.72, 0.54 (10). Length of prementum 230–246, 238  $\mu$ (10).

*Abdomen* — Procerus 30–44, 37  $\mu$ (7) high; 24–30, 28  $\mu$ (7) wide. Supraanal setae 160–195, 173  $\mu$ (6) long. Anal setae 540–736, 646  $\mu$ (6) long. Sa/An = 0.22–0.32, 0.27(6). Anal tubules 150–166, 160  $\mu$ (6) long; 27–38, 32  $\mu$ (5) wide at base; 44–70, 51  $\mu$ (6) wide in the middle; 18–38, 26  $\mu$ (5) wide at apex. Posterior parapods 210  $\mu$ (1) long.

#### Material Examined

Two males, Lake Kilpisjärvi, Finland, 28/5/68, B. Lindeberg; 1 male, Nordalsfjell, Sweden, 15/7/58, D. R. Oliver; 2 mature female pupae, depth 33–34 m, Lake Vättern, Sweden, May 1971, T. Wiederholm; 1 male, Swedish Lapland, 1936, A. Thienemann, det. F. W. Edwards; 26 exuviae, Upper, Central, and Lower Kårsavagga lakes, Katterjaure, Torneträsk, Abiskojaure, Swedish Lapland, 1936, A. Thienemann; 2 mature male pupae, 2 mature female pupae, 17 larvae, depth 17–20 m, Lake Vannaksvatn, Nordland, Norway, 11/6 and 2/8/66, A. Klemetsen; 1 larva, depth 31 m, Lake Langsjöen, Sör-Varanger, Finnmark, Norway, 27/7/66, O. A. Sæther.

#### Ecology and Distribution

*Heterotrissocladius subpilosus* is, according to Brundin (1949, p. 708; 1956b), a strongly cold-thermophilic and ultraoligotrophic species. In Scandinavia it is generally the dominant species in the profundal zone of mountain lakes. In southern Sweden it occurs as a glacial relict in the largest and deepest lakes. The species has two emergence periods a year in the Scandinavian subarctic lakes and in the deeper lakes of southern Sweden. The first emergence takes place primarily between the middle of May and the middle of July, the second emergence period between the middle of August and the beginning of October. In some lakes the pupae emerge through cracks in the ice.

*Distribution* — Bear Island (Kieffer and Lundbeck 1911:273, Edwards 1935b:537, Oliver 1962:8); Sweden (Ekman 1915:345 as *Psectrocladius* sp. (see Thienemann 1954, p. 821), Thienemann 1941:148; Brundin 1949:708, 1956b, Wiederholm 1973a, b, 1974b:36, 1974c); Finland; Norway (Brundin 1956b). The record by Edwards (1935a, p. 472) probably concerns *H. oliveri* s.p.n.

#### *Heterotrissocladius* sp. A.

(Fig. 3A, B; 4D, L)

Pupa characterized by conspicuously dark, brownish grey abdomen, T/A of 1.1–1.4, and weak setae dorsad of genital sac on sternite IX. Larval SI with relatively few lateral serrations, apically truncate labral lamellae, and head capsule about 0.41 mm long.

PUPA (N = 4, EXCEPT WHEN OTHERWISE STATED)

Length 5.12–5.68, 5.39 mm. Abdomen dark, brownish grey.

*Cephalothorax* — Thoracic horn (Fig. 3A) 318–393, 347  $\mu$  long; 40–58, 49  $\mu$  wide; length/width 6.4–8.3, 7.3. Anterior precorneal seta 100–140, 115  $\mu$  long located 8–16, 12  $\mu$  from median seta and 10–19, 16  $\mu$  from posterior seta. Median seta 75–140, 107  $\mu$  long located 4–8, 6  $\mu$  from posterior seta. Posterior seta 60–110, 80  $\mu$  long located 48–76, 61  $\mu$  from horn. Frontal seta 8–110, 61  $\mu$  long (8–40  $\mu$  in the Kenora specimen, 70–110  $\mu$  in the specimens from Babine Lake).

*Abdomen* — Pedes spurii B vestigial. Pedes spurii A present on sternites IV–VIII, longest spinules on IV–VI 6–12  $\mu$ (3), on VII 6–7  $\mu$ (3), on VIII 2–8  $\mu$ (3). Segments I–V with 3 hairlike L-setae, segment VI with 4 hairlike L-setae, segment VII with 3–4 filamentous and 0–1 hairlike L-setae, segment VIII with 5 filamentous L-setae. Sternite VIII of male with 9(1) posterior spines all longer than 10  $\mu$ . Anal macrosetae 245–294, 268  $\mu$  long; 3.5–4.0, 3.6  $\mu$  wide at base. Fringe of anal lobe with 21–23, 22 setae. Setae dorsad of genital sac on sternite IX 50–70  $\mu$ (2) long, weak and not very dark. Genital sac as in Fig. 3B.

LARVA (N = 1):

Length 7.7 mm. Head capsule length 0.41 mm.

*Head* — Antenna as in *H. subpilosus* (Fig. 4F). Length of antennal segments in microns: 90, 25, 5, 10, 4, 3, 1. AR = 1.88. Basal antennal segment 22.5  $\mu$  wide, 4.0 times as long as wide, distance from base to annular organ 12  $\mu$ , to distal mark of seta 22  $\mu$ ; blade at apex longer than segments 2–7 combined. Labrum and palatum about as in *H. subpilosus*, but with SI shorter and weaker, with fewer serrations and with labral lamellae apically truncate (Fig. 4D). Premandible 78  $\mu$  long. Mandible 158  $\mu$  long. Mentum as in Fig. 4L; width of one median tooth 24  $\mu$ ; width of ventromental plate 13  $\mu$ ; V/M = 0.54. Length of postmentum 210  $\mu$ .

*Abdomen* — Procerci 35  $\mu$  high, 29  $\mu$  wide. Supraanal seta 98  $\mu$  long. Anal setae 552  $\mu$  long. Sa/An = 0.18. Anal tubules 118  $\mu$  long, 37  $\mu$  wide at base, 18  $\mu$  wide at apex.

### Remarks

This species appears to be most closely related to *H. subpilosus*. The setae dorsad of the genital sac on sternite IX in the pupa are of the same strength in both species and the larvae of both lack pointed labral lamellae. The species can, however, be separated from *H. subpilosus* by means of its conspicuously dark exuviae, its lower T/A ratio, and, in the larva, by means of its weaker and less serrated SI, and its shorter head capsule.

The exuviae of *H. oliveri* sp.n. from Lake Huron also are darker and have a lower T/A ratio than *H. subpilosus*. However, the setae dorsad of the genital sac are, when present, much stronger than in *H. sp. A*.

The pupae from Hillock Lake differ from those of Babine Lake in having a shorter thoracic horn (318–331  $\mu$  against 346–393  $\mu$ ) and shorter frontal setae (8–40  $\mu$  against 70–110  $\mu$ ); it is not inconceivable that they in fact belong to different species.

### Material Examined

Two exuviae, one larva, depth 46 m, Hillock Lake, Kenora, Ont., 6/5/69, A. L. Hamilton and J. Johnson; 2 exuviae, on surface at dock, Babine Lake, B.C., 18/5/63, A. L. Hamilton.

### Ecology and Distribution

Hamilton (1971, p. 259) found this species (as *H. subpilosus*) in Hillock Lake, the deepest and most oligotrophic of the 15 lakes investigated in the Experimental Lakes Area in Northwestern Ontario. Babine Lake, B.C., also is a large very oligotrophic lake.

*Distribution* — Northwestern Ontario (Hamilton 1971:259), British Columbia. Possible records include Vancouver Island, B.C. (Henson 1966:47 as *H. subpilosus*).

*Heterotrissocladius oliveri* sp. n.

(Fig. 1E-H; 2E, F; 3C, D; 4C, G, J, K)

*Heterotrissocladius subpilosus*, Oliver 1963: 177, 1964:69, 1968:112; Henson 1966:47; Johnson and Brinkhurst 1971:1691; nec Kieffer 1911.

*Heterotrissocladius* cf. *subpilosus* Brinkhurst et al. 1968:17.

?*Spaniotoma* (*Orthocladius*) *subpilosus* var?, Edwards 1935a:472.

Imago characterized by strongly converging sides of the cibarial pump, and strong cornua; acrostichals usually present in low numbers, located centrally on scutum; LR<sub>1</sub> of 0.76-0.86. Male with about 16-33 weak setae on tergite IX and anal point; gonostylus rounded at apex with large, but not sharply protruding crista dorsalis.

Female with 24-32 setae on tergite IX, more or less pear-shaped seminal capsule, and spermathecal duct usually with a loop.

Pupa with pale abdominal segments, T/A of 1.3-1.6, and strong, long, dark setae dorsad of genital sac on sternite IX.

Larva with SI narrow, but long, apically pointed labral lamellae (occasionally rounded); median spine in pecten epipharyngis as long as and nearly as strong as lateral spines.

MALE IMAGO (N = 10, EXCEPT WHEN OTHERWISE STATED)

Length 3.71-4.57, 4.30 mm. Wing length 2.31-2.96, 2.61(20) mm. Total length/wing length 1.43-1.67, 1.59. Wing length/profemur 2.63-2.96, 2.73.

*Head* — AR = 1.43-1.80, 1.68. Temporal setae 16-21, 18. Postorbitals 2-5, 4; outer verticals 8-13, 10; inner verticals 3-8, 5. Clypeus 200-258, 224  $\mu$  wide; with 2-15, 10 setae. Width of clypeus/width of pedicel: 1.32-1.64, 1.42(20). Cibarial pump, tentorium, and stipes as in Fig. 1H. Minimum width of cibarial pump 41-58, 49  $\mu$ (20). Distance between apices of cornuae 61-80, 72  $\mu$ (20). Ratio of minimum width to distance between cornuae 0.62-0.76, 0.69(20). Tentorium 150-182, 163  $\mu$  long; 28-50, 37  $\mu$  wide; 11-14, 13  $\mu$  wide anterior of posterior tentorial pit; distance from apex to posterior tentorial pit 30-40, 35  $\mu$ . Stipes 158-196, 180  $\mu$  long; 50-78, 62  $\mu$  wide. Palp lengths in microns: 40-56, 49; 60-78, 68; 108-183, 149; 110-135, 120; 148-186, 170.

*Thorax* — Anteprepronotum with 6-11, 8 setae. Dorsocentrals 7-16, 11; prealars 6-9, 8; acrostichals 0-4, 0.4(40) (0-8 mentioned in Sæther 1969, p. 5). Scutellum with 13-21, 17 setae.

*Wing* — Anal lobe not protruding. VR = 1.11-1.17, 1.14. Brachiolum with 2 or 3, 2.2 setae; R with 11-22, 15; R<sub>1</sub> with 1-6, 3; R<sub>4+5</sub> with 4-8, 6 setae. Squama with 17-34, 25(20) setae. Cell r<sub>1+5</sub> with 4-10, 33; cell m<sub>1+2</sub> with 0-12, 2 setae.

*Legs* — Spur of front tibia 56-70, 65  $\mu$  long; spurs of middle tibia 30-49, 41  $\mu$ ; and 20-34, 29  $\mu$ ; of hind tibia 62-80, 71  $\mu$ ; and 22-36, 25  $\mu$ . Width at apex of front tibia 47-56, 51  $\mu$ ; of middle tibia 46-61, 54  $\mu$ ; of hind tibia 52-65, 58  $\mu$ . Comb with 9-11, 11 setae, shortest seta 20-34, 27  $\mu$  long; longest 47-64, 58  $\mu$ . Sensilla chaetica absent. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>
p <sub>1</sub>	846-1043,960	902-1141,1042	736-920,853	368-466,433	264-343,314
p <sub>2</sub>	834-1018,961	846-1043,979	435-540,503	239-313,280	172-227,206
p <sub>3</sub>	908-1153,1104	1006-1288,1179	577-748,673	307-417,378	165-202,303
	ta <sub>4</sub>	ta <sub>6</sub>	LR	BV	
p <sub>1</sub>	165-233,216	117-159,137	0.79-0.86,0.82(20)	2.49-2.91,2.62	
p <sub>2</sub>	129-159,153	110-135,124	0.50-0.53,0.52	3.13-3.43,3.22	
p <sub>3</sub>	165-202,190	117-159,140	0.56-0.58,0.57	2.77-3.12,2.92	
	SV	BR			
p <sub>1</sub>	2.24-2.39,2.35	2.94-3.68,3.29			
p <sub>2</sub>	3.74-3.96,3.86	3.60-4.79,4.10			
p <sub>3</sub>	3.26-3.42,3.37	5.63-6.54,5.96			

*Hypopygium* (Fig. 1E, F) — Ninth tergite with 16–33, 25(20) setae; including 12–25, 19(20) on anal point; laterosternites IX each with 4–8, 5 setae. Transverse sternapodeme 90–126, 107  $\mu$  long. Phallapodeme 110–148, 135  $\mu$  long. Anal point 4–10, 8  $\mu$  wide at apex. Gonocoxite 266–321, 301  $\mu$  long; gonostylus 134–157, 146  $\mu$  long. Crista dorsalis large, but not prominent, rounded. Gonostylus rounded at apex. HR 1.97–2.10, 2.05; HV = 2.75–3.09, 2.92.

#### FEMALE IMAGO

Length 4.02–4.45, 4.20 mm (7). Wing length 2.58–2.99, 2.74 mm (7). Total length/wing length 1.46–1.65, 1.54(7). Wing length/length of profemur 3.01–3.58, 3.20 (7).

*Head* — AR = 0.43–0.61, 0.53 (9). Pedicel length/width (microns): 50–64, 58/72–81, 79(9). 5–6 flagellomeres. Length/width (microns) of flagellum with 5 flagellomeres ( $n = 8$ ): 99–122, 111/34–44, 38; 64–75, 69/31–36, 34; 71–84, 78/26–33, 30; 75–90, 83/26–31, 29; 150–200, 184/28–31, 29. Lengths of flagellum with 6 flagellomeres (microns,  $n = 1$ ): 122, 72, 74, 63, 60, 150. Temporal setae 14–19, 16(8); postorbitals 2–4, 3(8), outer verticals 6–13, 8(8); inner verticals 4–7, 6(8). Clypeus with 6–16, 11(10) setae. Cibarial pump (Fig. 1G) posteriorly constricted with strong cornuae. Palp lengths in microns ( $n = 9$ ): 42–56, 46; 54–70, 60; 105–152, 133; 102–136, 117; 120–204, 170.

*Thorax* — Anteprenotum with 4–8, 7(8) setae. Dorsocentrals 14–23, 18(11); prealars 5–8, 7(10); acrostichals 0–4, 0.4(10). Scutellum with 14–24, 19(11) setae.

*Wings* — VR = 1.09–1.17, 1.14(8). Brachiolum with 2–4, 3(8) setae; R with 19–34, 24(8); R<sub>1</sub> with 18–26, 21(8); R<sub>4+5</sub> with 25–58, 40(7) setae. Squama with 21–40, 26(9) setae. Cell r<sub>4+5</sub> with 36–97, 66(6) setae; cell m<sub>1+2</sub> with 20–58, 39(6); cell m<sub>3+4</sub> with 0–48, 16(6); cell an with 0–22, 16(7) setae.

*Legs* ( $n = 8$ , except when otherwise stated) — Spur of front tibia 47–66, 55  $\mu$  long; spurs of middle tibia 27–46, 40  $\mu$  and 24–36, 30  $\mu$ ; of hind tibia 68–78, 72  $\mu$ (7) and 20–26, 25  $\mu$ (7). Width at apex of front tibia 48–55, 50  $\mu$ , of middle tibia 46–62, 56  $\mu$ ; of hind tibia 50–66, 62  $\mu$ . ta<sub>1</sub> of p<sub>2</sub> with 2–8, 4 sensilla chaetica; ta<sub>1</sub> of p<sub>3</sub> with 5–13, 8(9) sensilla chaetica. Lengths (in microns) and proportions of legs:

	fc	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	797–920,856	834–1043,973	687–810,764	356–417,390	258–294,274	172–227,195
p <sub>2</sub>	736–987,898	822–987,933	429–497,474	245–270,261	184–202,192	129–153,137
p <sub>3</sub>	957–1104,1025	1079–1233,1140	613–692,658	319–386,362	270–313,291	159–184,176
	ta <sub>5</sub>	LR	BV	SV	BR ( $n = 3$ )	
p <sub>1</sub>	123–141,132	0.76–0.82,0.79	2.48–2.74,2.62	2.30–2.52,2.40	2.83–3.00	
p <sub>2</sub>	98–135,122	0.50–0.52,0.51	3.00–3.39,3.23	3.63–3.98,3.86	3.15–3.55	
p <sub>3</sub>	116–141,135	0.56–0.59,0.58	2.84–3.07,2.93	3.19–3.40,3.29	4.17–4.69	

*Genitalia* (Fig. 2E, F) — Gonocoxite with 13–23, 18(11) setae. Tergite IX with 24–32, 27(11) setae. Cercus 130–162, 147  $\mu$ (10) long; 26–36, 30  $\mu$ (10) wide at apex. Notum 128–178, 151  $\mu$ (11) long. Seminal capsule more or less pear-shaped, more darkly sclerotized in oral half, 80–104, 91  $\mu$ (7) long including a 14–30, 26  $\mu$ (8) long neck; 54–70, 61  $\mu$ (8) wide. Spermathecal duct usually with a loop.

#### PUPA

Length 5.18–5.91, 5.46 mm (8). Abdomen pale brownish grey. T/A = 1.26–1.63, 1.40(10).

*Cephalothorax* — Thoracic horn (Fig. 3C) 294–380, 338  $\mu$ (10) long; 48–66, 53  $\mu$ (10) wide; length/width 5.09–7.60, 6.42(10). Anterior precorneal seta 82–120, 98  $\mu$ (6) long; located 7–21, 13  $\mu$ (7) from median setae and 11–27, 18  $\mu$ (7) from posterior seta. Median seta 60–110, 90  $\mu$ (5) long; located 2–8.5  $\mu$ (7) from posterior seta. Posterior seta 40–98, 67  $\mu$ (7) long; located 35–82, 53  $\mu$ (7) from horn. Frontal setae 20–96, 60  $\mu$ (5) long.

*Abdomen* ( $n = 10$ ) — Pedes spurii B vestigial. Pedes spurii A present on sternites IV–VIII, longest spinules on IV–VI 9–15, 12  $\mu$  long; on VII 5–10, 8  $\mu$ ; on VIII 1–6, 4  $\mu$  long. Segments I–V usually with 3 hairlike L-setae, occasionally with a minute fourth L-seta; segment VI usually with 4 hairlike L-setae; segment VII with 3–4 (usually 3) filamentous and 0–1 (usually 1) hairlike L-setae:

segment VIII with 5 filamentous L-setae. Sternite VIII of male with 14–38, 27(5) posterior spines, 6–24, 15(5) of which are longer than 10  $\mu$ . Anal macrosetae 220–276, 242  $\mu$  long; 3.0–4.0, 3.6  $\mu$ (9) wide at base. Fringe of anal lobe with 17–24, 20 setae. Setae dorsad of genital sac on sternite IX dark, conspicuous, but often lost, 160–220, 200  $\mu$ (4) long. Genital sac as in Fig. 3D or longer and with a longer apical projection.

#### FOURTH INSTAR LARVA

Length 6.82–9.49, 7.92 mm(14). Head capsule length 0.41–0.49, 0.44 mm(24).

*Head* — Antenna as in Fig. 4G. Lengths of antennal segments in microns ( $n = 14$ –16, 24 for basal segment): 73–88, 83; 24–30, 27; 4–5, 4.6; 8–14, 11; 3–4, 3.9; 2–4, 3; 1–2, 1.5. AR = 1.44–1.91, 1.69(21). Basal antennal segment 21–29, 24  $\mu$ (24) wide; 2.96–3.91, 3.41(24) times as long as wide; distance from base to annular organ 8–20, 14  $\mu$ (15); to basal mark of seta 8–16, 12  $\mu$ (10); to distal mark of seta 21–36, 30  $\mu$ (13); blade at apex 58–75, 65  $\mu$ (14) long; accessory blade 11–16, 13.5  $\mu$ (15) long. Subapical style of second segment 5–8, 6.2  $\mu$ (14) long. Labrum and palatum about as in *H. subpilosus* (Fig. 4A) but SI longer and more narrow, labral lamellae apically pointed (except in some larvae from Baffin Island), and medium spine of pecten epipharyngis as long as and only slightly weaker than lateral spines (Fig. 4C). Premandible 80–99, 91  $\mu$ (13) long. Mandible 150–195, 176  $\mu$ (12) long. Mentum as in Fig. 4J, K; width of one median tooth including lateral notch 21–32, 24  $\mu$ (42); width of ventromental plate 11–22, 18  $\mu$ (43); V/M = 0.47–0.94, 0.76(41). Length of postmentum 205–244, 221  $\mu$ (24).

*Abdomen* — Procerci 29–47, 36  $\mu$ (15) high; 22–36, 28  $\mu$ (15) wide. Supraanal seta 80–196, 140  $\mu$ (12) long. Anal setae 480–787, 604  $\mu$ (13) long. Sa/An = 0.15–0.27, 0.23(12). Anal tubules 110–165, 132  $\mu$ (10) long; 24–60, 45  $\mu$ (10) wide at base; 12–30, 21  $\mu$ (5) wide at apex. Posterior parapods 190–270, 219  $\mu$ (8) long.

#### THIRD INSTAR LARVA

Length 4.42–4.81, 4.63 mm (4). Head capsule length 0.28–0.30, 0.29 mm (5).

*Head* — Lengths of antennal segments in microns ( $n = 5$ ): 43–56, 51; 19–22, 20; 4; 7–10, 8.4; 3–4, 3.2; 2–3, 2.6; 1. AR = 1.16–1.43, 1.33(5). Basal antennal segment 14–16, 15  $\mu$ (5) wide; 2.69–3.86, 3.36(5) times as long as wide; distance from base to annular organ 6–12, 9  $\mu$ (5); to basal mark of seta 5–8  $\mu$ (2); to distal mark of seta 14–16  $\mu$ (2); blade at apex 46–60  $\mu$ (3); accessory blade 12  $\mu$ (1) long. Subapical style of second segment 4–5  $\mu$ (3) long. Premandible 46–62, 55  $\mu$ (5) long. Mandible 110–120, 114  $\mu$ (5) long. Width of one median tooth of mentum 13.5–17, 15  $\mu$ (9); of ventromental plate 9–14, 12  $\mu$ (9); V/M = 0.65–0.90, 0.80(9). Length of postmentum 134–150, 139  $\mu$ (5).

*Abdomen* — Procerci 20–26  $\mu$ (3) high, 14–20  $\mu$ (3) wide. Supraanal seta 65–120  $\mu$ (2) long. Anal setae 330–435,  $\mu$ (2) long. Sa/An = 0.20–0.28(2). Anal tubules 70–74  $\mu$ (2) long, 30  $\mu$ (2) wide at base, 10–14,  $\mu$ (2) wide at apex. Posterior parapods 130  $\mu$ (2) long.

#### Material Examined

Holotype and allotype: pair taken in copulation, Hazen Camp, Ellesmere Island, N.W.T., 8/8/63, R. E. Leech (CNC No. 13396).

Paratypes: male, 2 exuviae, Hazen Camp, Ellesmere Island, N.W.T., 24/7/62 and 31/7/61, D. R. Oliver; mature male pupa with larval exuvia, mature female pupa with larval exuvia, 4 larvae, Char Lake, Cornwallis Island, N.W.T., 24–28/6/68, 27/7–27/8/69, M. Charleton, D. R. Oliver, and H. E. Welch; 3 larvae, Kuhulu Lake, depth 60 m, Baffin Island, N.W.T., 23/8/74, B. Fallis; 3 larvae, depth 12 m, West Iwin Lake, Baffin Island, N.W.T., 27/8/74, B. Fallis; 3 larvae, East Iwin Lake, depth 4 m, Baffin Island, N.W.T., 30/8/74, B. Fallis; 1 larva, Ferguson Lake, depth 50 m, Mackenzie District, N.W.T. as *Heterotrissocladius* sp. *A.* in Sæther (1967b), 4/11/63, K. Elgmork; 2 larvae, Lake Tahoe, California, 19/8/65, collection of W. T. Mason; 29 males, 2 females, N.J. Mosquito Trap, University of Minn., Duluth, St. Louis Co., Minn., 17/6/68, 17/9–7/10/68, 18/5–24/6/69, 6/8–6/10/69, 21/5/70, and 27/8–27/9/70, E. F. Cook; 2 males, N.J. Mosquito Trap, Hovland, Cook Co., Minn., 9/6/69 and 28/9/69, E. F. Cook; 52 males, N.J. Mosquito Trap, 2 miles north

Hovland, U.S. 61, Cook Co., Minn., 28/9/69 and 16/6–27/6/70, E. F. Cook; male, Two Harbor, Lake Co., Minn., 4/6–38, D. Denning; 34 larvae, depth 27.5–120.5 m, off Isle Royale, Lake Superior 3–8/8/71, J. K. Hiltunen; 9 larvae, Georgian Bay, Lake Huron as *H. cf. subpilosus* in Brinkhurst et al. (1968), 2/5–23/8/64, Great Lakes Institute, Toronto; 1 mature female pupa, 35 larvae, Hammond Bay, Thunder Bay, and off Harbor Beach, Lake Huron, 12/7–11/9/70, J. K. Hiltunen; 4 males, 5 females, 1 mature female pupa, 5 exuviae, depths 65–90 m, Lake Huron, 8/10/74, J. K. Hiltunen; 2 larvae, Lake Erie, as *H. cf. subpilosus* in Brinkhurst et al. (1968), 26/8–24/10/63, Great Lakes Institute, Toronto; three larvae, Lake Ontario, 10–13/2/64, 7–10/8/65 and 26/6/67, Great Lakes Institute, Toronto, and P. Sly; 3 larvae, Cayuga Lake, New York, depth 91 m, 10/73 and 5/74, NUS Corp.

### Ecology and Distribution

*Heterotrissocladius oliveri* is a strongly cold-stenothermic and ultraoligotrophic species with apparently the same ecology as *H. subpilosus*. In the arctic lakes (Oliver 1964, 1968) it usually emerges at the end of July to the beginning of August often through cracks in the ice. *H. oliveri* appears to have a relict occurrence in the Great Lakes, Lake Tahoe, and Cayuga Lake (Stahl 1959, p. 97, Henson 1966, p. 47). In the Great Lakes the species has a spring emergence from the middle of May to the end of June, and a fall emergence from August to October.

*Distribution* (previous records as *H. subpilosus* unless otherwise stated) — Hazen Camp, Ellesmere Island, N.W.T. (Oliver 1963:177; 1968:111); Nettilling Lake (Oliver 1964:79; 1968:111), Kuhulu Lake, Iwin Lake, Baffin Island, N.W.T.; Char Lake, Cornwallis Island, N.W.T. (Welch 1973, 1115); Ferguson Lake, N.W.T. (Sæther 1967b:20, as *Heterotrissocladius* sp. A); Lake Tahoe, California (Frantz and Cordone 1966:10, as *Metricnemus* near *lundbecki* (Joh.)); Lake Superior (Hiltunen 1969b:129, as *Heterotrissocladius* sp., Henson 1966:47, probably only in part); Lake Huron (Brinkhurst et al. 1968:18, in part, probably in Schneider et al. 1969:83, as *Metricnemus* sp., Henson 1966:47, probably only in part); Lake Michigan (Henson 1966:47, Mozley and Garcia 1972:104, both probably only in part); Lake Erie (Brinkhurst et al. 1968:18, in part); Lake Ontario (Hiltunen 1969a:48, in part, as *Heterotrissocladius* spp., Johnson and Brinkhurst 1971:1686, probably only in part, Kinney 1972:58); Cayuga Lake (Stahl 1959:97, Henson 1966:47, probably only in part). The record from Greenland by Edwards (1935a, p. 472) probably also belongs to *H. oliveri*.

### *maeaeri* group

Imagines with normal clypeus; stipes with wide lateral extensions almost meeting at midline; antennal groove reaching third flagellomere, sensilla chaetica of flagellomeres only about 15  $\mu$  long; acrostichals stronger than normal but not as strong as in *marcidus* group, starting at about anterior  $\frac{1}{4}$ – $\frac{1}{3}$  of scutum; wings with apical setae in male, and with central and posterior parts bare in female. Pupa with pedes spurii B well developed, but narrow, about as high as wide; pedes spurii A present only on segments IV–VI; genital sac with an apicolateral conical extension; setae absent dorsad of genital sac; segment VII with 3, segment VIII with 3–4 filamentous L-setae. Larvae with antennal blade shorter than segments 2–7 combined, AR of 1.1–1.4, and only one median mental tooth.

### *Heterotrissocladius maeaeri* Brundin

(Fig. 5A–G)

*Heterotrissocladius määri* Brundin 1949: 12 (male, female, larva), Sæther 1967a:105 (larva).

Male characterized by AR of 1.1–1.2, LR<sub>1</sub> of 0.72–0.76; 29–44 weak setae on tergite IX including anal point; basal lobe of gonocoxite with only a few long posterior setae; gonostylus without an outer corner and with a long but little projecting crista dorsalis. Female has only a single row of

setae along the margin of the wing in cell an. Pupae separable from other known species by the characteristics of the *maeaeri* group (only the pupa of *H. maeaeri* is known in this group). Larva characterized by first lateral tooth of mentum being distinctly higher and wider than second lateral tooth; space between median and first lateral tooth approximately U-shaped.

MALE IMAGO (N = 4 EXCEPT WHEN OTHERWISE STATED)

Length 3.43–3.94, 3.74 mm. Wing length 2.01–2.26, 2.18 mm. Total length/wing length: 1.68–1.75, 1.72. Wing length/profemur: 2.52–2.62, 2.57.

*Head* — AR = 1.09–1.23, 1.15. Temporal setae 10–13, 12. Postorbitals 2–3, 2; outer verticals 4–8, 5; inner verticals 3–5, 4. Clypeus with 4–8, 7 setae. Cibarial pump, tentorium, and stipes as in Fig. 5B. Palp lengths in microns: 35–42, 39; 54–56, 55; 138–174, 156; 102–120, 109; 136–166, 146.

*Thorax* — Antepronotum with 12 or 13(2) setae. Dorsocentrals 18–24, 21; prealars 7–9, 8; acrostichals 5–10, 8, starting  $\frac{1}{4}$ – $\frac{1}{3}$  the length of scutum from scutal projection, about 30–40  $\mu$  long. Scutellum with 12–19, 16 setae.

*Wing* — Anal lobe well developed, slightly protruding. VR = 1.18–1.24, 1.20. Brachiolum with 2 setae; R with 14–21, 16 setae; R<sub>1</sub> with 6–8, 7 setae; R<sub>4+5</sub> with 2–7, 5 setae; M<sub>1+2</sub> with 0–2, 0.8 setae. Squama with 16–29(3) setae. Cell r<sub>4+5</sub> with 25–67, 49 setae; cell m<sub>1+2</sub> with 0–7, 3 setae; cell m<sub>3+4</sub> with 0–2, 0.5 setae.

*Legs* — Spur of front tibia 48–64, 59  $\mu$  long; spurs of middle tibia 38–49, 45  $\mu$  and 33–36, 35  $\mu$ ; of hind tibia 60–70, 67  $\mu$  and 28–33, 31  $\mu$ . Width at apex of front tibia 41–52, 47  $\mu$ ; of middle tibia 44–52, 49  $\mu$ ; of hind tibia 47–57, 54  $\mu$ . Sensilla chaetica absent. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>
p <sub>1</sub>	767–895,847	846–1006,946	613–742,701	307–374,350	233–276,253	165–202,185	92–123,112
p <sub>2</sub>	748–883,823	767–908,860	356–429,405	196–233,218	153–172,162	110–129,123	86–104,97
p <sub>3</sub>	810–957,905	932–1079,1023	534–644,592	288–350,321	233–276,256	141–178,163	92–123,111
	LR	BV	SV	BR			
p <sub>1</sub>	0.72–0.76,0.74	2.69–2.89,2.77	2.51–2.63,2.56	2.61–3.08,2.86			
p <sub>2</sub>	0.46–0.48,0.47	3.43–3.55,3.49	4.06–4.26,4.16	2.50–3.58,2.87			
p <sub>3</sub>	0.57–0.60,0.58	2.91–3.02,2.97	3.16–3.31,3.26	4.67–5.00,4.83			

*Hypopygium* (Fig. 5A) — Ninth tergite with 29–44, 36 weak setae including 22–31, 26 on anal point. Transverse sternapodeme 102–120  $\mu$ (3) long. Phallapodeme 114–130  $\mu$ (3) long. Anal point 4–10, 6  $\mu$  wide at apex. Gonocoxite 233–278, 257  $\mu$  long; gonostylus 131–146, 138  $\mu$  long. Crista dorsalis long, rounded near apex, not very prominent. Gonostylus with outer margin rounded. HR = 1.78–1.90, 1.86; HV = 2.62–2.79, 2.71.

FEMALE IMAGO

Only one nearly mature female pupa has been examined. The female is almost certainly separable from other known females by means of the stipes and the acrostichals which are similar to those found in the male (p. 5), and by the wing which has only a few apical setae on the membrane and a single row of setae along the margin of cell an (Brundin 1949, p. 873, 815). At least a few sensilla chaetica are present on ta<sub>1</sub> of p<sub>2</sub> and p<sub>3</sub>.

PUPA (N = 2, EXCEPT WHEN OTHERWISE STATED)

Length 3.78 mm (1). Abdomen pale. T/A = 2.08–2.20.

*Cephalothorax* — Thoracic horn (Fig. 5E) 331–350  $\mu$  long, 58–60  $\mu$  wide; length/width 5.52–6.03.

*Abdomen* — Pedes spurii B (Fig. 5F) well developed, but narrow, about as wide as high. Pedes spurii A present on sternites IV–VI, longest spinules on IV 8  $\mu$  long, on V and VI 2  $\mu$  long. Segments I–VI with 3 hairlike L-setae, segment VII with 3 filamentous L-setae and possibly with an additional

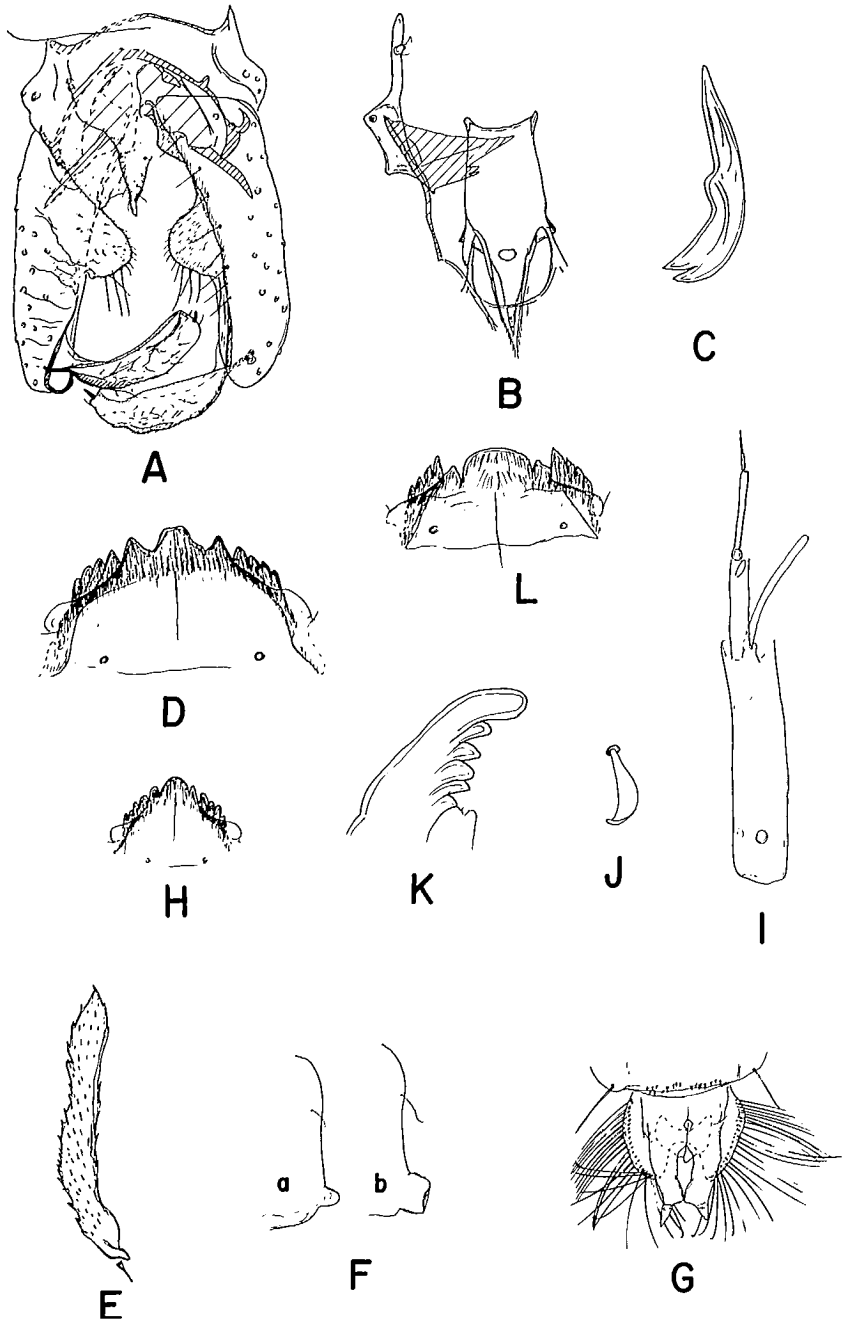


FIG. 5. *Heterotrissocladius maeeri* — group. A-G, *H. maeeri* Brund.: A) male hypopygium, B) cibarial pump, tentorium, and stipes of male, C) premandible of larva, D) mentum, E) thoracic horn, F) pedes spurii B (a) as compared with that of *H. changi* sp.n. (b), G) anal lobe of pupa, ventral view. H, *H. sp. B*, mentum of third instar larva. I-L, *H. sp. C*, larva: I) antenna, J) SII, K) apex of mandible, L) mentum.

hairlike L-seta, segment VIII with 4 filamentous L-setae in one specimen, 4 on one side 3 on the other in the second specimen. Sternite VII of male with 29(1) posterior spines, 4(1) of which are longer than 10  $\mu$ . Anal macrosetae 159  $\mu$  long. Fringe of anal lobe (Fig. 5G) with 23 or 24 setae. No setae dorsad of genital sac (Fig. 5G).

#### FOURTH INSTAR LARVA (N = 4, EXCEPT WHEN OTHERWISE STATED)

Length 5.72–6.46, 6.20 mm. Head capsule length 0.36–0.43, 0.39 mm.

*Head* — Length of antennal segments in microns: 86–90, 88; 34; 5–6(3); 16–18(3); 5–6(3); 3–4(3); 1(3). AR = 1.29–1.41(3). Basal antennal segment 19–21, 18  $\mu$  wide; 4.29–4.74, 4.47 times as long as wide; distance from base to annular organ 10–14  $\mu$ (3), to basal mark of seta 7–8  $\mu$ (3), to distal mark of seta 26–34  $\mu$ (3); blade at apex 30–36  $\mu$ (3) long; accessory blade 7–9, 8  $\mu$  long. Subapical style of second segment 4.5–6  $\mu$ (2) long. Labrum and palatum about as in *H. subpilosus* (Fig. 4A) but epipharyngeal comb apparently even more reduced. Premandible (Fig. 5C) 82–86  $\mu$ (3) long. Mandible 164–170  $\mu$ (2) long. Mentum as in Fig. 5D, sometimes with median tooth lower (more worn); median mental tooth 26–40, 33  $\mu$  wide; ventromental plate 20–25, 23  $\mu$  wide; V/M = 0.57–0.96, 0.72. Postmentum distinctly darker than surrounding areas of head capsule; 196–226, 212  $\mu$  long.

*Abdomen* — Proceri 36–50, 43  $\mu$  high; 24–28, 27  $\mu$  wide. Supraanal seta 130–150, 140  $\mu$  long. Anal setae 491–613, 545  $\mu$  long. Sa/An = 0.23–0.28, 0.26. Anal tubules 140–160  $\mu$ (3) long, 40–48  $\mu$ (2) wide at base, 26–36  $\mu$ (2) wide in middle, 28–38  $\mu$ (2) wide at apex. Posterior parapods 220  $\mu$ (1) long.

#### THIRD INSTAR LARVA (N = 1)

Length 3.15 mm. Head capsule length 0.23 mm.

*Head* — Length of antennal segments in microns: 42, 26, 5, 15, 4, 3, 1. AR = 0.81. Basal antennal segment 10  $\mu$  wide, 4.20 times as long as wide, distance from base to annular organ 8  $\mu$ , to distal mark of seta 16  $\mu$ , blade at apex 28  $\mu$  long, accessory blade 7  $\mu$  long. Postmentum 131  $\mu$  long.

*Abdomen* — Proceri 22  $\mu$  high, 16  $\mu$  wide. Supraanal seta 100  $\mu$  long. Anal setae 270  $\mu$  long. Sa/An = 0.37.

#### Remarks

Pankratova (1970, p. 148) gives *Chaetocladus maeaeri* Brund. (Brundin 1947, p. 24 figure 45) as the original citation for *H. maeaeri*. However, original description of the latter is in Brundin (1949, p. 812) and *C. maeaeri* is an accepted *Chaetocladus*.

#### Material Examined

Four males, Enontekiö, Kalkkoaiivi, Finland, 30/8/72, B. Lindeberg; 1 male hypopygium, near Lake Finsevatn, Finse, Norway, 19/8/64, E. Østbye; 1 larva, depth 5.5 m, Lake Nedre Spurvtjern, Pasvik, Sør-Varanger, Norway, 16/8/66, O. A. Sæther; 1 larva, depth 8 m, Lake Rundvann, Balsfjord, Troms, Norway, 19/8/63, R. Thomassen; 2 pupae, 3 larvae, depth 2 m, Lake Vannaksvatn, Nordland, Norway, 11/6/72, A. Klemetsen.

#### Ecology and Distribution

According to Brundin (1949, p. 707, 1956b, p. 203) *H. maeaeri* is a northern, cold-stenothermic species which constitutes a quantitatively important part of the littoral and upper profundal zones of subarctic Fennoscandian lakes. It seems to be lacking in the profundal of deeper subarctic lakes. In southern and central Sweden the species is stenobathic in the profundal zone of oligohumic oligotrophic lakes. According to Brundin (1949, p. 707) the main emergence takes place from August to the middle of October. However, he mentioned that a male found at Ankarvattnet on July 21, 1946, possibly may be a late member of an early spring emergence. The presence of pupae in the beginning of July in subarctic Lake Vannaksvatn in northern Norway seems to confirm that there are two generations or at least two emergence periods a year.

*Distribution* — Sweden (Brundin 1949:707, 1956b:203) [The record from Lake Vättern (Wiederholm 1974b, p. 36) belongs to *H. marcidus* and not *H. maeaeeri*]; Norway (Sæther 1967a:105, 1968:461).

### *Heterotrissocladius* sp. B

(Fig. 5H)

Larva separable from *H. maeaeeri* by its mentum which has approximately equal first and second lateral teeth; space between median and first lateral teeth approximately V-shaped.

#### FOURTH INSTAR LARVA (N = 1)

Length 7.29 mm. Head capsule length 0.40 mm.

*Head* — Length of antennal segments in microns: 80, 36, 6, 19, 6, 4, 2. AR = 1.08. Basal antennal segment 26  $\mu$  wide, 3.08 times as long as wide, distance from base to annular organ 10  $\mu$ , to basal mark of seta 6  $\mu$ , to distal mark of seta 22  $\mu$ , blade at apex 54  $\mu$  long. Premandible 80  $\mu$  long. Mandible 154  $\mu$  long. Mentum about as in third instar (Fig. 5H), median mental tooth 33  $\mu$  wide, ventromental plate 23  $\mu$  wide, V/M = 0.70. Postmentum 189  $\mu$  long.

*Abdomen* — Procerci 40  $\mu$  high, 32  $\mu$  wide. Supraanal seta 130  $\mu$  long. Anal seta 736  $\mu$  long. Sa/An = 0.18.

#### THIRD INSTAR LARVA (N = 1, EXCEPT WHEN STATED OTHERWISE)

Length 2.46 mm. Head capsule length 0.23 mm.

*Head* — Length of antennal segments in microns: 35, 22, 4, 12, 4, 3, 2. AR = 0.73. Basal antennal segment 13  $\mu$  wide, 2.69 times as long as wide, distance from base to annular organ 7  $\mu$ , blade at apex 35  $\mu$  long, accessory blade 5  $\mu$  long. Premandible 45  $\mu$  long. Mandible 95  $\mu$  long. Mentum as in Fig. 5H, median mental tooth 18–19  $\mu$ (3) wide, ventromental plate 11–13  $\mu$ (3) wide, V/M = 0.61–0.68(3). Postmentum 120–136  $\mu$ (2) long.

*Abdomen* — Procerci 37  $\mu$  high, 17  $\mu$  wide. Supraanal seta 90  $\mu$  long. Anal seta 380  $\mu$  long. Sa/An = 0.24. Anal tubules 64  $\mu$  long, 18  $\mu$  wide at base, 12  $\mu$  wide in middle, 8  $\mu$  wide at apex.

### Material Examined

One fourth instar larva, Cayuga Lake, New York, depth 45 m 17/4/74, NUS Corp.; 1 third instar larva, near Keewaunee, Lake Wisconsin, July 1972, C. Kondrat; 2 head capsules of third instar larvae, 39–40 cm in corer taken at 22 m, Glenora, Bay of Quinte, Lake Ontario, 17/3/72, W. F. Warwick.

### *Heterotrissocladius* sp. C

(Fig. 5I–L)

Larva characterized by having apical mark of seta in apical third, segment 4 conspicuously long, SII broad, premandible with brush, mandible with broad apical tooth, and mentum with very broad median tooth and reduced first laterals.

#### FOURTH INSTAR LARVA (N = 3, EXCEPT WHEN OTHERWISE STATED)

Length 4.23–6.74 mm. Head capsule 0.29–0.35 mm.

*Head* — Antenna as in Fig. 5I. Length of antennal segments in microns: 89–96, 36–40, 4–5, 30–34, 6–8, 3–4, 1–2. AR = 1.14–1.15. Basal antennal segment 20–21  $\mu$  wide, 4.23–4.80 times as long as wide, distance from base to annular organ 12–15  $\mu$ (2), to basal mark of seta 13–15  $\mu$ (2), to distal mark of seta 58–68  $\mu$ , blade at apex 48–52  $\mu$  long. Subapical style of second segment 8  $\mu$ (2) long. SII conspicuously broadened and longer than SI (Fig. 5J), labral lamella apparently single, pecten epipharyngis sclerotized with weak serrations on spines. Premandible 72–74  $\mu$  long, with brush. Mandible 126–131  $\mu$  long. Mentum as in Fig. 5L, median mental tooth 46–51  $\mu$  wide, ventromental plate 20  $\mu$

wide, V/M = 0.39–0.43. Postmentum blackish brown distinctly darker than surrounding areas of head capsule, 130–139  $\mu$  long.

*Abdomen* — Procerci 25–32  $\mu$  high, 18–22  $\mu$  wide. Supraanal seta 200–230  $\mu$  long. Anal setae 505–670  $\mu$  long. Sa/An = 0.34–0.42. Anal tubules 140–168  $\mu$ (2) long, 23–30  $\mu$ (2) wide at base, 18–20  $\mu$ (2) wide in middle, 4–8  $\mu$ (2) wide at apex. Posterior parapods 120–160  $\mu$  long.

#### THIRD INSTAR LARVA (N = 1)

Length 3.69 mm. Head capsule length 0.22 mm.

*Head* — Length of antennal segments in microns: 57, 31, 3.5, 21, 5, 3, 1. AR = 0.95. Basal antennal segment 12  $\mu$  wide, 4.75 times as long as wide, distance from base to annular organ 7  $\mu$ , to basal mark of seta 6  $\mu$ , to distal mark of seta 28  $\mu$ . Premandible 50  $\mu$  long. Mandible 86  $\mu$  long. Median mental tooth 29  $\mu$  wide, ventromental plate 11  $\mu$  wide, V/M = 0.38. Postmentum 92  $\mu$  long.

*Abdomen* — Procerci 14  $\mu$  high, 15  $\mu$  wide. Supraanal seta 150  $\mu$  long. Anal setae 393  $\mu$  long. Sa/An = 0.38. Anal tubules 78  $\mu$  long, 16  $\mu$  wide at base 8  $\mu$  wide in middle, 3  $\mu$  wide at apex. Posterior parapods 80  $\mu$  long.

#### Remarks

This species differs from other members of *Heterotrissocladius* by the form of its mentum, the placement of the apical mark of seta on the basal antennal segment and the broad SII. Pecten epipharyngis also appears to be more sclerotized than usual, but to have serrations. The only other known genus with the same kind of antenna is *Paratrissocladius* Zavřel. *Paratrissocladius*, however, has a double median mental tooth and usually only four lateral teeth, and possesses simple, strong, darkly sclerotized spines in the pecten epipharyngis. Both *Heterotrissocladius* sp. C and *Paratrissocladius* appear to have a single labral lamella. *Heterotrissocladius* sp. C also have a distinct premandibular brush not found in other species of the genus. The presence of this brush and of the simple labral lamella, however, are plesiomorphic characters, and do not necessarily mean that the larva belongs to another genus. For the moment it seems best to place the larva in *Heterotrissocladius*.

#### Material Examined

Four larvae, Lafayette Creek, Walton Co., Florida, 3/5/71, P. H. Carlson.

### *marcidus* group

Imagines with normal clypeus and stipes; acrostichals very strong starting in front at scutal projection; wing membrane with setae at least on distal half in males, on most of the surface in females. Pupa with pedes spurii B prominent, wider than high; pedes spurii A present on segments IV–VII; genital sac with long, apicolateral extension; no setae present dorsad of genital sac; segment VII and VIII with 3 or 4, nearly always 4, filamentous L-setae. Larva with antennal blade shorter than segments 2–7 combined, AR of 0.9–1.3, and two median mental teeth.

#### *Heterotrissocladius marcidus* (Walker)

(Fig. 6F; 7A–D; 8I–K; 9A, F; 10A, G)

*Metriocnemus marcidus* Walker, 1856:177 (male). Edwards 1929:313 (male, female); Chernovskii 1949:143.

*Metriocnemus aestivalis* Goetghebuer, 1921:76 (male).

*Metriocnemus* (*Heterotrissocladius*) *marcidus* Walk., Goetghebuer 1932:20 (male), 1940–50:6,22 (male, female).

*Metriocnemus alticola* Goetghebuer, 1934:339 (male).

*Brillia alticola* (Goetgh.), Thienemann 1935:92 (pupa, larva).

*Heterotrissocladius marcidus* (Walk.) Zavřel 1934:8 (pupa, larva); 1942:15, 19 (pupa); Edwards 1937:143; Thienemann 1941:216 (pupa), 1944:587, 633 (pupa, larva); Brundin 1947:fig. 32 (male); 1949:815 (male, female, larva); Pankratova 1970:146 (pupa, larva).

*Heterotrissocladius alticola* (Goetgh.), Thienemann 1941:216 (pupa); 1944:587, 633 (pupa, larva).  
*Metriocnemus cubitalis* Kieffer, 1911:200 (male); Potthast 1915: 362 (pupa, larva).  
 ? *Metriocnemus longicollis* Kieffer, 1913:34 (female).  
 ? *Metriocnemus triangulifer* Kieffer, 1924:99 (female).  
 ? *Heterotrissocladius longicollis* (Kieff.), Spärck 1922:92 (larva).  
 ? *Heterotrissocladius cubitalis* (Kieff.), Spärck 1922:92 (larva).  
 ? *Heterotrissocladius triangulifer* (Kieff.), Spärck 1922:93 (larva).  
 ? *Metriocnemus* (*Heterotrissocladius*) *longicollis* Kieff., Goetghebuer 1932:20 (female); 1940-50:6,21 (female).  
 ? *Metriocnemus* (*Heterotrissocladius*) *cubitalis* Kieff., Goetghebuer 1932: 26 (pupa, larva); 1942:17 (male).  
 nec *Heterotrissocladius marcidus* Sæther 1969:45 (male).

Imago characterized by hairy wings with at least a few hundred setae in cell an of male, and about 140 setae in cell m basad of RM in female. The AR of male low (1.2-1.3), anterior margin of cibarial pump moderately concave; number of thoracic setae higher than normal (21-29 dorsocentrals in male, 36-46 in female). Male gonostylus rounded on outer margin; with about 26-27 setae on tergite IX and anal point. Female with about 35-58 setae on tergite IX; relatively broad ventrolateral lobe of gonapophysis VIII with long caudolaterally directed setae on inner margin; labia with small, but distinct microtrichia.

Pupal exuvia with yellowish brown thorax, 26-36 setae in fringe of anal lobe, T/A of 1.3-1.6, and length to width of thoracic horn about 4.2-5.5.

Larva with brownish black submentum, conspicuously darker than surrounding areas of head capsule, VM of 1.1-1.6, basal antennal segment 80-95  $\mu$  long, 4.0-4.6 times as long as wide, and setae at base of mentum 2.2-3.3  $\mu$  wide at base.

MALE IMAGO (N = 3, EXCEPT WHEN STATED OTHERWISE)

Length 3.94-4.57 mm. Wing length 2.28-2.62 mm. Total length/wing length: 1.67-1.74. Wing length/length of profemur 2.48-2.61.

*Head* — AR = 1.23-1.33. Temporal setae 15-18(2). Postorbitals 5-7(2), outer verticals 4 or 5(2), inner verticals 6. Clypeus with 9-17 setae. Cibarial pump, tentorium and stipes as in Fig. 6F. Tentorium 180-220  $\mu$  long, 45-53  $\mu$ (2) wide, 11-20  $\mu$ (2) wide anteriorly of posterior tentorial pit, distance from apex to tentorial pit 25-40  $\mu$ . Stipes about 190  $\mu$ (1) long. Palp lengths in microns: 40-46, 50-70, 192-208, 144-160, 153-196.

*Thorax* — Anteprepronotum with 9-14 setae. Dorsocentrals 21-29, prealars 8-12, acrostichals 20-25(2). Scutellum with 19-21 setae.

*Wing* — Anal lobe well developed, distinctly protruding. VR = 1.16-1.21. Brachiolum with 2 or 3 setae; humeral crossvein with 1 or 2(2) setae; subcosta with 25-54(2) setae; R with 60-84 setae; R<sub>1</sub> with 56-90 setae, 6-33(2) of them ventrally; R<sub>4+5</sub> with 104-110 setae, 20-74 of them ventrally; RM with 0-2 setae; M with 2-8 setae; M<sub>1+2</sub> with 85-160 setae; M<sub>3+4</sub> with 82-102 setae; Cu with 50-66 setae; Cu<sub>1</sub> with 56-74 setae; vannal fold with 64-175 setae; An<sub>1</sub> with 75-82 setae. Cell an with 450(1) or more setae. Squama with 26-31 setae.

*Legs* — Spur of front tibia 73-82  $\mu$  long; spurs of middle tibia 44-50  $\mu$  and 28-41  $\mu$ , of hind tibia 78-91  $\mu$  and 27-34  $\mu$ . Width at apex of front tibia 48-50  $\mu$ , of middle tibia 50-57  $\mu$ , of hind tibia 56-62  $\mu$ . Comb with 11-14  $\mu$  setae, shortest seta 32-38  $\mu$  long, longest 65-78  $\mu$ . Sensilla chaetica absent on p<sub>2</sub>, 0-1, 0.4(5) on ta<sub>1</sub> of p<sub>3</sub>. Lengths (in microns) and proportions of legs:

	fc	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	920-1006	1055-1171	951-1012	503-527	368-405	258-270
p <sub>2</sub>	914-994	945-1030	509-564	270-307	196-227	135-165
p <sub>3</sub>	969-1067	1178-1263	730-785	362-393	282-331	184-215
	ta <sub>5</sub>	LR	BV	SV	BR	
p <sub>1</sub>	104-129	0.85-0.91	2.29-2.53	2.06-2.23	3.33(1)	
p <sub>2</sub>	92-104	0.54-0.55	3.22-3.42	3.55-3.65	3.36-3.93(2)	
p <sub>3</sub>	104-123	0.61-0.62	2.93-3.12	2.94-2.98	4.41-5.35(2)	

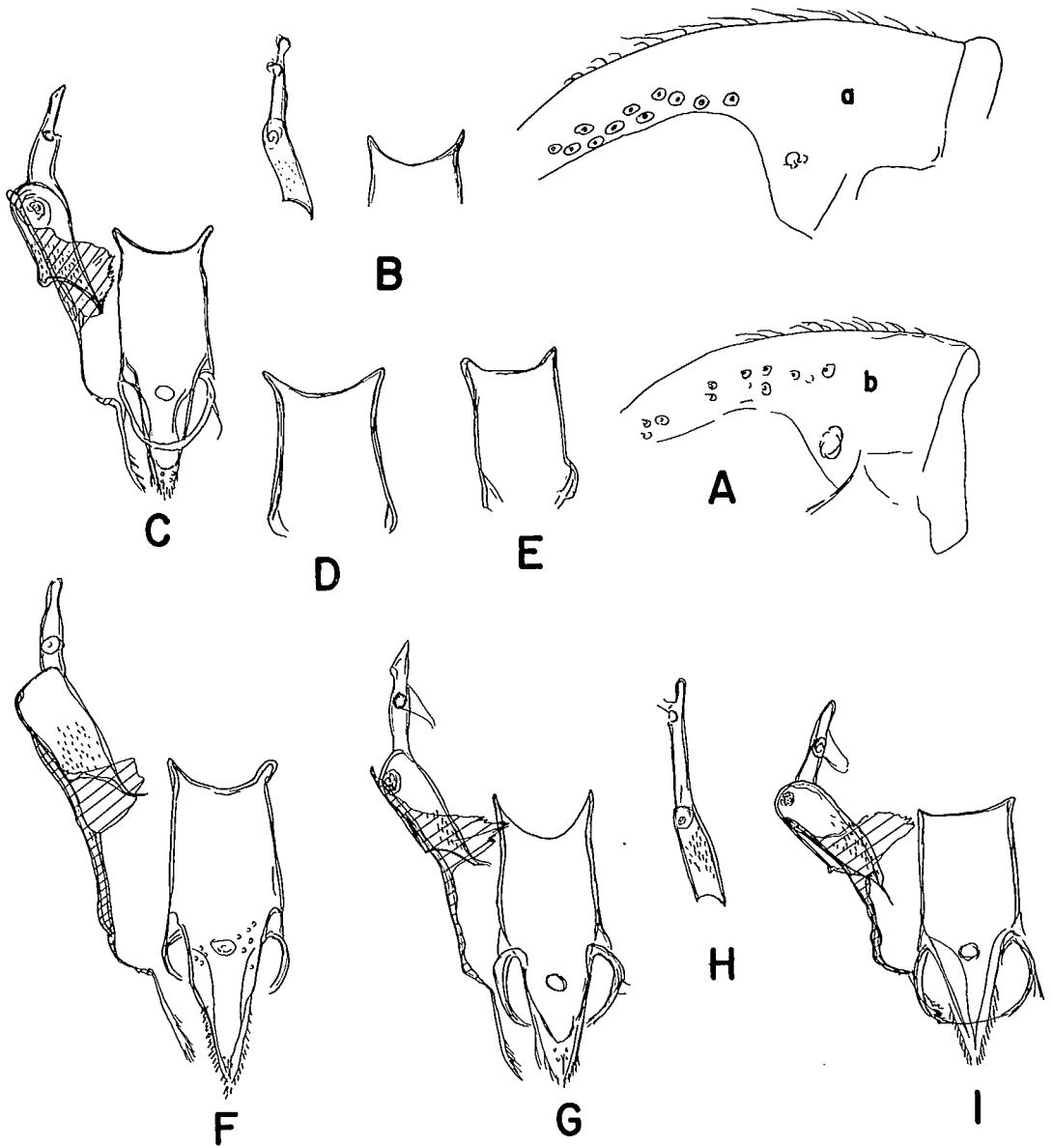


FIG. 6. *Heterotrissocladius marcidus* — group. A) thorax of *H. hirtapex* sp.n. (a) as compared with thorax of *Parametrioctenemus lundbecki* (Joh.) (b). B–I, cibarial pump, tentorium, and stipes: B–C) *H. changi*, female (B) and male (C), D) *H. scutellatus* (Goetgh.), E) *H. grimshawi* (Edw.), F) *H. marcidus* (Walk.), G–H) *H. hirtapex* sp.n. male (G) and female (H), I) *H. latilaminus* sp.n.

*Hypopygium* (Fig. 7A–D) — Ninth tergite with 26 or 27(2) weak setae including 16(1) on anal point; laterosternites IX each with 7(1) setae. Transverse sternapodeme 94  $\mu$ (1) long. Phallapodeme 110  $\mu$ (1) long. Anal point 4–6  $\mu$  wide at apex. Gonocoxite 258–282  $\mu$  long; gonostylus 123–127  $\mu$  long. Crista dorsalis triangular. Gonostylus mostly rounded on outer margin, sometimes with indications of a preapical corner. HR = 2.10–2.22; HV = 3.20–3.63.

FEMALE IMAGO (N = 3, EXCEPT WHEN OTHERWISE STATED)

Length 4.34–4.83 mm (2). Wing length 2.68–2.88 mm (2). Total length/wing length 1.62–1.68(2). Wing length/profemur 2.67–2.73(2).

*Head* — AR = 0.32–0.36. Pedicel length/width (microns): 64/78–80. Flagellomeres length/width (microns): 106–122/40–42, 79–95/33–38, 86–98/33–34, 90–92/32–34, 120–128/24–36. Temporal setae 14–17. Postorbitals 2, outer verticals 6–8, inner verticals 4–7. Clypeus with 15–22(6) setae. Tentorium 156–164  $\mu$  long, 29–30  $\mu$  wide, 10–11  $\mu$  wide anteriorly of posterior tentorial pit, distance from apex to posterior tentorial pit 14–20  $\mu$ . Stipes 154–174  $\mu$  long, 50  $\mu$ (1) wide. Coronal suture 40–110, 88  $\mu$ (6) long. Two ocelli 12–20  $\mu$ (2) apart. Palp lengths in microns: 44–49, 56–60, 186–200, 151–158, 205–232.

*Thorax* — Antepnotum with 12–14 setae. Dorsocentrals 36–46, 40(5); prealars 11–15, 12(5); acrostichals 10(1). Scutellum with 22–32, 29(5) setae.

*Wing* — VR = 1.21(1). Brachiolum with 5 or 6(2) setae; humeral crossvein with 3(2) setae; subcosta with 75–78(2) setae; R with 80–90(2) setae; R<sub>1</sub> with 93–113(2) setae, 28–38(2) ventrally; R<sub>4+5</sub> with 190(272(2)) setae, 63–100(2) ventrally; RM with 1–3 setae; M with 5–7(2) setae; M<sub>1+2</sub> with 170(1) setae, 52(1) ventrally; M<sub>3+4</sub> with 123(1) setae, 8(1) ventrally; Cu with 96(1) setae; Cu<sub>1</sub> with 86(1) setae, 4 ventrally; vannal fold with 142(1) setae; An<sub>1</sub> with 120(1) setae. Cell m basad of RM with 142(1) setae. Squama with 29–43, 34(4) setae.

*Legs* — Spur of front tibia 44–50  $\mu$  long; spurs of middle tibia 44–50  $\mu$  and 33–39  $\mu$ , of hind tibia 80–85  $\mu$  and 26–32  $\mu$ . Width at apex of front tibia 54–56  $\mu$ , of middle tibia 58–62  $\mu$ , of hind tibia 64–70  $\mu$ . Comb with 11–12 setae, shortest seta 35–38  $\mu$ (2) long, longest 68–70  $\mu$ (2). Sensilla chaetica 11–14 on ta<sub>1</sub> of p<sub>2</sub>, and 22–25 on ta<sub>1</sub> of p<sub>3</sub>. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	981–1055	1110–1190	963–1049	515–582	386–411	264–282
p <sub>2</sub>	981–1092	1043–1110	552–601	294–313	215–233	153–165
p <sub>3</sub>	1043–1141	1263–1386	797–846	411–435	313–331	202–209
	ta <sub>5</sub>	LR	BV	SV		
p <sub>1</sub>	110–123	0.87–0.90	2.36–2.42	2.08–2.17		
p <sub>2</sub>	98–104	0.53–0.55	3.35–3.46	3.55–3.67		
p <sub>3</sub>	110–117	0.61–0.63	2.94–3.09	2.89–2.99		

*Genitalia* (Fig. 8 I–K) — Gonocoxite with 13–20, 16(6) setae. Tergite IX with 35–58, 45(6) setae. Cercus 130–150  $\mu$  long. Seminal capsule 86–102, 96  $\mu$ (5) long; sclerotized in apical 64–70, 67  $\mu$ (5); 61–69, 66  $\mu$ (5) wide. Ventrolateral lobe of gonapophysis VIII relatively broad, with long posterolateral directed setae at anterior margin. Labia with small, but distinct microtrichia.

PUPA

Length 4.38–5.22, 4.91 mm (13). T/A = 1.31–1.65, 1.46(12). Thorax of exuvia yellowish brown, abdomen pale greyish brown.

*Cephalothorax* — Thoracic horn (Fig. 10A) 442–503, 467  $\mu$ (13) long; 86–110, 97  $\mu$ (11) wide; length/width: 4.24–5.46, 4.82(11). Anterior precorneal seta 78–125  $\mu$ (10) long; located 7–18, 11  $\mu$ (10) from median seta and 15–32, 22  $\mu$ (10) from posterior seta. Median seta 104–160, 138  $\mu$ (10) long; located 4–18, 10  $\mu$ (10) from posterior seta. Posterior seta 24–50, 38  $\mu$ (10) long, located 50–100, 81  $\mu$ (10) from horn. Frontal seta 40–90, 67  $\mu$ (10) long.

*Abdomen* — Pedes spurii A present on sternites IV–VII, longest spinules on IV and V 6–10, 8  $\mu$ (10), on VI 4–8, 7  $\mu$ (10) long, on VII 2–5, 3  $\mu$ (10) long. Segments I–V with 3 hairlike L-seta, segment VI with 4

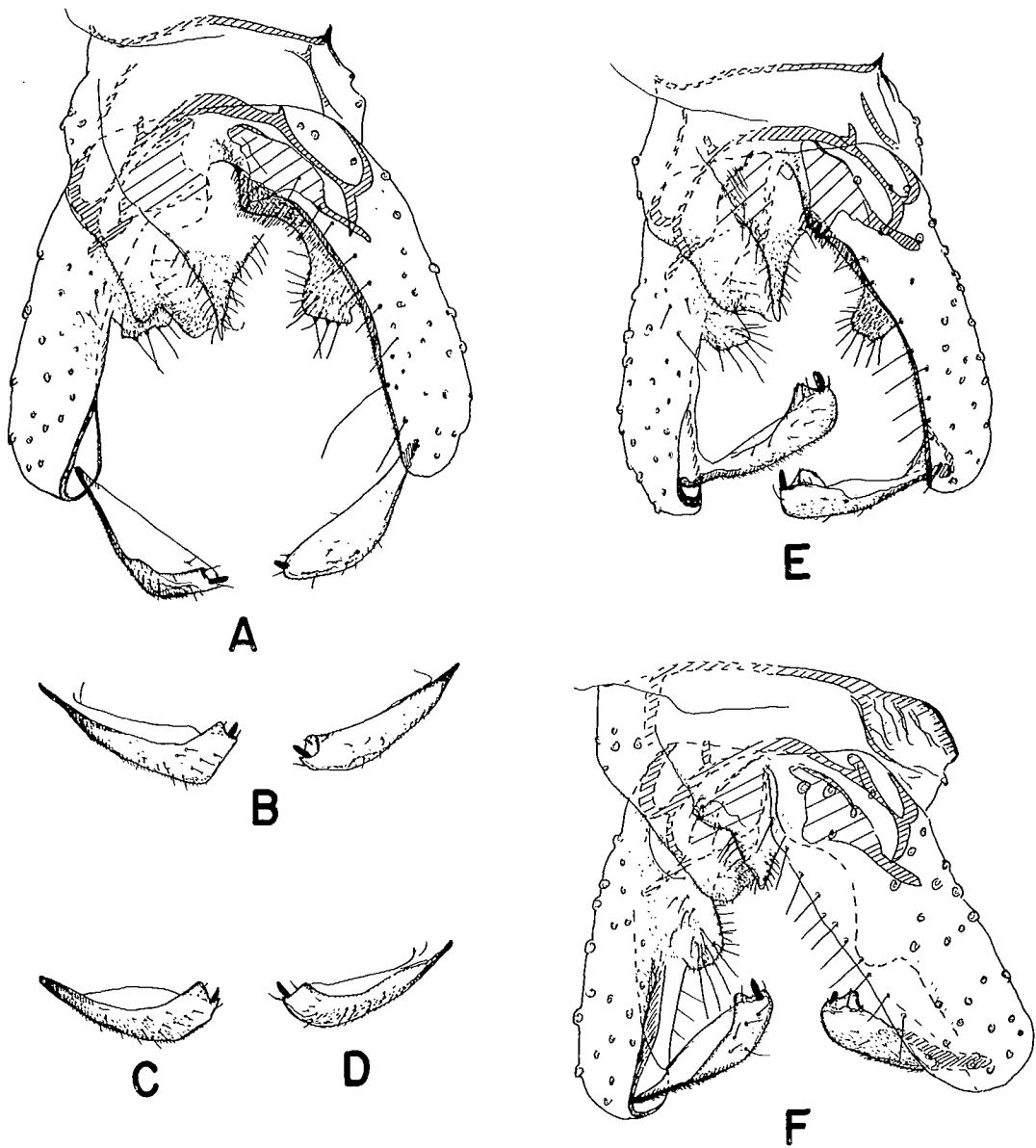


FIG.7. *Heterotrissocladius marcidus* — group, hypopygium. A–D, *H. marcidus* (Walk.): A–B) from Finland, C) from Marion Lake, B.C., D) from Bodensee, Germany. E, *H. latilaminus* sp.n. F, *H. hirtapex* sp.n.

hairlike L-setae, segments VII and VIII each with 4 filamentous L-setae. Sternite VIII of male with 34–55  $\mu$ (3) posterior spines, 25–45(3) of which are longer than 10  $\mu$ . Anal macrosetae 282–356, 322  $\mu$ (13) long. Fringe of anal lobe with 26–36, 31(13) setae. Genital sac and anal lobe as in Fig. 10F.

#### FOURTH INSTAR LARVA

Length 5.12–7.13, 6.27 mm (8). Head capsule length 0.35–0.47, 0.40 mm (9).

*Head* — Antenna as in Fig. 11G. Lengths of antennal segments in microns ( $n = 7-8$ ): 78–95, 86; 34–42, 38; 5–6.5, 5.7; 14–22, 17; 6–7, 6.3; 4–5, 4.7; 2–4, 3.3. AR = 1.05–1.25, 1.14(6). Basal antennal segment 18–23, 20  $\mu$ (7) wide; 4.09–4.51, 4.31(7) times as long as wide; distance from base to annular organ 10–18, 13  $\mu$ (6), to basal mark of seta 8–10, 8  $\mu$ (5); to distal mark of seta 19–40, 26  $\mu$ (6); blade at apex 42–59, 51  $\mu$ (5) long; accessory blade 6–10, 7  $\mu$ (4) long. Subapical style of second segment 6–8.5  $\mu$ (3) long. Labral lamella apically rounded, about as in *Heterotrissocladius latilaminus* sp.n. (Fig. 11M). Premandible 74–86, 80  $\mu$ (7) long. Mandible 130–162, 150  $\mu$ (8) long. Mentum as in Fig. 11A; width of one median mental tooth 18–21.5, 19  $\mu$ (9); width of ventromental plate 21–29, 24  $\mu$ (9); setae at base of mentum 2.0–3.3, 2.5  $\mu$ (9) wide at base; V/M = 1.16–1.53, 1.30(6). Length of postmentum 184–219, 202  $\mu$ (9); submentum brownish black, conspicuously darker than surrounding areas of head capsule.

*Abdomen* — Procerci 36–50, 44  $\mu$ (8) high; 22–40, 31  $\mu$ (8) wide. Supraanal seta 134–200, 166  $\mu$ (7) long. Anal setae 527–773, 664  $\mu$ (6) long. Sa/An = 0.22–0.27, 0.25(6). Anal tubules 180  $\mu$ (1) long, 60  $\mu$ (1) wide at base, 30  $\mu$ (1) wide at apex. Posterior parapods 190  $\mu$ (1) long.

#### Remarks

The larvae of *H. marcidus* are nearly identical to those of *H. latilaminus* sp.n. and the differences found in the width of the setae at the base of the mentum, and in the coloration of the submentum, may not hold up when more specimens are examined. The larval records from Lake Superior, Florida, and Quebec thus are somewhat uncertain.

#### Material Examined

Eight males, 3 females, 4 mature female pupae, 18 exuviae, Lake Kemiträsk, Finland, 30/7/68, M. Hirvenoja; 4 males, Lake Puruvesi, Finland, 13/9/67, B. Lindeberg; 4 males, Lake Inarijärvi, Finland, 26/6/71, P. Virtanen; 1 larva, depth 3 m, Lake Vaggatam, Sör-Varanger, Norway, 22/7/66, O. A. Sæther; 1 larva, depth 1 m, Lake Rundvann, Balsfjord, Norway, 14/4/63, R. Thomassen; 1 larva, depth 94 m, Lake Vättern, Sweden, May 1971, T. Wiederholm. 2 males, Lake Bodensee, Germany, 1/10/62 and 9/3/63, F. Reiss; 4 pupae, 56 larvae, Lunz, Austria, 1941 and 1942, A. Thienemann (as *H. alticola* (Goetgh.)); 1 male, 2 larvae, Marion Lake, B.C., 10/6/65 and 12/2/64, A. L. Hamilton; 9 larvae, depth 6.5 m, near Isle Royale, Lake Superior, 8/8/71, J. K. Hiltunen; 1 larva, small stream on Mt. St. Hilaire, Quebec, R. MacKay; 1 larva, depth 3 m, Canadarego Lake, near Cornell U., N.Y., 9/3/73 S. B. Smith; 3 larvae, Rileys Creek, Blackwater Drainage, Oxaloosa Co. Florida, 11/2/72, W. M. Beck Jr.

#### Ecology and Distribution

*Heterotrissocladius marcidus* occurs in ponds and puddles, in streams, rivers, and springs but seems to prefer the littoral zone of lakes (Brundin 1949; Thienemann 1954). It can be found both on minerogen and on organogen substrates with or without vegetation. According to Brundin (1949, p. 706) the greatest depth at which the species has been found is 15 m. However, one larva from a depth of 94 m in Lake Vättern, Sweden, is present in this material. Most likely the larva was washed out from shallower areas. The most common chironomid in the High Tatras is *H. marcidus* (Zavřel 1937, p. 490). In the pond Zielony Staw Gąsienicowy it is the only chironomid present (Gliwicz 1963, p. 31). Although *H. marcidus* is the least cold-stenothermic member of the genus it is still restricted to relatively cold waters. In most of the European localities the water temperature never exceeds 18° C throughout the year. The record from Florida thus seems peculiar. However, most or all streams in the Blackwater Drainage are fed by groundwater, not by surface drainage, and these streams stay cooler in the summer than could normally be expected (Beck 1973, p. 239).

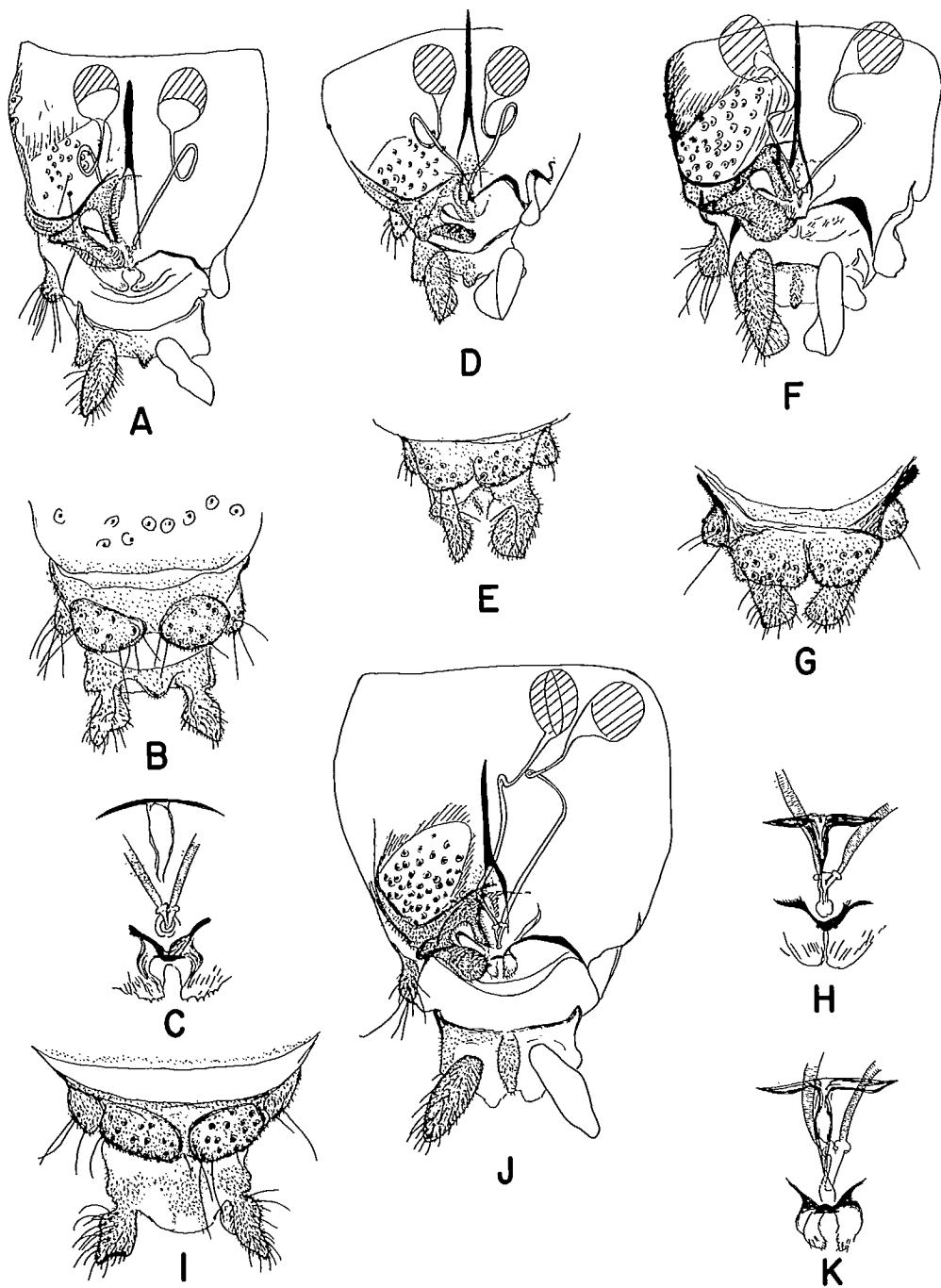


FIG. 8. *Heterotrissocladius marcidus* — group, female genitalia. A–C, *H. hirtapex* sp.n.: A) ventral view, B) dorsal view, C) labia, spermathecal eminence and membrane, D–E, *H. latilaminus* sp.n., ventral: D) and dorsal view, E); F–H, *H. changi* sp.n.: F) ventral view, G) dorsal view, H) labia, spermathecal eminence, and membrane. I–K, *H. marcidus* (Walk.): I) dorsal view, J) ventral view, K) labia, spermathecal eminence, and membrane.

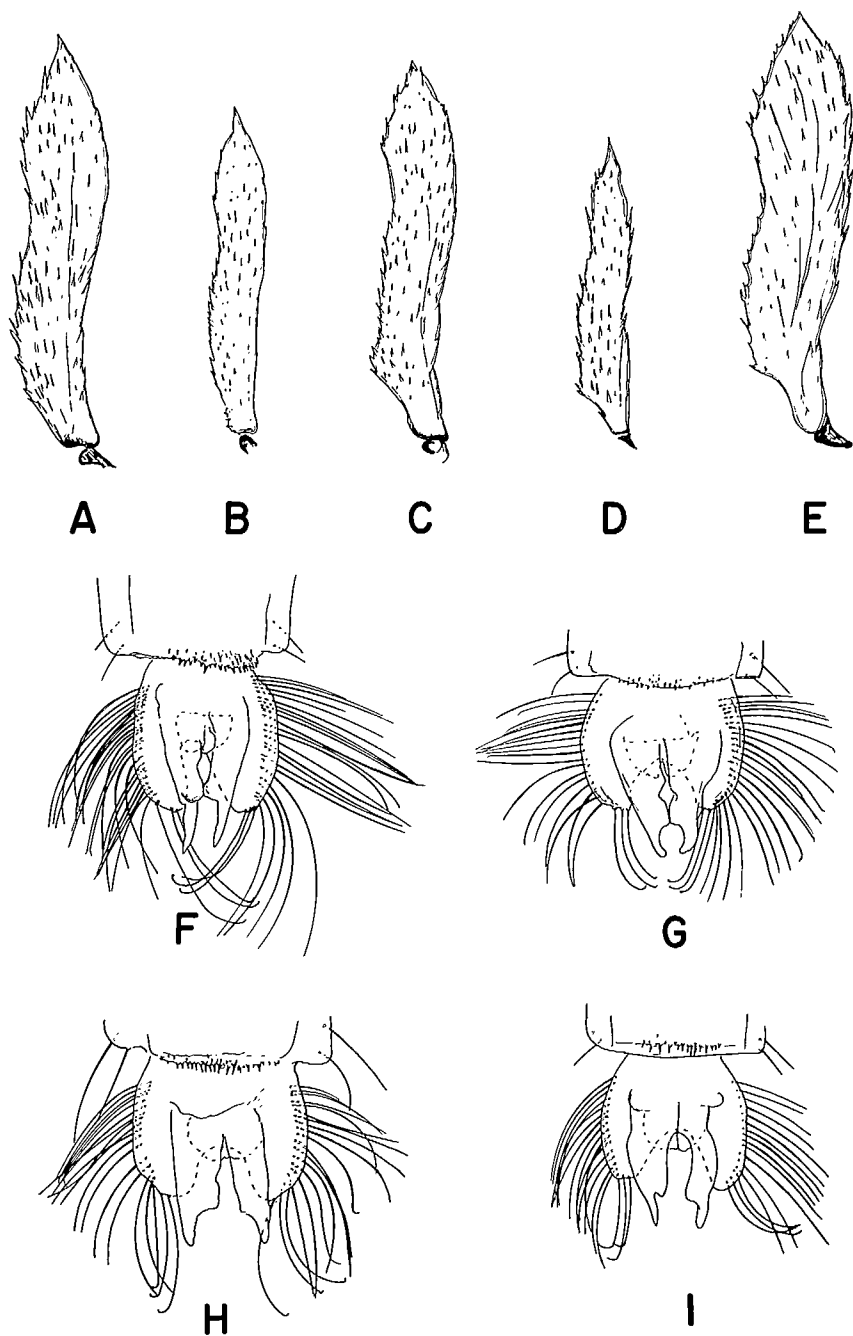


FIG. 9. *Heterotrissocladius marcidus* — group pupae. A–E, thoracic horn: A) *H. marcidus* (Walk.), B) *H. latilaminus* sp.n., C) *H. hirtapex* sp.n., D) *H. changi* sp.n., E) *H. scutellatus* sp.n. F–I, posterior end of segment VIII and anal lobe, ventral view: F) *H. marcidus* (Walk.), G) *H. latilaminus* sp.n., H) *H. hirtapex* sp.n., I) *H. changi* sp.n.

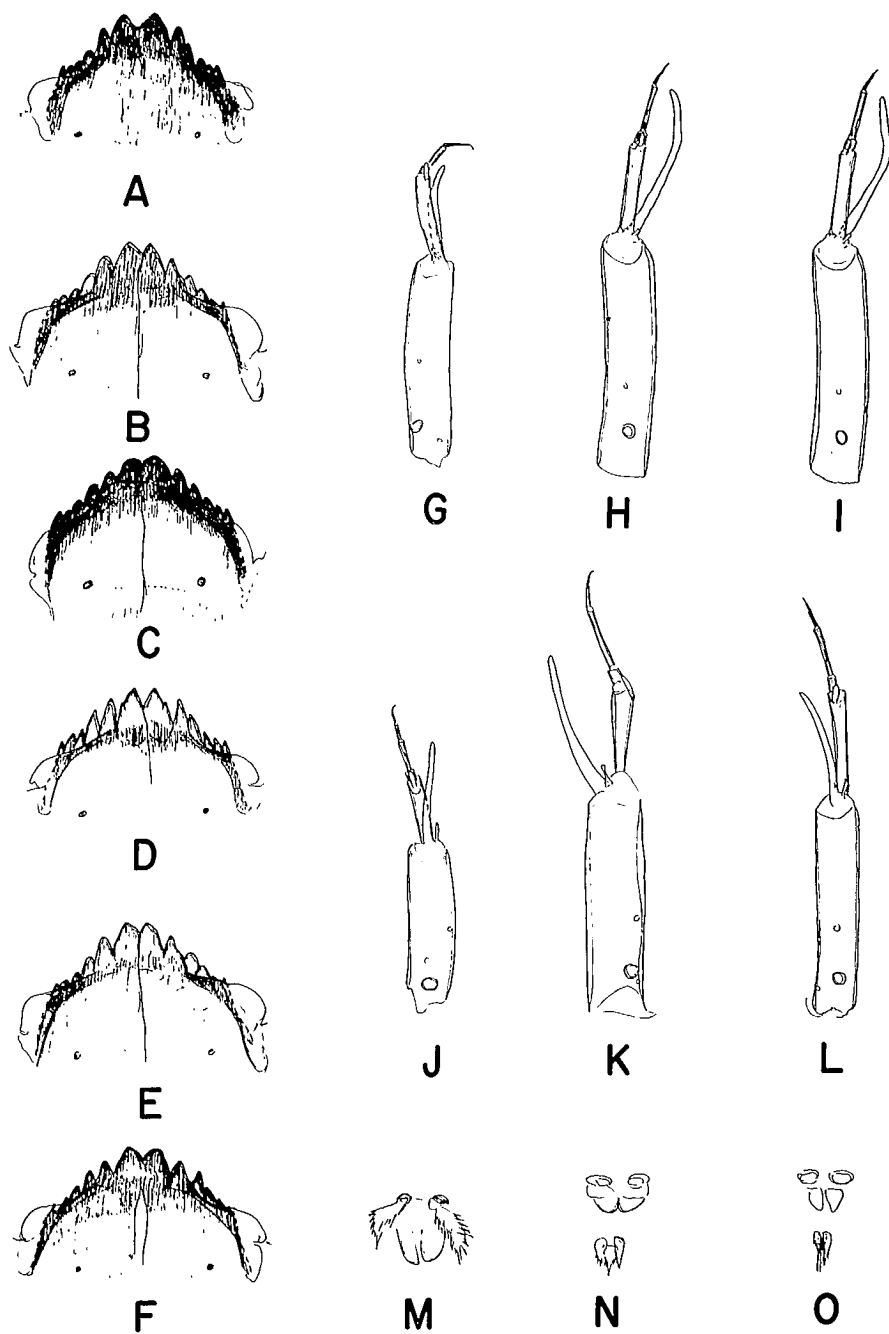


FIG.10. *Heterotrissocladius marcidus* — group, larvae. A–F, mentum: A) *H. marcidus* (Walk.), B) *H. latilaminus* sp.n., C) *H. hirtapex* sp.n., D) *H. changi* sp.n., E) *H. sp.n. D.*, F) *H. scutellatus* (Goetgh.). G–L, antenna: G) *H. marcidus* (Walk), H) *H. latilaminus* sp.n., I) *H. hirtapex* sp.n., J) *H. changi* sp.n., K) *H. sp. D.*, L) *H. scutellatus* (Goetgh.). M–O, SI, labral lamellae and pecten epipharyngis: M) *H. latilaminus* sp.n., N) *H. hirtapex* sp.n., O) *H. changi* sp.n.

*Heterotrissocladius marcidus* is bivoltine in most localities. However, in the subarctic lakes of northern Sweden there is probably only one generation a year (Brundin 1949:706).

*Distribution* — Finland; Sweden (Thienemann 1941:174, Brundin 1947:14, 1949:705, Sandberg 1969:132, Wiederholm 1974a:35, 1974b:36); Norway (Sæther 1967a:106); Iceland (Goetghebuer and Lindroth 1931:282); England (Walker 1856:177, Edwards 1929:313, Macan 1949:177); Belgium (Goetghebuer 1921:188); Germany (Thienemann 1936:201, Reiss 1968:231, Lehmann 1971:484); Austria (Albrecht 1924:197 as *Heterotrissocladius* sp., Brehm and Ruttner 1926:374 as *Heterotrissocladius*, Thienemann 1943:196, 1950:118, Bretschko 1974:27); the High Tatras (Zavřel 1934:8, 1935:443, 1937:490, Hrabě 1942:149, Gliwicz 1963:31, Kownacka and Kownacki 1965a:85, 1965b table 2, Kownacki 1971:444, Kownacki and Kownacka 1965:35); Hungary (Berczik 1968a:20, 1968b:19); the Juras (Vernaux 1968:35), the Pyrenees (Laville 1966:210, 1971:234, 1974:149), British Colombia, Lake Superior, Quebec, Florida.

### *Heterotrissocladius latilaminus* sp.n.

(Fig. 6I; 7E; 8D, E; 9B, G; 10B, H, M)

*Heterotrissocladius* sp. A. Hamilton 1965 part 2:58, pro parte.

*Heterotrissocladius* near *subpilosus* Sæther 1970a:table 6.

*Heterotrissocladius* f.l. *subpilosus* Sæther and McLean 1972:9.

Imago characterized by having dorsal margin of cibarial pump shallow. WL/Pfe of about 2.8 in male, 3.0–3.2 in female. Male wing with scattered setae in cells  $r_{4+5}$ ,  $m_{1+2}$ , and  $m_{3+4}$  but none in anal cell and none in cell m basad of RM. Female wing with about 20–55 setae in cell m basad of RM. Male with about 24 weak setae on tergite IX including anal point, gonostylus with indication of an outer corner, and triangular crista dorsalis. Female with about 23–26 setae on tergite IX, relatively narrow ventrolateral lobe of gonapophyses VIII, and spermathecal duct with a loop. Pupal exuvia pale on thorax and abdomen, with 20–30 setae in fringe of anal lobe, and a T/A of 1.4–1.7. Larva with blackish-brown submentum, conspicuously darker than surrounding areas of head capsule; V/M of 1.2–1.6; basal antennal segment 80–93  $\mu$  long and 4.0–4.6 times as long as wide; setae at base of mentum 1.1–1.9  $\mu$  wide at base.

#### MALE IMAGO (N = 1)

Length 4.14 mm. Wing length 2.57 mm. Total length/wing length: 1.61. Wing length/profemur 2.80.

*Head* — AR = 1.45, Temporal setae 13. Postorbitals 5, outer verticals 4, inner verticals 4. Clypeus with 7 setae. Cibarial pump, tentorium, and stipes as in Fig. 6I. Tentorium 155  $\mu$  long, 43  $\mu$  wide, 14  $\mu$  wide anteriorly of posterior tentorial pit, distance from apex to posterior tentorial pit 38  $\mu$ . Stipes 155  $\mu$  long, 65  $\mu$  wide. Palp lengths in microns: 45, 60, 150, 140, 175.

*Thorax* — Antepnotum with 9 setae. Dorsocentrals 13, prealars 6, acrostichals at least 6, 30–50  $\mu$  long. Scutellum with 14 setae.

*Wing* — VR = 1.15. Brachiolum with 2 setae; R with 25 setae;  $R_1$  with 20 setae, 1 ventrally;  $R_{4+5}$  with 56 setae, 7 ventrally;  $M_{1+2}$  with 63 setae;  $M_{3+4}$  with 39 setae, 3 ventrally;  $Cu_1$  with 21 setae;  $Cu$  with 2 setae; remaining veins without setae. Cell an and cell m basad of RM void of setae. Squama with 27 setae.

*Legs* — Spurs of middle tibia 28  $\mu$  and 38  $\mu$  long. Sensilla chaetica absent. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>
p <sub>1</sub>	920	1043	895	478	356	233	123
p <sub>2</sub>	883	945	509	294	215	141	104
p <sub>3</sub>	987	1159	705	372	301	178	116
	LR	BV	SV	BR			
p <sub>1</sub>	0.86	2.40	2.19	4.58			
p <sub>2</sub>	0.54	3.10	3.59	5.00			
p <sub>3</sub>	0.60	2.95	3.04	7.26			

*Hypopygium* (Fig. 7E) — Ninth tergite including anal point with 24 weak setae; laterosternites IX each with 4 setae. Transverse sternapodeme 96  $\mu$  long. Phallapodeme 106  $\mu$  long. Anal point 4  $\mu$  wide at apex. Gonocoxite 256  $\mu$  long, gonostylus 124  $\mu$  long. Crista dorsalis relatively prominent, triangular. Gonostylus with indication of an outer corner. HR = 2.08; HV = 3.37.

FEMALE IMAGO (N = 3 EXCEPT WHEN OTHERWISE STATED)

Length 2.54–3.31 mm. Wing length 2.29–2.62 mm. Total length/wing length 1.11–1.26. Wing length/profemur 3.02–3.16.

*Head* — AR = 0.37–0.41. Pedicel length/width (microns): 48–60(2)/60–74(2). Flagellomeres length/width (microns): 92–102/30–36; 56–70/26–30; 63–73/24–30; 66–71/24–30; 102–116/28–32. Temporal setae 10–12. Postorbitals 2 or 3, outer verticals 4, inner verticals 3–6. Clypeus with 11–14 setae. Tentorium 130–140  $\mu$  long, 20–24  $\mu$  wide; 8–10  $\mu$  wide anterior of posterior tentorial pit, distance from apex to posterior tentorial pit 14–20  $\mu$ . Stipes 136–164  $\mu$  long, 46  $\mu$  (1) wide. Coronal suture 35–80  $\mu$  long. Palp lengths in microns: 32–40, 48–60, 126–150, 108–126, 160–175.

*Thorax* — Antepnotum with 8 or 9 setae. Dorsocentrals 23–26, prealars 7–9, acrostichals 5(1). Scutellum with 16–21 setae.

*Wing* — VR = 1.17–1.20. Brachiolum with 2 setae; humeral crossvein with 0–1(2) setae; subcosta with 23–32 setae; R with 36–52 setae; R<sub>1</sub> with 47–52 setae, 12–13 of them ventrally; R<sub>4+5</sub> with 94–110 setae, 23–32 ventrally; M<sub>1+2</sub> with 77–90 setae, 1 or 2(2) of them ventrally; M<sub>3+4</sub> with 57–72 setae, 0–10 of them ventrally; Cu with 36–40(2) setae; Cu<sub>1</sub> with 37–48 setae, 0–2 of them ventrally; vannal fold with 37–63 setae; An<sub>1</sub> with 26–47 setae. Cell m basad of RM with 20–55 setae. Sqama with 22–26(2) setae.

*Legs* — Spur of front tibia 34–50  $\mu$  long; spurs of middle tibia 34–38  $\mu$  and 20–29  $\mu$  long, of hind tibia 64–82  $\mu$  and 19–30  $\mu$ . Width at apex of front tibia 44–53  $\mu$ , of middle tibia 48–53  $\mu$ (2), of hind tibia 52–60  $\mu$ . Comb with 12 or 13 setae, shortest seta 23–36  $\mu$  long, longest 52–62  $\mu$ . Sensilla chaetica 5–6  $\mu$  on ta<sub>1</sub> of p<sub>2</sub> and 8–11  $\mu$  on ta<sub>1</sub> of p<sub>3</sub>. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	724–865	877–1043	748–871	417–478	294–337	190–227
p <sub>2</sub>	754–865	822–926	435–509	245–270	172–209	110–129
p <sub>3</sub>	822–935	987–1171	626–736	319–368	251–294	141–165
	ta <sub>5</sub>	LR	BV	SV	BR	
p <sub>1</sub>	86–104	0.83–0.85	2.33–2.43	2.14–2.19	2.15–2.92	
p <sub>2</sub>	80–98	0.52–0.55	3.06–3.32	3.52–3.76	2.81–2.96	
p <sub>3</sub>	92–104	0.60–0.63	2.94–3.10	2.89–3.04	3.57–3.93	

*Genitalia* (Fig. 9D, E) — Gonocoxite with 13–17 setae. Tergite IX with 23–26 setae. Cercus 100–120  $\mu$  long. Seminal capsule 76–99  $\mu$  long, sclerotized in apical 56–70  $\mu$ , 52–55  $\mu$  wide. Spermathecal duct with loop. Ventrolateral lobe of gonapophysis VIII relatively narrow.

PUPA (N = 7, EXCEPT WHEN OTHERWISE STATED)

Length 4.34–4.63, 4.46 mm. T/A = 1.38–1.69, 1.51. Thorax and abdomen of exuvia pale.

*Cephalothorax* — Thoracic horn (Fig. 10B) 331–417, 372  $\mu$  long; 50–67, 60  $\mu$ (6) wide; length/width 5.48–6.62, 6.08(6). Anterior precorneal seta 92–125, 107  $\mu$ (6) long; located 4–16, 8  $\mu$  from median seta and 9–21, 14  $\mu$  from anterior seta. Median seta 95–132, 114  $\mu$  long; located 3–10, 7  $\mu$  from posterior seta. Posterior seta 50–65, 56  $\mu$ (6) long; located 75–88, 81  $\mu$  from horn. Frontal seta present but not measurable.

*Abdomen* — Pedes spurii A present on IV–VII, longest spinules on IV–VI 5–9, 6  $\mu$  long, on VII 4–9, 6  $\mu$  long. Segments I–VI with 3 hairlike L-setae, segments VII–VIII each with 4 filamentous L-setae. Sternite VIII of male with 25–39, 35(4) posterior spines, 13–28, 22(4) of which are longer than 10  $\mu$ . Anal macrosetae 221–270, 246  $\mu$  long. Fringe of anal lobe with 20–30, 25 setae. Genital sac and anal lobe as in Fig. 10G.

FOURTH INSTAR LARVA

Length 4.73–7.17, 6.31 mm (13). Head capsule length 0.36–0.42, 0.39 mm (16).

*Head* — Antenna as in Fig. 11H. Lengths of antennal segments in microns ( $n = 10-14$ ): 80-93, 86; 35-43, 38; 5-6.5, 6; 14-21, 18; 4-7, 6; 3-5, 3.9; 2-4, 2.3. AR = 1.04-1.26, 1.16(10). Basal antennal segment 19-22, 21  $\mu$ (11) wide; 4.00-4.58, 4.16(11) times as long as wide; distance from base to annular organ 10-14, 11  $\mu$ (9); to basal mark of seta 10-34, 25  $\mu$ (4); to distal mark 23-32, 27  $\mu$ (6); blade at apex 40-60, 53  $\mu$ (10) long; accessory blade 8-10, 9  $\mu$ (4) long. Subapical style of second segment 6-9, 7  $\mu$ (5) long. SI and labral lamellae as in Fig. 11M. Premandible 76-86, 82  $\mu$ (6) long. Mandible 136-164, 150  $\mu$ (8) long. Mentum as in Fig. 11B; width of one median mental tooth 16-20, 18  $\mu$ (16); width of ventromental plate 18-28, 24  $\mu$ (16); seta at base of mentum 1.1-1.9, 1.5  $\mu$ (16) wide at base; V/M = 1.16-1.56, 1.32  $\mu$ (16). Length of postmentum 192-216, 206  $\mu$ (16); submentum blackish brown to brown, usually conspicuously darker than surrounding areas of head capsule.

*Abdomen* — Procerci 42-50, 46  $\mu$ (15) high; 28-39, 33  $\mu$ (15) wide. Supraanal seta 110-200, 164  $\mu$ (12) long. Anal setae 552-797, 659  $\mu$ (14) long. Sa/An = 0.20-0.29, 0.25(12). Anal tubules 90-170, 142  $\mu$ (5) long; 40-63, 49  $\mu$ (5) wide at base; 16-30, 22  $\mu$ (5) wide at apex. Posterior parapods 170-195, 181  $\mu$ (4) long.

### Remarks

In some respects this species is intermediate between *H. marcidus* and *H. changi*. The male has some indications of an outer corner on its gonostylus, lacking in both *H. marcidus* and in *H. hirtapex* sp.n. but present in the remaining species. The number of setae is generally lower than in *H. marcidus* and *H. hirtapex*. The larva is almost indistinguishable from that of *H. marcidus*. The submentum, however, is usually lighter than in *H. marcidus* and in *H. hirtapex*, the setae at the base of the mentum are thinner than in *H. marcidus*, and the ventromental plates are wider than in *H. hirtapex*.

### Material Examined

Holotype and allotype: male, female, Marion Lake, B.C., 6/5/64, A. L. Hamilton (CNC No. 13397).

Paratypes: 2 females, 4 pupae, 5 exuviae, 6 larvae, 1/4-8/5/64, 5 larvae, July 1963-February 1964, 3 pupae, 4 larvae, 1/4/66, Marion Lake, B.C., A. L. Hamilton; 1 pupa reared from larva, Marion Lake, B.C., 7/5/69, V. J. E. McCauley; 1 larva, depth 26.5 m, at Kelowna, Okanagan Lake, B.C. 9/9/69, J. F. Flannagan and O. A. Sæther; 2 larvae, depths 1.5 and 2.5 m, Kalamalka Lake, B.C., 11/5/71, J. F. Flannagan and O. A. Sæther; 3 larvae, depths 5-52 m, Skaha Lake, B.C., 11/9/69 and 12/5/71, J. F. Flannagan and O. A. Sæther. Other possible material: 1 larva, Fraser River, B.C., 13/4/73, T. G. Northcote.

### Ecology and Distribution

*Heterotrissocladus latilaminus* has been found in the littoral and profundal zones of four lakes in British Columbia with one possible record from the Fraser River. The single larva from Okanagan Lake was found near the pipeline which discharges sewage from the city of Kelowna. However, the station had a typical oligotrophic fauna qualitatively, but very high densities were recorded relative to other stations in the lake (Sæther 1970a, p. 12). In Skaha Lake the larvae were found at depths of 5-52 m, in Kalamalka Lake only in the littoral zone (Sæther and McLean 1972, table 3), and in Marion Lake at all depths (Hamilton 1965, part 1, p. 33, but also including some *H. marcidus* at shallower stations). Skaha Lake shows clear signs of eutrophication (Sæther and McLean 1972, p. 17). Kalamalka and Okanagan lakes are oligotrophic, and Marion Lake is oligotrophic, probably with some modification by humic substances. The distribution of *H. latilaminus* seems to show that this species can tolerate a wider range of biotopes than usual for most lake-dwelling members of the genus, ranging from littoral to profundal, and from strongly oligotrophic to mesotrophic, and slightly polluted localities.

The species has two generations a year with emergence in April-June and August-October (Hamilton 1965, part 1, p. 36).

*Distribution* — British Columbia.

***Heterotrissocladius hirtapex* sp.n.**  
(Fig. 6A, G, H; 7F; 8A-C; 9C, H; 10C, I, N)

Imago characterized by strongly deepened dorsal margin of the cibarial pump, and conspicuously dark brownish grey wings, without setae in anal cell of males, and with about 65-88 setae in cell m basad of RM in females. Male with relatively short anal point, gonostylus rounded on outer dorsal margin, and crista dorsalis rounded. Female with numerous sensilla chaetica (8-21 on  $p_2$  and 20-34 on  $p_3$ ), setigerous protrusions of tergite IX well separated, tergite IX with 28-36 setae, and looped spermathecal duct. Pupal exuvium with conspicuously dark, brownish grey abdominal segments and tergite I occasionally with a few posterior spinules. Larva with V/M of 0.6-0.9, submentum conspicuously brownish black and darker than surrounding areas of head capsule; spines of pecten epipharyngis triangular and equal in size.

MALE IMAGO (N = 5, EXCEPT WHEN OTHERWISE STATED)

Length 4.26-4.65, 4.45 mm. Wing length 2.43-2.64, 2.57 mm. Total length/wing length 1.67-1.77, 1.73. Wing length/profemur 2.63-2.70, 2.66.

*Head* — AR = 1.55-1.62, 1.59. Temporal setae 12-16, 14. Postorbitals 5-7, 6; outer verticals 4-7, 5; inner verticals 1-5, 4. Clypeus with 10-14, 12 setae. Cibarial pump, tentorium, and stipes as in Fig. 6G. Tentorium 184-210, 193  $\mu$  long; 38-48, 42  $\mu$  wide; 14-18, 17  $\mu$  wide anterior of posterior tentorial pit; distance from apex to posterior tentorial pit 30-40, 35  $\mu$ . Stipes 170-190, 183  $\mu$  long; 60-72, 66  $\mu$  wide. Palp lengths in microns: 41-50, 45; 56-68, 63; 159-185, 169; 124-149, 137; 172-200, 186.

*Thorax* (Fig. 6A) — Anteprenotum with 7-12, 10 setae. Dorsocentrals 12-18, 15; prealars 6-8, 7; acrostichals 18-23, 21, anterior few about 15  $\mu$  long, followed by 56-80, 67  $\mu$  long, strong acrostichals, and by 7-11, 8 posterior setae 15-30, 27  $\mu$  long. Scutellum with 8-18, 14 setae.

*Wing* — VR = 1.13-1.14, 1.14. Brachiolum with 2 or 3 setae; R with 16-27, 23 setae;  $R_1$  with 12-18, 16 setae, including 0-2, 1.0 ventrally;  $R_{4+5}$  with 34-58, 43 setae including 0-6, 2.8 ventrally;  $M_{1+2}$  with 26-62, 47 setae;  $M_{3+4}$  with 9-33, 25 setae;  $Cu_1$  with 2-17, 10 setae; remaining veins without setae. Cell an and cell m basad of RM void of setae. Squama with 19-41, 29 setae.

*Legs* — Spur of front tibia 64-82, 73  $\mu$  long; spurs of middle tibia 42-45, 44  $\mu$  and 28-31, 29  $\mu$  long; of hind tibia 74-86, 81  $\mu(4)$  and 30-42, 33  $\mu(4)$  long. Width at apex of front tibia 47-54, 50  $\mu$ ; of middle tibia 49-54, 51  $\mu$ ; of hind tibia 56-60  $\mu(3)$ . Comb with 11-13, 12(4) setae; shortest seta 30-36, 33  $\mu(4)$  long; longest seta 56-80, 68  $\mu(4)$ . Sensilla chaetica 0-2, 0.8(4) on  $ta_1$  of  $p_3$ . Lengths (in microns) and proportions of legs:

	fc	ti	$ta_1$	$ta_2$	$ta_3$	$ta_4$
$p_1$	926-994,968	1043-1116,1090	926-1006,970	527-577,550	362-399,380	239-264,251
$p_2$	920-994,967	926-1043,1000	521-589,558	294-319,312	227-239,233	147-178,158
$p_3$	1006-1104,1065	1178-1288,1227	711-822,763	380-454,419	313-343,330	196-215,204
	$ta_5$	LR	BV	SV	BR	
$p_1$	110-129,117	0.84-0.94,0.89	2.28-2.38,2.34	2.01-2.23,2.12	3.21-3.48,3.90	
$p_2$	98-110,103	0.51-0.60,0.56	3.01-3.26,3.13	3.34-3.84,3.53	4.84-5.70,5.17(4)	
$p_3$	116-123,119	0.60-0.64,0.62	2.81-2.92,2.85	2.86-3.12,2.98	5.67-7.00,6.31	

*Hypopygium* (Fig. 7F) — Ninth tergite including anal point with 16-28, 24 weak setae; laterosternites each with 4-8, 6 setae. Transverse sternapodeme 96-117, 104  $\mu$  long. Phallapodeme 114-124, 119  $\mu$  long. Anal point 2-8, 5  $\mu$  wide at apex. Gonocoxite 264-305, 290  $\mu$  long; gonostylus 121-136, 130  $\mu$  long, without outer corner and with rounded crista dorsalis. HR = 2.17-2.29, 2.22; HV = 3.32-3.52, 3.42.

FEMALE IMAGO (N = 6, EXCEPT WHEN OTHERWISE STATED)

Length 3.47-4.30, 3.84 mm. Wing length 2.37-2.77, 2.56 mm (5). Total length/wing length: 1.42-1.56, 1.49(5). Wing length/profemur: 2.64-2.97, 2.79(5).

*Head* — AR = 0.39–0.48, 0.44. Pedicel length/width (microns): 58–86, 66/75–83, 79. Flagellomeres length/width (microns): 95–126, 106/38–48, 42; 64–75, 69/32–40, 35; 67–84, 77/31–35, 33; 72–92, 82/30–34, 32; 128–149, 141/31–36, 33. Temporal setae 9–16, 13. Postorbitals 2–6, 4; outer verticals 4–6, 5; inner verticals 3–5, 5. Clypeus with 12–17, 15 setae. Tentorium (Fig. 6H) 160–190, 176  $\mu$  long; 20–28, 26  $\mu$  wide; 9–11, 10  $\mu$  wide anterior of posterior tentorial pit; distance from apex to posterior tentorial pit 13–20, 17  $\mu$ . Stipes 176–190, 184  $\mu$  long; 54–78, 62  $\mu$  wide. Coronal suture 76–161, 105  $\mu$  long, complete in one specimen. Ocelli 0–2(4) located 10–12  $\mu$ (3) from coronal suture. Palp lengths in microns: 48–56, 50; 62–68, 65; 117–170, 151; 124–147, 134; 191–230, 205(5).

*Thorax* — Antepnotum with 9–12, 10 setae. Dorsocentrals 29–33, 31; prealars 8–11, 9; acrostichals 12–25, 21, anterior ones 60–105, 81  $\mu$ (5) long, posterior 7(5) 18–45, 29  $\mu$ (5) long. Scutellum with 24–28, 27(5) setae.

*Wing* — VR = 1.17–1.24, 1.20(5). Brachiolium with 3(4) setae; humeral crossvein with 0–3, 1.4(5); subcosta with 43–69, 55(5) setae; R with 59–79, 67 setae; R<sub>1</sub> with 63–75, 68 setae including 12–19, 15 ventrally; R<sub>4+5</sub> with 152–201, 172 setae including 40–58, 47 ventrally; RM with 0–1, 0.3 setae; M with 0–1, 0.2 setae; M<sub>1+2</sub> with 117–140, 132(5) setae including 4–21, 10(5) ventrally; M<sub>3+4</sub> with 91–138, 109(5) setae including 1–6, 3(5) ventrally; Cu with 65–77, 70(5) setae; Cu<sub>1</sub> with 52–70, 64(5) setae including 0–2, 0.8(5) ventrally; vannal fold with 76–93, 83(5) setae; An<sub>1</sub> with 58–66, 63(5) setae. Cell m basad of RM with 65–88, 78(5) setae. Squama with 28–40, 35 setae.

*Legs* — Spur of front tibia 40–47, 43  $\mu$  long; spurs of middle tibia 38–46, 44  $\mu$  and 26–38, 32  $\mu$ , of hind tibia 76–86, 82  $\mu$  and 25–33, 29  $\mu$ . Width at apex of front tibia 48–56, 50  $\mu$ ; of middle tibia 53–63, 57  $\mu$ ; of hind tibia 57–71, 62  $\mu$ . Comb with 11–13, 12 setae; shortest seta 30–35, 33  $\mu$  long; longest 64–70, 66  $\mu$ . Sensilla chaetica 8–21, 13(7) on ta<sub>1</sub> of p<sub>2</sub> and 20–34, 26(7) on ta<sub>1</sub> of p<sub>3</sub>. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
p <sub>1</sub>	859–994,908	963–1141,1022	853–945,891	454–527,498	319–380,355	215–258,225
p <sub>2</sub>	853–994,913	889–1043,953	497–552,516	258–313,286	196–233,211	135–165,144
p <sub>3</sub>	932–1092,990	1079–1300,1144	656–773,700	356–429,393	264–337,301	172–202,189
	ta <sub>5</sub>	LR	BV	SV	BR	
p <sub>1</sub>	98–123,108	0.83–0.89,0.88	2.32–2.49,2.38	2.12–2.26,2.17	3.03–3.85,3.45	
p <sub>2</sub>	80–98,90	0.53–0.57,0.54	3.20–3.41,3.26	3.48–3.69,3.62	3.13–4.17,3.61	
p <sub>3</sub>	104–123,111	0.59–0.64,0.61	2.74–2.95,2.86	2.92–3.16,3.05	3.53–4.44,4.05	

*Genitalia* (Fig. 9A–C) — Gonocoxite with 16–21, 18 setae. Tergite IX with 28–36, 33 setae; setigerous protrosions completely separated from each other. Cercus 132–153, 143  $\mu$  long. Seminal capsule 84–102, 92  $\mu$  long; sclerotized in apical 53–70, 60  $\mu$ ; 58–62, 60  $\mu$  wide. Spermathecal duct with loop. Labia usually serrated on margin.

PUPA (N = 9, EXCEPT WHEN OTHERWISE STATED)

Length 4.22–5.76, 5.23 mm. T/A = 1.25–1.54, 1.42. Exuvia conspicuously dark, brownish grey.

*Cephalothorax* — Thoracic horn (Fig. 10C) 368–478, 437  $\mu$ (10) long; 60–86, 75  $\mu$ (10) wide; length/width: 5.18–6.95, 5.88(10). Anterior precorneal seta 100–132, 115  $\mu$ (7) long; located 6–14, 9  $\mu$  from median seta and 8–23, 17  $\mu$  from posterior seta. Median seta 119–130, 122  $\mu$ (7) long; located 4–14, 9  $\mu$  from posterior seta. Posterior seta 50–80, 69  $\mu$ (8) long; located 64–106, 90  $\mu$  from horn. Frontal seta 93–105  $\mu$ (3) long.

*Abdomen* — Pedes spurii A present on sternites IV–VII; longest spinules on IV and V 6–18, 11  $\mu$ ; on VI 5–14, 8  $\mu$ ; on VII 5–9, 6  $\mu$ . Segments I–VI with 3 hairlike L-setae, segments VII and VIII with 4 filamentous L-setae, and segment VIII occasionally (in 3 of 11 specimens) with one additional hairlike L-seta. Sternite VIII of male with 18–33, 28(5) posterior spines, 10–20, 17(5) of which are longer than 10  $\mu$ . Anal macrosetae 290–350, 312  $\mu$  long. Fringe of anal lobe with 23–28, 25(10) setae. Genital sac and anal lobe as in Fig. 10H.

FOURTH INSTAR LARVA (N = 3, EXCEPT WHEN OTHERWISE STATED)

Head capsule length 0.44–0.47 mm.

*Head* — Antenna as in Fig. 11I. Length of antennal segments in microns: 90–92, 37–42, 6, 19–22, 5–6, 3–4, 2. AR = 1.14–1.26. Basal antennal segment 20–22  $\mu$  wide, 4.09–4.50 times as long as wide, distance from base to annular organ 12–14  $\mu$ (2), to basal mark of seta 14–30  $\mu$ (2), to distal mark of seta 33  $\mu$ (1), blade at apex 54–62  $\mu$ . Subapical style of second segment 8–10  $\mu$ (2). Labral lamellae and pecten epipharyngis as in Fig. 11N. Premandible 74–80  $\mu$  long. Mandible 139–158  $\mu$  long. Mentum as in Fig. 11C; width of one median tooth 18  $\mu$ , width of ventromental plate 12–14  $\mu$ , V/M = 0.67–0.78. Length of postmentum 188–212  $\mu$ , submentum brownish black and conspicuously darker than surrounding areas of head capsule.

*Abdomen* — Procerci 48–52  $\mu$ (2) long, 32–36  $\mu$ (2) wide. Supraanal seta 130–150  $\mu$ (2) long. Anal setae 834–853  $\mu$ (2) long. Sa/An = 0.16–0.18(2).

### Remarks

This species seems most closely related to *H. marcidus* from which it is easily separated by means of its less hairy wings. The dark wing should also separate this species from other *Heterotrissocladius*; however, in some species, (e.g. *H. changi* sp.n.) the coloration of the wings may vary from pale and transparent to nearly as dark as in *H. hirtapex* sp.n. The species is the only member of the *marcidus* group in which the pupal exuvium has a dark colored abdomen; the same coloration is found in *Heterotrissocladius* sp. *A* of the *subpilosus* group and in some *H. oliveri*. The larva has a very dark submentum as in *H. marcidus* and in some *H. latilaminus*; but is separable from these by means of its narrow ventromental plates.

### Material Examined

Holotype and allotype: male with larval and pupal exuviae, female with larval and pupal exuviae, depth 0.2–0.3 m, large stream, Kenora, Ontario, 3/5/68, A. P. Wiens, P. Chang, and A. L. Hamilton (CNC No. 13398).

Paratypes: 4 males and 5 females, all reared from pupa, same data as holotype; 1 mature female pupa reared from larva, depth 0.5 m, muddy bottom, Rideau River, Manotick, Ontario, 3/6/66, A. L. Hamilton.

### Ecology and Distribution

The species occurs in streams and probably the littoral zone in lakes, as its recorded localities were very close to the outlet of a lake. So far it has only been found in Ontario.

### *Heterotrissocladius cooki* sp.n.

(Fig. 11B–D)

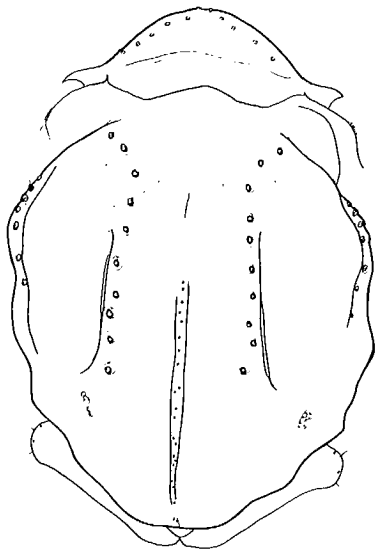
Male imago characterized by relatively high AR (1.56–1.84); numerous prealars (9–14), dorso-centrals (23–35) and acrostichals (18–33); and by having 0–2 setae on subcosta and 5–148 setae in the anal cell. Gonostylus with distinct outer corner and triangular crista dorsalis.

MALE IMAGO (N = 10, EXCEPT WHEN OTHERWISE STATED)

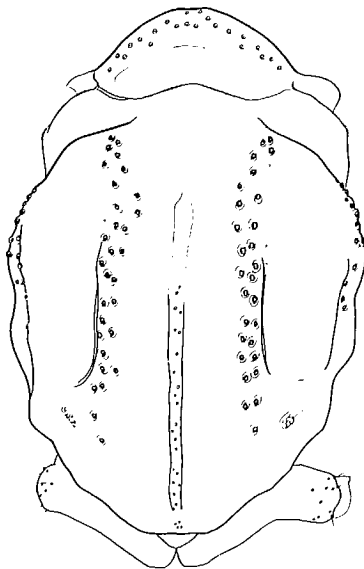
Length 4.10–4.89, 4.53 mm. Wing length 2.55–3.06, 2.74 mm. Total length/wing length: 1.59–1.69, 1.66. Wing length/profemur: 2.51–2.65, 2.56.

*Head* — AR = 1.56–1.84, 1.68(15). Temporal setae 14–41, 17. Postorbitals 2 or 3, 3: outer verticals 4–11, 8; inner verticals 5–8, 6. Clypeus with 12–24, 17 setae. Cibarial pump, tentorium, and stipes as in Fig. 11C. Tentorium 176–230, 198  $\mu$  long; 42–52, 46  $\mu$  wide; 17–22, 19  $\mu$  wide anterior of posterior tentorial pit; distance from apex to posterior tentorial pit 35–50, 43  $\mu$ . Stipes 192–210, 201  $\mu$  long; 68–91, 78  $\mu$  wide. Palp lengths in microns: 46–54, 50; 60–74, 68; 162–202, 192; 146–169, 161; 190–212, 202.

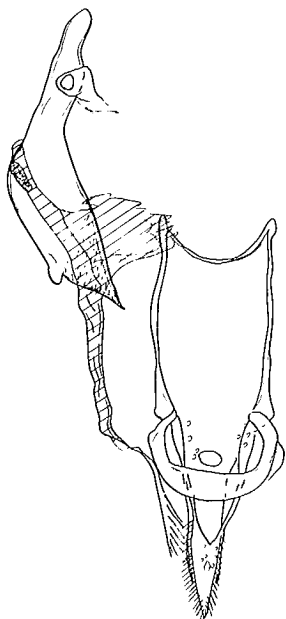
*Thorax* (Fig. 11B) — Anteprepronotum with 11–16, 14 setae. Dorsocentrals irregular biserial 23–35, 28(16); prealars 9–14, 12(16); acrostichals 18–33, 26(16). Scutellum with 13–24, 17(16) setae.



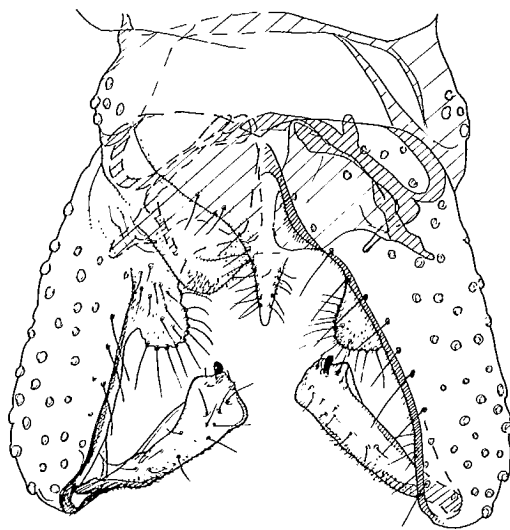
A



B



C



D

FIG. 11. *Heterotrissocladius marcidus* — group male. A, *H. changi* sp.n., thorax, dorsal view. B–D, *H. cooki* sp.n.: B) thorax, dorsal view, C) cibarial pump, tentorium and stipes, D) hypopygium.

*Wing* — VR = 1.10–1.17, 1.14. Brachiolum with 2 or 3, 2 setae; subcosta with 0–2, 0.7(16) setae. R with 27–59, 41(16) setae; R<sub>1</sub> with 20–46, 29(16) setae including 1–4, 2(16) ventrally; R<sub>4+5</sub> with 59–107, 76(16) setae including 1–10, 5(16) ventrally; M<sub>1+2</sub> with 48–120, 76(16) setae; M<sub>3+4</sub> with 42–88, 64(16) setae; Cu with 1–47, 10(16) setae; Cu<sub>1</sub> with 21–64, 37(16) setae; vannal fold with 0–8, 2(16) setae; An<sub>1</sub> with 15–58, 39(16) setae. Cell m basad of RM with 0–9, 5(16) setae; cell an with 5–148, 59(16) setae. Squama with 24–39, 31(16) setae.

*Legs* — Spur of front tibia 71–90, 82  $\mu$  long; spurs of middle tibia 41–49, 45  $\mu$  and 27–34, 31  $\mu$  long; of hind tibia 70–90, 85  $\mu$  and 24–32, 29  $\mu$  long. Width at apex of front tibia 49–56, 54  $\mu$ ; of middle tibia 54–64, 58  $\mu$ ; of hind tibia 60–69, 64  $\mu$ . Comb with 10 or 11, 11 setae; shortest seta 28–40, 31  $\mu$  long; longest seta 68–78, 74  $\mu$ . Sensilla chaetica absent. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>
p <sub>1</sub>	1012–1153,1067	1135–1282,1208	969–1110,1044	527–613,560
p <sub>2</sub>	1006–1135,1057	1030–1178,1086	564–662,606	301–356,325
p <sub>3</sub>	1104–1276,1164	1306–1485,1378	822–932,876	454–497,469
	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
p <sub>1</sub>	368–423,397	258–288,274	117–129,122	0.84–0.90,0.86(16)
p <sub>2</sub>	221–270,237	153–190,166	104–129,110	0.54–0.59,0.56
p <sub>3</sub>	343–386,362	202–239,220	117–135,127	0.62–0.66,0.63
	BV	SV	BR	
p <sub>1</sub>	2.35–2.55,2.45	2.08–2.23,2.18	2.86–2.90(3)	
p <sub>2</sub>	3.21–3.41,3.28	3.38–3.64,3.54	4.06–5.16,4.66(8)	
p <sub>3</sub>	2.81–2.98,2.91	2.79–2.96,2.91	5.29–6.67,5.75	

*Hypopygium* (Fig. 11D) — Ninth tergite including anal point with 29–42, 36 setae; laterosternites each with 5–9, 7 setae. Transverse sternapodeme 79–128, 101  $\mu$  long. Phallapodeme 115–134, 126  $\mu$  long. Anal point 3–8, 6  $\mu$  wide at apex. Gonocoxite 285–336, 303  $\mu$  long; gonostylus 133–149, 141  $\mu$  long, with outer corner and bluntly triangular crista dorsalis. HR = 2.03–2.33, 2.14; HV = 2.99–3.38, 3.21.

### Remarks

This species appears to be closely related to *H. scutellatus*, but differs by having more numerous dorsocentrals and acrostichals, and by having none, or very few, setae on the subcosta.

It is unlikely that any of the species known only from immatures belong to this species.

### Material Examined

Holotype: male, N.J. Mosquito Trap. Lower LaSalle Lake, Hubbard Co., Minn., 7/5/70, E. F. Cook (CNC No. 13606).

Paratypes: 14 males, same locality as holotype, 27/4–22/5/70, E. F. Cook; male, N.J. Mosquito Trap, Cedar Creek Nat. Hist. area, Anoka Co., Minn., 5/5/68, R. A. Hellenthal.

### Ecology and Distribution

The species has been taken in light traps near two small lakes in Minnesota situated in coniferous forest. Lower LaSalle Lake is 62.5 m deep, and though small is one of the deeper lakes of Minnesota. The lake is moderately eutrophic but morphometrically oligotrophic (J. Underhill, personal communication).

### *Heterotrissocladius scutellatus* (Goetghebuer)

(Fig. 6D; 9E; 10F, L; 12E, F; 13A–C)

*Metriocnemus* (*Heterotrissocladius*) *scutellatus* Goetghebuer 1942:15 (male).

*Heterotrissocladius scutellatus* (Goetgh.), Thienemann 1943:196 (pupa, larva), 1944:489, 633. Pankratova 1970:145 (pupa, larva).

*Heterotrissocladius grimshawi* Brundin 1949:704, pro parte, nec Edwards 1929.

(Some of the cited references may actually concern *H. grimshawi* if this species occurs outside of the Boreal region of Europe.)

Male imago characterized by 51–162 setae in the anal cell, about 9–30 setae in cell m basad of RM, 19–45 setae on Cu, 73–114 setae on  $M_{1+2}$ , gonostylus with indistinct outer corner and crista dorsalis small, triangular, and pointed. Pupa with T/A of about 1.8 and thoracic horn about 4.1 times as long as wide. Larva with V/M ratio of 0.9–1.3, submentum usually slightly darker than surrounding areas of head capsule, Sa/An of 0.22–0.30, and segment 4 of antenna 2.9–3.8 times as long as segment 3.

MALE IMAGO (N = 2, EXCEPT WHEN OTHERWISE STATED)

Length 4.85–4.97 mm. Wing length 2.62–3.02 mm. Total length/wing length: 1.71–1.73. Wing length/profemur: 2.70–2.79.

*Head* — AR = 1.47–1.52. Temporal setae 18. Postorbitals 4–7, outer verticals 5, inner verticals 6–9. Clypeus with 14–24 setae. Cibarial pump as in Fig. 6D. Palp lengths in microns: 45–46, 66–72, 212–213, 144–175, 182–202.

*Thorax* — Anteprenotum with 11 or 12 setae. Dorsocentrals 17 or 18, prealars 12–14, acrostichals 12, longest 70–85  $\mu$  long. Scutellum with 22 or 23 setae.

*Wing* — VR = 1.13–1.17, 1.14(7). Brachiolum with 2–4, 3(4) setae; humeral crossvein with 0–5, 1.2(5) setae; subcosta with 17–54, 32(7) setae, R with 41–58, 53(7) setae;  $R_1$  with 36–49, 40(7) setae including 8–15, 10(7) ventrally;  $R_{4+5}$  with 81–120, 95(7) setae including 7–31, 18(7) ventrally; RM with 0–1, 0.3(7) setae; M with 0–2, 0.4(7) setae;  $M_{1+2}$  with 73–114, 89(7) setae;  $M_{3+4}$  with 43–65, 59(7) setae; Cu with 19–45, 31(7) setae;  $Cu_1$  with 30–53, 37(7) setae; vannal fold with 0–40, 17(7) setae;  $An_1$  with 10–41, 28(7) setae;  $An_2$  with 0–10, 1.4(7) setae. Cell an with 51–162, 102(7) setae; cell m basad of RM with 9–30, 24(7) setae. Squama with 25–48, 34(7) setae.

*Legs* — Spur of front tibia 74–75  $\mu$  long; spurs of middle tibia 41–43  $\mu$  and 26  $\mu$  long, of hind tibia 76–86  $\mu$  and 23–39  $\mu$  long. Width at apex of front tibia 54–58  $\mu$ , of middle tibia 60–62  $\mu$ , of hind tibia 57–64  $\mu$ . Comb with 12 or 13 setae, shortest seta 32  $\mu$ (1) long, longest 74  $\mu$ (1). Sensilla chaetica absent. Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>
P <sub>1</sub>	1030–1049	1214–1227	1030–1040	558–564	423–429	282–288
P <sub>2</sub>	1055–1079	1116–1135	564–613	307–313	233–239	165–172
P <sub>3</sub>	1190	1355–1417	810–871	423–442	337–343	215–221
	ta <sub>5</sub>	LR	BV	SV	BR	
P <sub>1</sub>	123	0.85–0.86	2.34–2.39	2.17–2.18	3.61–3.87	
P <sub>2</sub>	104–110	0.51–0.54	3.38–3.39	3.57–3.89	3.50–4.48	
P <sub>3</sub>	116–135	0.60–0.61	3.05–3.08	2.99–3.14	5.29–5.54	

*Hypopygium* (Fig. 12E, F) — Ninth tergite with 23–29, 27(6) weak setae including 13–19, 16(6) on anal point. Transverse sternapodeme 100–130, 115  $\mu$ (5) long. Phallapodeme 110–130, 121  $\mu$ (5) long. Anal point 3–5, 4  $\mu$ (7) wide at apex. Gonocoxite 270–332, 293  $\mu$ (7) long; gonostylus 128–153, 139  $\mu$ (7) long, with outer corner and small, triangular, and sharply pointed crista dorsalis. HR = 2.04–2.17, 2.11(7); HV = 3.60–3.67(2).

FEMALE IMAGO (N = 1, EXCEPT WHEN OTHERWISE STATED)

Two mature female pupae were examined.

*Head* — Temporal setae 14. Clypeus with 15 setae.

*Thorax* — Anteprenotum with 8 setae. Dorsocentrals 33, prealars 8. Scutellum with 16 setae.

*Wing* — Squama with 26 setae.

*Genitalia* (Fig. 13) — Gonocoxite with 15–19(2) setae. Tergite IX with 22–26(2) setae, setigerous protrusions separated. Cercus 120  $\mu$  long. Seminal capsule 77–83  $\mu$ (2) long including a 24–30  $\mu$ (2) long neck. Spermathecal duct with angle, but no loop. Labia triangular, pointed.

PUPA

Length 4.23–5.12 mm (3). T/A = 1.66–1.84, 1.78(4). Exuvia pale.

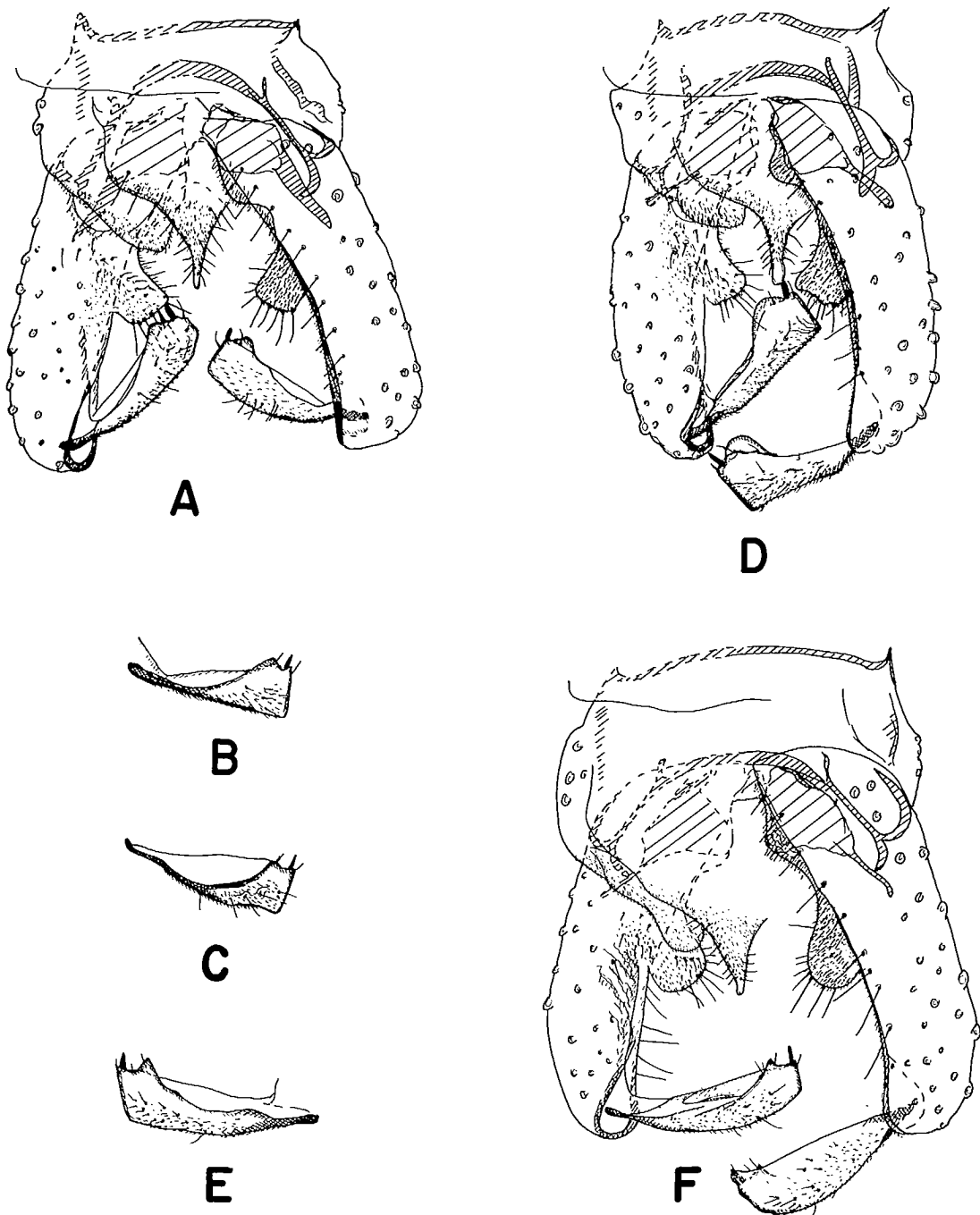


FIG. 12. *Heterotrissocladius marcidus* — group, hypopygium. A–C, *H. changi* sp.n.: A) from Lake Winnipeg, B) from Lake Waterton, Alberta, C) from L. 122, Kenora, Ontario. D, *H. grimshawi* (Edw.). E–F, *H. scutellatus* (Goetgh.).

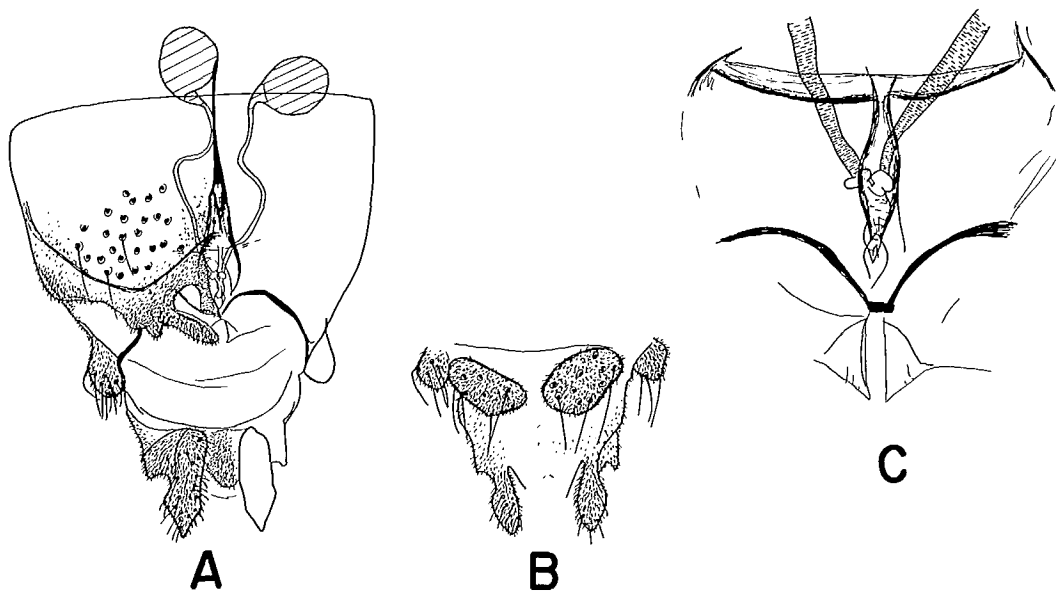


FIG. 13. *Heterotrissocladus scutellatus* (Goetgh.), female genitalia. A, ventral view. B, dorsal view. C, labia spermathecal eminence and labia.

*Cephalothorax* — Thoracic horn as in Fig. 9E, 294–491, 378  $\mu$ (5) long; 60–120, 78  $\mu$ (5) wide; length/width: 4.09–6.65, 5.01(5). Frontal setae apparently absent, (none of the exuviae in good condition).

*Abdomen* — Segments I–VI each with 3 hairlike L-setae, segments VII and VIII with 4 filamentous L-setae. Pedes spurii A present on sternites IV–VII, about 3–6  $\mu$ (2) long. Sternite VIII of male with 10–56, 25(4) posterior spines; 4–50, 18(4) of which are longer than 10  $\mu$  in length. (Exuviae from Lunzer Untersee with 10–20 posterior spines, larger exuvia from Bodensee with 56 posterior spines.) Anal macrosetae 200–270, 223  $\mu$ (4) long. Fringe of anal lobe with 27–31, 29(4) setae.

#### FOURTH INSTAR LARVA (N = 7, EXCEPT WHEN OTHERWISE STATED)

Length 5.81–8.14, 6.96 mm(8). Head capsule length 0.34–0.40, 0.37 mm(8).

*Head* — Antenna as in Fig. 11L. Lengths of antennal segments in microns ( $n = 7-8$ ): 75–86, 81; 36–40, 39; 5–7, 6.1; 18–24, 21; 6–7, 6.3; 3–5, 4; 2–3, 2.3. AR = 0.96–1.19, 1.05. Basal antennal segment 18–20, 19  $\mu$ (8) wide; 4.00–4.67, 4.32(8) times as long as wide; distance from base to annular organ 8–13, 10  $\mu$ (8); to basal mark of seta 4–8, 6  $\mu$ ; to distal mark of seta 16–30, 25  $\mu$ ; blade at apex 54–66, 60  $\mu$ (8) long; accessory blade 7–10, 9  $\mu$  long. Subapical style of second segment 6–9, 7  $\mu$ (6) long. SI and labral lamellae about as in *H. changi*. sp.n. (Fig. 10 O). Premandible 74–78, 75  $\mu$ (5) long. Mandible 140–169, 150  $\mu$  long. Mentum as in Fig. 11 F; width of one median mental tooth 16–19, 17  $\mu$ ; width of ventromental plate 16–23, 19  $\mu$ ; V/M = 0.94–1.28, 1.10. Length of postmentum 180–208, 191  $\mu$ ; submentum usually slightly darker than, but may be of same color as, surrounding areas of head capsule.

*Abdomen* — Proceri 38–46, 41  $\mu$  high; 25–36, 30  $\mu$  wide. Supraanal seta 130–180, 149  $\mu$ (8) long. Anal setae 430–675, 589  $\mu$ (8) long. Sa/An = 0.22–0.30, 0.25(8). Anal tubules 140–190, 175  $\mu$  long; 38–48, 43  $\mu$ (6) wide at base. Posterior parapods 200–225, 212  $\mu$ (6) long.

## Remarks

The male of *H. scutellatus* most closely resembles that of *H. cooki* sp.n. The differences are to be found in the higher HV, the more numerous setae on the subcosta, the lower numbers of dorsocentrals and acrostichals, and the more pointed crista dorsalis in *H. scutellatus*. The pupa has a higher T/A ratio (1.66–1.84) than *H. changi* (1.30–1.66) and apparently a higher number of setae in the fringe of the anal lobe (27–31) than in *H. grimshawi* (24). However, the pupa from Bodensee is larger and has 56 spines posteriorly on male sternite VIII, whereas the pupae from Lunzer Untersee have only 10–20 spines and are considerably smaller. It is, therefore, conceivable that there are two species of this type in the Alps. The differences between *H. scutellatus* and *H. grimshawi* larvae are very small (see key on p. 10). The Sa/An ratio is not good unless many larvae are measured, and the ratio of antennal segment 4 to segment 3 is difficult to measure accurately because of the small size of segment 3. However, the two species should presumably be separated geographically with *H. scutellatus* restricted to the Alps and Schwarzwald.

## Material Examined

Male with pupal exuvia, 1 male, wings and hypopygia of 5 males, 1 larva, Lake Bodensee 20/4/62, 22/4/63, 30/4/63, 14/9/60, F. Reiss; 3 male pupae, 2 female pupae, 81 larvae, Lake Lunzer Untersee, Austria, 1941–42, A. Thienemann.

## Ecology and Distribution

*Heterotrissocladius scutellatus* is a typical lake-dweller occupying the sublittoral and upper profundal zones of oligotrophic lakes. It has two generations a year with the spring emergence from March to June dominating (Thienemann 1943, p. 196, Reiss 1968, p. 231 as *H. grimshawi*).

*Distribution* — Austria (Goetghebuer 1942:16, Brehm 1942:299 as *Heterotrissocladius* sp., Thienemann 1943:196, 1950:118; Bretschko 1974:27); Germany: Schwarzwald (Wülker 1958:810), Bodensee (Reiss 1968:231).

## *Heterotrissocladius changi* sp.n.

(Fig. 5F; 6B, C; 8F–H; 9D, I; 10D, J, O; 11A; 12A–C)

*Heterotrissocladius* cf. *subpilosus* Brinkhurst et al. 1968:17, pro parte nec Kieff.

*Heterotrissocladius marcidus* Sæther 1969:45 nec Walk.

Male imago characterized by 0–95 setae in anal cell, subcosta at most with 4 setae, cell m basad of RM with 0–4 setae, and gonostylus with outer corner and small apically rounded crista dorsalis. Female imago with WL/Pfe of 2.7–3.0, spermathecal duct without loop but with a sharp angle, and broad ventrolateral lobe of gonapophysis VII. Pupal exuvia pale, with T/A of 1.3–1.7, and 3 or 4 filamentous L-setae on VII and VIII. Larva nearly always with lateral notch on median mental teeth, submentum not or only slightly darker than surrounding areas of head capsule, and V/M ratio of 1.0–1.6.

MALE IMAGO (N = 11, EXCEPT WHEN OTHERWISE STATED)

Length 3.07–4.86, 4.07 mm. Wing length 1.93–2.71, 2.37 mm (12). Total length/wing length: 1.59–1.79, 1.69. Wing length/profemur: 2.54–2.80, 2.67.

*Head* — AR = 1.30–1.69, 1.45(28). Temporal setae 11–17, 14. Postorbitals 3–7, 5(10); outer verticals 3–7, 5(10); inner verticals 3–6, 4(10). Clypeus with 6–11, 9(12) setae. Cibarial pump, tentorium, and stipes as in Fig. 6C. Tentorium 144–188, 171  $\mu$ (10) long; 27–44, 38  $\mu$ (10) wide; 12–17, 15  $\mu$ (10) wide anteriorly of posterior tentorial pit; distance from apex to posterior tentorial pit 26–46, 37  $\mu$ (10). Stipes 142–182, 168  $\mu$ (10) long; 46–70, 55  $\mu$ (9) wide. Palp lengths in microns: 32–44, 39; 50–67, 58; 120–190, 159; 110–143, 131; 130–210, 174.

*Thorax* (Fig. 11A) — Anteprenotum with 8–14, 11(12) setae. Dorsocentrals 7–19, 13(28); prealars 5–9, 7(28); acrostichals 11–26, 18(25), anterior few about 30  $\mu$  long, followed by 50–80, 64  $\mu$ (7) long acrostichals and by 6 or 7, 7(5) shorter 22–30, 26  $\mu$ (5) long acrostichals. Scutellum with 9–15, 11(12) setae.

*Wing* — VR = 1.13–1.20, 1.15(12). Brachiolum with 2(12) setae; subcosta with 0–4, 0.3(26) setae; R with 13–38, 26(27) setae; R<sub>1</sub> with 2–26, 19(27) setae including 0–5, 2(12) ventrally; R<sub>4+5</sub> with 7–68, 46(28) setae including 2–8, 4(12) ventrally; M<sub>1+2</sub> with 2–90, 19(26) setae; M<sub>3+4</sub> with 0–51, 31(27) setae; Cu with 0–22, 4(27) setae; Cu<sub>1</sub> with 0–34, 30(26) setae; vannal fold with 0–2, 0.1(27) setae; An<sub>1</sub> with 0–29, 7(27) setae; remaining veins without setae. Cell an with 0–95, 15(27) setae; cell m basad of RM with 0–4, 0.3(27) setae. Squama with 10–29, 20(26) setae.

*Legs* — Spur of front tibia 57–70, 65  $\mu$ (9) long; spurs of middle tibia 32–44, 39  $\mu$  and 22–36, 29  $\mu$ (10) long; of hind tibia 61–79, 71  $\mu$  and 24–34, 29  $\mu$ (10) long. Width at apex of front tibia 36–48, 43  $\mu$ (10); of middle tibia 37–54, 46  $\mu$ (10); of hind tibia 42–59, 52  $\mu$ (10). Comb with 8–11, 10 setae; shortest seta 23–40, 29  $\mu$  long; longest seta 48–66, 58  $\mu$ . Sensilla chaetica 0–2, 0.7 on ta<sub>1</sub> of p<sub>3</sub>. Lengths (in microns) and proportions of legs:

	fc	ti	ta <sub>1</sub>	ta <sub>2</sub>
p <sub>1</sub>	736–1018,902	810–1129,998	748–987,877	399–546,479
p <sub>2</sub>	711–969,891	736–1006,912	417–552,491	209–313,271
p <sub>3</sub>	773–1104,975	932–1276,1153	577–791,698	313–435,382
	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
p <sub>1</sub>	294–417,346	196–245,232	98–135,112	0.81–0.92,0.88
p <sub>2</sub>	165–233,206	110–159,139	80–110,95	0.51–0.57,0.54
p <sub>3</sub>	245–337,296	147–209,181	98–123,112	0.56–0.63,0.61
	BV	SV	BR	
p <sub>1</sub>	2.21–2.46,2.38	2.07–2.34,2.18	4.08–4.95,4.40	
p <sub>2</sub>	2.88–3.32,3.20	3.22–3.86,3.64	4.58–5.83,5.43	
p <sub>3</sub>	2.79–3.02,2.91	2.87–3.17,3.05	5.71–6.80,6.33	

*Hypopygium* (Fig. 12A–C) — Ninth tergite with 19–33, 27 weak setae; laterosternites IX with 4–10, 6 setae. Transverse sternapodeme 73–116, 93  $\mu$  long. Phallapodeme 100–126, 112  $\mu$  long. Anal point 3.0–9.5, 5  $\mu$  wide at apex. Gonocoxite 210–295, 256  $\mu$  long; gonostylus 104–132, 119  $\mu$  long with outer corner and rounded crista dorsalis. HR = 1.98–2.33, 2.15; HV = 2.96–3.68, 3.41.

FEMALE IMAGO (N = 15, EXCEPT WHEN OTHERWISE STATED)

Length 2.78–3.59, 3.24 mm. Wing length 2.15–2.64, 2.40 mm (19). Total length/wing length: 1.21–1.47, 1.34. Wing length/profemur: 2.72–2.96, 2.88(16).

*Head* — AR = 0.32–0.44, 0.40. Pedicel length/width (microns): 42–64, 57/64–82, 72. Flagellomeres length/width (microns): 90–111, 102/30–48, 35; 50–70, 62/26–34, 30; 45–77, 68/26–34, 29; 64–83, 72/25–34, 29; 92–142, 120/22–33, 29. Temporal setae 9–16, 12. Postorbitals 1–4, 3; outer verticals 3–6, 5; inner verticals 3–5, 4. Clypeus with 8–15, 12 setae. Tentorium (Fig. 6 B) 120–170, 143  $\mu$  long; 18–26, 22  $\mu$  wide; 8–12, 10  $\mu$  wide anterior of posterior tentorial pit; distance from apex to posterior tentorial pit 15–23, 18  $\mu$ . Stipes 140–184, 162  $\mu$  long; 41–62, 52  $\mu$ (14) wide. Coronal suture 50–110, 84  $\mu$ (13) long. Ocelli 0–1, 0.1(14); located 6–12  $\mu$ (2) from coronal suture. Palp lengths in microns: 34–44, 40; 46–65, 56; 125–155, 140; 106–138, 125; 150–200, 174.

*Thorax* — Anteprenotum with 7–12, 9 setae. Dorsocentrals 20–34, 26; prealars 7–13, 8; acrostichals 14–24, 19(8), longest 40–100, 69  $\mu$ (3) long, posterior 5–9, 7(6) 22–36, 29  $\mu$ (6) long. Scutellum with 14–22, 17 setae.

*Wing* — VR = 1.13–1.121, 1.16(19). Brachiolum with 2 or 3, 2.6 setae; subcosta with 24–46, 33 setae; R with 30–60, 43 setae; R<sub>1</sub> with 43–63, 51 setae including 6–15, 11 ventrally; R<sub>4+5</sub> with 105–192, 131 setae including 24–51, 32 ventrally; M<sub>1+2</sub> with 70–131, 93 setae; M<sub>3+4</sub> with 63–90, 75 setae. Cu with 19–56, 38(19) setae; Cu<sub>1</sub> with 43–65, 51 setae; vannal fold with 42–87, 62 setae; An<sub>1</sub> with 38–71, 53 setae; remaining veins without setae. Cell r with 0–5, 0.4 setae; cell m basad of RM with 36–86, 64 setae. Squama with 21–30, 27 setae.

*Legs* — Spur of front tibia 30–44, 38  $\mu$ (14) long; spurs of middle tibia 34–49, 38  $\mu$  and 20–33, 26  $\mu$ ; of hind tibia 60–80, 70  $\mu$  and 20–31, 26  $\mu$ . Width at apex of front tibia 44–56, 48  $\mu$ (14); of middle tibia 44–55, 50  $\mu$ ; of hind tibia 49–61, 55  $\mu$ (13). Comb with 10–11, 10 setae; shortest seta 26–34, 30  $\mu$

(14) long; longest 52–66, 57  $\mu$ (14) long. Sensilla chaetica 3–14, 7(14) on  $ta_1$  of  $p_2$  (4–9 in Lake Winnipeg population, 3–5 in Lake Waterton population, 11–14 in Kenora population); and 8–25, 13(14) on  $ta_1$  of  $p_3$  (9–15 in Lake Winnipeg population, 8–11 in Lake Waterton population, 16–25 in Kenora population). Lengths (in microns) and proportions of legs:

	fc	ti	$ta_1$	$ta_2$
$p_1$	761–895,838	853–1079,984	724–895,795	374–503,438
$p_2$	761–920,848	773–981,890	399–503,458	233–282,256
$p_3$	822–1030,929	969–1214,1103	582–724,663	311–411,364
	$ta_3$	$ta_4$	$ta_5$	LR
$p_1$	270–356,314	147–233,207	92–110,102	0.72–0.86,0.81
$p_2$	159–227,190	98–147,125	67–104,86	0.50–0.53,0.51
$p_3$	245–313,283	135–184,168	86–110,103	0.56–0.62,0.60
	BV	SV	BR	
$p_1$	2.35–2.83,2.48	2.17–2.63,2.30	2.80–3.57,3.12	
$p_2$	3.14–3.55,3.34	3.61–3.91,3.80	3.00–4.06,3.41	
$p_3$	2.79–3.13,2.94	2.91–3.25,3.07	3.64–4.81,4.19	

**Genitalia** (Fig. 8F, G, H) — Gonocoxite with 13–21, 17(16) setae. Tergite IX with 22–32, 28(16) setae; setigerous protrusions in contact with each other. Cercus 118–140, 126  $\mu$  long. Seminal capsule 70–100, 86  $\mu$  long; sclerotized in apical 40–60, 50  $\mu$ ; 45–68, 59  $\mu$  wide. Spermathecal duct without loop, but with a strong angle.

**PUPA** (N = 3, EXCEPT WHEN OTHERWISE STATED)

Length 3.55–4.67, 4.22 mm (6). T/A = 1.30–1.66, 1.49(6). Exuvia pale.

**Cephalothorax** — Thoracic horn (Fig. 9D) 331–410, 368  $\mu$ (7) long; 49–96, 67  $\mu$ (6) wide; length/width: 4.27–6.76, 5.73(6). Anterior precorneal seta 80–114  $\mu$  long, located 7–12  $\mu$  from median seta, and 14–20  $\mu$  from posterior seta. Median seta 80–121  $\mu$  long, located 4–10  $\mu$  from posterior seta. Posterior seta 50–54  $\mu$  long, located 70–86  $\mu$  from horn. Frontal seta 34–50  $\mu$ (2) long.

**Abdomen** — Pedes spurii A present on sternites IV–VII, longest spinules on IV 1–4  $\mu$ , on V 2–7  $\mu$ , on VI 3–5  $\mu$ , on VII 2–3  $\mu$  long. Segments I–VI each with 3 hairlike L-seta, segments VII and VIII each with 3 or 4 filamentous L-seta (usually 4 on VIII) and 0–1 hairlike L-seta (specimens from Kenora with 3 filamentous L-setae on VII, specimens from Lake Michigan 4 setae). Sternite VIII of male with 30–40 posterior spines, 9–21 of which longer than 10  $\mu$ . Anal macrosetae 200–270, 245  $\mu$ (6) long. Fringe of anal lobe with 19–24, 23(6) setae. Genital sac and anal lobe as in Fig. 9I.

**FOURTH INSTAR LARVA**

Length 4.77–6.95, 5.87 mm(13). Head capsule length 0.33–0.43 0.37 mm(19).

**Head** — Antenna as in Fig. 10J. Lengths of antennal segments in microns ( $n = 16$ –18). 58–86, 69; 26–38, 31; 5–7, 5.4; 14–23, 18.3; 4–7, 5.7; 2–5, 3.6; 1–3, 2. AR = 0.95–1.21, 1.08(16). Basal antennal segment 16.5–23, 19  $\mu$ (18) wide; 3.00–4.15, 3.63(18) times as long as wide; distance from base to annular organ 5–16, 11  $\mu$ (13); to basal mark of seta 8–23, 14  $\mu$ (12); to distal mark of seta 22–34, 29  $\mu$ (9); blade at apex 32–56, 45  $\mu$ (14) long; accessory blade 6–11, 9  $\mu$ (11) long. Subapical style of second segment 5–8, 7  $\mu$ (13) long. SI and labral lamellae as in Fig. 10O. Premandible 60–86, 75  $\mu$ (17) long. Mandible 118–163, 138  $\mu$ (17) long. Mentum as in Fig. 10D; width of one median tooth including lateral notch 14–19, 16  $\mu$ (22); width of ventromental plate 17–24, 20  $\mu$ (22); V/M = 1.03–1.57, 1.29(22). Length of postmentum 157–210, 183  $\mu$ (19) long; submentum of same color as, or only slightly darker than, surrounding areas of head capsule.

**Abdomen** — Procerci 35–46, 41  $\mu$ (11) high; 21–34, 29  $\mu$  wide. Supraanal seta 125–165, 143  $\mu$ (11) long. Anal setae 410–730, 572  $\mu$ (12) long. Sa/An = 0.21–0.36, 0.25(10). Anal tubules 90–166, 119  $\mu$ (12) long; 32–70, 43  $\mu$ (7) wide at base; 16–30, 23  $\mu$ (7) wide at apex. Posterior parapods 150–260, 186  $\mu$ (10) long.

**THIRD INSTAR LARVA** (N = 10, EXCEPT WHEN OTHERWISE STATED)

Length 2.66–3.69, 3.34 mm. Head capsule length 0.20–0.27, 0.24 mm.

*Head* — Lengths of antennal segments in microns: 38–48, 43; 27–40, 29; 4.0–5.5, 4.5; 9.5–17, 14; 3–6, 4.6; 3–4, 3.7; 1–2, 1.6. AR = 0.69–0.86, 0.77. Basal antennal segment 12–14, 12  $\mu$  wide; 3.17–4.00, 3.52 times as long as wide; distance from base to annular organ 6  $\mu$ ; to basal mark of seta 9–12, 10  $\mu$ ; blade at apex 31–45, 34  $\mu$  long; accessory blade 7–11, 9  $\mu$  long. Subapical style of second segment 5.0–6.5, 5.5  $\mu$  long. Premandible 42–60, 50  $\mu$  long. Mandible 80–112, 91  $\mu$  long. Width of one median mental tooth 9–12, 11  $\mu$ ; width of ventromental plate 10–16, 13  $\mu$ ; V/M = 1.00–1.45, 1.31. Length of postmentum 114–146, 126  $\mu$ .

*Abdomen* — Procerci 20–31, 25  $\mu$  high; 14–20, 17  $\mu$  wide. Supraanal seta 80–105, 92  $\mu$  long. Anal setae 300–480, 445  $\mu$  long. Sa/An = 0.20–0.30, 0.23. Anal tubules 60–84, 75  $\mu$ (7) long; 24–30, 27  $\mu$ (7) wide at base; 10–16, 13  $\mu$ (7) wide at apex. Posterior parapods 110–140, 126  $\mu$ (7) long.

#### SECOND INSTAR LARVA (N = 1, EXCEPT WHEN OTHERWISE STATED)

Length 0.96–2.37 mm (3). Head capsule length 0.11–0.15 mm (3).

*Head* — Lengths of antennal segments in microns: 23, 15, 4, 10, 3, 3, 2. AR = 0.58. Basal antennal segment 8  $\mu$  wide, 2.89 times as long as wide. Premandible 28–32  $\mu$ (2) long. Mandible 48–56  $\mu$ (3) long. Width of one median mental tooth 6–7  $\mu$ (2), width of ventromental plate 7–12  $\mu$ (2); V/M = 1.17–1.71(2). Length of postmentum 64–76  $\mu$ (3).

*Abdomen* — Procercus 14  $\mu$  high, 4  $\mu$  wide. Supraanal seta 40  $\mu$  long. Anal setae 200–245  $\mu$ (2) long. Sa/An = 0.16.

#### FIRST INSTAR LARVA (N = 2, EXCEPT WHEN OTHERWISE STATED)

Length 1.05 mm (1). Head capsule length 0.09 mm.

*Head* — Lengths of antennal segments in microns: 6.3, 12.6, 2.9–3.2, 6.3–6.9, 2.1–2.5, 1.9, 1.6–1.9. AR = 0.23–0.24. Basal antennal segment 6.3–7.6 mm wide; 0.71–1.00 times as long as wide; blade at apex 20–23  $\mu$  long. Mandible 39  $\mu$  long. Length of postmentum 46–47  $\mu$ .

*Abdomen* — Procerci 7.5  $\mu$ (1) high, 5.5  $\mu$ (1) wide. Supraanal seta 29  $\mu$ (1) long. Anal setae 76  $\mu$ (1) long. Sa/An = 0.38(1). Anal tubules 29  $\mu$  long(1). Posterior parapods 43  $\mu$ (1) long.

#### Remarks

There is a large variation in some characters in this species and it is possible that more than one species is involved. However, it is difficult to evaluate the findings as there are two generations a year in the Kenora lakes, in Lake Winnipeg, and in the Great Lakes, but probably not in Lake Waterton; the two generations differ from each other in several details. In Kenora the second generation has only 10–13 setae on the squama, whereas the first generation has 18–26 setae. In Lake Winnipeg, the single second generation male found, has 22 setae on the squama, whereas the first generation has 18–29 setae. In both localities the number of setae on the rest of the wing are higher in the second generation which has 27–95 setae on the anal lobe compared with 0–15 setae in first generation. The specimens from Lake Waterton are intermediate in this respect. In Lake Superior the differences are less apparent; the majority of the second generation appear to have fewer setae on the squama than the majority of the first generation.

The number of sensilla chaetica on the metatarsi of the female is clearly higher in one specimen from Kenora which has 11–14 on the middle leg and 16–25 on the hind leg, compared with 4–9 and 8–15 in the other specimen. The pupae from the Kenora lakes have only 3 filamentous L-setae on segment VII and may occasionally have only 3 also on VIII. The pupae from Lake Michigan, however, have 4 filamentous L-setae on both VII and VIII. The Lake Michigan larvae, are closest to those from Kenora. Both have a longer basal antennal segment (70–81  $\mu$  long; 4.00–4.15 times as long as wide) than other specimens except a few from Lake Superior and Lake Huron. In specimens from Lake Winnipeg, Lake Erie, and most specimens from Lake Huron the basal antennal segment is 60–64  $\mu$  long and 3.00–3.56 times as long as wide. However, a few specimens from Lake Huron and the specimens from Lake Superior are intermediate in this respect and have a basal antennal segment, 64–86  $\mu$  long, which is 3.56–3.80 times as long as wide. It seems likely that there are several ecotypes

within *H. changi*. The differences found can be explained as variations between generations and ecotypes. The Kenora population particularly may well be shown to deserve specific status.

The male of *H. changi* is very close to that of *H. grimshawi*. The latter has a larger, more rounded crista dorsalis, a smaller anal lobe, and generally less setae on the wing than *H. changi*.

### Material Examined

Holotype and allotype: male, female,  $\frac{1}{3}$  mile offshore George Island, Lake Winnipeg, Man., 6/6/69, S. S. Chang (CNC No. 13299).

Paratypes: 1 male, 4 females, same data as for holotype; 1 male, 5 females, 1 mile off Horse Island, Lake Winnipeg, Man., 7/6/69, S. S. Chang; 1 male, Creek at Biscuit Harbour, Lake Winnipeg, Man., 26/8/71, E. Johnson and M. Roberts; 1 mature pupa, 7 larvae, depths 5.5–8.5 m, northern half of Lake Winnipeg, Man., 8/6–31/7/69, S. S. Chang; 4 males, 8 females, Waterton Lakes Townsite, Alta., 20/7/67, A. L. Hamilton and O. A. Sæther; 4 males, 2 females, 2 exuviae, emergence trap, Lake 122, Experimental Lakes Area, Kenora, Ont., 7–17/5 and 2–4/9/68, A. Wiens and S. S. Chang; 2 larvae, depth 5 m, Lake 239, Experimental Lakes Area, Kenora, Ont., 1/5/69, A. L. Hamilton and G. P. McRae; 1 larva, depth 8 m, Lake 240, Experimental Lakes Area, Kenora, Ont., 1/5/69, A. L. Hamilton and G. P. McRae; 1 larva, depth 2 m, Lake 3, Mackenzie River delta, N.W.T., 23/5/73, N. B. Snow; 1 larva, depth 3 m, East Channel, delta of Mackenzie River, N.W.T., 3/3/73, N. B. Snow; 1 male, North Boulder Creek at Green Lake 5, Colo., 2/8/71, O. A. Sæther; 5 larvae, depth 6.5 m, near Isle Royale, Lake Superior, 8/8/71, J. K. Hiltunen; 5 males, tow net above depths 5–12 m, off mouth of Gooseberry River, 42 miles northeast of Duluth, Minn., Lake Superior, 8/10/74, D. E. Maschwitz; 12 larvae, fine sand and debris, depths 5–7 m, off mouth of Gooseberry River, Lake Superior, 8/10/74, D. E. Maschwitz; 16 larvae, artificial substrate placed at depth of 5.5 m, 1.5 miles northeast of mouth of Gooseberry River, Lake Superior, 20/11/74, D. E. Maschwitz; 1 larva, depth 13 m,  $\frac{3}{4}$  miles northeast of Duluth shipping channel, Lake Superior, 11/11/74, D. E. Maschwitz; 13 males, N.J. Mosquito Trap, 2 miles north of Hovland on U.S. 61, Cook Co., Minn., 2–8/6/70 and 21/9/70, E. F. Cook; 7 males, N.J. Mosquito Trap, Hovland, Cook Co., Minn., 1/9–30/9/68 and 16/9/69, E. F. Cook; 73 males, N.J. Mosquito Trap, FWPCA Lab, Duluth, St. Louis Co., Minn., 9/9/68, 9/6/69, 6/8–6/10/69, 31/5–15/6/70, and 23/7–13/9/70, E. F. Cook; 3 males, N.J. Mosquito Trap, Beaver Creek St. Park, Houston Co., Minn., 22/4–5/6/70, E. F. Cook; 1 male, Crookston Exp. Sta., Polk Co., Minn., 15/9/69, E. F. Cook; 3 larvae, depth 15 m, 1 mile north of Chambers Island, Green Bay, Lake Michigan, 28/8/72, J. R. Ball; 3 pupae, 5 larvae, near Kewaunee, Wis. and Zion, Ill., Lake Michigan, 7/10/72, C. Kondrat; 6 larvae outside Gary and Michigan City, Ind., Lake Michigan, 25/8–4/12/71, S. H. Gurney; 1 larva, Georgian Bay, Lake Huron, 25–30/9/64, Great Lakes Institute, University of Toronto; 9 larvae, Hammond Bay, Lake Huron, 11/5/70, J. K. Hiltunen; 1 mature female pupa, 3 larvae, Lake Erie, 3/6–24/11/63, Great Lakes Institute, University of Toronto; pupa reared from larva, 9 larvae, depths 15–17 m, George Lake, La Cloche Mountain Region, Ont., 21–28/5/68 and 23–30/9/68, R. J. Beamish; 2 larvae, depth 8 m, Lumsden Lake, La Cloche Mountain Region, Ont., 21–28/5/68, R. J. Beamish; 3 larvae, depth 3–45 m, Cayuga Lake, N.Y., 10/73, NUS Corp. Other material: 104 head capsules, 5–164 cm in corer taken at 22 m, Glenora, Bay of Quinte, Lake Ontario, 17/3/72, W. F. Warwick.

### Ecology and Distribution

*Heterotrissocladius changi* is a typical lake-dweller occupying the lower littoral to upper profundal zones of oligotrophic lakes. The male from North Boulder Creek, Colorado, probably originated from Green Lake 5 (Elgmork and Sæther 1970), not from the stream itself.

The species has two generations a year in most areas, with a dominant spring emergence from the end of April to the middle of June, and a weaker fall emergence from August to late September. In Lake Waterton as well as in Green Lake 5 there probably is only one emergence period from the middle of July to the middle of August.

*Distribution* — Northwest Territories, Alberta (Sæther 1969:45 as *H. marcidus*), Manitoba, Ontario, Minnesota, Lake Superior, Lake Huron (Brinkhurst et al. 1968:18, as *H. cf. subpilosus*, in part), Lake Michigan, Lake Erie (Brinkhurst et al. 1968:20, as *H. cf. subpilosus*, in part), Lake Ontario (Brinkhurst et al. 1968:23, as *H. cf. subpilosus*, in part), New York, Colorado.

*Heterotrissocladius* sp. *D*

(Fig. 10E, K)

Pupa characterized by pale exuvia, about 15 posterior spinules on tergite I, and length to width of thoracic horn as 7.0–8.1. Larva with pale submentum and V/M of 0.8–0.9.

PUPA (N = 3, EXCEPT WHEN OTHERWISE STATED)

Length 4.28–4.66 mm. T/A = 1.28–1.55(2). Exuvia pale.

*Cephalothorax* — Thoracic horn about as in *H. changi* (Fig. 9D), 307–380  $\mu$ (2) long, 44–47  $\mu$ (2) wide, length/width: 6.98–8.09(2). Anterior precorneal seta 82–88  $\mu$ (2) long, located 8–12  $\mu$  from median setae, and 11–22  $\mu$  from posterior seta. Median seta 94–105  $\mu$  long, located 4–10  $\mu$  from posterior seta. Posterior seta 45–80  $\mu$  long, located 40–85  $\mu$  from horn. Frontal seta 45  $\mu$ (1) long.

*Abdomen* — Tergite I with about 15 posterior spinules. Pedes spurii A present on segments IV–VII, longest spinules on IV and V 5–6  $\mu$ , on VI 6–9  $\mu$ , on VII 4–6  $\mu$ . Segments I–VI each with 3 hairlike L-setae, segments VII and VIII each with 4 filamentous L-setae. Sternite VIII of male with 30–48(2) posterior spines, 18–25(2) of which are longer than 10  $\mu$ . Anal macrosetae 244–245  $\mu$  long. Fringe of anal lobe with 25–27 setae.

FOURTH INSTAR LARVA

Length 4.41–7.98, 5.84 mm (12). Head capsule length 0.37–0.43, 0.41 mm (12).

*Head* — Antenna as in Fig. 10K. Lengths of antennal segments in microns ( $n = 11$ –13): 77–92, 85; 32–39, 36; 6–7, 6.4; 19–28, 23; 4–6, 5.3; 2–4, 3.4; 1–2, 1.6. AR = 1.02–1.25, 1.16(11). Basal antennal segment 22–25, 24  $\mu$ (13) wide; 3.33–3.83, 3.58(13) times as long as wide, distance from base to annular organ 6–18, 11  $\mu$ (11); to basal mark of seta 8–12, 10  $\mu$ (6); to distal mark of seta 19–40, 29  $\mu$ (11); blade at apex 40–54, 48  $\mu$ (9) long; accessory blade 8–11, 9  $\mu$ (9) long. Subapical style of second segment 7–10, 9  $\mu$ (12) long. SI and labral lamellae about as in *H. changi* (Fig. 10O). Premandible 80–90, 83  $\mu$ (9) long. Mandible 146–170, 157  $\mu$ (12) long. Mentum as in Fig. 10E; width of one median tooth 18–23, 20  $\mu$ (13); width of ventromental plate 15–21, 17  $\mu$ (13); V/M = 0.77–0.86(13). Length of postmentum 202–222, 209  $\mu$ (13); submentum of same color as or only slightly darker than surrounding areas of head capsule.

*Abdomen* — Proceri 40–50, 44  $\mu$ (11) high; 25–33, 30  $\mu$ (11) wide. Supraanal seta 140–185, 166  $\mu$ (8). Anal setae 601–720, 672  $\mu$ (10). Sa/An = 0.21–0.28, 0.25(8). Anal tubules 100–140, 121  $\mu$ (5) long; 38–48, 42  $\mu$ (5) wide at base; 21–25, 23  $\mu$ (5) wide at apex. Posterior parapods 200–225, 207  $\mu$ (5) long.

THIRD INSTAR LARVA (N = 3, EXCEPT WHEN OTHERWISE STATED)

Length 3.06–3.75 mm. Head capsule length 0.25–0.26 mm.

*Head* — Lengths of antennal segments in microns ( $n = 2$ ): 44–46, 29–30, 5, 16–22, 3–4, 2, 1. AR = 0.77–0.79(2). Basal antennal segment 14–15  $\mu$ (2) wide, 3.07–3.14(2) times as long as wide, distance from base to annular organ 7–13  $\mu$ (2), to basal mark of setae 5–6  $\mu$ (2), to distal mark of seta 15–20  $\mu$ (2), blade at apex 37–39  $\mu$ (2), accessory blade 8  $\mu$ (1) long. Subapical style of second segment 7  $\mu$ (1) long. Premandible 52–55  $\mu$ (2) long. Mandible 89–100  $\mu$ (2) long. Width of one median mental tooth 11–12  $\mu$ , width of ventromental plate 9–12  $\mu$ , V/M = 0.82–1.00. Length of postmentum 135–140  $\mu$ .

*Abdomen* — Proceri 24–26  $\mu$  high, 18–19  $\mu$  wide. Supraanal seta 80–85  $\mu$  long. Anal setae 390–491  $\mu$  long. Sa/An = 0.17–0.22. Anal tubules 70–130  $\mu$  long, 26  $\mu$ (1) wide at base, 12  $\mu$ (1) wide at apex. Posterior parapods 120–140  $\mu$ (2) long.

## Remarks

This species seems to be most closely related to *H. changi* and may occupy the same ecological niche west of the Rocky Mountains. The combination of pale exuviae with spinules on tergite I, low V/M ratio, and a light submentum will separate it from other members of the *marcidus* group.

## Material Examined

Three exuvia, 16 larvae, depth 19–79 m, Okanagan Lake, B.C., 9–10/9/69, J. F. Flanagan and O. A. Sæther.

## Ecology and Distribution

The species occupies the sublittoral and profundal zones of Okanagan Lake, a large, deep, and oligotrophic lake of British Columbia. The species is likely to have two generations a year so the exuvia found probably belong to the second generation.

## *Heterotrissocladius grimshawi* (Edwards)

(Fig. 6E; 12D; 14A–C)

*Metriocnemus grimshawi* Edwards 1929:313 (male).

*Metriocnemus (Heterotrissocladius) grimshawi* Edw., Goetghebuer 1932:20 (male), 1940–50: 6, 19 (male, female).

*Heterotrissocladius grimshawi* (Edw.) Thienemann 1941:174. Brundin 1947:14 (male), 1949:815 (male, female, larva), 1956a:79 (male). Pankratova 1970:149 (pupa, larva). Hofmann 1971b:7 (larva).

*Heterotrissocladius grimshawi* (Edw.) pro parte. Brundin 1949:704 (not *H. scutellatus* (Goetgh.)) nec *Heterotrissocladius grimshawi* Thienemann 1950:118 (*H. scutellatus* (Goetgh.)).

Male imago characterized by absence of setae in cell m basad of RM, by none or only a few setae in the anal cell, and low number of setae on veins with none on Cu and 2–20 on  $M_{1+2}$ . Gonostylus with distinct outer corner and prominent semicircular crista dorsalis. Pupa with T/A of about 1.7–1.8, and thoracic horn about 6.0 times as long as wide. Larva with V/M ratio of 0.8–1.1, submentum of same color as surrounding areas of head capsule, Sa/An of 0.16–0.22, and segment 4 of antenna 4.0–4.6 times as long as segment 3 in normal specimens.

### MALE IMAGO (N = 6, EXCEPT WHEN OTHERWISE STATED)

Length 3.55–3.92, 3.75 mm. Wing length 2.11–2.40, 2.30 mm. Total length/wing length: 1.60–1.70, 1.64. Wing length/profemur: 2.61–2.82, 2.71.

*Head* — AR = 1.38–1.54, 1.48. Temporal setae 11–17, 13. Postorbitals 6–9, 7; outer verticals 2–6, 4; inner verticals 1–3, 3. Clypeus with 8–13, 10 setae. Cibarial pump as in Fig. 6E. Palp lengths in microns: 40–46, 42; 48–60, 53; 124–156, 143; 80–126, 107; 124–190, 156.

*Thorax* — Anteprepronotum with 8–10(2) setae. Dorsocentrals 12–21, 15(16); prealars 6–9, 7; acrostichals 13–16, 15(4), longest about 40  $\mu$ (2). Scutellum with 10–20, 14 setae.

*Wing* — VR = 1.10–1.13, 1.12. Brachiolum with 2 setae; R with 17–34, 25 setae;  $R_1$  with 11–20, 16 setae including 0–2, 0.5 ventrally;  $R_{4+5}$  with 12–33, 28 setae including 0–2, 0.3 ventrally;  $M_{1+2}$  with 2–20, 9 setae;  $M_{3+4}$  with 0–25, 7 setae;  $Cu_1$  with 0–15, 5 setae; vannal fold with 0–3, 0.6 (5) setae; remaining veins without setae. Cell an with 0–4, 1.8(5) setae; cell m basad of RM without setae. Squama with 15–25, 20 setae.

*Legs* — Spur of front tibia 54–78, 65  $\mu$  long; spurs of middle tibia 37–42, 40  $\mu$  and 23–32, 29  $\mu$  long, of hind tibia 50–74, 66  $\mu$  and 24–30, 27  $\mu$  long. Width at apex of front tibia 45–56, 50  $\mu$ ; of middle tibia 44–54, 49  $\mu$ ; of hind tibia 50–57; 53  $\mu$ (5). Comb with 10–12, 11(4) setae; shortest seta 24–28, 27  $\mu$  (4) long; longest 45–60, 50  $\mu$ (4). Sensilla chaetica absent.

Lengths (in microns) and proportions of legs:

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>
P <sub>1</sub>	767-908,850	895-1043,968	681-828,765	368-448,405
P <sub>2</sub>	791-920,856	816-957,896	393-491,438	221-264,248
P <sub>3</sub>	871-1061,969	994-1165,1093	582-711,654	319-374,351
	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
P <sub>1</sub>	258-319,288	178-209,195	92-110,101	0.76-0.82,0.79
P <sub>2</sub>	172-202,183	110-147,127	80-104,94	0.46-0.52,0.49
P <sub>3</sub>	251-313,282	159-190,175	92-116,102	0.58-0.61,0.60
	BV	SV	BR	
P <sub>1</sub>	2.51-2.70,2.62	2.31-2.48,2.38	3.33-3.92,3.76	
P <sub>2</sub>	3.24-3.53,3.37	3.76-4.22,4.01	3.52-5.56,4.49	
P <sub>3</sub>	2.91-3.06,2.99	3.06-3.42,3.19	5.67-6.83,6.29	

*Hypopygium* (Fig. 12D) — Ninth tergite with 21-23, 22(5) weak setae including 13-19, 15(5) on anal point. Transverse sternapodeme 94-128, 105  $\mu$ (4) long. Phallapodeme 102-108  $\mu$ (3) long. Anal point 7-12, 9  $\mu$  wide at apex. Gonocoxite 215-268, 237  $\mu$  long; gonostylus 110-130, 119  $\mu$  long, with sharp outer corner and prominent, rounded crista dorsalis. HR = 1.89-2.07, 2.00; HV = 2.96-3.26, 3.16.

#### FEMALE IMAGO

No female imagines have been examined. However, according to previous descriptions the female is likely to have fewer setae on the wings than any other species in the *marcidus* group.

#### PUPA (N = 1, EXCEPT WHEN OTHERWISE STATED)

Length 4.73 mm. T/A = 1.73-1.83(2). Pupal exuvia clear, transparent.

*Cephalothorax* — Thoracic horn as in *H. latilaminus* sp.n. (Fig. 9B), 380-393  $\mu$ (2) long, 66-70  $\mu$ (2) wide, length/width: 5.43-5.95(2). Anterior precorneal seta 85  $\mu$  long, located 14  $\mu$  from median seta, 16  $\mu$  from posterior seta. Median seta 85  $\mu$  long, located 10  $\mu$  from posterior seta. Posterior seta 60  $\mu$  long, located 76  $\mu$  from horn.

*Abdomen* — Pedes spurii A present on segments IV-VII, longest spinules 4-6  $\mu$ . Segments I-VI with 3 hairlike L-setae, segments VII and VIII each with 4 filamentous L-setae, segment VIII with 1 additional hairlike L-seta. Sternite VIII of male with 38 posterior spines, 22 longer than 10  $\mu$ . Anal macrosetae 215-220  $\mu$ (2) long. Fringe of anal lobe with 24 setae.

#### FOURTH INSTAR LARVA

Length 6.31-8.08, 6.88 mm (8). Head capsule length 0.36-0.39, 0.38 mm (9).

*Head* — Antenna as in Fig. 14A. Lengths of antennal segments in microns (n = 7-9): 68-78, 74; 30-36, 33; 4-5, 4.6; 18-23, 20 (with only 10 in an abnormal specimen); 4-5, 4.8; 4-5, 4.4; 1. AR = 1.00-1.12, 1.07 (6) with 1.26 in the abnormal specimen. Basal antennal segment 18-21, 19  $\mu$ (9) wide; 3.58-4.35, 3.93 (9) times as long as wide; distance from base to annular organ 6-14, 10  $\mu$ (7); to basal mark of seta 7-8  $\mu$ (3); to distal mark 16-28, 25  $\mu$ (7); blade at apex 42-58, 50  $\mu$ (6) long; accessory blade 4-8, 6  $\mu$ (4) long. Subapical style of second segment 6-10, 7  $\mu$ (9) long. SI and labral lamellae about as in Fig. 14B. Premandible 72-80, 74  $\mu$ (5) long. Mandible 138-148, 142  $\mu$ (5) long. Mentum as in Fig. 14C; width of one median mental tooth 15-19, 17  $\mu$ (8); width of ventromental plate 14-18, 16  $\mu$ (8); V/M = 0.84-1.07, 0.95(8). Length of postmentum 170-196, 184  $\mu$ (9); submentum same color as surrounding areas of head capsule.

*Abdomen* — Procerci 38-48, 42  $\mu$ (8) high; 27-34, 27  $\mu$ (8) wide. Supraanal seta 110-150, 134  $\mu$ (5) long. Anal setae 675-740, 714  $\mu$ (6) long. Sa/An = 0.16-0.22, 0.18(5). Anal tubules 120-144, 136  $\mu$ (4) long; 42-52, 46  $\mu$ (4) wide at base; 10-18, 13  $\mu$ (4) wide at apex. Posterior parapods 220-260  $\mu$ (2) long.

#### Remarks

It may not be practical to separate the pupa and larva of this species from *H. scutellatus* (Goetgh.). However, the male genitalia and the wing chaetotaxy are quite different from *H. scutellatus*. In fact, the species closest to *H. scutellatus* appears to be *H. cooki* sp.n. and not *H. grimshawi*.

## Material Examined

Four males, Utsjoki, Kevojärvi, Finland, 2/7/68, B. Lindeberg; 2 males Lake Puruvesi, Finland, 24/5/69, B. Lindeberg; 1 pupa, 10 larvae changing to pupae, depth 19–23 mm, Lake Vättern, Sweden, May 1971 and May 1972, T. Wiederholm; 1 larva, depth 2 m, Lake Vannaksvatn, Nordland, Norway, 11/7/72, A. Klemetsen.

## Ecology and Distribution

*Heterotrissocladus grimshawi* is a typical lake inhabitant which attains its maximum abundance in the profundal and sublittoral zones of lakes in southern Sweden, and in the littoral zones of subarctic lakes. It forms a northern element of the fauna (Brundin 1949, p. 704). It may occur in polyhumic lakes as well as moderately eutrophic lakes, but is most abundant in oligotrophic lakes (Brundin 1949, p. 705). Brundin assumed that the species has two generations with a dominant spring generation in April–May in southern Sweden, and June–July in the subarctic lakes. However, he never found a second generation and Sandberg (1969, p. 132) shows there is only one generation a year in Lake Erken. This is an additional difference between the boreal *H. grimshawi* and the alpine *H. scutellatus*.

*Distribution* — Norway; Finland; Sweden (Thienemann 1941:174; Brundin 1947: 14, 1949:704, Sandberg 1969:132, Wiederholm 1974a:35, 1974b:35); Ireland (Edwards 1929:313), Scotland (Edwards 1929:313); Belgium (Goetghebuer 1935:64). Probably subfossil in Schöhsee, Northern Germany (Hofmann 1971a:19).

## *Heterotrissocladus* sp. E.

(Fig. 14D–F)

Larva characterized by mentum with first lateral tooth as high as median teeth, light submentum, and high V/M (1.2–1.4) and AR (1.2–1.4).

### FOURTH INSTAR LARVA (N = 6, EXCEPT WHEN OTHERWISE STATED)

Length 4.93–6.70, 5.75 mm. Head capsule length 0.36–0.41, 0.39 mm.

*Head* — Antenna as in Fig. 14D. Lengths of antennal segments in microns ( $n = 5-6$ ): 84–90, 87; 32–42, 36; 4–5, 4.6; 16–17, 16; 4–5, 4.6; 2–4, 2.8; 1–2, 1.6. AR = 1.20–1.43, 1.33(5). Basal antennal segment 19–21, 20  $\mu$  wide; 4.23–4.52, 4.40 times as long as wide; distance from base to annular organ 10–20, 14  $\mu$ (5); to basal mark of seta 8–16, 12  $\mu$ ; to distal mark of seta 22–38, 30  $\mu$ ; blade at apex 48–60, 53  $\mu$ (4) long; accessory blade 8–10, 9  $\mu$ (5) long. Subapical style of second segment 5–6, 6  $\mu$ (5) long. SI, labral lamellae, and spines of pecten epipharyngis as in Fig. 14E. Premandible 64–82, 75  $\mu$ (4) long. Mandible 156–165  $\mu$ (3) long. Mentum as in Fig. 14F; width of one median tooth including lateral notch 13–15, 14  $\mu$ ; width of ventromental plate 18–20, 19  $\mu$ ; V/M = 1.20–1.42, 1.34. Length of postmentum 206–226, 219  $\mu$ ; submentum of same color as surrounding areas of head capsule.

*Abdomen* — Procerci 40–52, 44  $\mu$ (4) high; 28–32, 31  $\mu$ (4) wide. Supraanal seta 170–190  $\mu$ (3) long. Anal setae 564–626  $\mu$ (3) long. Sa/An = 0.29–0.34(3). Anal tubules 128–160  $\mu$ (3) long, 35–44  $\mu$ (3) wide at base, 13–16  $\mu$ (3) wide at apex. Posterior parapods 230–250  $\mu$ (2) long.

### THIRD INSTAR LARVA (N = 1)

Head capsule length 0.23 mm.

*Head* — Basal antennal segment 38  $\mu$  long, 12  $\mu$  wide, 3.17 times as long as wide, distance from base to annular organ 6  $\mu$ , to basal mark of seta 6  $\mu$ , to distal mark of seta 11  $\mu$ . Mandible 94  $\mu$  long. Width of one median tooth of mentum 8  $\mu$ , width of ventromental plate 10  $\mu$ , V/M = 1.25. Length of postmentum 117  $\mu$ .

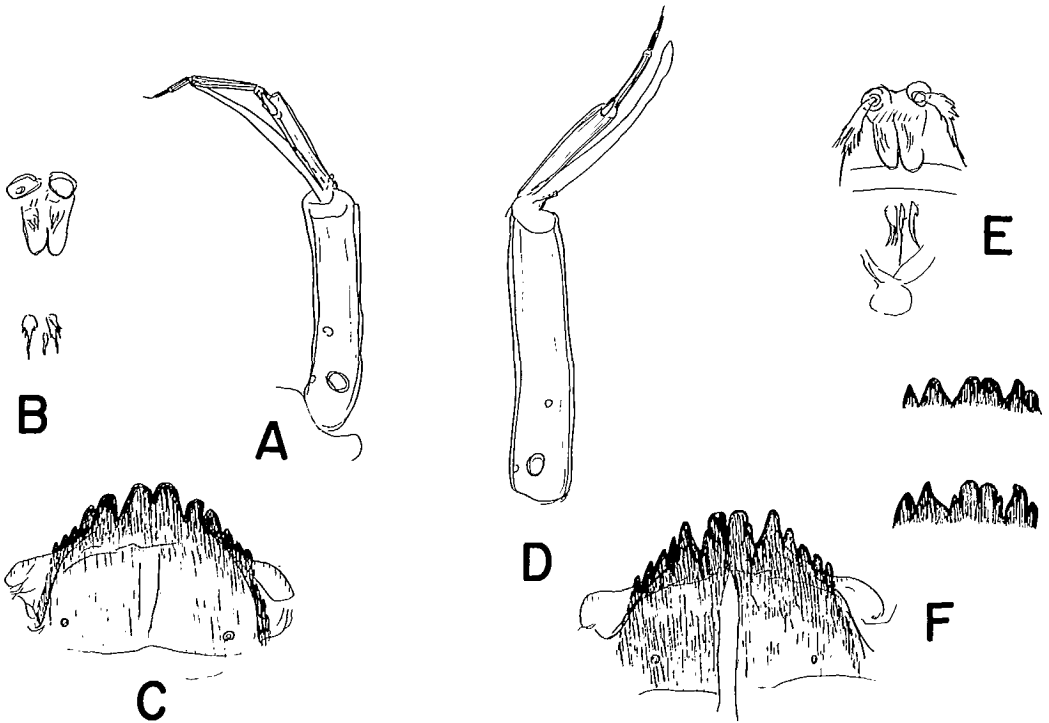


FIG. 14. *Heterotrissocladius grimshawi* (Edw.), A-C, larva: A) antenna, B) labial lamellae and pecten epipharyngis, C) mentum. D-F, *Heterotrissocladius* sp. E, larva: D) antenna, E) SI, labial lamellae and pecten epipharyngis, F) mentum with variation in shape and wear of median teeth.

#### Remarks

This species appears to be intermediate between the *marcidus* and the *maeaeri* groups. The mentum has two median teeth as in the *marcidus* group but the size and shape of the first lateral teeth are very similar to *H. maeaeri*. Also the antennal ratio is nearly identical to that of *H. maeaeri* and higher than in the other members of the *marcidus* group.

#### Material Examined

Seven larvae, depth 33-44 m, near Isle Royale, Lake Superior, 6-8/8/71, J. K. Hiltunen.

#### Ecology and Distribution

The distribution of the different species of *Heterotrissocladius* around Isle Royale, Lake Superior, with *H. marcidus* and *H. grimshawi* in shallower waters, followed by *H. sp. E* and *H. oliveri* in the upper profundal, and *H. oliveri* alone at the deepest stations, indicates that *H. sp. E* has an ecology similar to that of *H. maeaeri*, i.e., more cold-stenothermic and typical of ultraoligotrophy than *H. grimshawi* and *H. changi*, but less than *H. subpilosus* and *H. oliveri*.

#### *Heterotrissocladius incomptus* (Zetterstedt)

*Chironomus incomptus* Zetterstedt, 1840: 816 (female), 1850: 3586 (female).

*Heterotrissocladius incomptus* (Zett.), Fittkau et al. 1967: 358.

This species, known only from females, has not been examined. It may well be a senior synonym of one of the other species of *Heterotrissocladius*.

## *Heterotrissocladius cubitalis* (Kieffer)

*Metriocnemus cubitalis* Kieffer, 1911: 200 (male). Potthast 1915, 362 (pupa) larva.

*Metriocnemus longicollis* Kieffer, 1913: 34 (female)

*Metriocnemus triangulifer* Kieffer, 1924: 99 (female)

*Heterotrissocladius longicollis* (Kieff.), Spärck 1922: 92 (larva)

*Heterotrissocladius cubitalis* (Kieff.), Spärck 1922: 92 (larva)

*Heterotrissocladius triangulifer* (Kieff.), Spärck 1922: 93 (larva)

*Metriocnemus* (*Heterotrissocladius*) *longicollis* Kieff., Goetghebuer 1932: 20 (female), 1940-50: 6, 21 (female)

This species is the type species of the genus. It is, according to Brundin (1956a, p. 80), probably a junior synonym of *H. marcidus* (see p. 27). According to the description and the figures given by Potthast (1915, p. 362-366) the pupa could belong to *H. marcidus*, *H. grimshawi*, or *H. scutellatus*. Figure 159 in Potthast, however, seems to indicate that the submentum is dark and thus, if *H. cubitalis* is identical with any other known species, *H. marcidus* is the only possible one.

## Phylogeny

Brundin (1956a) gave a general account of the systematics of the Orthocladiinae. He regarded the genus *Heterotrissocladius* as closely related to *Heterotanytarsus* Spärck and these two genera closely related to *Trissocladius* in his sense. However, he overlooked some important characteristics and the features on which he based the assumption of relationships are symplesiomorphic within the Orthocladiinae. Brundin mentioned the acrostichals as being absent in *Heterotrissocladius*, but, as pointed out by Oliver (1962, p. 8), they are absent in *H. subpilosus* only. In fact the acrostichals in the *marcidus* group are as long and as strong as in *Parametriocnemus* Goetgh., *Paraphaenocladus* Thien., *Metriocnemus* v.d. Wulp, *Thienemannia* Kieff., and *Pseudorthocladus* Goetgh. (see Fig. 6A). Similarly the  $Cu_1$  is not nearly straight, but distinctly curved in all *Heterotrissocladius* (and also in *Paratrissocladius* Zavř.) to the same extent as in *Parametriocnemus* and *Paraphaenocladus*. Furthermore, FCu ends distinctly distad of RM giving a relatively high VR in *Heterotrissocladius*. These characters will place *Heterotrissocladius* in the Metriocnemini in the sense of Brundin and not in his Orthocladiini.

It is essential when trying to assess the phylogenetic position, particularly of an apparent plesiomorphic genus, to examine which characters should be regarded as plesiomorphic and which apomorphic within the subfamily as a whole. Brundin (1956a, p. 51) criticized Goetghebuer (1914) for regarding the fringe of the pupal anal lobe as a very important phylogenetic character. The error, however, did not lie in regarding it as important, but in regarding this character as apomorphic, whereas in fact it seems certain to be plesiomorphic within the Orthocladiinae (see Hirvenoja 1973, p. 63). The fringe is present in the Prodiamesini, the Chironominae, and most or many of the plesiomorph Orthocladiinae. This indicates that the fringe is synapomorphic for these three groups, and plesiomorphic within each subfamily. Another neglected but important feature seems to be the relatively large ventromental plate (with setae beneath found in some plesiomorph Orthocladiinae). Again only the Prodiamesini (all), the plesiomorph Orthocladiinae, and the Chironominae (whose striation probably developed by the incorporation of setae, see Hirvenoja (1973, p. 39)) have this kind of plate. The large ventromental plate and the presence of setae (or striation) has to be regarded as synapomorphic for the Prodiamesini, the Orthocladiinae, and the Chironominae and plesiomorphic within each subfamily.

Particularly the pupa, but also the larva of *Heterotrissocladius*, primarily possess plesiomorphic characters. The key to understanding the relationships with other genera to a large extent rests with the imagines (see Brundin 1956a, p. 22). Comparing the male hypopygia with those of other genera there are three genera only, *Paratrissocladius*, *Parametriocnemus*, and *Paraphaenocladus*, with species whose hypopygia are not separable from those of *Heterotrissocladius*. These four genera also agree in a number of other characters. The diagnosis of *Heterotrissocladius* given on p. 3 will fit each of these genera in most details. In fact the only difference between a male of *Parametriocnemus*

and a male of *Heterotrissocladius* consists of the extended costa and the shorter  $R_{4+5}$  in *Parametriccnemus*. The four genera have many symplesiomorphic features, as follows: the dorsally elongated eyes, the well-developed temporals, the numerous dorsocentrals and prealars, the long and strong acrostichals starting at the scutal projection in the more plesiomorph species (in *Paratrissocladius* the acrostichals are shorter than in *Heterotrissocladius*, but longer than in any other Orthoclaidiini in the sense of Brundin, and start at the scutal projection), the wings with setae or very strong microtrichia (*Paratrissocladius*) on the membrane, the well-developed anal lobe, the fully fringed squama, the absence of tarsal pseudospurs, the long and strong anal point, the presence of frontal setae in the pupa, the long thoracic horn covered with spinules, the absence of strong spines on the medial surfaces of tergites, the presence of pedes spurii A and B, the presence of a long fringe of setae on the anal lobe (except in *Paraphaenocladius*), the sexual dimorphism in the pupae (except in *Paratrissocladius* where it is probably secondarily reduced), the long genital sac, the plumose SI, the presence of labral lamellae, the relatively large ventromental plate, and the well-developed parapods, procerci, and anal tubules. Common characters which are difficult to evaluate as plesiomorphic or apomorphic include the shape of the anteprepronotum which is normally developed and not in contact anteriorly of the scutal projection, and the presence of a crista dorsalis of about same type and size in all four genera. A number of synapomorphies can also be found and are outlined below (trend 60).

Following the theoretical synapomorphic diagram of Hennig (1950, 1957) and Brundin (1966) an attempt has been made to erect a kladogram for the four related genera and for the species of *Heterotrissocladius* (Fig. 15). The phylogeny within the genus *Heterotrissocladius* is difficult to establish in detail. Although the genus can be easily separated into three groups, the species within each group are very close to each other. A closer examination of the other stages of the species known only from larvae may well cause a revision within each group. As the species are so close to each other, it makes little sense to draw an anagenetic diagram by means of the "Evolutionindex" (Illies 1960) and the "adjusted evolution index" (Sæther 1970b). The kladogenesis can be demonstrated by means of the following trends used in Fig. 15 (p = plesiomorph, a = apomorph):

- 1 Vein  $R_{4+5}$  ends above end of  $M_{3+4}$  (p), ends proximal of end of  $M_{3+4}$  (a).
- 2 Pedes spurii B very long (p), normal, or reduced (a).
- 3 Anal lobe of pupa with fringe of setae (p), without (a).
- 4 Anal lobe of pupa with normal anal macrosetae (p), without (a).
- 5 Gonocoxite of female with setae of normal length (about as long as cerci) (p), more than twice as long as cerci (a).  
— Only one female *Paraphaenocladius* mounted with the genitalia in lateral view has been examined, and some setae may have fallen off. Furthermore, only two species of *Parametriccnemus* have been examined. This trend may, therefore, be invalid. However, no other female genitalia are known to have such long setae on the gonocoxite as *Parametriccnemus*.
- 6 Tergites of pupa without strong posterior spines (p), with (a).
- 7 Vein  $R_{4+5}$  ends distinctly distad of end of  $M_{3+4}$  (p), ends above or proximal to end of  $M_{3+4}$  (a).  
— This trend and trend 1 can be regarded as steps of same trend.
- 8 Costa not extended (p), extended (a).  
— This trend should perhaps not be regarded as separate from trend 7 as costa essentially ends on the same point whereas only  $R_{4+5}$  is contracted.
- 9 Ventrolateral lobe of gonapophysis VIII of female much larger than dorsomesal lobe (p), of similar size (a).  
— The female genitalia of *Heterotrissocladius* are very characteristic. Only *Paratrissocladius* has similar genitalia.
- 10 Antenna of larva without hairlike seventh segment (p), with (a).  
— The larval antennae of *Heterotrissocladius* and *Paratrissocladius* are apparently identical, and differ from any other known chironomid larvae. Thus, this trend really covers a number of other possible trends regarding the antenna.

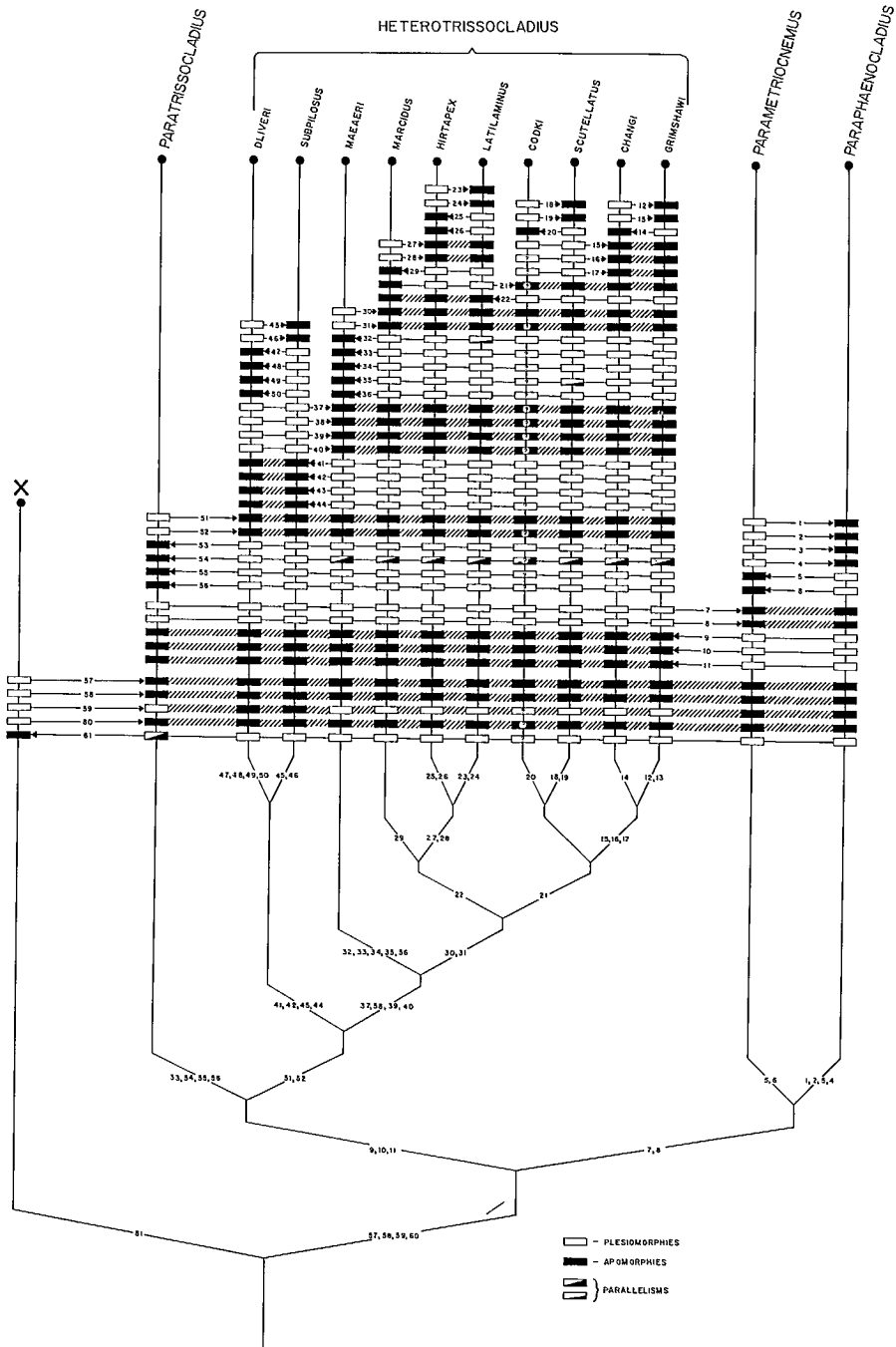


FIG. 15. Synapomorphic diagram giving the phylogeny of the genera *Paratrissocladius* Zavř., *Heterotrissocladius* Spärck, *Parametrioctenemus* Goetgh., *Paraphaenocladus* Thien., and the species known as adults in the genus *Heterotrissocladius*. The numbers represent the different trends given on p. 58–62. Crosshatched connections between rectangles show the synapomorphies, single lines the symplesiomorphies.

- 11 Lauterborn organ present and large (p), absent, or vestigial (a).
- 12 Anal lobe of wing well developed, slightly protruding (p); small, not protruding (a).
- 13 Wing membrane and veins of male with relatively numerous setae ( $R_{4+5}$  usually with more than 35,  $M_{1+2}$  usually with more than 20 setae) (p), fewer setae ( $R_{4+5}$  with less than 35 setae,  $M_{1+2}$  with less than 20 setae) (a).
- 14 Crista dorsalis large and rounded (p); small, bluntly triangular (a).  
—This trend could be regarded as two separate trends. However, the change in shape and the change in size appear to be interrelated. The same applies to several of the following trends.
- 15 Prealars (9–14), scutellars (13–24), and setae on clypeus (12–24) numerous (p); less numerous (prealars 5–9, scutellars 9–15, clypeus with 6–11 setae) (a).
- 16 Thoracic horn of pupa long (about 0.49 mm) and wide (about 4.1 times as long as wide) (p); shorter (less than 0.40 mm) and narrower (about 5.4–6.0 times as long as wide) (a).  
—Although the pupa of *H. cooki* is not known it is highly likely to conform to that of *H. scutellatus*.
- 17 Pupa with many setae (27–31) in fringe of anal lobe (p), fewer (19–24) (a).  
—There is apparently no synapomorphic trend for *H. cooki* and *H. scutellatus* as compared to *H. changi* and *H. grimshawi*.
- 18 Dorsocentrals (23–35) and acrostichals (18–33) numerous (p); less numerous (17 or 18 and about 12 respectively) (a).
- 19 Crista dorsalis relatively large, bluntly triangular (p); small, sharply pointed (a).
- 20 Subcosta with 17–54 setae, cell m basad of RM with 9–30 setae (p); subcosta with 0–2 setae, cell m basad of RM with 0–9 setae (a).
- 21 Submentum (gula o.a.) of larva dark (p), light (a).  
—Although the dark submentum probably is a synapomorphic trend for the *maeaeeri* and *marcidus* groups and to some extent for the whole genus, a reversion seemingly has taken place. Within *H. changi* there is a variation in color from light to nearly as dark as in *H. latilaminus*.
- 22 Gonostylus with an outer corner (p), without (a).  
—The three probably most plesiomorph genera of Orthoclaadiinae, *Brillia*, *Eurynemus*, and *Diplocadius*, all have a bilobed gonostylus. Within *Trissocladius* Kieff. sensu Brundin the development from near bilobation to a sharp outer corner apparently can be followed.  
—Another trend which almost certainly belongs here is: spermathecal duct without a loop (p), with (a). However, as the female genitalia of *H. grimshawi* and *H. cooki* have not been examined the trend is not included here.
- 23 Acrostichals numerous (10–35) (p), reduced in number (5–7) (a).
- 24 Cibarial pump with dorsal margin deepened (p), almost flat (a).  
—The dorsal margin of *H. hirtapex* is deepened more than usual, in *H. latilaminus* much less than normal. An additional trend thus could be made for the deepening of the dorsal margin.
- 25 BR higher than 4.5 on  $p_1$  and 7.1 on  $p_3$  (p), BR lower than 4.4 on  $p_1$  and 7.0 on hind leg (a).
- 26 Ventromental plate wide (18–28  $\mu$ ) (p), narrow (12–14  $\mu$ ) (a).
- 27 Wing membrane and veins with numerous setae, setae present and numerous on Sc, Cu, An, cell an, and cell m basad of RM (p); above veins and cells without setae (a).
- 28 Setae in fringe of anal lobe of pupa numerous (26–36) (p); less numerous (20–30) (a).  
—A parallel development takes place between *H. cooki* plus *H. scutellatus* and *H. changi*, plus *H. grimshawi* (trend 18).
- 29 BR of  $p_3$  high (5.7–7.3) (p), lower (4.4–5.4) (a).
- 30 Tergite IX of male with 29–44 setae (p), fewer setae (16–33) (a).

- 31 AR of larva high (1.29–1.41) (p), lower (0.95–1.26) (a).
- 32 Acrostichals very long, starting at scutal projection (p); shorter, starting some distance from scutal projection (a).
- 33 Pedes spurii B broader than high (p); reduced in width (a).
- 34 Pedes spurii A present on IV–VII (p), on IV–VI (a).
- 35 Segment VII and VIII of pupa with 4 filamentous L-setae (p); segment VII with 3, segment VIII with 3 or 4 filamentous L-setae (a).
- 36 Mentum with two median teeth (p), with one (a).
- 37 Wing sheaths of pupa with “pearls” (p), without (a).  
—A secondary reduction, see trends 54 and 59.
- 38 Pedes spurii A present on IV–VIII (p), on IV–VII (a).
- 39 Segment VIII of pupa with 5 filamentous L-setae (p), with 3 or 4 (a).
- 40 Setae present dorsad of genital sac (p), absent (a).  
—Indication of similar setae has been found in several other genera, and dorsal setae on IX is present for instance in *Monodiamesa* Kieff.
- 41 Clypeus and cibarial pump normal (p); clypeus enlarged, cibarial pump constricted posteriorly, with thickened cornua (a).  
—This trend could, with some justification, be regarded as two trends. However, the development of the clypeus is probably connected with that of the cibarial pump.
- 42 Acrostichals long and numerous (p); few, short, or absent (a).  
—Parallel reductions in size and/or number of the acrostichals take place in *H. maeaeeri* (trend 30) and in *H. latilaminus* (trend 21).
- 43 Setae of wing membrane numerous (p), few (a).  
—Parallel reductions take place also within the *maeaeeri* and *marcidus* groups, however, not to the same extent as in the *subpilosus* group.
- 44 Pedes spurii B well developed (p), absent, or vestigial (a).
- 45 Acrostichals often present (p), absent (a).
- 46 LR<sub>1</sub> high (0.78–0.86) (p), lower (0.77–0.79) (a).
- 47 Cibarial pump moderately constricted (p), strongly (a).
- 48 Crista dorsalis large, protruding (p); smaller, less protruding (a).
- 49 Seminal capsule ovoid (p), pear-shaped (a).
- 50 Spermathecal duct shorter, with angle (p); longer, with loop (a).
- 51 Spermathecal duct straight (p); with angle or loop (a).  
—Trends 50 and 51 would, in calculating the anagenesis, contain steps 1 and 2, and 2 and 3 respectively of a 3-step trend.  
—Another trend which apparently takes place here is: Labral lamella simple (p), divided (a). However, *Heterotrissocladius* sp. C. from Florida has a simple labral lamella and without knowing the phylogenetic position of this species it seems better not to use this trend. The trend apparently takes place as a parallelism in *Paratriocnemus* (simple) and *Paraphaenocladus* (divided) (see Thienemann and Strenzke (1941, figure 4) and Strenzke (1950, p. 223, figure 14)).
- 52 Pecten epipharyngis consists of three dark, sclerotized, smooth spines (p); consists of three very weakly sclerotized, small serrated scales (a).  
—The larva of *Heterotrissocladius* sp. C from Florida, however, have sclerotized but serrated spines or scales in the pecten.

- 53 Wing membrane with setae (p); with strong microtrichia (a).
- 54 Wing sheaths of pupa with row of "pearls" (p); without (a).  
—This trend is the opposite of trend 59 and the same as trend 37. In other words the "pearls" are regarded as secondarily reduced in *Paratrissocladius* and in the *maeaeri* and *marcidus* groups as they also are in some members of *Parametrioctenus* and *Paraphaenocladus*.
- 55 Sexual dimorphism present in pupa (p), absent (a).
- 56 Mentum with 5 pairs of lateral teeth (p); with 4 (a).  
—Some abnormal specimens of *Paratrissocladius* still have 5 lateral teeth.
- 57 Setae of anal point long and strong (p), short and weak (a).
- 58 Sensilla chaetica present and numerous on  $p_2$  and  $p_3$  of male, and on  $p_1$  to  $p_3$  or  $p_2$  and  $p_3$  of female (p); absent or at most 0–2 on  $p_3$  of male, present on proximal fourth of  $p_2$  and  $p_3$  in female (a).
- 59 Wing sheaths of pupa without row of "pearls" (p); with (a).  
—See trends 54 and 37.
- 60 Larval antenna with segment 3 longer than segment 4 (p); shorter (a).  
—Other synapomorphic trends of the four genera treated, which, however, also may be apomorphic for their sister group (x) consist of:  $Cu_1$  straight (p); distinctly curved (a).  
VR lower than 1.1 (p); higher than 1.1 (a).  
Pulvilli present (p); absent (a).  
Tergite IX of female undivided (p); divided (a).  
Ventromentum with setae underneath (p); without (a).
- 61 Sexual dimorphism present in pupa (p), absent (a).  
—This trend is the same as trend 55. There are a few other pupa of Orthoclaudiinae with sexual dimorphism usually of same type as in *Paraphaenocladus*, i.e. sternite VIII in the male has posterior spines whereas sternite VIII in the female has not. However, only *Brillia* Kieff. has bilobed sternite VIII in the female pupa and thus resembles *Heterotrissocladius* and *Parametrioctenus*. Several other symplesiomorphies are mentioned on p. 58.

Although it seems well established that the four genera of Fig. 15 belong to one monophyletic group it is possible that one or two other genera may belong to the same group. Genera such as *Pseudorthocladus* Goetgh., *Gymnetrioctenus* Goetgh., and *Psilometrioctenus* Sæth. seem at least closely related particularly to *Parametrioctenus* and *Paraphaenocladus*. However, the male genitalia of these genera do not conform to those of the treated group and the sensilla chaetica of the legs, the females, and the immatures need closer examination.

## Concluding Remarks on the Ecology of the Species

According to Brundin (1949, p. 709) the European species of *Heterotrissocladius* possess different tolerance ranges with respect to temperature. Arranged according to increasing cold-stenothermy the following series emerges *H. marcidus*, *H. grimshawi*, *H. maeaeri*, *H. subpilosus*. However, as shown, *H. grimshawi* in the sense of Brundin includes two species, namely the Boreal *H. grimshawi* and the Alpine *H. scutellatus*.

Many of the Nearctic species are known from only one or two localities. Nevertheless, it seems apparent that they can be placed on a similar scale. If all the Nearctic and Palaearctic species are arranged according to increasing cold-stenothermy the following preliminary series is obtained: *H. sp. C*; *H. marcidus*; *H. hirtapex*, *H. latilaminus*; *H. grimshawi*, *H. scutellatus*, *H. changi*, and probably *H. cooki*; *H. sp. D*, *H. maeaeri*, *H. sp. B*, and *H. sp. E*; *H. sp. A*, *H. oliveri*, and *H. subpilosus*. It should be noted, however, that even *H. marcidus* and *H. sp. C* are relatively cold-stenothermic; the latter is probably restricted to streams; *H. marcidus* is present in springs, streams, rivers, ponds, and puddles, but seems to prefer the littoral zone of lakes. *Heterotrissocladius hirtapex* has been found in a stream,

but probably occurs in the littoral zone of lakes; *H. latilaminus* has been found in the littoral to the upper profundal zone of lakes. *Heterotrissocladius grimshawi*, *H. scutellatus*, *H. changi*, *H. sp. D*, and probably *H. cooki* are primarily found in the sublittoral to the upper profundal zone of lakes in the temperate region, but probably are more common in shallower waters in the Arctic, Subarctic, and Alpine areas. *Heterotrissocladius maeaeeri*, *H. sp. B*, and *H. sp. E* are probably present mostly in the upper profundal zone of temperate lakes, while *H. sp. A*, *H. oliveri*, and *H. subpilosus* are found also in the deeper parts of the profundal zone of temperate lakes. In Arctic, Subarctic, and Alpine lakes the last-mentioned species may occur in the sublittoral and littoral zones.

Thus, all lake species of *Heterotrissocladius* seem to be characteristic of ultraoligotrophic to moderately oligotrophic lakes. However, *H. latilaminus* and *H. cooki* may also occur in mesotrophic and even moderately eutrophic lakes. Particularly the members of the *subpilosus* group but also the members of the *maeaeeri* group are typical for ultraoligotrophic or at least strongly oligotrophic lakes. *Heterotrissocladius grimshawi*, *H. scutellatus*, *H. changi*, and probably *H. cooki* are present in strongly oligotrophic lakes and in more oligotrophic parts of mesotrophic lakes.

### Acknowledgments

I am much indebted to Dr E. F. Cook, Department of Entomology, University of Minnesota, St. Paul., Minn., for the types of *H. cooki* and other material; to Dr D. R. Oliver, Entomology Research Institute, Ottawa, Ont., for the types of *H. oliveri*; to Dr A. L. Hamilton, Department of Environment, Freshwater Institute, Winnipeg, Man., for the types of *H. latilaminus*; to Dr F. Reiss, Max-Planck Institut für Limnologie, Germany BRD; Dr B. Lindeberg and Dr M. Hirvenoja, Zoological Institute, University of Helsinki, Helsinki, Finland; Dr W. M. Beck Jr., Department of Entomology, Florida A & M University, Tallahassee, Fla.; Mr J. K. Hiltunen, Great Lakes Fishery Laboratory, Ann Arbor, Mich.; Mr D. E. Maschwitz, Minnesota Pollution Control Agency, Roseville, Minn.; Dr T. Wiederholm, Zoological Institute, University of Uppsala, Sweden; cand. real. A. Klemetsen, Tromsø Museum, Tromsø, Norway; Mr S. H. Gurney, Department of Biology, Ball State University, Muncie, Ind.; Mr D. L. Andersen, Industrial Bio-Test Laboratories, Auburn, Neb.; Dr R. J. Beamish, Department of Environment, Biological Station, Nanaimo, B.C.; Mr W. T. Mason, Interstate Commission on the Potomac River Basin, Bethesda, Md.; Mr J. R. Ball, Department of Natural Resources, State of Wisconsin, Madison, Wis.; Mr W. F. Warwick, Canada Centre for Inland Waters, Burlington, Ont.; Mrs P. Dahlberg, NUS Corporation, Cyrus W. M. Rice Division, Pittsburgh, Pa.; and Dr N. B. Snow, Department of Environment, Freshwater Institute, Winnipeg, Man., for other material, and to Miss M. P. McLean for making the preparations.

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