Zootaxa 974: 1–56 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

974

A new subgenus and new species of *Orthocladius* van der Wulp, with a phylogenetic evaluation of the validity of the subgenera of the genus (Diptera: Chironomidae)

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Abstract

A new subgenus, *Mesorthocladius*, of the genus *Orthocladius* v. d. Wulp is erected and diagnoses are provided for all stages and both sexes. *Orthocladius* (*Mesorthocladius*) *lamellatus* sp. n. and *O.* (*Mesorthocladius*) *nimidens* sp. n. are described in both sexes and all stages. *Orthocladius* (*Euorthocladius*) *annellae* sp. n. is described in both sexes and the pupa. The females of *O.* (*Euorthocladius*) *rivicola* Kieffer, *O.* (*Eurthocladius*) *ashei* Soponis, and *O.* (*Orthocladius*) *dentifer* Brundin

Accepted by P. Adler: 24 Apr. 2005; published: 9 May 2005

are described for the first time. The larva of *O.* (*Orthocladius*) *nitidoscutellatus* Lundström (syn. *Orthocladius trigonolabis* Edwards) is described for the first time. A parsimony analysis of all species of *Orthocladius* with known pupae and male imagines is performed. The subgenera *Eudactylocladius* Thienemann and *Euorthocladius* Thienemann are always monophyletic, while *Symposiocladius* Cranston is paraphyletic before successive reweighting, but monophyletic after; *Mesorthocladius* is monophyletic before reweighting, but paraphyletic after; and *Orthocladius* s. str. is polyphyletic before reweighting and monophyletic after. Keys to subgenera for both sexes and all stages are given.

Key words: *Orthocladius* subgenera, *Mesorthocladius* new subgenus, *Euorthocladius*, new species, keys, phylogeny, Chironomidae

Introduction

Larvae of *Orthocladius* van der Wulp inhabit all types of flowing water. In addition, representatives are found in lakes, ponds, swamps, thermal waters, hygropetric rock faces, and moist soil, and one species, *O.* (*Symposiocladius*) *lignicola* (Kieffer in Potthast 1915) mines wood. The genus is recorded from all zoogeographical regions except Antarctica, but with few exceptions the records outside of the Holarctic Region are based on misidentifications. However, in the Holarctic Region the genus is widespread and common.

The genus presently is divided into five subgenera, *Eudactylocladius* Thienemann, *Pogonocladius* Brundin, *Symposiocladius* Cranston, *Euorthocladius* Thienemann, and *Orthocladius* s. str. *Pogonocladius* is monotypic, whereas *Eudactylocladius* undoubtedly is monophyletic with several autapomorphies. However, *Euorthocladius,* as defined by Soponis (1990), may not be monophyletic, and *Orthocladius* s. str. is unlikely to be monophyletic. It is not possible to find a single synapomorphy combining all species of the nominal subgenus that is not present in some species in one of the other subgenera.

Michael J. Bolton, Columbus, Ohio, sent me material containing all stages and both sexes of two new species of *Orthocladius.* The pupae of both will key to *Orthocladius* s. str. as presently defined, while the larvae of both key to *Euorthocladius.* One species has a male of the *Euorthocladius* type and a female of the *Eudactylocladius* type, whereas the other species keys to *Orthocladius* s. str. as presently defined in both sexes. While comparing these two new species with specimens of *Euorthocladius* from our collection, it was discovered that some specimens from the Northwest Territories identified as *O. rivicola*, in fact belonged to a closely related new species.

Methods and terminology

Some of the material is mounted on slides in Euparal, the rest in Canada balsam, following the procedure outlined by Sæther (1969: 1).

The general terminology follows that of Sæther (1980), with the exception that the apical "spine" of the male gonostylus is termed the megaseta, and the apodeme lobe is regarded as primarily belonging to gonapophysis IX (not VIII). In the larvae, the posterior “extensions of the ventromental plates” are not part of the ventromentum and are here called mental extensions.

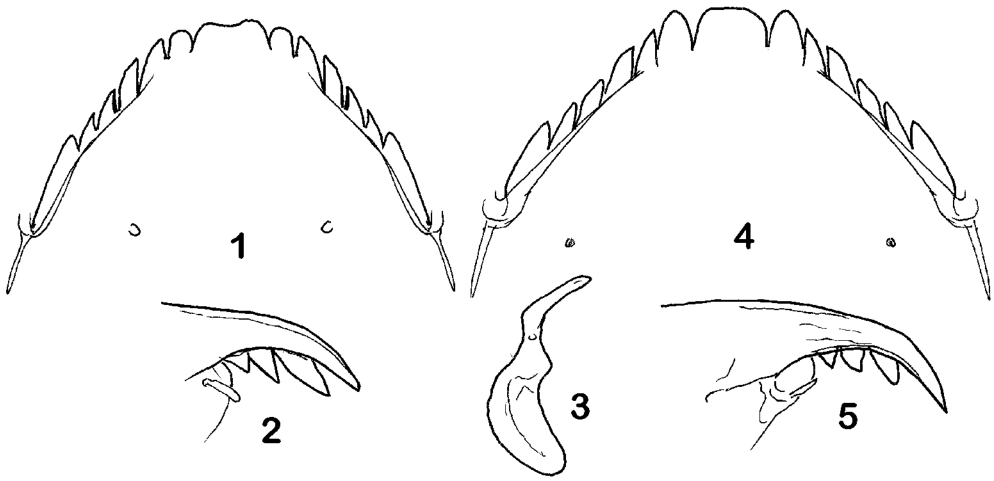
In the figures of the male genitalia, the dorsal view is shown to the left, and the ventral aspect and the apodemes to the right. The measurements are given as ranges followed by a mean when four or more measurements are made, followed by the number measured in parentheses (*n*).

Material

Two species of *Orthocladius* inhabiting seeps and small streams in Ohio were sent to me by Michael Bolton, Ohio EPA. This material includes associated material of male and female imagines, pupae, and larvae. The species, however, did not fit well into any of the recognised subgenera. A phylogenetic analysis was deemed necessary to place these species. In order to complete a data matrix including all species with at least the male imago and the pupa known all material present in the collections of the Museum of Zoology in the University of Bergen and all material in the Zoologische Staatssammlung, Munich, was examined. Previously undescribed material from the collection in Bergen included the male, female, and pupa of a new species of the subgenus *Euorthocladius* from the Northwest Territories in Canada; the females of *O.* (*Euorthocladius*) *ashei* Soponis, *O.* (*Euorthocladius*) *rivicola* Kieffer, and *O.* (*Orthocladius*) *dentifer* Brundin; and the larvae of *O.* (*Orthocladius*) *nitidoscutellatus* Lundström (= *O. trigonolabis* Edwards).

In the Zoologische Staatssammlung there were larvae mounted on two slides labelled *Orthocladius* (*Rheorthocladius*) *rivinus* and on one slide labelled *Rheorthocladius mitisi* Goetgh. v. *mitisi* No 29 in the handwriting of A. Thienemann, but without any further information. *Orthocladius mitisi* is a junior synonym of *O. glabripennis* (Goetghebuer). As Thienemann regarded the larvae of both these species as inseparable from their closest congeners (see for instance Thienemann 1944, p.650 footnote), the larvae must originate from the same localities and samples (mass rearings?), as adult males were described. Although it is not unusual that several species of *Orthocladius* occur in the same sample, it is at least likely that these larvae belong to *O. rivinus* Kieffer and *O. glabripennis*, respectively, and for the purpose of the data matrix they are regarded as correctly identified. Some details are illustrated in Figs. 1–5, but the conditions of the larvae allow no further descriptions.

The type material is in the Museum of Zoology, University of Bergen (ZMBN).



FIGURES 1–5. *Orthocladius* (*Orthocladius*) spp., larvae, 1–3: *O.* (*O.*) ?*glabripennis* (Goetghebuer) as *O. mitisi* v. *mitisi* Goetghebuer, 1: mentum, 2: apex of mandible, 3: premandible, 4, 5: *O.* (*O.*) ?*rivinus* Kieffer, 4: mentum, 5: apex of mandible.

The delimitation of subgenera of *Orthocladius*

Few genera have been so difficult to delimit in a satisfactory way as the genus *Orthocladius.* This primarily is caused by incongruence between immatures and imagines. A satisfactory delimitation of all stages was first reached by Brundin (1956). He and also Soponis (1977) outlined some of the historical, nomenclatorial, and taxonomic problems concerning the genus. However, the male imagines of *Orthocladius* are not generically distinct from those of *Stackelbergina* Shilova & Zelentzov, and not all immatures are separable from those of *Cricotopus* van der Wulp.

Subgeneric diagnoses were given by Thienemann (1935) for the immatures of *Eudactylocladius, Euorthocladius,* and *Orthocladius* s. str. (as *Rheorthocladius* Thienemann), by Brundin (1956) for the imagines, and by Soponis (1977) for all stages. The originally monotypic *Symbiocladius* described by Cranston (1982) was enlarged to include several other species by Sæther (2004a).

Soponis (1977) did not include *O. frigidus* (Zetterstedt) in any of the subgenera, whereas Brundin (1956) included the species in *Euorthocladius.* Soponis (1987) later transferred *O. frigidus* to *Orthocladius* s. str. primarily based on the pupa. Sæther et al (2000), however, transferred the species back to *Euorthocladius* primarily based on the similarity with *O. rousellae* Soponis. Diagnoses and descriptions of all stages of *O.* (*Euorthocladius*) in the limited sense were given by Soponis (1990). The exclusion of *O. frigidus* from *Euorthocladius* by Soponis (1987) was based only on the fact that the pupae possess normally developed anal macrosetae. Other characters and stages are more similar to those of *O.* (*E.*) *rousellae* which apparently is the sister species of *O. frigidus*. Their male hypopygia as well as their pupal thoracic horn are mainly identical. However, reincluding *O. frigidus* in *Euorthocladius* makes it necessary to also evaluate the position of two new species, *O. lamellatus* and *O. nimidens* as well as of *O. vaillanti* Langton & Cranston, which has a pupal thoracic horn of the *frigidus* type. *Orthocladius lamellatus* has a hypopygium nearly identical to those of *O*. *frigidus* and *O. rousellae,* whereas the larvae of *O*. *nimidens* are similar to those of *O. rousellae.*

Hamilton et al. (1969) recommended that a genus should have all three life stages in a relatively discernable group, whereas subgenera should be used when one or more of the life stages in a group are very difficult to separate while the remaining stage or stages show consistent morphological differences. Soponis (1990) used this rule of thumb not to place *O*. (*Euorthocladius*) *abiskoensis* Thienemann & Krüger in a separate genus, i.e. *Lapporthocladius* Thienemann, or in a separate subgenus. However, the pupa of *O*. (*E.*) *abiskoensis* has several unique autapomorphies and the male is easily separable by a unique combination of characters. Accordingly, a subgeneric status of *Lapporthocladius* could be justified. Soponis (1990) also doubted the validity of having a separate monotypic subgenus for *O.* (*Pogonocladius*) *consobrinus*. Here, however, both the larva and the pupa and to some extent the female have unique autapomorphies. The subgenus *Eudactylocladius* Thienemann is the best-defined subgenus, with unique autapomorphies in all stages and both sexes, although the autapomorphy for the larvae, head capsule dark reddish brown, is rather obscure. The subgenus *Euorthocladius* Thienemann is particularly distinct in the pupa. However, if *O. rousellae* is removed from the subgenus, the vestigial macrosetae of the pupa is no longer a unique synapomorphy. The subgenus *Symposiocladius* Cranston has a unique autapomorphy in the large, rounded Lauterborn organs of the larvae, whereas the other stages are separable only by a combination of characters. For the nominal subgenus, there apparently are no unique synapomorphies in any stages or sex although a well-developed superior volsella is found only in this subgenus plus *O.* (*E.*) *abiskoensis*, and only *O.* (*O.*) *charensis* Soponis, *O.* (*O.*) *chuzeseptimus*, *O.* (*O.*) *wetterensis*, and *O.* (*O.*) *glabripennis* have a collar-like or no superior volsella.

Several species have such unique autapomorphies in one or two stages or sex that they could be regarded as belonging to a separate genus. The hypopygium of *O. nitidoscutellatus* Lundström with the triangular gonostylus, is unique within *Orthocladius*, resembling that of *Zalutschia* Lipina. Also for the male and female genitalia of *O.* (*Symposiocladius*) *bilyji* Sæther, and for the female genitalia of the new species *O. nimidens*, there are no remotely similar configurations. The larval mentum of *O.* (*Symposiocladius*) *lignicola* is unique as is the four-segmented antenna of *O.* (*Pogonocladius*) *consobrinus*. Other unique apomorphies normally indicating generic status are shared between two or more species and include the labral lamellae present in *O. frigidus* and the new species *O. lamellatus*, and the absence of a seta interna in *O. frigidus, O. rousellae, O. vaillanti*, and *O. lamellatus*.

TABLE 1. A mosaic of characters within *Orthocladius* v. d. Wulp

	Sct	SCh	AP	SCa	SDu	FW	TH1	TH2	PSB	AM	AL	Head	LL	Pm	PmB	SI	M
O. frigidus	1	0	1	0	1/0	1	1	1	1	0	1/0	1	1	0	1	1	1
O. rousellae	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1
O. vaillanti	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	1	0
O. lamellatus	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0
O. nimidens	0	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	1
O. (E.) calvus	0	1/0	1/0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
O. (E.) kanii	0	?	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1
O. (E.) rivulorum	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1
O. (E.) saxosus	1/0	0	1	0	0	0	0	1	0	1	0	1	0	1/0	0	0	0
O. (E.) suspensus	1	?	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1
Other *Euorthocladius*	1/0	1/0	1/0	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Pogonocladius	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Eudactylocladius	0	1/0	0	0	1	0	0	1	0	0	1	1	0	1/0	0	0	0
O. charensi	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
O. decoratus	0	0	0	0	0	1	0	1	0	0	1/0	0	0	0	0	0	0
O. excavatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. lapponicus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. nitidoscutellatus	1/0	0	0	0	0	0	0	1/0	0	0	0	0	0	0	0	0	0
O. oliveri	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
O. marchetti	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. rhyacobius	0	0	0	0	0	0	0	0	0	0	1/0	0	0	0	0	0	0
O. wetterensis	1	0	1	0	0	0	0	0	0	0	1/0	0	0	0	0	0	0
Other *O.* s.str.	0	0	0	0	0	1/0	0	0	0	0	0	0	0	0	0	0	0
Symposiocladius	1/0	1/0	0	0	0	1/0	0	1/0	0	0	1/0	1/0	0	0	1	0	0

The number 1 means: Sct = scutellars multiserial; SCh = sensilla chaetica absent; AP = anal point of *Euorthocladius* type; SCa= seminal capsule with tubercle or rugulosity; SDu = spermathecal ducts with several loops; FW = frontal warts strong; TH1 = thoracic horn long, smooth and filamentous; TH2 = thoracic horn bare; PSB = pedes spurii B spinulose or rugulose; AM = anal macrosetae vestigial; AL = anal lobe with lateral threads; Head = head light to dark brown; LL = labral lamellae present; Pm= premandible bifid; PmB = at least vestigial premandibular brush present; SI = seta interna of mandible absent; M = mentum at least sometimes with more than 13 teeth.

As shown in Table 1, apomorphous characters within the genus as a whole show incongruous distribution where apparent synapomorphies are contradicted by other equally good apparent synapomorphies. These numerous apparent parallelisms must to a large extent consist in underlying synapomorphies and thus are not multiply derived, but inherited. Even the more distant parallelisms often are expressions of canalised evolutionary potentials. As shown by Sæther (1989), phylogenetic trends often consist in a change from a stable plesiomorphic character alternative to a condition of underlying synapomorphy and further to a stable apomorphy, a stable plesiomorphy or to a condition of apomorphy, but with the plesiomorphous alternative potentially present. In the last case reversals can take place without violating Dollo's law. Trends of this type, however, appear unstable only at a few furcations of a phylogenetic tree. In a manual quantitative cladogenetic analysis it thus is important to keep significant parallelism as close as possible. For instance, if it is decided that *O. rousellae* and *O. frigidus* are sister species, other apparent synapomorphic trends between *O. rousellae* and *O. lamellatus* or between *O. frigidus* and *O. lamellatus* or *O. nimidens* are underlying synapomorphies (or secondary reductions). However, these parallelisms nevertheless indicate close relationships if their bearers are not separated by more than a few furcations or nodes on a phylogenetic tree.

In an attempt to examine the validity of the different subgenera and their delimitations, a parsimony analysis including all species with at least known male imago and pupa was performed. The data matrix is based on a number of publications including Brundin (1947, 1949, 1956), Caldwell (1998), Cranston (1982, 1984, 1999), Cranston & Oliver (1988), Cranston et al. (1983,1989), Coffman et al. (1986), Edwards (1924), Epler (2001), Goetghebuer (1940, 1942), Goetghebuer & Dorier (1939), Kieffer (1911), Langton (1991), Langton & Cranston (1991), Langton & Visser (2003), Pinder & Cranston (1976), Potthast (1915), Rossaro et al. (2002, 2003), Sæther (1969, 1977, 2004a, 2004b, 2004c), Sæther et al. (2000), Sasa (1979, 1981, 1984, 1988), Sasa & Kimamura (1987), Sasa & Okazawa (1992), Sasa & Suzuki (1999), Schmid (1993), Soponis (1977, 1983, 1987, 1990), and Thienemann (1935, 1941, 1944). Dr. Bruno Rossaro gave additional information particularly on *O. wetterensis* Brundin and *O. ruffoi* Rossaro & Prato. All slide-mounted material of *Orthocladius* in the collections of the Zoologische Staatssammlung, Munich, and the Museum of Zoology were examined in order to fill out details not mentioned in previous descriptions. For instance, most descriptions, including those of Soponis (1977), do not mention the presence or absence of tarsal sensilla chaetica and the descriptions of females, when in existence, are deficient.

Taxonomic interpretations in *Orthocladius* s. str. Follow those of Rossaro et al. (2003), but as shown by Spies & Sæther (2004), further revisions are necessary to clarify the status of several species and their correct names.

The characters and character alternatives used in the parsimony analysis are given in Table 2 and the character states for each taxon in Table 3. Characters 69, 70, 71, 73, 77, 79, 80, 84, 102, and 103 were ordered, the remaining characters unordered. The genera *Stackelbergina* Shilova & Zelentsov and *Paracladius* Hirvenoja and the subgenera of *Cricotopus* v. d. Wulp combined were used as the outgroup. The constraint that the genus is monophyletic was used, because some results for some trees placed the subgenus *Nostococladius* Ashe & Murray of *Cricotopus* within *Orthocladius*. When characters are given equal weight, the analysis yields more than 80,000 trees, each with 614 steps, a consistency index (CI) of 0.23, retention index (RI) of 0.61, and rescaled consistency index (RC) of 0.14 (Fig. 6). Analysis with successive reweighting based on RC gives 333 trees, each of 630 steps (when character weights are reset to 1), CI 0.46, RI 0.81 and RC 0.37 (Fig. 7). The results are constant after three reweightings. However, the differences between one, two, and three reweightings are minimal with *O. appersoni* Soponis as the sister species of *O. nimidens* after one reweighting and *O. tamarutilus* Sasa or *O. makabensis* Sasa after both one and two reweightings.

TABLE 2. Characters and character alternatives used in parsimony analysis.

Imagines

1 *Antennal ratio*: (0) higher than 1.8, (1) 1.8–1.00, (2) lower than 1.0 or antenna reduced.
2 *Dorsomedian eye extension*: (0) well developed; (1) weak or absent, eyes widely separated.
3 *Eyes*: (0) bare, (1) hairy.
4 *Temporals*: (0) at least inner verticals bi- to multiserial, (1) uniserial, postorbitals present, (2) uniserial, postorbitals absent.
5 *Antepronotal lobes*: (0) robust, not or only slightly narrowed medially; (1) not robust, often distinctly narrowed medially.
6 *Dorsocentrals*: (0) uniserial, (1) bi- to multiserial.
7 *Dorsocentrals*: (0) erect, (1) decumbent.
8 *Acrostichals*: (0) present, (1) absent.
9 *Prealars*: (0) 1– 7, (1) more than 7.
10 *Supraalars*: (0) present, (1) absent.
11 *Scutellars*: (0) bi- or multiserial, (1) uniserial.
12 *Scutellars*: (0) uni- or biserial, (1) multiserial.
13 *Anal lobe of wing*: (0) distinctly to strongly projecting, (1) at most moderately projecting.
14 *Costal extension*: (0) distinct, more than 40 µm long; (1) absent or less than 40 µm long.
15 R_{4+5} *in male*: (0) setose, (1) bare.
16 *Setae on squama*: (0) more than 40, (1) 10–40, (2) less than 10.
17 *Sensilla chaetica of* p_2 *of male*: (0) present, (1) absent.
18 *Sensilla chaetica of* p_3 *of male*: (0) present, (1) absent.
19 *Anal point*: (0) tapering to triangular, pointed or absent, with setae directed posterolaterally: (1) robust, triangular to parallel-sided with rounded apex and lateral setae which often are laterally or even anterolaterally directed.
20 T IX basal of anal point: (0) with 0–14 setae, (1) with more than 14 setae.
21 *Superior volsella*: (0) collar-like, weak or absent; (1) rectangular to rounded, (2) triangular, pointed or blunt.
22 *Inferior volsella*: (0) present and well developed, (1) absent or present only as a projection of inner margin of gonocoxite.
23 *Inferior volsella*: (0) ventral part not prominently extended below dorsal part, (1) prominent extended.
24 *Inner margin of gonocoxite*: (0) without strong, short dense setae; (1) with.
25 *Transverse sternapodeme*: (0) nearly straight, (1) slightly arched, (2) strongly arched.
26 *Oral projections of transverse sternapodeme*: (0) weak, (1) moderate, (2) strong.

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27 *Setae on dorsal surface of gonostylus*: (0) fine and sparse, (1) strong and dense.
28 *Crista dorsalis*: (0) robust, preapical to apical, triangular to rounded, occasionally elongate; (1) weak, long and low to absent.
29 *Gonostylus*: (0) without median or proximal projection, (1) with.
30 *Virga*: (0) present, consisting of cluster of spines or of single spine; (1) consisting of scattered minute spines or of short teeth, (2) absent.
31 *Female tergite IX*: (0) divided, broad, plate-like or conspicuous and consisting of two bulbous projections; (1) divided, narrow, band-like; (2) essentially undivided, but with setae in two lateral groups.
32 *Female tergite IX*: (0) margins well delimited, (1) margins poorly delimited.
33 *Female gonocoxite IX*: (0) without projection, (1) with narrow apical or broader median projection.
34 *Female gonocoxite IX*: (0) with more than 15 setae, (1) with 15 or fewer setae.
35 *Female gonocoxite IX*: (0) well developed; (1) small, reduced, [at least in some *Cricotopus* (*Isocladius*)].
36 *Gonapophysis VIII*: (0) ventrolateral lobe clearly larger than dorsomesal lobe, (1) lobes about equal in size.
37 *Seminal capsules*: (0) not small, rounded to oval with parallel-sided neck; (1) relatively small, rounded, with small, but distinct and often well sclerotised more or less parallel-sided neck.
38 *Seminal capsules*: (0) not pear-shaped, (1) pear-shaped.
39 *Seminal capsules*: (0) not large and spherical; (1) large and spherical to oval, without distinct neck or with pale scarcely delimited neck.
40 *Seminal capsules*: (0) not with neck placed perpendicular and lateral; (1) pear-shaped to spherical with wide and prominent perpendicular and often laterally placed neck, [at least in some *Cricotopus* (*Isocladius*)].
41 *Seminal capsules*: (0) bare, (1) with microtrichiae, apical rugulosity or apical wart.
42 *Spermathecal ducts*: (0) straight, meandering or with short loop; (1) very long, with two to several loops.
43 *Spermathecal ducts*: (0) straight or nearly straight, (1) with two to several loops.
44 *Spermathecal ducts*: (0) of about even width throughout, (1) with strongly broadened portion(s).

Pupa

45 *Frontal seta*: (0) on praefrons or lacking, (1) on frontal apotome.
46 *Frontal warts*: (0) strong, (1) weak or absent.
47 *Thoracic horn*: (0) present; (1) sometimes absent.
48 *Thoracic horn*: (0) not stalked; (1) stalked.
49 *Thoracic horn*: (0) not small, rounded and bare; (1) small, rounded, bare.
50 *Thoracic horn*: (0) not very long, smooth and filamentous; (1) very long, filamentous, smooth.
51 *Thoracic horn*: (0) not sausage-shaped and smooth; (1) sausage-shaped and smooth.
52 *Thoracic horn*: (0) not tubular and bubbled, (1) tubular and sometimes bubbled.
53 *Thoracic horn*: (0) not oval and robust, (1) oval or leaf-like and robust.
54 *Thoracic horn*: (0) more than 200 µm long, (1) shorter or absent.
55 *Thoracic horn*: (0) covered with points or at least with serrated edge, (1) bare or at most a few points indicated in some specimens or bubbled or absent.
56 *Dorsocentrals*: (0) four pairs, (1) three or fewer pairs.
57 *Dorsocentrals*: (0) narrow or absent; (1) robust to conspicuously strong, spine-like.

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TABLE 2 (continued)

58 *Anterior point band on T III*: (0) extending further laterally than the posterior band, or absent or weak with posterior row consisting of spines or hooklets, or with paired median point patches (1) extending shorter or equally far laterally.
59 *T III–VII or VIII*: (0) without anterior spinous plate, (1) with.
60 *T III–VI or VII*: (0) without or with single median patch of spinules, (1) with pair of median spinule patches.
61 *T II–VII(VIII), TIII–VII(VIII) or IV–VII(VIII):* (0) without conspicuous posterior transverse band of small points although there may be a transverse band of points or hooklets, (1) T IV–VII with, (2) T III–VII with, (3) TII–VII or T II–VI with.
62 *Median point bands of T III–VI*: (0) fused to posterior band forming single mostly trapezoidal patch or posterior band absent; (1) transverse anterior or median bands separate from posterior band, but sometimes joined to it laterally or joined to it medially as well.
63 *Shagreen spinules of T III*: (0) similar in size or at least posterior spinules absent, (1) central median spinules larger, (2) posterior spinules larger.
64 *Shagreen spinules of T IV–VI:* (0) similar in size or at least posterior spinules absent, (1) central median spinules larger, (2) posterior spinules larger.
65 *Tergites IV–VI*: (0) without circular spinule patch medially or patch not set off from surrounding shagreen spinules or with two patches; (1) with single circular spinule patch medially or anterior.
66 *Tergites II or III–VII*: (0) without two central patches of strong spinules or robust points, (1) with.
67 *Hooklets or straight posterior spines on T II*: (0) absent, (1) hooklets in 2–3 rows or posterior straight spines, (2) hooklets in 3–5 or numerous rows.
68 *T II*: (0) “true” hooklets present; (1) without true hooklets, but with posterior group of straight spines; (2) no posterior spines or hooklets.
69 *Pedes spurii B on segment I*: (0) strong, (1) weak, (2) absent.
70 *Pedes spurii B on segment II*: (0) strong, (1) weak, (2) absent.
71 *Pedes spurii B on segment III*: (0) strong, (1) weak, (2) absent.
72 *Pedes spurii B*: (0) bare or absent, (1) spinulose or granulose.
73 Pedes spurii A: (0) present on IV–VII or IV–VI, (1) on V–VI or V–VII, (2) on VI and/or VII, (3) absent.
74 *Chitinous rings or small dark spots on conjunctives*: (0) absent, (1) present.
75 *Conjunctives III/IV to V/VI*: (0) with spinules or hooklets, (1) bare.
76 *T III– V or conjunctives III/IV to V/VI*: (0) bare or with spinules different from hooklets posterior on T II, (1) with hooklets or spinules similar to those on II/III or T II.
77 *Pleural spinules*: (0) absent, (1) on segments III–V or III–VI; (2) at least on segments II–V or II–VI.
78 *Dorsal O setae*: (0) present, (1) absent.
79 *L setae on segment VII*: (0) 4, (1) 3.
80 *L setae on segment VIII*: (0) 5, (1) 4, (2) 3, (3) 1or 2.
81 *Anal macrosetae*: (0) 3 subequal, well developed; (1) posterior anal macroseta reduced in strength and length relative to remaining two macrosetae; (2) absent or all hair-like.
82 *Anal macrosetae*: (0) strongly hooked at apex, absent or reduced; (1) at most weakly curved at apex, often straight.
83 *Number of anal macrosetae*: (0) 3 vestigial or normal, (1) 1–2 vestigial, (2) absent.
84 *Length of anal macrosetae*: (0) absent or less than 0.2 of anal lobe length; (1) 0.20–0.40 anal lobe length; (2) 0.41–0.79 anal lobe length; (3) more than 0.80 anal lobe length.

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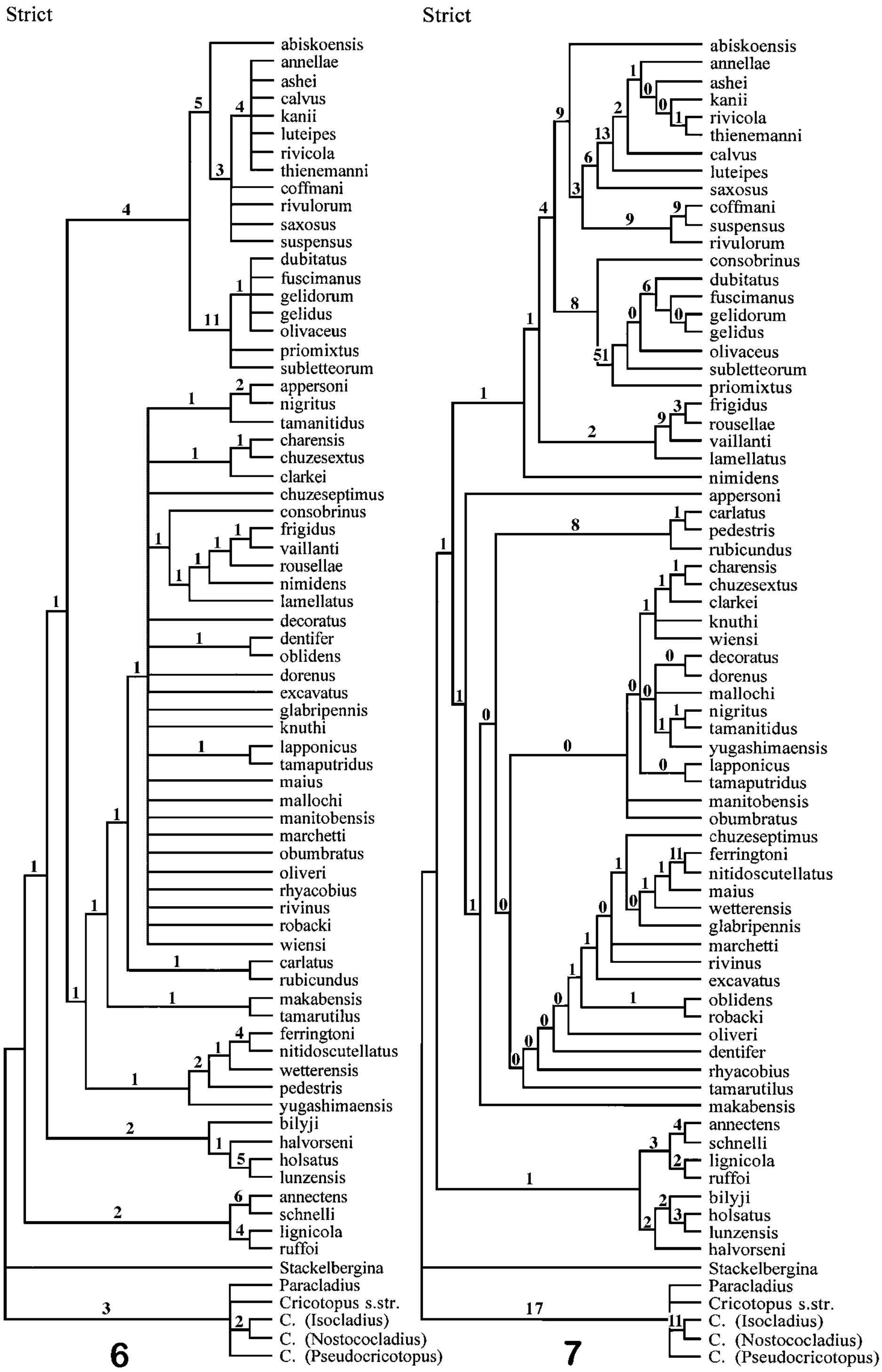
TABLE 2 (continued)

85 *Anal lobe*: (0) well developed, (1) reduced.
86 *Anal lobe*: (0) not extended, (1) extended distally as long lobes or spinous extension in at least some specimens.
87 *Anal lobe*. (0) no apical points or spines; (1) with apical points or spines.
88 *Anal lobe*: (0) no lateral spines or threads; (1) with fine, sclerotised lateral threads or spines.
89 *Genital sac of male*: (0) not conspicuously broad at apex; (1) conspicuously broad at apex.
Larva
90 *Head coloration*: (0) yellow or yellowish brown, (1) light to dark brown, (2) dark reddish brown to black.
91 *Antenna*: (0) well developed, (1) sometimes reduced.
92 *Antenna*: (0) 5-segmented, (1) 4-segmented.
93 *Antennal blade*: (0) shorter than flagellum, (1) longer than flagellum
94 *Lauterborn organs*: (0) absent, or narrow, weak to moderately developed; (1) well developed, but longer than wide; (2) conspicuous, about as wide as long.
95 *Labral lamellae*: (0) absent, (1) vestigial, (2) distinct.
96 *S I*: (0) bifid, (1) simple or weakly serrate.
97 *Pecten epipharyngis*: (0) 3 subequal separate scales, (1) scales fused or median scale shorter.
98 *Premandible*: (0) single, (1) bifid.
99 *Premandibular brush*: (0) absent, (1) vestigial or weak; (2) relatively distinct, consisting of spines or setae.
100 *Seta interna of mandible*: (0) present, (1) absent.
101 *Outer margin of mandible*: (0) smooth, (1) weakly or strongly rugose or crenulate.
102 *Mentum*: (0) with 13 or fewer teeth; (1) occasionally with 15 teeth, (2) always with 15 teeth, (3) with 17–21 teeth.
103 *Median mental tooth*: (0) more than 3.5 times as wide as first lateral tooth, (1) 1.5 ñ3.5 times as wide as first lateral tooth. (2) less than 1.5 times as wide as first lateral tooth.
104 *Mentum*: (0) more convex in outline, without teeth projecting far beyond their neighbours; (1) more triangular in outline, first and second lateral teeth often projecting above remaining lateral teeth.
105 *Extensions of mentum*: (0) not extended far posteriorly, not or barely exceeding line drawn through setae submenti; (1) extended far posteriorly, distinctly exceeding line drawn through setae submenti.
106 *Pecten galearis*: (0) present, (1) absent.
107 *Body seta L_4*: (0) simple, (1) brush-like.

The Bremer supports for each branch are indicated in Figs. 6 and 7 as numbers above the branches. For the reweighted tree, the character weights are reset to 1, resulting in some supports becoming lower than 0.5, and the supports adjusted to the shortest tree. Except for support for the monophyly of *Eudactylocladius* and to some extent *Euorthocladius* the supports are low when characters are not reweighted. When the characters are reweighted the supports are very high for *Eudactylocladius* and high for *Euorthocladius* and part of *Mesorthocladius*. For many branches, however, the support after successive reweighting is less than 0.5.



FIGURES 6, 7. Parsimony analyses of the relationships within *Orthocladius* v. d. Wulp, 6: strict consensus tree of the more than 80 000 trees obtained with no characters weighted, 7: strict consensus tree of the 333 trees obtained with characters successively reweighted according to the rescaled consistency index. Numbers above each branch indicate the Bremer support, for the reweighted characters when character weights are reset to 1 and the supports adjusted to the shortest tree.

TABLE 3. Character states for characters 1–107 in *Orthocladius* v. d. Wulp and outgroup. Polymorphies: A= 0&1, B= 0&1&2, C=1&2, D= 1&2&3, E=0&2, F=2&3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
abiskoensis	1	1	0	1	?	0	0	0	0	1	A	0	1	?	A	1	0	A	0	0	C	0	0	0	C	1	0
annectens	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	C	A	0	0	0	0	0	0	0	0	1	0
annellae	1	1	0	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	1	C	0
appersoni	1	0	0	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0	0	2	0	0	0	1	2	0
ashei	1	1	0	1	0	0	0	0	0	1	0	A	1	1	1	C	1	1	1	0	0	0	0	0	2	2	0
bilyji	1	0	0	1	0	0	0	0	0	1	A	0	0	1	A	C	0	A	0	1	0	0	0	0	1	2	0
calvus	A	1	0	1	?	0	0	0	0	1	0	0	1	1	A	1	A	1	A	0	A	0	0	0	1	2	0
carlatus	1	0	0	2	0	0	0	0	0	1	1	0	1	0	1	1	0	1	0	0	2	0	0	0	1	1	0
charensis	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	9	1	1	0	0	0	0	0	0	2	0
chuzeseptimus	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1	1	?	?	0	0	0	0	0	0	?	?	0
chuzesextus	A	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	?	?	0	A	2	0	0	0	1	1	0
clarkei	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	?	?	0	1	2	0	0	0	1	1	0
coffmani	?	1	0	1	?	0	0	1	0	1	0	1	?	?	1	1	?	?	0	1	0	0	1	0	1	0	0
consobrinus	0	1	0	1	0	0	0	0	A	1	1	0	0	1	1	A	0	1	0	0	0	0	0	0	1	1	0
decoratus	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	2	0	0	0	1	1	0
dentifer	A	0	0	2	0	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0
dorenus	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	0	0	2	0	0	0	1	1	0
dubitatus	C	0	0	1	1	0	0	0	0	1	1	0	0	A	A	C	0	0	0	A	0	1	0	1	1	1	1
excavatus	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	A	0	1	0	0	2	0	0	0	1	1	0
ferringtoni	2	1	0	C	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	2	0	0	0	1	1	0
frigidus	A	0	0	1	0	0	0	0	A	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0
fuscimanus	C	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	1	0	1	2	1	0
gelidorum	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	C	0	A	0	A	0	1	0	1	1	1	0
gelidus	1	0	0	1	1	0	0	0	0	1	A	0	0	A	1	1	0	1	0	A	0	1	0	0	1	1	0
glabripennis	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	2	0	0
halvorseni	1	?	0	1	0	0	0	0	0	1	1	0	?	?	?	1	?	?	0	0	0	0	0	0	1	1	0
holsatus	1	1	0	1	0	1	0	0	0	1	A	A	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0
kanii	1	1	0	1	0	0	0	1	0	1	0	0	1	1	1	A	?	?	1	0	0	0	0	0	1	0	0
knuthi	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	?	?	0	0	2	0	0	0	1	1	0
lamellatus	1	0	0	1	0	0	0	0	A	1	A	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0
lapponicus	1	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	2	0	1	0	1	1	0
lignicola	1	0	0	0	1	0	0	0	0	0	1	0	1	0	1	2	1	1	0	0	0	0	0	0	C	C	0
lunzensis	1	1	0	1	0	1	0	0	1	0	0	A	1	1	1	1	0	1	0	1	0	0	0	0	0	1	0
luteipes	0	1	0	1	?	0	0	A	A	1	0	A	1	?	1	1	0	1	1	0	0	0	0	0	0	1	0
maius	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	1	0	1	0	2	1	0
makabensis	1	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	?	?	0	0	2	0	0	0	?	?	0
mallochi	A	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	?	?	0	0	2	0	0	0	1	1	0

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TABLE 3 (continued)

	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
abiskoensis	1	0	2	1	0	0	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0	0	1
annectens	1	0	2	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
annellae	0	0	0	A	0	1	0	0	0	A	A	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
appersoni	1	0	2	1	0	0	A	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
ashei	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1
bilyji	1	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	A
calvus	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
carlatus	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
charensis	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
chuzeseptimus	1	0	0	1	?	?	?	?	?	0	1	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0
chuzesextus	1	0	0	1	?	?	?	?	?	0	1	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0
clarkei	1	0	2	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
coffmani	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	1	0	0
consobrinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
decoratus	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	0	0	0
dentifer	0	0	0	1	0	0	9	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
dorenus	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
dubitatus	0	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	1
excavatus	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	?	1	0	0	0	0	0	0	0	0
ferringtoni	1	1	2	?	?	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
frigidus	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	A	0	1	0	0	0	0	1	0	0	0	0
fuscimanus	1	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	A
gelidorum	?	0	2	2	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	0	1	0	0	1
gelidus	?	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	1
glabripennis	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
halvorseni	9	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
holsatus	1	0	2	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
kanii	0	0	0	?	?	?	?	?	?	1	0	0	0	?	?	?	?	0	1	0	1	1	0	0	0	0	1
knuthi	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
lamellatus	A	0	0	1	A	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
lapponicus	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
lignicola	1	0	2	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
lunzensis	1	0	2	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
luteipes	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	0	0	0	1
maius	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
makabensis	A	0	0	1	?	?	?	?	?	1	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	A
mallochi	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1

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TABLE 3 (continued)

	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
abiskoensis	1	0	0	0	0	0	0	1	2	2	0	0	1	0	2	2	2	0	3	0	0	1	0	1	0	1	2
annectens	1	0	0	0	0	0	0	1	2	1	1	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
annellae	1	1	1	0	0	0	1	0	0	0	0	0	0	2	2	2	2	0	3	0	1	0	0	1	1	3	2
appersoni	0	0	1	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	2	0
ashei	1	1	1	0	0	0	1	0	0	0	0	0	0	2	2	2	2	0	3	0	1	0	0	1	1	3	2
bilyji	0	0	0	1	0	0	0	1	2	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
calvus	1	1	1	0	0	0	3	0	0	0	0	0	1	1	2	2	2	0	3	0	1	0	0	1	1	3	2
carlatus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	1	0	0	0	0	0	2	0
charensis	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
chuzeseptimus	0	0	0	1	0	0	0	0	2	2	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
chuzesextus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	2	2	0	0	0	0	0	0	0	A	A	0
clarkei	0	0	0	1	0	0	0	0	2	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
coffmani	1	0	0	0	1	0	0	0	1	1	1	0	2	0	2	1	2	0	3	0	1	1	0	1	1	2	2
consobrinus	0	0	0	0	0	0	0	0	C	C	0	1	2	1	2	0	2	0	0	0	0	1	0	0	0	1	0
decoratus	1	0	0	?	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
dentifer	0	0	0	1	0	0	0	1	2	2	0	0	2	0	2	0	2	0	0	0	0	0	0	0	1	1	0
dorenus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
dubitatus	1	0	0	0	0	1	3	0	0	0	0	1	2	1	0	0	0	0	0	0	0	1	1	1	0	1	0
excavatus	0	0	0	1	0	0	0	0	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ferringtoni	0	0	0	1	0	0	0	0	1	1	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
frigidus	1	0	0	1	0	0	0	0	2	2	0	0	2	0	2	0	2	1	0	0	0	0	0	0	1	A	0
fuscimanus	1	0	0	0	0	1	3	1	0	0	0	1	2	1	1	0	1	0	0	0	0	1	2	1	0	C	0
gelidorum	1	0	0	0	0	1	3	1	0	0	0	1	2	1	2	2	2	0	A	0	0	1	2	1	0	1	1
gelidus	1	0	0	0	0	1	3	1	0	0	0	1	2	1	1	1	1	0	A	0	0	1	2	1	0	1	0
glabripennis	0	0	0	0	0	0	0	0	1	1	0	0	2	0	2	0	2	0	0	0	0	0	0	0	A	A	0
halvorseni	0	0	0	1	0	0	0	1	2	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
holsatus	0	0	0	1	0	0	0	1	1	1	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	1	0
kanii	1	1	0	0	0	0	1	0	0	0	0	0	0	2	2	2	2	0	3	0	1	0	0	0	1	3	2
knuthi	0	0	0	?	0	0	0	0	?	?	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
lamellatus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	2	2	0	0	0	0	0	0	0	A	1	0
lapponicus	0	0	0	?	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
lignicola	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	2	2	0	0	0	0	0	0	0	0	0	0
lunzensis	0	0	0	1	0	0	0	1	1	1	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	1	0
luteipes	1	1	1	0	0	0	1	1	0	0	0	0	0	2	2	2	2	0	1	0	1	0	0	0	1	2	2
maius	0	0	0	1	0	0	0	0	1	C	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
makabensis	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
mallochi	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0

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TABLE 3 (continued)

	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107
abiskoensis	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	1	0
annectens	0	0	F	0	0	1	0	0	0	0	0	0	2	0	0	1	0	2	0	0	0	1	1	0	1	1
annellae	0	1	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
appersoni	0	0	2	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ashei	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	1	0
bilyji	0	0	2	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
calvus	0	2	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	2	0	1	1	0
carlatus	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
charensis	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	A	0	2	0	1	1	0
chuzeseptimus	0	0	F	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
chuzesextus	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
clarkei	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
coffmani	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
consobrinus	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	C	0	1	0	0
decoratus	0	0	?	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
dentifer	1	0	2	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0
dorenus	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0
dubitatus	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0
excavatus	0	0	2	0	0	1	A	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ferringtoni	0	0	2	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0
frigidus	0	0	2	0	0	0	A	0	1	0	0	A	0	2	0	0	0	1	1	1	1	2	0	1	1	0
fuscimanus	0	0	F	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0
gelidorum	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	0
gelidus	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0
glabripennis	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0
halvorseni	0	0	2	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0
holsatus	1	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1
kanii	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	2	0	1	1	0
knuthi	0	0	2	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lamellatus	0	0	2	0	0	0	0	0	1	0	0	0	1	2	0	0	1	C	1	0	0	2	0	1	1	0
lapponicus	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	C	0	1	1	0
lignicola	1	0	3	0	1	1	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	0	1	0	0	A
lunzensis	1	0	C	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1
luteipes	0	2	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0
maius	0	0	F	0	0	A	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
makabensis	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
mallochi	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0

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TABLE 3 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
manitobensis	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	?	?	0	0	2	0	0	0	1	1	0
marchetti	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	2	0	0	0	1	1	0
nigritus	0	0	0	2	0	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	2	0	0	0	1	1	0
nimidens	A	0	0	1	0	0	0	0	A	0	A	0	A	A	1	1	1	1	0	A	0	0	0	0	A	1	0
nitidoscutellatus	1	1	0	2	1	0	0	0	0	1	0	A	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0
oblidens	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	2	0	0	0	1	1	0
obumbratus	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	2	0	0	0	1	1	0
olivaceus	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	C	0	1	0	0	0	1	0	0	0	1	0
oliveri	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	1	1	0
pedestris	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	?	?	0	0	2	0	1	0	1	1	0
priomixtus	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	A	0	1	0	0	1	2	A
rhyacobius	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	C	0	1	0	0	1	0	0	0	1	1	0
rivicola	1	1	0	1	0	1	0	A	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	1	0
rivinus	A	0	0	1	0	0	0	0	0	1	1	A	0	1	1	1	?	?	0	0	C	0	1	0	1	0	0
rivulorum	1	1	0	C	0	1	0	1	0	1	0	0	A	1	1	1	0	0	1	0	0	0	A	0	1	1	0
robacki	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	?	?	0	0	2	0	0	0	1	1	0
rousellae	1	1	0	0	0	A	0	0	1	1	0	1	0	1	A	1	1	0	1	A	0	0	0	0	1	2	0
rubicundus	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	C	?	?	0	0	C	0	0	0	1	1	0
ruffoi	1	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	1	A	0	0	0	0	0	0	1	1	0
saxosus	1	1	0	1	1	1	0	1	0	1	0	A	1	1	1	1	0	0	1	A	0	0	1	0	1	1	0
schnelli	1	1	0	1	1	0	0	0	0	1	1	0	1	A	1	C	A	0	0	0	0	0	0	0	0	0	0
subletteorum	C	0	0	1	1	0	0	0	0	1	1	0	0	0	1	C	1	1	0	A	0	1	0	0	1	0	A
suspensus	1	1	0	2	?	1	0	1	0	1	0	1	A	1	1	1	?	?	1	0	0	0	0	0	1	1	0
tamanitidus	A	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	?	?	0	0	2	0	0	0	1	0	0
tamaputridus	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	?	?	0	1	2	0	0	0	?	?	0
tamarutilus	1	0	0	1	1	0	0	0	0	1	1	0	1	0	1	2	?	?	0	A	1	0	0	0	?	?	0
thienemanni	A	1	0	1	?	1	0	1	0	1	0	A	0	1	1	A	0	1	1	0	A	0	0	0	1	1	0
vaillanti	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0
wetterensis	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	0	1	0	1	1	1
wiensi	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	?	?	0	0	2	0	0	0	1	1	0
yugashimaensis	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	?	?	0	0	?	0	1	0	?	?	0
Stackelbergina	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	2	0
Paracladius	A	A	1	A	0	1	1	0	A	1	0	0	1	A	A	1	1	0	0	1	0	0	0	0	1	2	0
Cricotopus s.str.	B	A	1	A	0	A	1	0	A	A	A	A	1	A	A	B	A	0	0	A	0	0	0	0	A	C	A
C. (Isocladius)	B	A	1	A	0	A	1	0	A	A	A	A	1	A	A	B	A	0	0	A	A	0	A	0	A	C	A
C. (Nostococladius)	1	0	1	1	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	2	1
C. (Pseudocricotopus)	C	0	1	1	0	1	1	0	0	1	0	1	?	?	A	?	?	?	0	A	1	0	0	0	1	1	0

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TABLE 3 (continued)

	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
manitobensis	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
marchetti	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	1
nigritus	1	0	2	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
nimidens	1	0	2	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0
nitidoscutellatus	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
oblidens	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
obumbratus	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
olivaceus	0	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	1
oliveri	1	0	2	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
pedestris	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	0	0	0
priomixtus	0	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	1
rhyacobius	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
rivicola	1	0	E	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
rivinus	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
rivulorum	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	1	0	A
robacki	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	1
rousellae	0	0	E	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1	0	A	0	0
rubicundus	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	A
ruffoi	1	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	A
saxosus	0	0	E	?	?	?	?	?	?	1	0	0	0	?	?	?	?	0	0	0	0	1	0	0	0	0	1
schnelli	1	0	2	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
subletteorum	1	0	2	2	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	1
suspensus	0	0	E	?	?	?	?	?	?	0	0	0	1	?	?	?	?	0	1	0	0	0	0	0	1	0	0
tamanitidus	1	0	0	?	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0
tamaputridus	1	0	?	?	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0
tamarutilus	1	0	0	?	?	?	?	?	?	1	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	A
thienemanni	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	0	0	0	1
vaillanti	A	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0	0	0	1
wetterensis	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	0
wiensi	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
yugashimaensis	1	0	?	1	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0
Stackelbergina	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0
Paracladius	0	0	2	2	1	0	A	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	A
Cricotopus s.str.	A	0	2	C	1	A	A	0	0	0	A	0	0	A	0	A	0	A	1	1	0	A	0	0	0	A	A
C. (Isocladius)	A	0	2	C	1	0	A	1	0	0	A	0	1	0	0	A	0	A	1	0	A	A	A	A	A	0	A
C. (Nostococladius)	1	0	2	?	?	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1
C. (Pseudocricotopus)	1	1	1	1	A	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1

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TABLE 3 (continued)

	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
manitobensis	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
marchetti	0	0	0	1	0	0	0	0	2	1	0	0	2	0	2	1	2	0	0	0	0	0	0	0	A	A	0
nigritus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	2	0
nimidens	0	0	1	1	0	0	0	0	2	2	0	0	2	0	2	0	2	1	0	0	0	0	0	0	0	A	0
nitidoscutellatus	A	0	0	1	0	0	0	0	0	0	0	0	C	0	2	0	2	0	0	0	0	0	0	0	0	0	0
oblidens	0	0	0	1	0	0	0	0	2	2	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
obumbratus	0	0	0	1	0	0	0	0	E	B	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
olivaceus	1	0	0	0	0	1	0	1	0	0	0	1	2	1	0	0	0	0	0	0	0	1	1	1	A	1	1
oliveri	0	0	0	1	0	0	0	0	2	2	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
pedestris	0	0	0	0	0	0	0	0	1	1	0	0	2	0	2	0	2	0	0	1	0	0	0	0	0	0	0
priomixtus	1	0	0	0	0	1	0	1	0	0	0	1	2	1	2	1	2	0	2	0	0	1	0	1	0	1	0
rhyacobius	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
rivicola	1	1	0	0	0	0	1	1	0	0	0	0	0	2	2	2	2	0	3	0	1	0	0	1	1	3	2
rivinus	0	0	0	1	0	0	0	1	1	1	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
rivulorum	1	0	0	0	0	0	3	1	0	0	1	0	2	0	2	0	2	0	3	0	1	1	0	0	1	1	2
robacki	0	0	0	1	0	0	0	0	C	C	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
rousellae	1	0	0	0	0	0	0	1	2	C	0	0	2	0	2	0	0	1	0	0	0	0	0	0	0	1	2
rubicundus	0	0	0	1	0	0	0	1	0	0	0	0	2	0	2	0	2	0	0	1	0	0	0	0	0	1	0
ruffoi	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	2	2	0	0	0	0	0	0	0	1	0	0
saxosus	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	2	0	1	1	0	0	0	2	2
schnelli	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
subletteorum	1	0	0	0	0	1	0	1	0	0	0	1	2	1	0	0	2	0	2	0	0	1	1	1	0	1	0
suspensus	1	0	?	0	1	0	0	0	0	0	0	0	2	0	2	0	2	0	3	0	0	1	0	?	1	2	2
tamanitidus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
tamaputridus	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	1	0
tamarutilus	0	0	0	1	0	0	0	1	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	1	1	0
thienemanni	1	1	A	0	0	0	2	0	0	0	0	0	0	2	2	2	2	0	3	0	1	0	0	1	1	1	0
vaillanti	1	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	0	0	0	0	1	0	A
wetterensis	0	0	0	1	0	0	0	A	1	1	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0
wiensi	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	1	0
yugashimaensis	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	0	0	0	0	0	0
Stackelbergina	0	0	A	1	0	0	0	1	2	C	1	0	1	0	2	C	2	0	0	0	0	0	0	0	0	0	0
Paracladius	0	0	0	1	0	0	0	1	0	0	0	0	1	0	2	0	A	0	0	0	0	0	0	0	A	1	1
Cricotopus s.str.	A	0	0	1	0	0	0	A	0	0	0	0	1	0	2	B	B	0	0	0	0	0	0	0	A	A	A
C. (Isocladius)	A	0	0	1	0	0	0	0	A	2	0	0	1	0	2	C	C	A	0	0	0	0	0	0	A	A	0
C. (Nostococladius)	1	1	0	1	0	0	0	0	0	0	0	0	2	0	2	2	2	0	3	0	0	0	0	0	A	A	2
C. (Pseudocricotopus)	0	1	0	0	0	0	0	1	0	0	0	0	1	0	2	A	1	0	?	0	0	0	0	0	1	1	0

......continued on the next page

TABLE 3 (continued)

	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107
manitobensis	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0
marchetti	0	0	2	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
nigritus	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0
nimidens	0	0	F	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	F	0	0	1	1	0
nitidoscutellatus	0	0	2	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0
oblidens	1	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
obumbratus	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	1	1	0
olivaceus	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
oliveri	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	A	1	0
pedestris	0	0	2	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
priomixtus	1	0	2	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
rhyacobius	0	0	2	0	0	1	A	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	?	0	0
rivicola	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	1	0
rivinus	0	0	F	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
rivulorum	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	1	0
robacki	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
rousellae	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	1	2	2	0	1	1	0
rubicundus	0	0	F	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
ruffoi	1	0	3	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
saxosus	0	2	0	1	0	0	0	0	1	0	0	1	1	0	0	0	A	0	0	0	0	2	0	1	1	0
schnelli	0	0	3	0	0	1	0	0	0	0	0	0	2	0	0	1	0	2	0	0	0	1	1	0	1	1
subletteorum	?	0	2	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
suspensus	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	3	1	0	1	1	0
tamanitidus	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
tamaputridus	0	0	2	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
tamarutilus	0	0	2	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
thienemanni	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0
vaillanti	A	0	C	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	A	0	1	0	1	1	0
wetterensis	0	0	F	0	0	0	A	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
wiensi	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0
yugashimaensis	0	0	F	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
Stackelbergina	0	0	3	0	0	0	0	0	?	0	0	0	0	0	1	0	0	?	0	0	0	1	0	0	?	1
Paracladius	1	0	F	0	0	0	0	0	0	0	0	0	1	0	0	0	A	1	0	0	0	0	0	1	1	0
Cricotopus s.str.	1	0	2	0	0	0	0	0	A	0	0	0	A	0	0	0	A	B	0	A	0	B	A	0	0	A
C. (Isocladius)	0	0	2	0	0	0	0	0	A	1	A	0	A	0	A	1	A	0	A	A	0	C	A	0	A	1
C. (Nostococladius)	0	2	2	1	1	0	0	0	2	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0
C. (Pseudocricotopus)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?	1

Weighting the apparently more important characters also was attempted. However, nearly half of the different characters could be regarded as important and given higher weight and the results differed little from those resulting from unweighted characters. The main differences consisted in making *Symposiocladius* monophyletic both before and after reweighting, placing *Eudactylocladius* basally above *Symposiocladius* before reweighting, but in the same position as with unweighted characters after reweighting, and making both *Mesorthocladius* and *Orthocladius* polyphyletic before reweighting and paraphyletic after.

There are no unique synapomorphies for all members of *Mesorthocladius*, but as is shown in Table 1 there are several for two to four species. These include sculptured seminal capsules, filamentous and stalked thoracic horn, granulose or spinulose pedes spurii B, presence of labral lamellae, and absence of seta interna. Other characters are mostly limited to the subgenus, but appear also elsewhere, such as multiserial scutellars, strong frontal warts of the pupa and bifid premandible.

The subgenus *Euorthocladius*, following the removal of *O. rousellae*, also lacks unique synapomorphies for the full subgenus, but has several unique synapomorphies within the subgenus. These include pupal characters such as a small, rounded and bare thoracic horn, bubbled thoracic horn, absence of hooklets on tergite II, absence of spinules on conjunctives, and reduced number of L setae. There are a number of synapomorphies mostly limited to the subgenus, but occurring also elsewhere. These include female-like eyes in the male, bi-multiserial dorsocentrals, absence of acrostichals, robust anal point, absence of pedes spurii B, and vestigial pupal anal lobe megasetae.

The subgenus *Eudactylocladius* has several unique synapomorphies in both sexes and all stages. However, the only unique character of the larva is in the reddish brown coloration of the head capsule. The lack of posterolateral mental extensions in the larva, however, is nearly limited to the subgenus.

The large female tergite IX, the spinous pupal tergites and the four-segmented larval antenna are all unique autapomorphies for the monotypic subgenus *Pogonocladius*. The subgenus, however, lacks unique synapomorphies in the male imago.

In the subgenus *Symposiocladius* the large, rounded Lauterborn organs appear to be a unique synapomorphy. A brush-like body seta L_4 is found only within this subgenus. Absence of a virga, prominent frontal warts in the pupa, and absence of pedes spurii B all are common within the subgenus and rare outside.

The subgenus *Orthocladius* does not show any unique synapomorphies for the subgenus as a whole. A well developed triangular to rounded superior volsella and apical spines on the pupal anal lobe, however, are nearly limited to the subgenus, and most pupae have the median point band on tergites III and IV fused to the posterior band while they more often are separated outside the subgenus. A few unique synapomorphies, such as the presence of chitinous rings or small dark spots on the pupal conjunctives, define some groups within the subgenus.

Keys to subgenera

Male imagines

1. Hypopygium without well-developed dorsal part of inferior volsella; virga absent ....*Orthocladius* (*Eudactylocladius*)
- Hypopygium with well-developed dorsal part of inferior volsella, virga present or absent 2
2. Superior volsella well developed, triangular to rounded.. 3
- Superior volsella reduced or collar-like 4
3. Eyes widely separated, female-like; virga absent .... *O.* (*Euorthocladius)*, pro parte [*O.* (*E.*) *abiskoensis* Thienemann & Krüger]
- Eyes extended dorsomedially, male-like; virga usually present..................................... .... *Orthocladius* s.str., pro parte
4. Anal point robust, triangular to parallel-sided with rounded apex and lateral setae which often are laterally or even anterolaterally directed 5
- Anal point pointed, not robust... 8
5. Eyes widely separated, female-like 6
- Eyes extended dorsomedially, male-like 7
6. Anal lobe of wing well developed, projecting ....*Orthocladius* (*Mesorthocladius*), pro parte [*O.* (*M.*) *rousellae* Soponis]
- Anal lobe of wing at most slightly projecting .... *Orthocladius* (*Euorthocladius*), pro parte
7. Either vein R_{4+5} setose or ventral part of inferior volsella prominently extended below dorsal part... *Orthocladius* s. str., pro parte
- Vein R_{4+5} bare, ventral part of inferior volsella not extended below dorsal part .... *Orthocladius* (*Mesorthocladius*), pro parte
8. Eyes widely separated, female-like 9
- Eyes extended dorsomedially, male-like 13
9. Virga absent 10
- Virga present.. 11
10. Ventral part of inferior volsella extended below dorsal part, scutellars multiserial ....*Orthocladius* (*Euorthocladius*), pro parte [*O.* (*E.*) *coffmani* Soponis]
- Ventral part of inferior volsella not extended below dorsal part, scutellars uni- multiserial .... *Orthocladius* (*Symposiocladius)*, pro parte.
11. Dorsal part of inferior volsella long and narrow .... *Orthocladius* (*Pogonocladius*)
- Dorsal part of inferior volsella not long and narrow 12
12. Anal lobe of wing strongly projecting... ....*Orthocladius* s.str., pro parte [*O.* (*O.*) *chuzeseptimus* Sasa]
- Anal lobe of wing not strongly projecting ....*Orthocladius (Euorthocladius*), pro parte [*O.* (*E.*) *calvus* Pinder]

13. Virga absent, gonostylus conspicuously curved..
................................*Orthocladius* (*Symposiocladius)*, pro parte [*O.* (*S.*) *bilyji* Sæther]
- Virga present, gonostylus approximately straight 14
14. Anal point broadly triangular with base not clearly separated from apical part ....
............................*Orthocladius* (*Mesorthocladius*), pro parte [*O.* (*M.*) *nimidens* sp. n.]
- Anal point with triangular base and clearly differentiated, tapering apical portion........
.... *Orthocladius* s.str., pro parte.

Female imagines

1. Spermathecal ducts with two to several loops, with broadened portions; tergite IX essentially undivided, but with setae in two groups....*Orthocladius* (*Eudactylocladius*)
- Spermathecal ducts straight, meandering or with loops, when more than one loop [*O* (*M.*). *nimidens*] without broadened portions; tergite IX divided.................................. 2
2 Tergite IX broad, plate-like, with margins relatively poorly delimited; gonocoxite strongly developed with more than 15 setae; seminal capsule pear-shaped; spermathecal ducts straight to slightly meandering........................ *Orthocladius* (*Pogonocladius*)
- Tergite IX less broad and plate-like, margins often well delimited; gonocoxite variously developed with few to many setae; seminal capsule pear-shaped, small and rounded or large and spherical to oval; spermathecal ducts with or without loops, or meandering 3
3 Seminal capsule pear-shaped with apical wart or rugulosity, or small, rounded and bare; when small rounded and bare, margins of tergite IX relatively poorly delimited; spermathecal ducts meandering or with one or more loops ....
.... *Orthocladius* (*Mesorthocladius*)
- Seminal capsule when pear-shaped, without apical wart or rugulosity, but may have microtrichiae; when small and rounded, margins of tergite IX well delimited [not known for *O. (O.) makabensis* Sasa and *O. (O.) tamarutilus* Sasa]; spermathecal ducts without loops.. 4
4. Seminal capsule small, rounded, and bare; tergite IX divided with margins well delimited ....*Orthocladius* (*Euorthocladius*) pro parte
- Seminal capsules pear-shaped to ovoid, tergite IX divided with margins poorly or well delimited 5
5. Dorsomesal and ventrolateral lobe of gonapophysis VIII about equal in size................
.... *Orthocladius* (*Symposiocladius*) pro parte
[except *O.* (*S.*) *lignicola* Kieffer, *O.* (*S.*) *halvorseni* Sæther]
- Ventrolateral lobe clearly larger than dorsomesal lobe ....
Orthocladius (Orthocladius), *O*. (*Euorthocladius*) pro parte, *O*. (*Symposiocladius*) pro parte

Pupae

1. Anal lobe without or with vestigial macrosetae; thoracic horn not long and filamentous; frontal setae absent .... *Orthocladius* (*Euorthocladius*)
- Anal lobe with well-developed macrosetae or when vestigial, thoracic horn long, filamentous and smooth; frontal setae usually on frontal apotome 2
2. Tergite II without hooklets, but with posterior group of straight spines; thoracic horn stalked, smooth, sausage-shaped or perhaps occasionally absent .... *Orthocladius* (*Eudactylocladius*)
- Tergite II with posterior hooklets; thoracic horn not smooth and sausage-shaped 3
3. Tergites III–VII with two central clumps of points; thoracic horn oval and robust .... *Orthocladius* (*Pogonocladius*)
- Tergites without clumps of points, but may have central area of stronger shagreen spinules; thoracic horn never oval and robust 4
4. Thoracic horn stalked, long, filamentous and smooth or robust with tapered apex and covered with points; when spinous, anal lobe with fine sclerotised lateral threads and frontal warts strong and some dorsocentrals spine-like .... *Orthocladius* (*Mesorthocladius*) pro parte [except *O.* (*M.*) *lamellatus* sp. n.]
- Thoracic horn not stalked, not filamentous, slender to robust, bare or mostly covered with points; anal lobe usually without lateral threads [except *O.* (*S.*) *ruffoi* Rossaro & Prato and *O.* (*O.*) *rhyacobius* Kieffer] 5
5. Transverse anterior or median point bands of tergites III to VI separate from posterior bands, but sometimes joined to it laterally. Tergites IV–VI sometimes with single circular patch of strong spinules [*O.* (*S.*) *annectens* Sæther, *O.* (*S.*) *schnelli* Sæther]. Anal macrosetae often straight combined with pedes spurii B on segment II absent [*O.* (*S.*) *lignicola, O.* (*S.*) *ruffoi*], or straight combined with pedes spurii B on segment III strong [*O.* (*S.*) *holsatus* Goetghebuer, *O.* (*S.*) *lunzensis* Dettinger-Klemm], when anal macrosetae hooked at apex pedes spurii B on segment III present, but weak [*O.* (*S.*) *halvorseni*] .... *Orthocladius* (*Symposiocladius*) pro parte
- Transverse point bands fused or separate; tergites without circular patch of strong spinules; none of the above combinations present 6
6. Pedes spurii B absent on segments II and III, no apical or lateral spines on anal lobe, median point band on tergites III and IV fused with posterior band............................ 7
- Pedes spurii present at least on segment II, apical or lateral spines usually present on anal lobe, median point band on tergites III and IV often separate from posterior band 8
7. Total length 3.0–3.6 mm, anal macrosetae 184–223 µm long .... *O. (Orthocladius) chuzesextus* Sasa
- Total length 4.1–5.4 mm, anal macrosetae 225–278 µm long .... *O. (Mesorthocladius) lamellatus* sp. n.
8. Median point band on tergites III and IV fused to posterior band ....

....*Orthocladius* (*Orthocladius*) pro parte
- Median point band on tergites III and IV separated from posterior band 9
9. Frontal setae on praefrons or absent, or anal lobe without apical spines, or pedes spurii B present on segment III, or conjunctives with chitinous rings or small dark spots....... ....*Orthocladius* (*Orthocladius*) pro parte
- Frontal setae on frontal apotome, anal lobe with apical spines, pedes spurii B absent on segment III, conjunctives without chitinous rings 10
10. Central median shagreen spinules on tergites III–VI larger than posterior spinules....... .... *O. (O.) rivinus* Kieffer
- Posterior shagreen spinules slightly larger than median spinules on tergite III, of about the same size on tergites IV–VI............................... *O.* (*Symposiocladius*) *bilyji* Sæther

Larvae
1. Antenna 4-segmented, premandible bifid, pecten galearis present................................. .... *Orthocladius* (*Pogonocladius*)
- Antenna 5-segmented or when 4-segmented premandible simple, premandible bifid or usually simple, pecten galearis usually absent 2
2. Seta interna of mandible absent or when present, mentum with 15 or 17 teeth and premandible bifid; when mentum with 13 teeth, labral lamellae distinct and premandible bifid with weak brush or seta interna of mandible absent and premandible simple with apical notch and vestigial brush .... *Orthocladius* (*Mesorthocladius*)
- Seta interna of mandible present; premandible usually simple, when bifid brush absent; mentum usually with 13 or fewer teeth, when with 15–21 teeth, premandible simple 3
3. Lauterborn organs robust and circular; mentum either with single broad, elongate median tooth and 2 pairs of basal, lateral teeth, or triangular in outline with first and second lateral teeth projecting above remaining lateral teeth or more convex in outline with median tooth more than 3.5 times as wide as first lateral tooth; body segments 4-9 often with lateral seta L_4 developed as setal brush; pecten galearis often present; premandible simple often with vestigial brush .... *Orthocladius* (*Symposiocladius*)
- Lauterborn organs vestigial to well developed, when long and robust, not circular; when mentum triangular in outline or median tooth of mentum more than 3.5 times as wide as first lateral tooth setal brushes of abdomen and pecten galearis absent........... 4
4. Head capsule yellow... *Orthocladius* (*Orthocladius*)
- Head capsule brown to reddish brown 5
5. Head capsule light to dark brown, not reddish; mentum sometimes with more than 13 teeth; mental extensions extended far posteriorly, distinctly exceeding line drawn through setae submenti...*Orthocladius* (*Euorthocladius*)
- Head capsule dark reddish brown; mentum with 13 teeth, with median tooth less than 1.5 times as wide as first lateral tooth; mental extensions not extended far posteriorly,

not or barely exceeding line drawn through setae submenti ....*Orthocladius* (*Eudactylocladius*)

Orthocladius subgen. *Mesorthocladius* new subgenus

Orthocladius subgen. *Rheorthocladius* Thienemann, 1944 pro parte, not Thienemann 1935: 235.
Orthocladius subgen. *Euorthocladius* Brundin 1947, pro parte, not Thienemann 1935: 201.
Orthocladius subgen. *Orthocladius* Goetghebuer, 1932, not v. d. Wulp 1874: 132.

Type species

Orthocladius (*Mesorthocladius*) *frigidus* Kieffer.

Other included species

Orthocladius (*M.*) *rousellae* Soponis, *O.* (*M*) *vaillanti*, *O.* (*M*) *lamellatus* sp. n., *O.* (*M.*) *nimidens* sp. n.

Etymology

From Greek, *mesos*, middle, and *Orthocladius*, a genus of Orthocladiinae, referring to the phylogenetic position of the subgenus.

Diagnostic characters

The male imagines are separable from those of other subgenera by a combination of characters: collar-like superior volsella; inferior volsella with ventral part not extended below dorsal part; anal point robust with rounded apex or broadly triangular (*O. nimidens*); eyes extended dorsomedially, male-like or when female-like (*O. rousellae*) scutellars multiserial, antepronotals numerous (9–27) and crista dorsalis prominent; scutellars usually multiserial, when uniserial to biserial eyes not female-like and anal point broadly triangular or anal lobe strongly projecting and sensilla chaetica present on both mid and hind leg; anal lobe of wing usually strongly projecting. Tergite IX of female divided, seminal capsule pear-shaped with apical wart or rugulosity, or small, rounded and bare; when small rounded and bare, margins of tergite IX relatively poorly delimited; spermathecal ducts meandering or with one or more loops. Pupae (except *O. lamellatus*) with thoracic horn stalked, long, filamentous and smooth or robust with tapered apex and covered with points; when spinous anal lobe with fine sclerotised lateral threads and frontal warts strong and some dorsocentrals spine-like. *Orthocladius lamellatus* differs from species of the nominal subgenus except *O.* (*O.*) *chuzesextus* Sasa by having pedes spurii B absent on segments II and III, no apical or lateral spines on anal lobe, and median point band on tergites III and IV fused with posterior band. From *O.* (*O.*) *chuzesextus* it differs by its larger size (total length 4.1–5.4 mm, anal macrosetae 225–278 µm long versus 3.0–3.6 mm, anal macrosetae 184–223 µm long). The larva differs from that of other species of the genus by lacking seta interna of the mandible or when seta interna present, the mentum has 15 or 17 teeth and the premandible is bifid; labral lamellae sometimes present; premandible often bifid.

Imago

Moderately large species, wing length 1.7–3.4 mm. Thorax with brown to blackish brown vittae and other markings and with the ground colour varying from pale to nearly as dark as markings.

Eye bare, reniform, with small or no dorsomedian elongation, occasionally female-like.

Antenna with 13 flagellomeres in male, 5 in female; male antenna fully plumed; groove beginning on flagellomere 4 or 5; sensilla chaetica present on flagellomere 2, 3 and 13; apex without straight apical seta in male, with in female; AR 1.0–2.1. Palpomeres long, normal; palpomere 3 with 2–3 short lanceolate sensilla clavata. Temporals numerous. Tentorium and stipes normally developed. Cibarial pump with anterior margin deeply concave, cornua moderately to strongly developed. Clypeus with several setae.

Antepronotal lobes with several to numerous lateral antepronotals. Acrostichals starting close to antepronotum, dorsocentrals uniserial to occasionally biserial, few to many prealars, supraalars absent or occasionally present. Scutellum with setae usually transversely bi- multiserial, occasionally uniserial.

Wing membrane with fine punctation; anal lobe well developed, moderately to strongly projecting; costa not to clearly extended; R_{2+3} running in the middle between R_1 and R_{4+5}; R_{4+5} and costa ending distal to end of M_{3+4}; VR 1.00–1.12; Cu_1 straight to slightly curved, occasionally slightly sinuous apically; postcubitus ending far distal to cubital fork, anal vein ending distal to cubital fork. Brachiolum with 1 seta, R with a few setae; R_1 occasionally with 1 seta, R_{4+5} of male bare or occasionally with 1 non-marginal seta, in female R_1 and R_{4+5} with setae; other veins bare. Squama with 17–37 setae. Sensilla campaniformia about 13–14 basally on brachiolum, about 8–10 apically on brachiolum, three below setae on brachiolum; one present basally on subcosta, and one basally on R_1 or on RM.

Front leg ratio 0.62–0.72. Tibial spurs and hind tibial comb normal. Tarsal pseudospurs present on ta_1 of mid and hind legs, usually on ta_2 of mid leg and often on ta_2 of hind leg. Pulvilli absent. Sensilla chaetica 0–21 on ta_1 of mid leg, 0–16 on hind leg in male; 0–22 on ta_1 of each middle and hind leg in female.

Tergites with scattered setae without a distinct pattern. Sternites with median and lateral setae.

Male anal point usually robust, partly parallel-sided with rounded apex and short, stiff lateral setae often directed laterally or even anteriorly; occasionally (*O. nimidens*) anal point broadly triangular and pointed. None to few setae at base on tergite IX; laterosternite IX with several setae. Sternapodeme slightly curved, oral projections well developed. Phallapodeme hooked apically, aedeagal lobe well developed. Virga present and consisting of several small teeth or of cluster of spines or absent. Gonocoxite well developed; superior volsella collar-like or absent; inferior volsella well developed with weak ventral part not extended below dorsal part. Gonostylus with weak to prominent rounded preapical crista dorsalis, megaseta normal.

Female genitalia with evenly curved gonocoxapodemes meeting or indicated anterior of vagina. Gonocoxite well developed, with numerous setae. Tergite IX strongly divided with several setae. Segment X normal. Postgenital plate weak, indistinct, bluntly triangular. Cercus large. Gonapophysis VIII divided into large, brush-like ventrolateral lobe covering part of nearly equally large dorsomesal lobe with or without oral rounded projection. Rami indistinct, barely sclerotised. Apodeme of apodeme lobe distinct. Coxosternapodeme strong laterally, moderately strong to weak and indistinct medially, evenly curved, but sometimes with anterior projection or bend. Seminal capsules small and rounded to pear-shaped, sometimes with apical rugulosity or distinct apical wart; darkly sclerotised for most of their length; with or without neck. Spermathecal ducts slightly meandering, with small loop, or very long with several loops; equally wide throughout; with separate openings. Labia bare.

Pupa

Moderately large pupae, 4.4–6.5 mm long. Exuviae pale greyish brown to pale brown with brown to blackish brown apophyses. Frontal warts prominent, weak or occasionally absent. Frontal setae mostly well developed, Thoracic horn stalked, very long, filamentous, and smooth or robust, tapering and covered with spinules. Three precorneals, 3–4 antepronotals, at least one postorbital and 4 dorsocentrals present; dorsocentrals in two pairs or equidistant. Wing sheath smooth without pearls or nose.

Tergite I bare or with a few posterior spinules, II with weak median or posteromedian shagreen; tergites III–VI with median portion covered with single mostly subrectangular patch of often coarse spinules; tergites III–V with 4–7 rows of anteriorly directed spinules posteriorly on tergites or more usually on conjunctives; tergite VII–IX with weak anterior group shagreen, occasionally with additional median shagreen. Sternites I bare, II–VIII with lateral or anterolateral shagreen; II–III or IV often with additional large patch of spinules. Pedes spurii A on sternites IV–VI or VII. Pedes spurii B well developed, spinulose or granulose or occasionally absent (*O. lamellatus*), sometimes present also on tergite III. Caudal hooklets on tergite II 40–160; in 2–6 rows. Segments II–V each with 3 L setae, VI and VII each with 3–4, and VIII with 4–5 L setae.

Anal lobe either large, rounded, without apical spurs, but with minute to very long lateral threads, and apically curved, subequal anal macrosetae; or slightly extended with heavy spines on tips and vestigial macrosetae (*O. rousellae)*. Male genital sac nearly reaching to or slightly overreaching anal lobe.

Larva

Moderately large larvae, up to 8.6 mm long. Head capsule brown to dark brown.

Antenna with 5 segments, antennal ratio 1.7–3.0. Ring organ in basal third. Lauterborn organs weak to moderately developed. Labrum with one branch of S I occasionally split into weak branches; two labral lamellae each with 3–7 spines sometimes present; about 12 chaetae and 2–5 spinulae. Pecten epipharyngis consisting of 3 subequal spine- to lobe-like teeth. Chaetulae laterales all smooth or one chaetulae laterales slightly serrated. Premandible simple or bifid, brush present and distinct to vestigial or absent. Mandible often without seta interna. Mentum with 13–17 teeth, median tooth slightly wider than first lateral tooth to more than four times as wide, ventromental plate occasionally with weak setae underneath on cardo. Pecten galearis apparently absent.

Claws of anterior parapods strongly serrated. Body with simple setae, some long and robust. Procercus higher than wide, with 6–7 anal setae; supraanal seta about 1/3 to 1/4 as long as anal setae. Anal tubules shorter than posterior parapods, rounded, subequal or one pair slightly shorter.

***Orthocladius* (*Mesorthocladius*) *lamellatus* sp. n.**
(Figs. 8–12, 13–17, 23, 24, 31, 32, 35, 36)

Type material

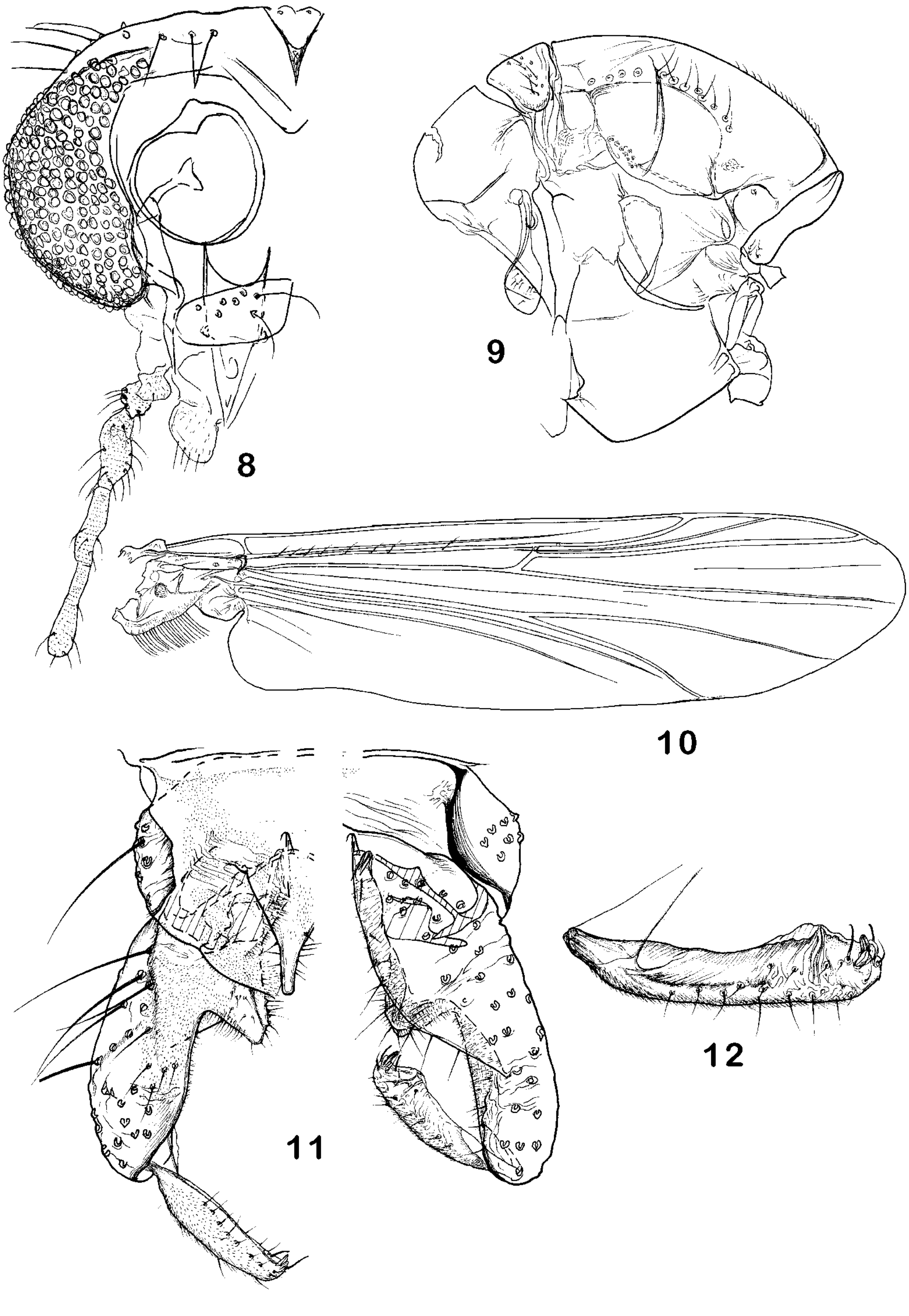
Holotype ♂ reared from larva, USA: Ohio, Delaware Co., Olentangy R., N. of Winter Road, 5 ii emerged 14 iii 1987, M. J. Bolton (ZMBN Type No. 406). Paratypes: USA: Ohio, Franklin Co., Sciota park, spring-stream, mature ♂ pupa reared from larva, mature ♀ pupa reared from larva, 26 iv 1987, M. J. Bolton (ZMBN); Ohio, Franklin Co., spring-stream tributary to Sciota R., 4 larvae, 1 v 1986, M. J. Bolton (ZMBN); Ohio, Delaware Co., Highbanks Metro Park, small stream, 1♂, mature ♂ pupa reared from larva, 3 larvae, 4 iv 1987, 26 iii 1989. M. J. Bolton (ZMBN).

Etymology

From Latin, *lamella*, small plate and -*atus*, equipped with, referring to the presence of labral lamellae in the larva.

Diagnostic characters

The male imago is separable from the other species of the subgenus by having a well developed virga consisting of a cluster of spines combined with uni-biserial scutellars, robust anal point and sensilla chaetica on both mid and hind leg. The pear-shaped seminal capsule with apical rugulosity separates the female from other species. The pupa differs from other members of the subgenus by lacking pedes spurii B, from other members of the genus except *O. chuzesextus* by having median point band on tergites III and IV fused with posterior band and lacking apical spurs or lateral threads on the anal lobe. From *O. chuzesextus* it differs only by its larger size (4.1–5.4 mm versus 3.0–3.6 mm). The larva can be separated from other members of the genus by the presence of labral lamellae combined with a bifid premandible.



FIGURES 8–12. *Orthocladius* (*Mesorthocladius*) *lamellatus* sp. n., male imago, 8: head, 9: thorax, 10: wing, 11: hypopygium, 12: gonostylus, different view.

Male imago (*n* = 2–3 except when otherwise stated)

Total length 4.49–4.57 mm. Wing length 2.24–2.41 mm. Total length/wing length 1.90–2.00. Wing length/length of profemur 2.60–2.76. Coloration dark brown with blackish brown vittae.

Head (Fig. 8). AR 1.95–2.28. Ultimate flagellomere 775–841 µm long. Temporal setae 12–15, including 3–6 inner verticals, 6 outer verticals, and 3 postorbitals. Clypeus with 10–12 setae. Cibarial pump, tentorium and stipes as in Fig. 8. Tentorium 195–199 µm long, 56 µm wide. Stipes 165–184 µm long, 68 µm wide. Palpomere lengths (in µm): 41–47, 53–64, 86–109, 75–90, 105–135.

Thorax (Fig. 9, *n* = 4). Antepronotum with 6–8, 7 setae. Dorsocentrals 10–14, 12; anterior dorsocentral 15–79, 45 µm long, second 26–98, 71 µm long, third 86–106, 97 µm long; acrostichals 13–18(3); prealars 7–9, 8. Scutellum with 13–21, 17 setae, uni-biserial.

Wing (Fig. 10). Anal lobe moderately produced. VR 1.03 (1). Costal extension 15–17 µm long. Brachiolum with 1 seta, R with 9–10 setae, other veins bare. Squama with 25–31 setae.

Legs. Spur of front tibia 71–79 µm long, spurs of middle tibia 30 and 23–26 µm long, of hind tibia 75 and 23–24 µm long. Width at apex of front and middle tibia each 56 µm, of hind tibia 68 µm. Pseudospurs present on ta_1 of mid and hind leg, 23–34 µm long; one specimen with additional pseudospur on ta_2 of mid leg. Sensilla chaetica 3 at 0.10–0.13 to 0.22–0.24 of ta_1 of mid leg, 6–8 at 0.10–0.16 to 0.25–0.33 on ta_1 of hind leg. Lengths (in µm) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3
p_1	813–926	888–1153	614–756	357–482	293–331
p_2	756–954	888–1049	425–482	274–302	217–222
p_3	857–1068	1134–1276	605–671	394–416	284–302

	ta_4	ta_5	LR	BV	SV	BR
p_1	148–203	132–142	0.66–0.69	2.27–2.45	2.75–2.77	1.6–2.
p_2	151	113–132	0.46–0.49	3.30	4.49–4.53	2.6–2.8
p_3	175–189	132–142	0.53	2.96–3.10	3.14–3.49	2.9–3.0

Hypopygium (Figs. 11, 12). Anal point 86–120, 109 µm long including triangular base; robust, tapering with rounded apex; with 10–14, 13 setae including on base; laterosternite IX with 10–11, 11 setae. Phallapodeme 53–86, 74 µm long; transverse sternapodeme 83–99, 95 µm long, oral projections moderately to well developed. Gonocoxite 308–364, 342 µm long; superior volsella collar-like; inferior volsella with ventral part not extended beyond dorsal part.. Gonostylus 135–167, 152 µm long; crista dorsalis apical, rounded; megaseta 10–19 µm (3) long. Virga 26–36, 32 µm long; consisting of cluster of 7 spines. HR 2.18–2.37, 2.26; HV 2.74–3.12 (2).

Female imago (*n* = 1 mature pupa)

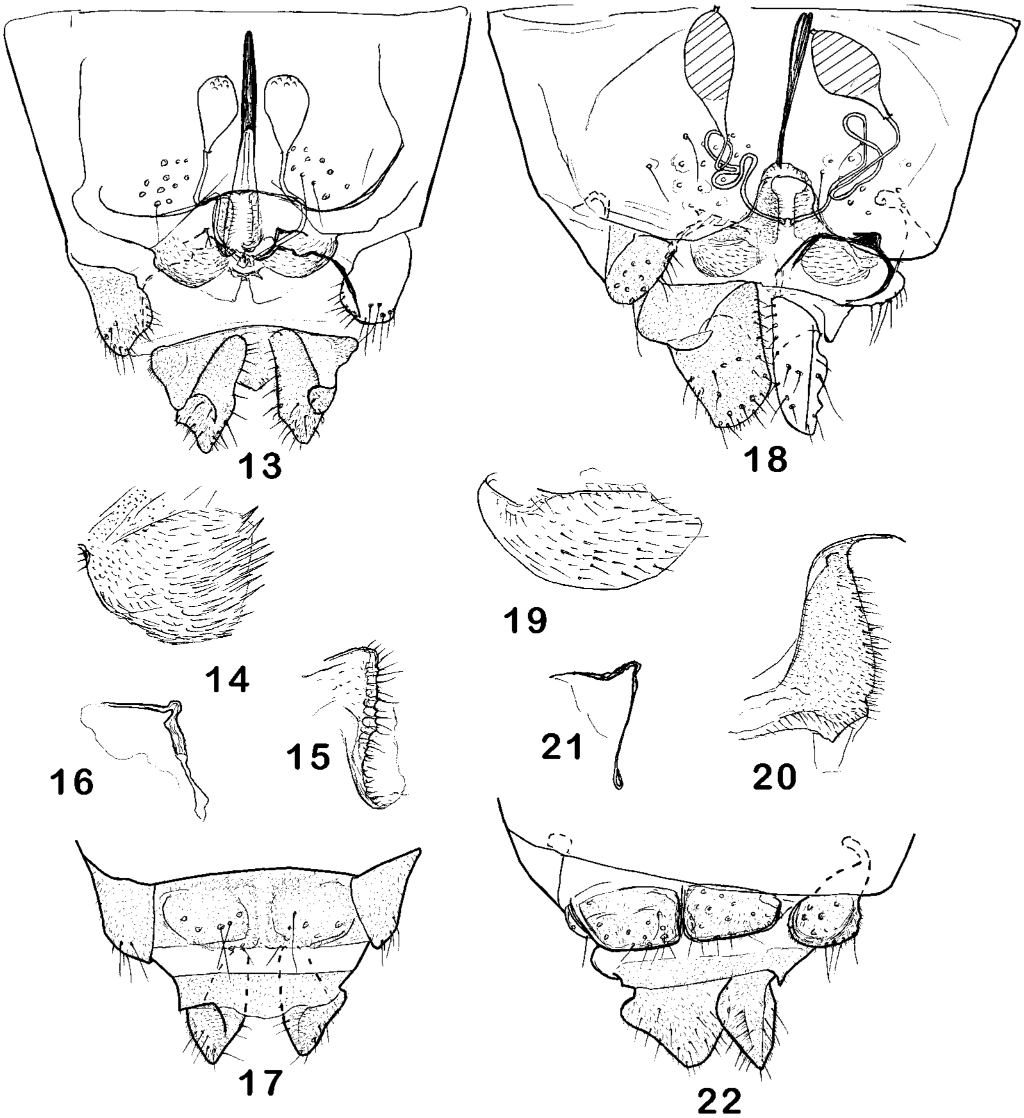
Total length about 4.10 mm. Coloration apparently not as dark as in male.

Head. AR 0.75. Flagellomere lengths (in µm): 56, 38, 38, 49, 154. Coronal suture 56 µm long. Temporal setae not measurable. Clypeus with 14 setae. Tentorium 150 µm long, 41 µm wide. Palpomere lengths (in µm): 38, 45, 70, 86, 90.

Thorax. Dorsocentrals 12, acrostichals 11, prealars 6. Scutellum with 13 setae.

Wing. Squama with 25 setae.

Legs not measurable.



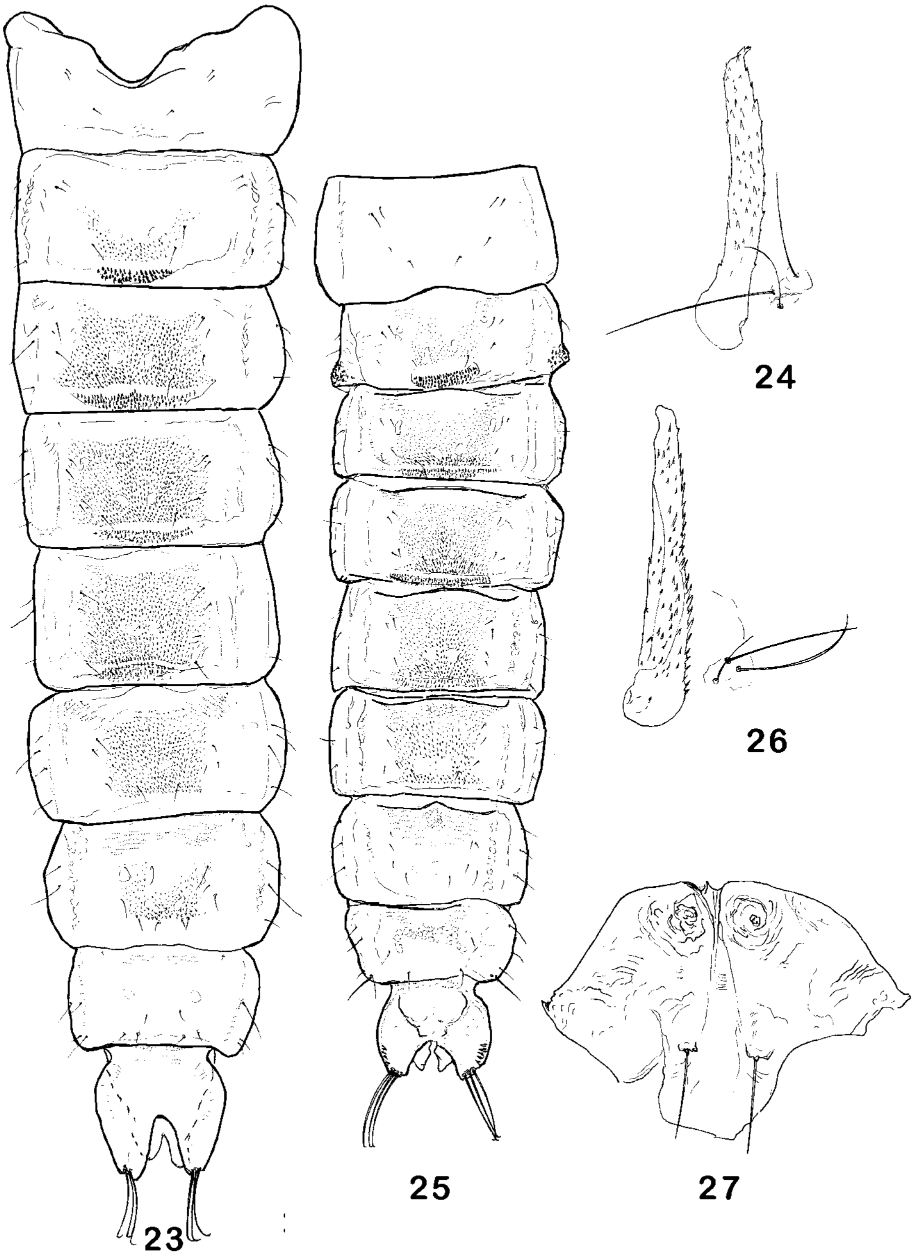
FIGURES 13–22. *Orthocladius* (*Mesorthocladius*) spp., female imagines, genitalia, 13–17: *O.* (*M.*) *lamellatus* sp. n., 13: ventral view, 14: ventrolateral lobe, 15: dorsomesal lobe, 16: apodeme lobe, 17: dorsal view, 18–22: *O.* (*M.*) *nimidens* sp. n., 18: ventral view, 19: ventrolateral lobe, 20: dorsomesal lobe, 21: apodeme lobe, 22 dorsal view.

Abdomen. Tergite VIII with 32 setae, sternite VIII with 23 setae.

Genitalia (Figs. 13–17). Tergite IX divided, with 24 setae. Gonocoxite with 19 setae. Cercus 131 µm long. Seminal capsule pear-shaped with apical rugulosity, 84 µm long, 53 µm wide. Spermathecal ducts with one bend and separate openings. Notum 98 µm long.

Pupa (*n* = 3–4 except when otherwise stated)

Total length 4.16–5.39 mm. Exuviae pale greyish brown with brownish apophyses.



FIGURES 23–27. *Orthocladius* (*Mesorthocladius*) spp., pupae, 23: *O.* (*M.*) *lamellatus* sp. n., tergites, 24: thoracic horn, 25–27: *O.* (*M.*) *nimidens* sp. n., 25: tergites, 26: thoracic horn, 27: frontal apotome.

Cephalothorax. Frontal setae143–150 µm long. Thoracic horn (Fig. 24) 270–428, 340 µm long; 41–53, 49 µm wide; 4.14–8.77, 7.00 times as long as wide; 1.16–1, 54, 1.35 times as long as anal macrosetae. Precorneal setae respectively 94–128, 105 µm; 150–171, 166 µm; and 68–101, 91 µm long. Anterior dorsocentral (Dc_1) 79–90, 83 µm long; Dc_2, 49–79, 66 µm; Dc_3 56–75, 71 µm; and Dc_4 64–83, 71 µm long. Distances (in µm): Dc_1–Dc_2 26–49, 40; Dc_2–Dc_3 98–131, 113; Dc_3–Dc_4 19–34, 24.

Abdomen (Fig. 23). Tergite I bare, tergite II with weak mediolateral shagreen, stronger posterior shagreen on tergites III–VII, shagreen relative extensive on tergites VIII–IX. Shagreen spinules about equal in size, anterior and posterior bands joined, anterior band not extending as far lateral as posterior bands. Sternites I and IX bare; II–III with anterolateral plus posterolateral shagreen, IV with lateral, V–VII with lateral plus anterolateral, VIII with anterolateral shagreen. Pedes spurii A on sternites IV–VII. Pedes spurii B absent. Caudal hooklets on tergite II 46–69, 57; in 3 rows. Segments II–V each with 3 L setae, VI and VII each with 3–4, and VIII with 4 L setae. Lengths of L_1–L_4 setae on segment VIII (in µm) as: 64–113; 75–124, 98; 38–116, 65; 68–101, 85. Occasionally a forked V seta present on sternite III.

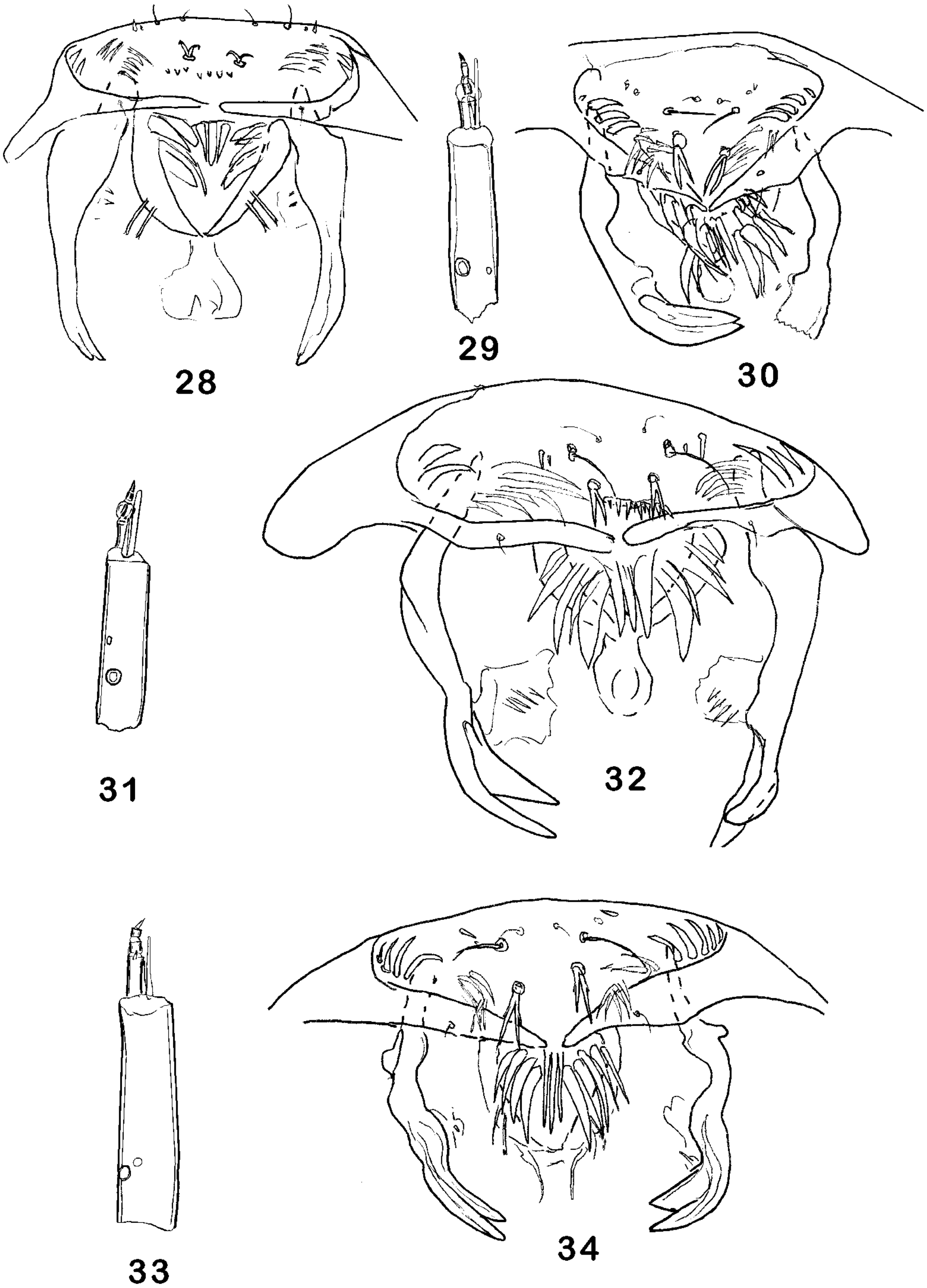
Anal lobe 364–443, 400 µm long. Anal macrosetae subequal in length; 225–278, 249 µm long; 0.59–0.64, 0.62 as long as anal lobe. Male genital sac overreaching anal lobe by 30 µm (2), female genital sac ending 105 µm short of apex of anal lobe.

Fourth instar larva (*n* = 9–11 except when otherwise stated)

Total length 4.68–8.60, 6.06 mm. Head capsule 0.44–0.50, 0.47 mm long. Postmentum 195–212, 203 µm long. Head capsule dark brown.

Head. Antenna as in Fig. 31. Length of antennal segments (in µm): 49–64, 55; 12–15, 13; 4–7, 5; 3–4, 4; 3–4, 4. AR 1.75–2.32, 1.96. Ring organ 10–19, 15 µm from base; basal setal mark 14–22, 19 µm from base; apical setal mark 20–37, 26 µm from base. Basal antennal segment 19–23, 20 µm wide; blade 20–26, 23 µm (7) long; accessory blade12–17, 15 µm (7) long. Lauterborn organs 5–9, 7 µm long; style 5–9, 7 µm long. Two labral lamellae (Fig. 32) each with 3–7, 5 spines. With 12 chaetae and 2–3 spinulae. One pair of chaetulae laterales slightly serrated, chaetulae basales tapering, bifid, with 1 long and 1 short apical tooth. Premandible (Fig. 32) bifid, 79–109, 89 µm long; brush consisting of 11–16, 14 (7) spines present. Mandible (Fig. 35) 146–165, 157 µm long, without seta interna. Mentum (Fig. 36) 120–144, 133 µm wide; median tooth 19–23, 20 µm wide; ventromental plate 4–12, 8 µm wide; with 5–7, 7 setae underneath on cardo.

Abdomen. Claws of anterior parapods strongly serrated. Longest body setae 131–278, 186 µm long. Posterior parapods 293–450, 352 µm (7) long. Procercus 38–53, 46 µm high; 34–45, 41 µm wide. Anal setae 506–675, 595 µm long; supraanal seta 64–105, 84 µm (7) long, 0.11–0.20, 0.15 (8) as long as anal setae. Longer anal tubules 150–278, 183 µm (6) long, 56–83, 72 µm (4) wide at base; shorter anal tubules 113–184, 153 µm (6) long, 41–60, 54 µm (7) wide at base.



FIGURES 28–34. *Orthocladius* spp., larvae, 28: *Orthocladius* (*Mesorthocladius*) *frigidus* (Zetterstedt) labrum, epipharyngeal area and premandible, 29, 30: *Orthocladius* (*Orthocladius*) *nitidoscutellatus* Lundström, 29: antenna, 30: labrum, epipharyngeal area and premandible, 31, 32: *Orthocladius* (*Mesorthocladius*) *lamellatus* sp. n., 31: antenna, 32: labrum, epipharyngeal area and premandible, 33–34: *Orthocladius* (*Mesorthocladius*) *nimidens* sp. n., 31: antenna, 32: labrum, epipharyngeal area and premandible.

Comments

The pupa of this species shows no synapomorphies with the other members of the subgenus and is practically inseparable from *O.* (*Orthocladius*) *chuzesextus*. However, the male imago has the characteristic anal point of the other species except *O.* (*M.*) *nimidens* and the larva shares several apparent synapomorphies such as presence of labral lamellae, absence of seta interna, and bifid premandible with one or more of the other species of the genus. The phylogenetic placement of this and the next species, however, cannot be regarded as completely ascertained.

Ecology and distribution

The species is known only from Ohio, inhabiting small streams and seeps.

***Orthocladius* (*Mesorthocladius*) *nimidens* sp. n.**
O. sp. “Jacobsen” (Epler 2001: 7.99, 7.109)
(Figs. 18–22, 25–27, 33, 34, 37, 38, 41–46)

Type material

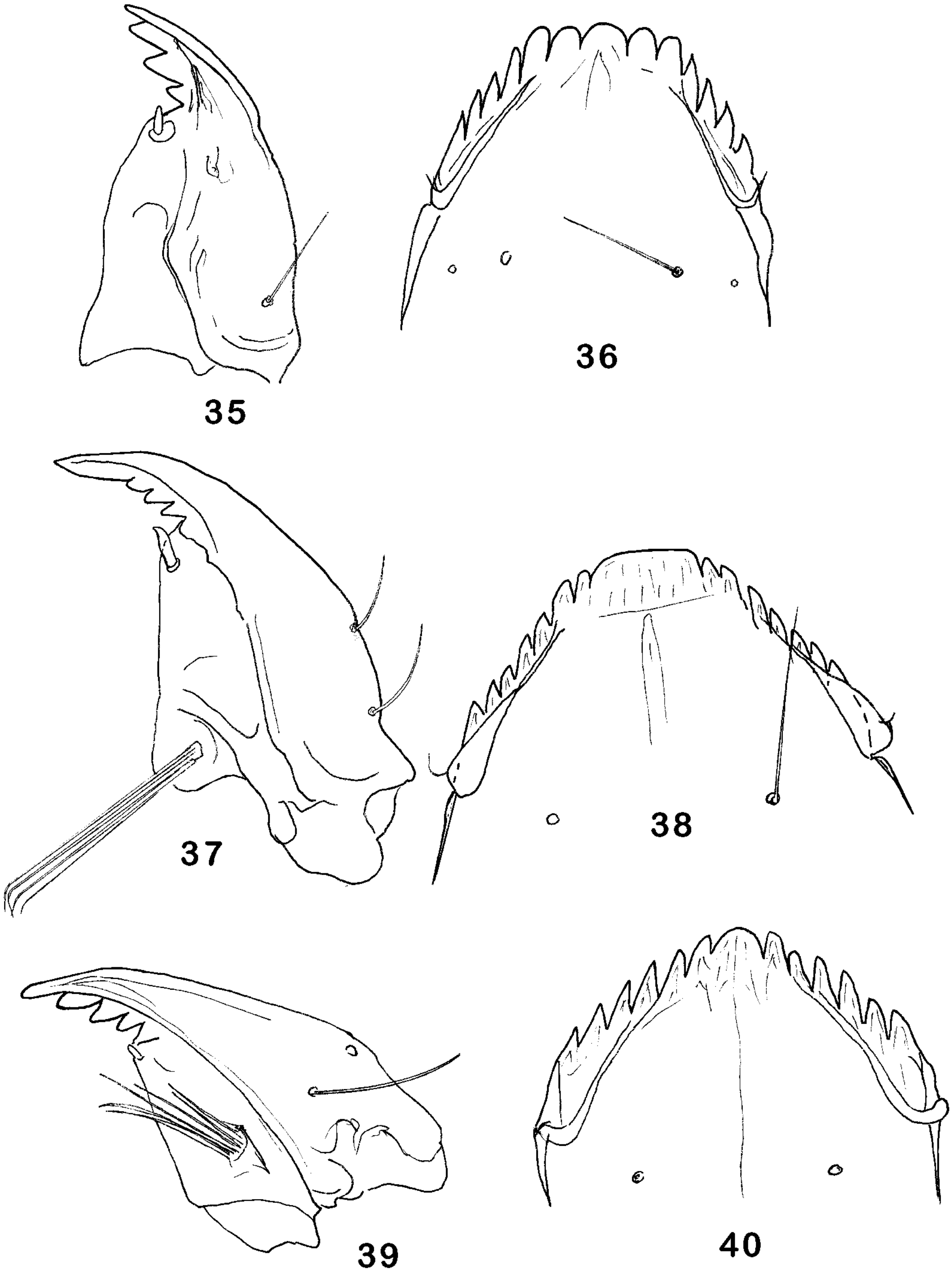
Holotype ♂ reared from larva, USA: Ohio, Franklin Co., Sharon Woods Park, woodland trickle, 28 iii emerged 2 iv 1987, M. J. Bolton (ZMBN Type No.407). Paratypes: 3 mature ♂ pupae reared from larva, 3 mature ♀ pupae reared from larva, 3 pupal exuviae, 3 larvae, as holotype except 22–26 iv 1987, M. J. Bolton (ZMBN)

Etymology

From Latin, *nimius*, excessive, and *dens*, tooth, referring to the 15–17 teeth of the larval mentum.

Diagnostic characters

The male imago differs from all other species of the genus by means of the triangular anal point. The apical wart of the seminal capsule, the evenly wide spermathecal ducts with several loops, and the lack of an anterior projection of the dorsomesal lobe of gonapophysis VIII all are unique within the genus. The combination of prominent frontal warts, granulose pedes spurii B on segment II, thoracic horn covered with spinules, and minute lateral threads but no apical spines on the anal lobe separates the pupa from other members of the genus. The mentum with 15–17 teeth combined with a bifid premandible, very broad median tooth of the mentum, and presence of seta interna of the mandible separate the larva from other members of the genus.



FIGURES 35–40. *Orthocladius* spp., larvae, 35, 36: *Orthocladius* (*Mesorthocladius*) *lamellatus* sp. n., 35: mandible, 36: mentum, 37–38: *Orthocladius* (*Mesorthocladius*) *nimidens* sp. n., 37: mandible, 38: mentum, 39–40: *Orthocladius* (*Orthocladius*) *nitidoscutellatus* Lundström, 39: mandible, 40: mentum

Male imago (*n* = 3–4 except when otherwise stated)

Total length 3.35–4.30, 3.95 mm. Wing length 1.72–1.96 mm (2). Total length/wing length 1.95–2.07 (2). Wing length/length of profemur 2.44–2.49 (2). Coloration brown with dark brown vittae.

Head (Fig. 41). AR 1.76–1.92, 1.84. Ultimate flagellomere 567–652, 614 µm long. Temporal setae 11–14, including 4–5 inner verticals, 4–5 outer verticals, and 3–4 postorbitals. Clypeus with 5–8, 6setae. Cibarial pump, tentorium and stipes as in Fig. 41. Tentorium 195–206 µm (2) long, 49 (2) µm wide. Stipes 146–158 µm (2) long, 56–60 µm (2) wide. Palpomere lengths (in µm): 34–47, 53–64, 75–101, 68–86, 113–135 (2).

Thorax (Fig. 42). Antepronotum with 6–8, 7 setae. Dorsocentrals 15–18, 16, uni-biserial; acrostichals 6–11, 8; prealars 7–8, 8; 1 supraalar. Scutellum with 14–17, 16 setae; uni-biserial.

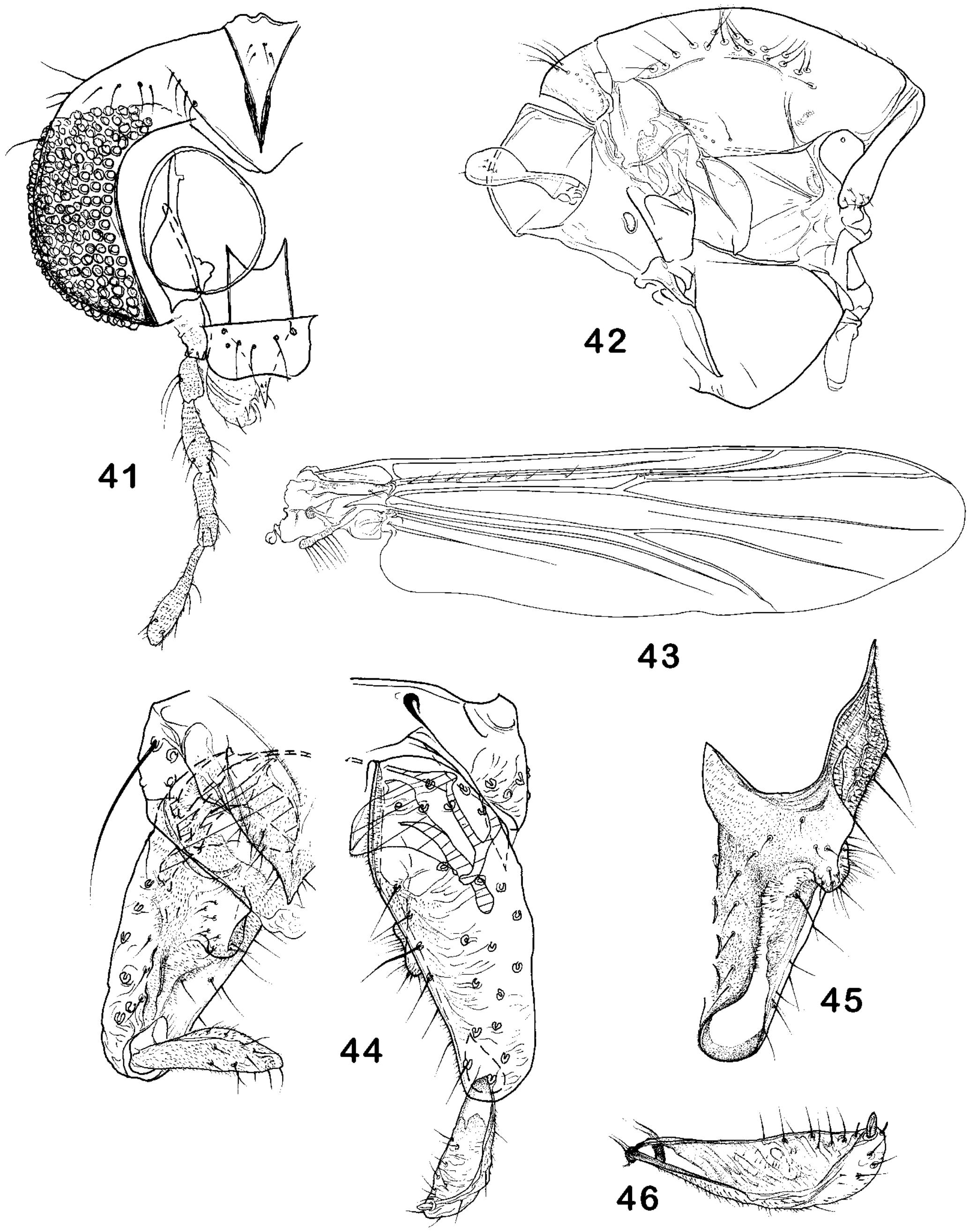
Wing (Fig. 43). Anal lobe moderately to strongly produced. VR 1.03–1.06 (2). Costal extension 38–49 µm (2) long. Brachiolum with 1 seta, R with 7–9, 8 setae; other veins bare. Squama with 17–24, 19 setae.

Legs (*n* = 2). Spur of front tibia 71–94 µm long, spurs of middle tibia 34–45 and 24–41 µm long, of hind tibia 68–83 and 26–38 µm long. Width at apex of front and middle tibia each 45–56 µm, of hind tibia 56–68 µm. Pseudospurs present on ta_1 of mid and hind leg, ta_2 of mid leg and occasionally ta_2 of hind leg, 26–32 µm long. Sensilla chaetica absent. Lengths (in µm) and proportions of legs:

	Fe	ti	ta_1	ta_2	ta_3
p_1	690–803	775–926	548–624	340–378	236–255
p_2	690–813	699–851	340–435	198–208	170–189
p_3	778–888	851–1021	454–517	265–322	198–246

	ta_4	ta_5	LR	BV	SV	BR
p_1	151–170	99–118	0.67–0.71	2.45–2.55	2.67–2. 77	2.4–2.5
p_2	113–132	95–109	0.49–0.51	2.95–3.34	3.83–4.08	2.9
p_3	123–161	99–118	0.53–0.56	2.95–2.96	3.37–3.45	3.1

Hypopygium (Figs. 44–46). Anal point 86–120, 109 µm long, triangular with pointed apex. Tergite IX including anal point with 16–20, 19 setae; laterosternite IX with 7–10, 9 setae. Phallapodeme 124–135, 130 µm long; transverse sternapodeme 94–131 µm long, oral projections moderately developed. Gonocoxite 266–311, 288 µm long; inferior volsella with ventral part reduced, not extended beyond dorsal part. Gonostylus 113–131, 122 µm long; crista dorsalis low or absent; megaseta 11–15 µm long. Virga absent. HR 2.34–2.37, 2.36; HV 2.97–3.50, 3.24.



FIGURES 41–46. *Orthocladius* (*Mesorthocladius*) *nimidens* sp. n., male imago, 41: head, 42: thorax, 43: wing, 44: hypopygium, 45: inner margin of gonocoxite, 46: gonostylus, different view.

Female imago (n = 3)

Total length 3.83–4.19 mm. Wing length 1.95–2.28 mm. Total length/wing length 1.80–2.05. Wing length/length of profemur 2.61–2.84. Coloration not as dark as in male with more distinct markings.

Head. AR 0.46–0.49. Flagellomere lengths (in µm): 90–101, 56, 49–56, 60–68, 124–135. Coronal suture 113–128 µm long. Temporal setae 14–16, including 4–6 inner verticals, 6–7 outer verticals, and 4–5 postorbitals. Clypeus with 8–12 setae. Tentorium 154–191 µm long, 38–49 µm wide. Palpomere lengths (in µµm): 41–45, 53–64, 90–124, 79–94, 129–143.

Thorax. Dorsocentrals 14–19, acrostichals 6–17, prealars 7–10. Scutellum with 18–21 partly biserial setae.

Wing. Anal lobe very slightly produced. VR 1.06–1.11. Costal extension 56–60 µm long. Brachiolum with 1–3 setae, R with 79–18, R_1 with 6–11. R_{4+5} with 11–18 setae. Squama with 17–24, 19 setae.

Legs. Spur of front tibia 41–45 µm long, spurs of middle tibia 30–38 and 28–34 µm long, of hind tibia 68–85 and 26–38 µm long. Width at apex of front tibia 45–56 µm, of middle tibia 53–62 µm, of hind tibia 60–71 µm. Pseudospurs present on ta_1 of mid and hind leg, ta_2 of mid leg and occasionally ta_2 of hind leg, 30–34 µm long. Sensilla chaetica absent. Lengths (in µm) and proportions of legs:

	Fe	ti	ta_1	ta_2	ta_3
p_1	747–803	841–983	510–614	331–350	227–246
p_2	756–851	803–973	378–435	217–236	165–180
p_3	813–936	954–1153	529–643	312–369	227–265

	ta_4	ta_5	LR	BV	SV	BR
p_1	142–161	104–113	0.61–0.63	2.58–2.76	2.91–3.13	1.6–1.9
p_2	104–123	95–109	0.45–0.48	3.12–3.49	4.02–4.20	1.4–1.8
p_3	132–151	104–113	0.54–0.56	2.89–3.04	3.10–3.39	1.4–2.6

Abdomen. Tergite VIII with 30–50 setae, sternite VIII with 35–39 setae.Genitalia (Figs. 18–22). Tergite IX strongly divided with margins well delimited, with 33–40 setae. Gonocoxite with 14–19 setae. Cercus 169–188 µm long. Seminal capsule pear-shaped with more or less well developed apical wart, 105–130 µm long including about 45 µm long tapering neck, 64–68 µm wide, sclerotised in anterior 75–94 µm. Spermathecal ducts with several loops and apparently separate openings. Notum 98 µm long. Dorsomesal lobe of gonapophysis VIII without anterior projection. Labia with very fine microtrichiae medially, apodeme of apodeme lobe strong.

Pupa (*n* = 9–10) Total length 4.29–5.78, 4.89 mm. Exuviae pale brown with darker thorax and apex of anal lobe and blackish brown apophyses.

Cephalothorax. Frontal warts (Fig. 27) relatively pronounced. Frontal setae 64–139, 103 µm long. Thoracic horn (Fig. 26) 266–428, 363 µm long; 49–68, 56 µm wide; 5.46–7.85, 6.54 times as long as wide; 0.95–1.23, 1.11 times as long as anal macrosetae. Precorneal setae respectively 68–113, 96 µm; 86–169, 133 µm; and 56–98, 84 µm long. Anterior dorsocentral (Dc_1) 71–120, 95 µm long; Dc_2, 53–105, 75 µm; Dc_3 71–94, 69 µm; and Dc_4 79–116, 94 µm long. Distances (in µm): Dc_1–Dc_2 30–60, 46; Dc_2–Dc_3 26–64, 49; Dc_3–Dc_4 34–71, 55.

Abdomen (Fig. 25). Tergite I bare, tergite II with weak median and anterolateral group shagreen and stronger posterior shagreen; strong, extensive shagreen on tergites III–VI, posterior spinules on tergite III stronger than anterior ones, of about the same size on IV–VI, spinule bands confluent with anterior shagreen reaching about as far lateral as posterior shagreen; tergite VII with weak median shagreen, VIII and IX with anterior group shagreen. Sternite I bare; II with weak lateral shagreen, II–V with stronger lateral, VI with lateral, anterolateral and posteromedian shagreen, VII with fewer anterolateral and posteromedian spinules, VIII with anterolateral V–VII with lateral plus anterolateral, VIII and IX with anterolateral shagreen. Pedes spurii A on sternites IV–VII. Pedes spurii B well developed, granulose, on tergite II only. Caudal hooklets on tergite II 61–160, 111; in 4–5 rows. Segments II–VI each with 3 L setae, VII with 4, and VIII with 4–5 L setae. Lengths of L_1–L_5 setae on segment VIII (in µm) as: 79–165, 123; 86–199, 138; 90–184, 132; 139–240, 186; 105–120 (present in 2 of 10 specimens).

Anal lobe 338–401, 374 µm long; each lobe with 9–14, 12 fine lateral spines; no posterior spines. Anal macrosetae subequal in length; 281–375, 326 µm long; 0.79–0.94, 0.87 as long as anal lobe. Male genital sac reaching about to apex of anal lobe.

Fourth instar larva (*n* = 8–9 except when otherwise stated)

Total length about 4.8–8.1, 6.2 mm. Head capsule 0.48–0.53, 0.51 mm long. Postmentum 225–263, 240 µm long. Head capsule light brown.

Head. Antenna as in Fig. 31. Length of antennal segments (in µm): 73–86, 79; 15–17, 16; 4–7, 6; 3–4, 4; 5–6, 6. AR 2.38–2.81, 2.62. Ring organ 13–19, 17 µm from base; basal setal mark 16–25, 20 µm from base; apical setal mark 20–35, 28 µm from base. Basal antennal segment 20–25, 22 µm wide; blade 20–26, 23 µm (6) long; accessory blade10–17, 14 µm (8) long. Lauterborn organs 5–7, 6 µm (7) long; style 5–9, 7 µm long. Labrum (Fig. 32) with one branch of S I split into 2–6 weak branches, S II double on one side in one specimen, 12 chaetae and 5 spinulae. Chaetulae laterales smooth. Premandible bifid (Fig. 32), 98–109, 105 µm (8) long; vestigial brush indicated. Pecten galearis apparently absent. Mandible (Fig. 37) 176–210, 189 µm long; seta interna of 7–8 branches. Mentum (Fig. 38) 161–180, 169 µm wide; with 15 or 17 teeth, median tooth 35–47, 40 µm wide; ventromental plate 10–16, 14 µm wide; about 4 very weak setae present underneath ventromental plates on cardo.

Abdomen. Claws of anterior parapods strongly serrated. Longest body setae 131–278, 186 µm long. Posterior parapods 225–323, 280 µm (5) long. Procercus 41–56, 48 µm high; 26–45, 39 µm wide. Anal setae 544–675, 618 µm long; supraanal seta 143–206, 167 µm (8) long, 0.24–0.31, 0.27 (8) as long as anal setae. Longer anal tubules 151–188, 162 µm (6) long, 75–113, 94 µm (6) wide at base; shorter anal tubules 105–143 µm (3) long, 56–68 µm (3) wide at base.

Comments

The female imago is unique within the genus, with the apical wart on the seminal capsule, spermathecal ducts with several loops but no widened portions, dorsomesal lobe without the anterior projection characteristic for the *Cricotopus-Orthocladius* group of genera, and no discernible rami. The genitalia are surprisingly similar to those of some *Diamesa* Waltl. Other apparent autapomorphies within the genus are the triangular anal point of the male imago and the rounded, instead of concave, posterior part of the larval ventromental plates. However, the pupa shares several synapomorphies with other members of the subgenus such as prominent frontal warts, granulose pedes spurii B, and lateral threads on the anal lobe.

Ecology and distribution

The species inhabits vernal woodland shallow pools and springs. This habitat is only present in the spring when the groundwater level is high enough to supply them, or possibly they are created where an impermeable clay lens is pooling snow-melt and spring rains. The species is known from Ohio, Indiana, and North Carolina.

Orthocladius* subgen. *Euorthocladius

Orthocladius subgen. *Euorthocladius* Thienemann, 1935: 201.
Lapporthocladius Thienemann in Thienemann & Krüger, 1937: 266.

Diagnostic characters

As in Soponis (1990: 6) except for the exclusion of *O. rousellae*.

***Orthocladius* (*Euorthocladius*) *annellae* sp. n.**

(Figs. 47–55, 66, 67)

Orthocladius (*Euorthocladius*) *rivicola* Soponis, 1990: 26, pro parte not Kieffer, 1911.

Type material

Holotype mature ♂ pupa, CANADA: Northwest Territories, FWI Pipeline Project, ?Oscar Creek, 25 v 1972, det. A. Soponis as *O. rivicola* (ZMBN Type No. 408). Paratypes: 5 ♂, 1 ♀, 1 ♂ reared from pupa, 2 mature ♂ pupae, 15 pupal exuviae; as holotype (ZMBN)

Etymology

Named in honour of Annelle R. Soponis who has revised both the subgenus *Euorthocladius*, and the nominal subgenus, and has additional publications on this important genus.

Diagnostic characters

The male imago is separable from those of the other species of the subgenus *Euorthocladius*, except *O.* (*E.*) *rivicola*, by having uniserial scutellar setae, robust crista dorsalis, sensilla chaetica on ta_1 of p_2, low antennal ratio (1.0–1.2), virga present, and inferior volsella with ventral part extended relatively prominently below dorsal part (see Remarks). The female imago differs from those of *O.* (*E.*) *rivicola* and *O.* (*E.*) *ashei* by having smaller seminal capsules and completely straight spermathecal ducts. The pupa differs from those of other members of the subgenus by lacking posterior spines or hooklets on tergites II and III, no pedes spurii A on sternite VI, precorneals and dorsocentrals not spine-like and less than 30 spines on tergite VI. The larva is unknown.

Male imago (*n* = 9 except when otherwise stated)

Total length 2.66–3.13, 2.95 mm (7). Wing length 1.75–2.24, 1.95 mm (5). Total length/wing length 1.39–1.69, 1.53 (5). Wing length/length of profemur 3.02–3.08, 3.05 (5). Coloration light brown with vittae, lower part of preepisternum and postnotum blackish brown.

Head (Fig. 47). AR 1.02–1.23, 1.09. Ultimate flagellomere 394–529, 442 µm long. Temporal setae 13–18, 15; including 3–8, 6 inner verticals; 3–9, 6 outer verticals; and 1–6, 3 postorbitals. Clypeus with 7–12, 10 setae. Tentorium 131–173, 167 µm (6) long; 38–41, 39 µm (6) wide. Stipes 105–169, 131 µm (6) long; 23–49, 36 µm (6) wide. Palpomere lengths (in µm, *n* = 5–6): 36–41, 39; 53–71, 61; 86–128, 101; 71–98, 87; 120–150, 135.

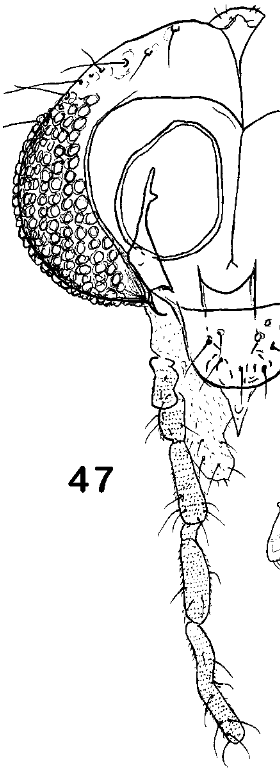
Thorax (Fig. 48). Antepronotum with 3–5, 3 (7) setae. Dorsocentrals 7–14,10; acrostichals 0–5, 2; prealars 4–6, 5. Scutellum with 10–13, 12 setae, uniserial.

Wing (Fig. 49). Anal lobe moderately produced. VR 1.03–1.12 (2). Costa not extended. Brachiolum with 1 seta; R with 4–8, 5 setae; other veins bare. Squama with 12–21, 16 setae.

Legs (*n* = 5–6). Spur of front tibia 45–64, 55 µm long; spurs of middle tibia 23–34, 29 and 23–30, 27 µm long; of hind tibia 49–71, 66 and 23–26, 25 µm long. Width at apex of front and middle tibia each 36–43, 39 µm: of hind tibia 41–49, 46 µm. Pseudospurs present on ta_1 and ta_2 of mid and hind leg, 26–38 µm long. Sensilla chaetica 5–10, 7 at 0.06–0.11, 0.08 to 0.19–0.26, 0.23 of ta_1 of mid leg; absent on of hind leg. Lengths (in µm) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3
p_1	576–728, 641	680–860, 760	454–586, 513	312–425, 354	227–265, 243
p_2	605–765, 680	624–813, 715	302–387, 336	198–247, 228	161–184, 172
p_3	699–851, 762	775–992, 870	397–520, 456	236–350, 278	194–265, 220

	ta_4	ta_5	LR	BV	SV	BR
p_1	137–161, 154	90–113, 101	0.66–0.68, 0.67	2.19–2.30, 2.24	2.67–2.79, 2.73	2.5–3.0, 2.8
p_2	95–113, 103	95–109, 98	0.45–0.49, 0.47	2.66–3.04, 2.88	4.03–4.28, 4.14	2.7–3.9, 3.0
p_3	109–146, 126	95–118, 107	0.50–0.53, 0.51	2.69–2.91, 2.86	3.50–3.81, 3.64	4.6–5.9, 5.1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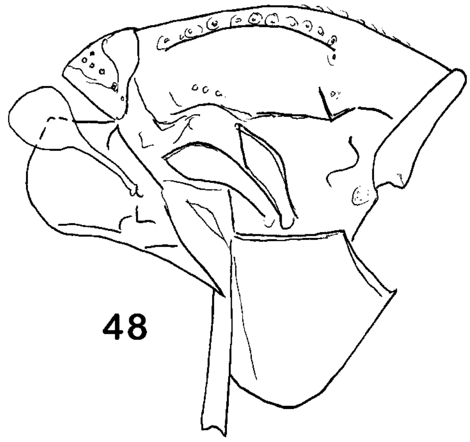
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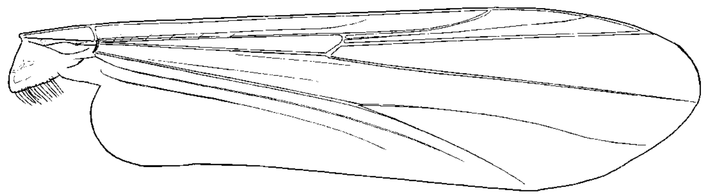
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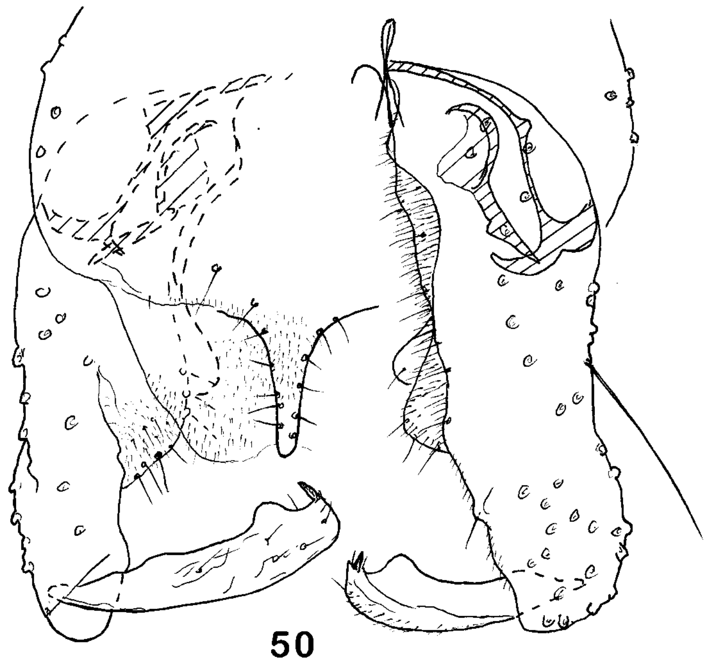
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FIGURES 51–65. *Orthocladius* (*Euorthocladius*) spp., female imagines, genitalia, 51–55: *O.* (*E.*) *annellae* sp. n., 51: ventral view, 52: dorsomesal lobe, 53: apodeme lobe, 54: ventrolateral lobe, 55: dorsal view, 56–60: *O.* (*E.*) *ashei* Soponis, 56: ventral view, 57: dorsomesal lobe, 58: apodeme lobe, 59: ventrolateral lobe, 60: dorsal view, 61–65: *O.* (*E.*) *rivicola* Kieffer, 61: ventral view, 62: dorsomesal lobe, 63: apodeme lobe, 64: ventrolateral lobe, 65: dorsal view.

Hypopygium (Fig. 50). Anal point including triangular base 41–54, 49 µm long; robust, tapering with rounded apex; with 10–17,12 setae including on base, some directed lateral and even anterior; laterosternite IX with 4–7, 6 setae. Phallapodeme 64–79, 68 µm long; transverse sternapodeme 83–105, 87 µm long, oral projections well developed. Gonocoxite 195–244, 205 µm long; superior volsella collar-like to rounded; inferior volsella with ventral part prominently extended beyond dorsal part. Gonostylus 94–109, 101 µm long; crista dorsalis apical, rounded; megaseta 8–11, 9 µm long. Virga 23–43, 32 µm long; consisting of cluster of about 5 spines. HR 1.93–2.24, 2.03; HV 2.63–3.15, 2.91 (7).

Female imago (*n* = 1)

Total length 4.10 mm. Wing length 2.08 mm. Total length/wing length 1.51. Wing length/length of profemur 3.33. Coloration not as dark as in male.

Head. AR 0.65. Flagellomere lengths (in µm): 79, 41, 38, 39, 128. Coronal suture 68 µm long. Temporal setae about 10, consisting of 5 inner and 5 outer verticals, postorbitals not observed. Clypeus with 8 setae. Tentorium 135 µm long, 24 µm wide. Stipes 139 µm long, 19 µm wide. Palpomere lengths (in µm): 38, 49, 90, 86, 135.

Thorax. Dorsocentrals 10, acrostichals 6, prealars 4, no supraalar. Scutellum with 12 setae.

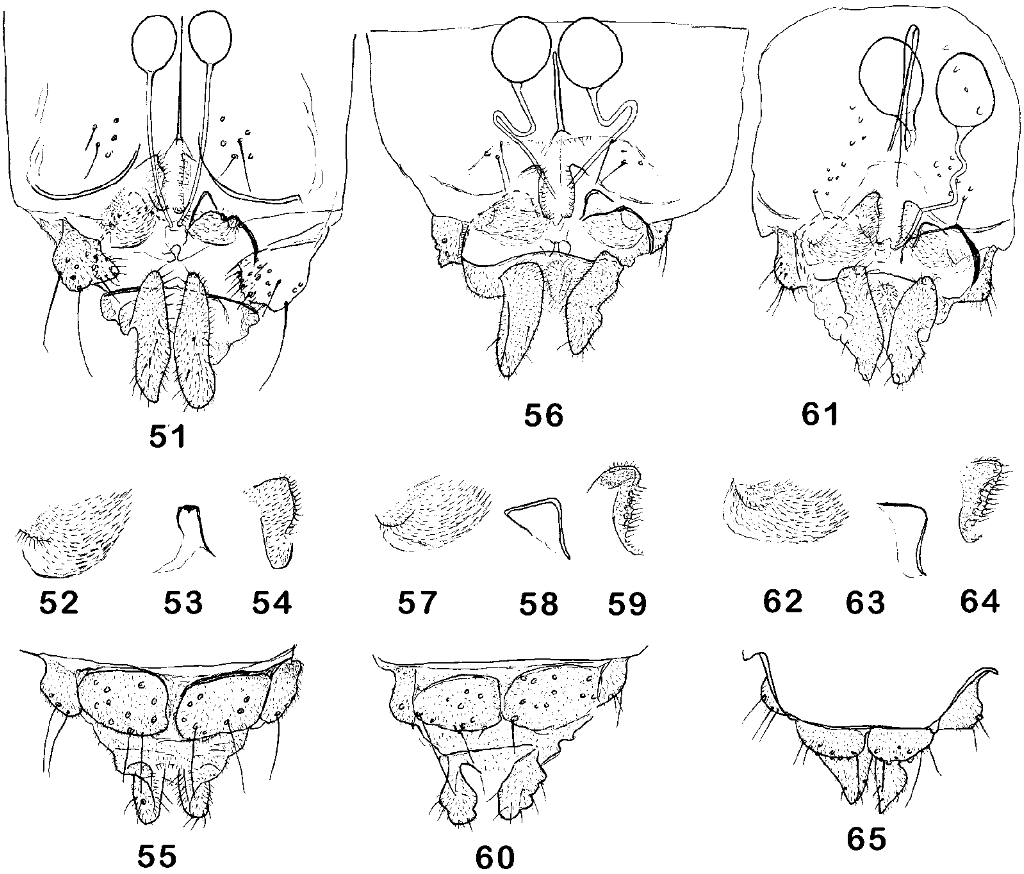
Wing. Brachiolum with 1 seta; R with more than 8 setae, R_1 with more than 2 and R_{4+5} with more than 3 setae. Squama with 14 setae. Other details not measurable.

Legs. Spur of front tibia 38 µm long, spurs of middle tibia 26 and 21 µm long, of hind tibia 53 and 19 µm long. Width at apex of front and middle tibia each 38 µm, of hind tibia 45 µm. Pseudospurs present on ta_1 of mid leg and hind leg and ta_2 of mid hind leg, 26–34 µm long. Sensilla chaetica 14 at 0.06–0.23 on ta_1 of mid leg, 7 at 0.13–0.16 on ta_1 of hind leg. Lengths (in µm) and proportions of legs:

	Fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	634	690	473	321	208	132	90	0.68	2.38	2.78	2.5
p_2	633	662	340	184	146	95	90	0.50	3.16	3.91	2.5
p_3	728	784	435	246	189	113	95	0.55	3.03	3.48	2.8

Abdomen. Number of setae on tergites I–VIII as: 55, 36, 26, 26, 26, 22, 19, 17; on sternites I–VIII: 0, 2, 8, 10, 18, 17, 22, 15.

Genitalia (Figs. 51–55). Tergite IX strongly divided with margins clearly delimited, with 24 setae. Gonocoxite with 24 setae of which 12 are shorter. Cercus 143 µm long. Seminal capsule ovoid with 15 µm long sclerotised neck, 56 µm long, anterior 38 µm darker sclerotised, 28 µm wide. Spermathecal ducts completely straight with separate openings. Notum 124 µm long.



FIGURES 51–65. *Orthocladius* (*Euorthocladius*) spp., female imagines, genitalia, 51–55: *O.* (*E.*) *annellae* sp. n., 51: ventral view, 52: dorsomesal lobe, 53: apodeme lobe, 54: ventrolateral lobe, 55: dorsal view, 56–60: *O.* (*E.*) *ashei* Soponis, 56: ventral view, 57: dorsomesal lobe, 58: apodeme lobe, 59: ventrolateral lobe, 60: dorsal view, 61–65: *O.* (*E.*) *rivicola* Kieffer, 61: ventral view, 62: dorsomesal lobe, 63: apodeme lobe, 64: ventrolateral lobe, 65: dorsal view.

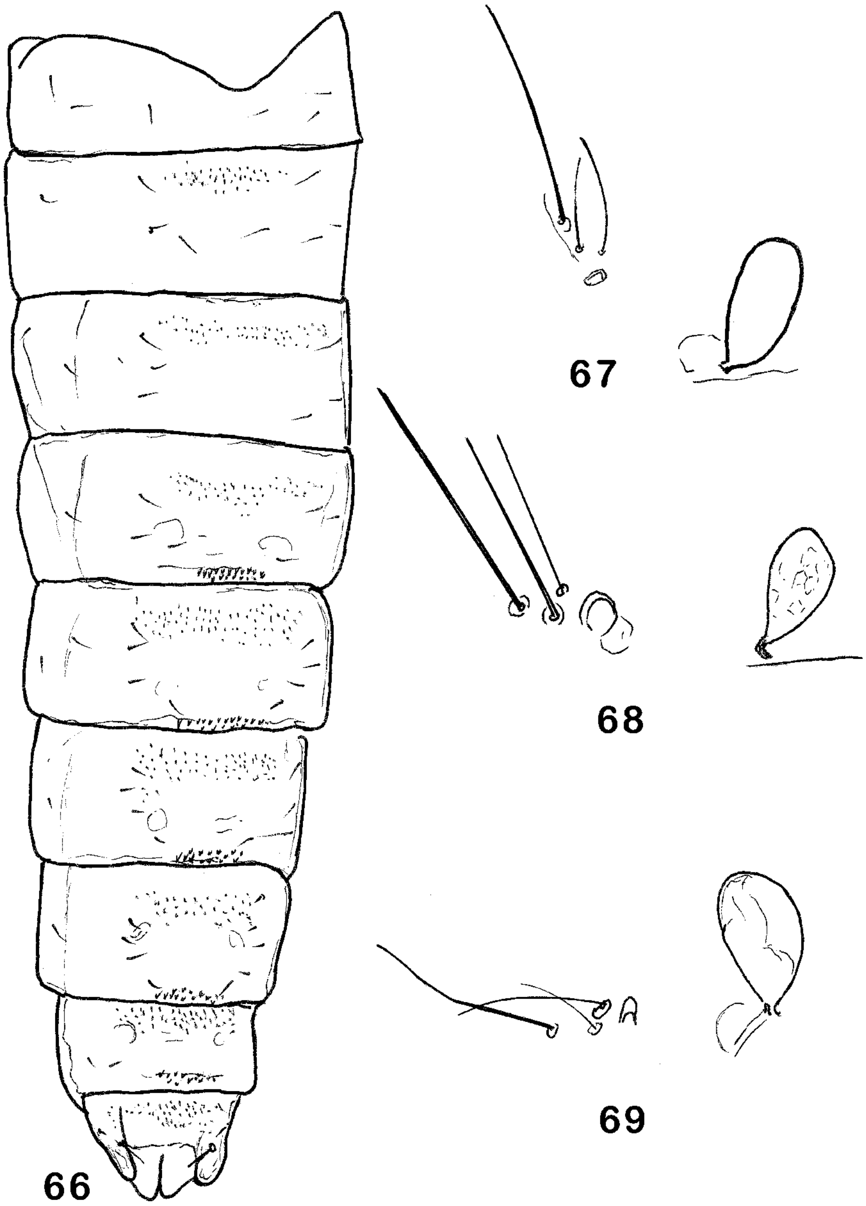
Pupa (n = 13–15 except when otherwise stated)

Total length 2.28–3.31, 2.94 mm. Exuviae pale greyish brown with area of tergite points blackish brown.

Cephalothorax. Frontal setae absent. Thoracic horn (Fig. 67) ellipsoid, clear, stalked, 34–60, 49 µm long; 19–26, 23 µm wide; 1.80–2.60, 2.04 times as long as wide; 1.00–1.62, 1.22 times as long as anal macrosetae. Precorneal setae respectively 68–94, 82 µm; 30–60, 39 µm; and 38–64, 52 µm long. Anterior dorsocentral (Dc_1) 56–86, 68 µm (12) long; Dc_2, 60–86, 71 µm; and Dc_3 56–86, 67 µm long. Distances (in µm): Dc_1–Dc_2 30–68, 42; Dc_2–Dc_3 21–64, 41.

Abdomen (Fig. 66). Tergite I bare, tergite II with 2 weak anterior patches of spinules, tergites III–IX with stronger anterior patches. Sternites bare. Pedes spurii A and B absent. Caudal hooklets on tergite II absent. Posterior points on tergites IV–VIII in 2–3 rows.

Number of points on tergites IV–VIII in male as (n = 7–8): 9–29, 15; 14–34, 22; 11–22, 18; 10–18, 12; 8–14, 12. Number of points in female as (n = 7–8): 16–30, 23; 24–35, 31; 20–27, 23; 17–21, 29; 19–21, 16. Segments II–VII each with 3 L setae, VIII with 2 L setae. L_1 and L_2 setae on segment VIII less than 25 µm long. No O setae.



FIGURES 66–69. *Orthocladius* (*Euorthocladius*) spp., pupae, 66, 67: *O.* (*E.*) *annellae* sp. n., 66: tergites, 67: thoracic horn, 68: *O.* (*E.*) *ashei* Soponis sp. n., thoracic horn, 69: *O.* (*E.*) *rivicola* Kieffer, thoracic horn.

Anal lobe 150–191, 160 µm long. Two strongly reduced anal macrosetae in distal half, 30–60, 38 µm long. Male genital sac overreaching anal lobe by 45–135, 101 µm (7); female genital sac overreaching anal lobe by 15 µm to ending 30 µm short of apex of anal lobe, mean 7 µm short.

Remarks

The description by Soponis (1990: 26) of *O.* (*E.*) *rivicola* includes *O.* (*E.*) *annellae*. At least some and probably all the specimens from the Northwest Territories and probably the specimens from Yukon and Alaska belong to the new species. The two species may perhaps be separated by *O.* (*E*) *annellae* having the ventral part of the inferior volsella more prominently extended below the dorsal part, as illustrated in Fig. 50 and Soponis (1990 Fig. 33c). However, several of the specimens of *O.* (*E.*) *rivicola* from Norway appear to have a nearly equally extended ventral part.

Orthocladius* (*Euorthocladius*) *ashei
(Figs. 56–60, 68)

Orthocladius (*Euorthocladius*) *ashei* Soponis, 1990: 17.

Material: *examined*: NORWAY: Hordaland, Vaksdal, Ekse, paratype ♂ reared from larva, 11 vi 1979, E. Willassen; same locality, mature ♂ pupa, mature ♀ pupa, 7 vi 1988, Ø. A. Schnell; same locality, 1 ♂, 1 ♀, 9 vii 1979 & 24 vi 1980, G. A. Halvorsen; Hordaland, Vaksdal, Fosse at Storeglupen, 6 pupal exuviae, 6 vi 1985, Ø. A. Schnell; Hordaland, Vaksdal, Storelva, 1 pupal exuviae, 9 vi 1986, Ø. A. Schnell; Hordaland, Årdal, Hæreidelva, 1 pupal exuviae, 2 vi 1986, Ø. A. Schnell (all ZMBN).

The male imago, pupa, and larva were described by Soponis (1990). The female, however, remained undescribed.

Female imago (*n* = 1–2)

Total length 2.91 mm. Wing length not measurable.

Head. AR 0.65–0.74. Flagellomere lengths (in µm): 60–68, 34–41, 34–41, 34–45, 105–116. Coronal suture 0–60 µm long. Temporal setae 8, consisting of 2–4 inner, 4–6 outer verticals, and no postorbitals. Clypeus with 10–12 setae. Tentorium 146 µm long, 26 µm wide. Stipes 98 µm long, 26 µm wide. Palpomere lengths (in µm):41, 45, 79, 56–79, 83–109.

Thorax. Antepronotum with 4–6 setae. Dorsocentrals 8–15, acrostichals not observed, prealars 34, no supraalar. Scutellum with 10–16 setae.

Wing. Brachiolum with 1 seta; R with 7–8 setae, R_1 with 4–5, R_{4+5} with 4–5 setae. Squama with 14–16 setae.

Legs. Sensilla chaetica 10 on ta_1 of mid leg, 4 on ta_1 of hind leg. Other details not measurable.

Abdomen. Number of setae on tergites I–VIII as: 25–51, 21–42, 18–32, 14–25, 13–25, 8–22, 14–22, 14–19; on sternites I–VIII: 0, 0–2, 2–5, 4–8, 5–10, 6–15, 6–14, 8–9.

Genitalia (Figs. 56–60). Tergite IX strongly divided with margins clearly delimited, with 18–22 setae. Gonocoxite with 7–9 setae including 3 short setae. Cercus 109–128 µm long. Seminal capsule ovoid with 13–15 µm long, tapered, sclerotised neck; 49–71 µm long; anterior 56 µm more darkly sclerotised; 34–66 µm wide. Spermathecal ducts with loops and separate openings. Notum 86–98 µm long.

***Orthocladius* (*Euorthocladius*) *rivicola* Kieffer**
(Figs. 61–65, 69)

Orthocladius rivicola Kieffer, 1911: 181.
Orthocladius fusiformis Goetghebuer, in Goetghebuer & Dorier 1939: 30.
Euorthocladius rivicola Kieffer; Thienemann 1936: 191.
Orthocladius (*Euorthocladius*) *rivicola* Kieffer; Brundin 1956: 101, Soponis 1990: 26, pro parte.

Material: *examined*: NORWAY: Hordaland, Vaksdal, Ekse, 4 ♂ reared from larva, 2 ♀ reared from larva, 3 ♂ reared from pupa, 10 mature ♂ pupa, mature ♀ pupa, 21 vi, 11 vii, & 9 vii 1970, E. Willassen; same locality, 3 ♂ 1976, 8–15 vii & 5–10 viii 1976, T. Andersen; same locality, 8 pupal exuviae, 9 vi 1987, Ø. A. Schnell; same locality, ♂ reared from larva, 5 pupal exuviae, 7 vi 1988, Ø. A. Schnell; Hordaland, Vaksdal, Storelva, 6 pupal exuviae, 9 vi 1986, Ø. A. Schnell; Buskerud, Hol, Ustaoset, Smettbakgrovi stream below waterfall, 1 pupal exuviae, 27 vii 1993, P. H. Langton & O. A. Sæther (all ZMBN). CANADA: Alberta, Waterton National Park, Rows Creek above highway, ♂ reared from pupa, 21 vii 1967, A. L. Hamilton & O. A. Sæther (ZMBN). USA: Arizona, Summerhaven on Mt. Lemmon near Tucson, Sabino Creek, ♂ reared from pupa, ii 1986, Doughman (ZMBN).

The male imago, pupa, and larva were described by Soponis (1990). The female, however, remained undescribed.

Female imago (*n* =1–2)

Total length 2.36 mm. Wing length 1.81 mm. Total length/wing length 1.31. Wing length/length of profemur 3.20.

Head. AR 0.62–0.65. Flagellomere lengths (in µm): 53–68, 34–38, 34–48, 34–41, 86–110. Coronal suture 30–38 µm long. Temporal setae11–13, consisting of 3–5 inner, 7 outer verticals, and 1 postorbital. Clypeus with 8–11 setae. Tentorium 135 µm long, 26 µm wide. Stipes 135 µm long, 26 µm wide. Palpomere lengths (in µm): 30–38, 41–60, 68–98, 60–79, 83–116.

Thorax. Antepronotum with 4–6 setae. Dorsocentrals 7, acrostichals about 2, prealars 3–5, no supraalar. Scutellum with 11–13 setae.

Wing. Brachiolum with 1 seta; R with 8–13 setae, R_1 with 4–8, R_{4+5} with 6–10 setae. Squama with 14 to about 24 setae.

Legs. Spur of front tibia 49 µm long, spurs of middle tibia 26 and 21 µm long, of hind tibia 56 and 23 µm long. Width at apex of front tibia 39 µm, of and middle tibia 41 µm, of hind tibia 45 µm. Pseudospurs present on ta_1 and ta_2 of mid leg and hind leg, 23–27 µm long. Sensilla chaetica 9 at 0.07–0.32 on ta_1 of mid leg, 2 at 0.07–0.15 on ta_1 of hind leg. Lengths (in µm) and proportions of legs:

	Fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	567	662	463	312	208	132	99	0.70	2.25	2.65	2.3
p_2	614	633	284	184	142	90	95	0.45	3.00	4.40	2.5
p_3	643	747	387	236	189	109	95	0.52	2.83	3.59	3.7

Abdomen. Tergites VIII with 12–20 setae, sternite VIII with 15–29 setae.

Genitalia (Figs. 61–65). Tergite IX strongly divided with margins clearly delimited, with 16 setae. Gonocoxite with 7–8 long and 3–5 short setae. Cercus 105–120 µm long. Seminal capsule ovoid with 15 µm long, tapered, sclerotised neck; 64–75 µm long; anterior 51–64 µm darker sclerotised; 54–60 µm wide. Spermathecal ducts meandering with separate openings. Notum 120–135 µm long.

Orthocladius subgen. *Orthocladius*

Orthocladius subgen. *Orthocladius* v. d. Wulp, 1874: 132.
Rheorthocladius Thienemann, 1935: 205.

Diagnostic characters

As in Soponis (1977: 18) except for the exclusion of *O.* (*Symposiocladius*) *annectens* Sæther and *O. tryoni* Soponis [= *O.* (*Symposiocladius*) *lignicola* Kieffer).

Orthocladius (*Orthocladius*) *nitidoscutellatus*

(Figs. 29, 30, 39, 40)

Orthocladius nitidoscutellatus Lundström, 1915: 11
Orthocladius trigonolabis Edwards, 1924: 170.
Orthocladius aquilonaris Goetghebuer, 1940: 63.
Trichocladius thienemanni Thienemann 1941: 217, not Goetghebuer 1940: 69.
Orthocladius (*Orthocladius*) *nitidoscutellatus* Lundström; Sæther 2004 c: 14.

Material examined

NORWAY: Svalbard, Danskøya, Lake Arresjøen, 2 ♂ reared from pupa, 1 mature ♂ pupae, 2 prepupa larvae, 14 viii 1993, Ø. A. Schnell (ZMBN); Svalbard, Vasa Peninsula, Lake Birgersjøen, ♂ reared from pupa, 15 viii 1993, Ø. A. Schnell (ZMBN); Svalbard, Ny Friesland, Lake N. Mosselvatn, pupal exuviae, 27 viii 1977, H. A. Støen (ZMBN); Oppland, Vågå, Lake Nedre Sjodalsvatn, 1 mature ♂ pupa reared from larva, 26 v 1990, Ø. A. Schnell (ZMBN).

Male imago

The description in Soponis (1977: 96) can be supplemented by the presence of about 6 sensilla chaetica at the base of ta_1 of the mid leg and sensilla chaetica apparently absent from the hind leg.

Pupa (*n* = 3)

The description in Soponis (1977: 99) and Langton & Visser (2002) and Rossaro et al (2003: 234) can be supplemented by:

Total length about 4.7–5.7 mm.

Cephalothorax. Frontal setae 94–120 mm long. Thoracic horn with sparse points over most of its length [bare according to Soponis (1977), with a few apical points according to Langton & Visser (2002), with points in apical half according to Rossaro et al. (2003)], 195–218 µm long; 32–41 µm wide; 4.73–6.82 times as long as wide; 10.88–1.02 times as long as anal macrosetae. Precorneal setae 114–188 µm long. Anterior dorsocentral (Dc_1) 83–90 µm long, Dc_2, 75–94 µm, Dc_3 68–79 µm, Dc_4 34–49 µm long. Distances (in µm): Dc_1–Dc_2 30–86, Dc_2–Dc_3 83–109, Dc_3–Dc_4 28–41.

Abdomen. With 31–62 caudal hooklets on tergite II in 4–5 rows in specimens from Lake Arresjøen, only two rows in the other specimen. Segments II–VI each with 3 L setae, VII with 4, VIII with 5 L setae. Lengths of L_1–L_5 on segment VIII in µm as: 64–94, 75–94, 79–86, 124–128, 131–154.

Anal lobe 329–371 µm long. Anal macrosetae 214–225 µm long. Male genital sac conspicuous, overreaching anal lobe by 56–68 µm, about 86 µm wide at apex.

Fourth instar larva (*n*= 2–3 except when otherwise stated)

Total length about 5.0–6.1 mm. Head capsule 0.43–0.45 mm long. Postmentum 195–199 µm long. Head capsule yellowish brown.

Head. Antenna as in Fig. 29. Length of antennal segments (in µm): 57–62, 14–17, 6–8, 4–6, 4–6. AR 1.36–2.08. Ring organ 7–9 µm from base, basal setal mark 14–19 µm from base, apical setal mark 50 µm (1) from base. Basal antennal segment 19–21 µm wide, blade 21–31 µm long, accessory blade 12–20 µm long. Lauterborn organs well developed, 7–8 µm long, style 7–9 µm long. Labrum (Fig. 30) with 12–14 chaetae and 6 spinulae. Chaetulae laterales apparently all smooth. Premandible (Fig. 30) simple with distinct apical notch, 92–95 µm long, brush absent. Mandible (Fig. 39) 169–173 µm long, seta interna of about 7 smooth branches. Mentum (Fig. 40) 150–161 µm wide, median tooth 11–12 µm wide, about twice as wide as first lateral tooth; ventromental plate 6 µm wide.

Abdomen. Claws of anterior parapods strongly serrated. Posterior parapods 284–331 µm long. Procercus 38–41 µm high, 30–38 µm wide. Anal setae 578–614 µm long, supraanal seta 131–143 µm long, 0.58 times as long as anal setae. Longer anal tubules 150–169 µm long, 71–86 µm wide at base.

Remarks. The larva from Lake Nedre Sjodalsvatn has a considerably longer antennal flagellum than the ones from Svalbard, resulting in a lower antennal ratio. In other details, however, it is nearly identical.

Orthocladius* (*Orthocladius*) *dentifer
(Figs. 70–74)

Orthocladius dentifer Brundin, 1947: 21.
Orthocladius (*Orthocladius*) *dentifer* Brundin; Brundin 1949: 888; Brundin 1956: 104; Soponis 1977: 45.

Material examined

NORWAY: Hordaland, Vaksdal, Ekse, 1 ♂ reared from larva, 2 ♀ reared from larva, 9 xi 1978, T. Andersen; same locality, 1 ♂ reared from larvae, 4 mature ♂ pupae, 5 vii 1979, E. Willassen (ZMBN). USA: Georgia, Rabun Co. West Fork Chattooga River, 1♂, 10 v 1980. P. L. Hudson (ZMBN).

Description

Male imago

As mentioned by Soponis (1977), the North American material mostly agrees with the European except for the smaller size and the distinct scutal stripes. In addition, at least the specimen from Georgia has only about 3 sensilla chaetica at 0.13–0.18 of ta_1 of mid leg and a 26 µm long virga, while the specimens from Ekse have 10–14 sensilla chaetica at 0.05–0.07 to 0.13–0.18 and the virga is only 0–15 µm long. In all other counts and measurements the differences are not significant.

Female imago (*n* = 3 except when otherwise stated)

Total length 3.64–3.97 mm. Wing length 2.36–2.69 mm. Total length/wing length 1.45–1.54. Wing length/length of profemur 3.21–3.36.

Head. AR 0.67–0.75. 0.71 (4). Flagellomere lengths (in µm, n= 4–6): 83–86, 84; 53–56, 55; 49–56, 47; 49–56, 50, 161–180, 168. Flagellomeres 3 and 4 fused in one specimen. Temporal setae 8–13, 10 (5); consisting of 3–5, 4 inner; 5–7, 6 outer verticals; and 0–3, 1 postorbital. Clypeus with 16–19, 17 (5) setae. Tentorium 150–169 µm long, 26–30 µm wide. Stipes 150–161 µm long, 41–53 µm wide. Palpomere lengths (in µm): 38; 53–64; 105–124; 83–116, 101 (5); 143–199, 165 (5).

Thorax (*n* = 6). Antepronotum with 8–13, 10 setae. Dorsocentrals 7–13, 10; acrostichals14–16 (3); prealars 3–6, 4; no supraalar. Scutellum with 8–12, 10 setae.

Wing. VR 1.05–1.11. Costal extension 56–75 µm long. Brachiolum with 1(6) seta; R with 11–20, 16 (6) setae; R_1 with 6–12, 10 (6), R_{4+5} with 12–20, 16 (6); costal extension with 1–2, 1 (6) non-marginal seta. Squama with 16–27, 21 (6) setae.

Legs. Spur of front tibia 49 µm long, spurs of middle tibia 30–38 and 26–30 µm long, of hind tibia 60–79 and 26 µm long. Width at apex of front tibia 45–49 µm, of middle tibia 45–51 µm, of hind tibia 49–56 µm. Pseudospurs present on ta_1 of mid leg and hind leg and

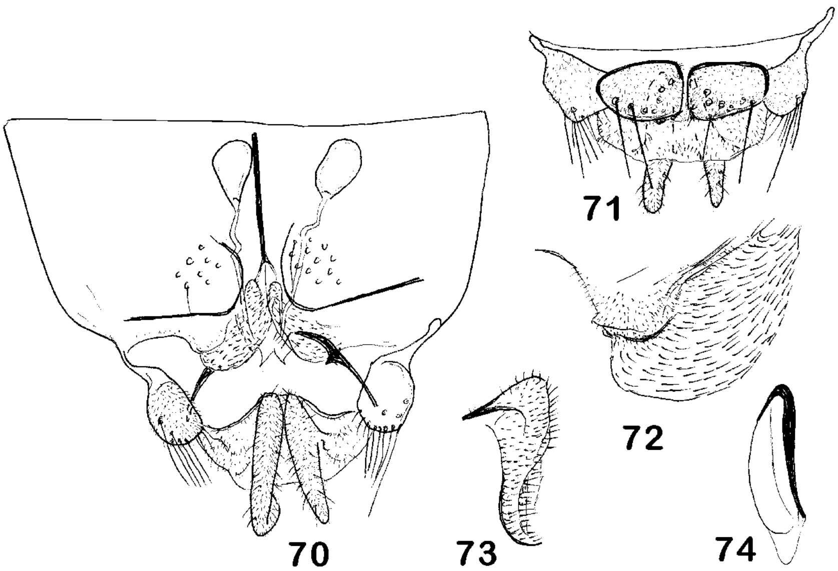
ta_2 of mid leg, 23–34 µm long. Sensilla chaetica 17–23 at 0.06–0.08 to 0.20–0.30 on ta_1 of mid leg, 7–17 at 0.06–0.07 to 0.17–0.26 on ta_1 of hind leg. Lengths (in µm) and proportions of legs:

	Fe	ti	ta_1	ta_2	ta_3
p_1	737–822	907–1040	586–666	387–435	265–293
p_2	765–879	860–936	378–425	222–246	170–189
p_3	803–898	901–1077	529–610	307–340	246–265

	ta_4	ta_5	LR	BV	SV	BR
p_1	175–198	109–113	0.64–0.65	2.38–2.43	2.79–2.84	2.0–2.4
p_2	113–123	99–109	0.46–0.47	3.19–3.38	4.15–4.24	1.9–2.6
p_3	142–161	109–118	0.54–0.57	2.89–2.93	3.24–3.39	2.7–2.9

Abdomen (*n* = 6). Number of setae on tergites I–VIII as: 61–73, 67; 36–45, 40; 26–38, 33; 25–34, 31; 28–34, 31; 23–33, 27; 17–29, 22: 17–25, 21; on sternites I–VIII: 0; 2–5, 4; 7–11, 9; 10–19, 13; 18–25, 20; 20–28, 23; 28–31, 23; 22–30, 27.

Genitalia (Figs. 70–74, *n* = 5–6). Tergite IX strongly divided with margins clearly delimited, with 20–31, 24 setae. Gonocoxite with 23–34, 28 setae. Cercus 120–180, 160 µm long. Seminal capsule pear-shaped; 60–78, 69 µm long; anterior 34–45, 41 µm darker sclerotised; 45–54, 50 µm wide. Spermathecal ducts slightly meandering with separate openings. Notum 116–150, 142 µm long.



FIGURES 70–74. *Orthocladius* (*Orthocladius*) *dentifer* Brundin, female imago, genitalia, 70*:* ventral view, 71: dorsal view, 72: ventrolateral lobe, 73: dorsomesal lobe, 74: apodeme lobe.

Remarks

It is not unlikely that the Nearctic specimens represent a different species as evidenced by the differences in sensilla chaetica on the legs and the length of the virga. However, more material from a wider range of localities is needed before any conclusion can be drawn.

Acknowledgements

I am grateful to Michael Bolton, Ohio EPA, Groveport, Ohio, for the material of *O. lamellatus* and *O. nimidens*. I would also like to thank Martin Spies and Marin Kotrba, Zoologische Staatssammlung, Munich, for all their hospitality and help during my visit to Munich in order to examine the collection of *Orthocladius*. Trond Andersen, Museum of Zoology, Bergen, carefully read the manuscript and suggested improvements. Gladys Ramirez made the slide preparations.

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