CENTROPTILUM EATON AND *PSEUDOCENTROPTILUM* BOGOESCU OF MANITOBA (EPHEMEROPTERA; BAETIDAE): CLASSIFICATION, SPECIES GROUPS, AND POST-GLACIAL DISPERSAL

by

© Robert G. Lowen

A thesis submitted to the
Faculty of Graduate Studies
The University of Manitoba
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of
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ABSTRACT

The life stages of seven Manitoba species of Centroptilum Eaton sensu lato species are described or redescribed and keys are provided to identify nymphs and male and female imagines. The species are C. album, C. bifurcatum, C. conturbatum, C. infrequens, C. quaesitum, C. rufostrigatum, and C. victoriae. Nymphal and imaginal character states were evaluated phylogenetically using the Hennigian system with Callibaetis as the out-group. Centroptilum quaesitum and C. infrequens are closely related and together with C. rufostrigatum form a monophyletic group that should be transferred to Pseudocentroptilum sensu Keffermller and Sowa. The remaining four species form a monophyletic group that is phylogenetically more similar to Centroptilum sensu stricto than it is to Pseudocentroptilum. It is recommended that the name Centroptilum be used for these four species.

Literature references and museum specimens were compiled and known geographical ranges are drawn. Centroptilum bifurcatum is a western species known from the interior of British Columbia eastward to Winnipeg, Manitoba. It ranges north to the Pembina River, Alberta and south to Yellowston National Park, Wyoming. Centroptilum victoriae is an eastern species known from Cape Breton Island, southern Ontario, and west-central Manitoba. Centroptilum album is a transcontinental species. Its northern record is in Churchill, Manitoba and its southern record is in North Carolina. It has not yet been found in the

western United States. Centroptilum conturbatum is a western species that ranges east from southern British Columbia to west-central Manitoba and south to Waddell Creek, California. Pseudocentroptilum rufostrigatum is an eastern species that ranges from New Brunswick to west-central Manitoba. Its northern record is in Rivire du Castor, Quebec and its southern record is in Meade County, Kentucky. Pseudocentroptilum infrequens is a northwestern species. Its northern and western record is in the Nahanni National Park, Northwest Territories. It ranges east and south to southeastern Manitoba. It has not yet been found in British Columbia or in the Yukon Territory. Pseudocentroptilum quaesitum is a western species that ranges from the Okanagan area of British Columbia to eastern Manitoba. Its northernmost record is in Churchill, Manitoba and its southern Canadian record is in Medicine Hat, Alberta. There is one disjunct record of this species from Cairo, Illinois. It has not otherwise been found in the United States. Distribution patterns are classified according to postglacial dispersal routes of Flannagan and Flannagan (1982). C. album has a South Transcontinental distribution. C. victoriae and P. rufostrigatum have an East Agassiz distribution. P. infrequens has a West Agassiz distribution while C. bifurcatum, C. conturbatum, and P. quaesitum all have a Saskatchewan-Montane distribution.

PART I. INTRODUCTION

The genus Centroptilum sensu lato, of the family Baetidae, is found on all continents except South America and Antarctica. There are 24 described North American species (Edmunds et al. 1976; Edmunds 1984). The genus was first described by Eaton (1869). He defined species belonging in it as having hind wings and single marginal intercalaries in the fore wings. This separated it from Cloeon Leach the members of which lack hind wings and from Baetis Leach which have double marginal intercalaries. These definitions sufficed until more detailed work brought about a redefinition of this family.

Recently, one of the most important developments in the taxonomy of this family occured when it was realized that the Baetidae included several subfamilies. Kazlauskas (1969) suggested the Baetidae be divided into the two subfamilies Baetinae and Cloeoninae. His description only weakly defined these groups and later authors attempted to clarify this division. Riek (1973) was the first to suggest that the family Siphlaenigmatidae should be reduced to a subfamily of Baetidae and that it should be considered the sister taxon to the remainder of the baetids together. McCafferty and Edmunds (1979) supported this idea and clarified the definitions through more detailed structural descriptions. Riek (1973) also suggested that Baetidae be split into three subfamilies. He characterized the subfamilies by using nymphal characters but as he was apparently

unaware of Kazlauskas (1969), he named the subfamilies Baetinae, Callibaetinae, and Siphlaenigmatinae. Landa and Soldn (1985) compared the internal structure of species from these subfamilies, confirmed that the Siphlaenigmatinae should be considered baetids and that the remaining Baetidae should be split into two subfamilies. This last division was based primarily on the position of the gonads and corresponded well to previous subdivisions. They gave priority of this division to Kazlauskas (1969) and accepted the names Siphlaenigmatinae, Baetinae, and Cloeoninae. Centroptilum was placed in the subfamily Cloeoninae together with the following genera: Baetopus Keffermller, Callibaetis Eaton, Centroptella Braasch and Soldan, Cloeodes Traver, Cloeon Leach, Notobaetis Morihara and Edmunds, Paracloeodes Day, Procloeon Bengtsson, and Symbiocloeon Mller-Liebenau.

The limits of most of these genera are poorly understood. Ideally genera should be defined along evolutionary lines (Hennig 1966; Wiley 1981). This has not been the general practice. New genera are usually erected on the basis of one or two apotypic characters with little consideration for resultant paraphylies created in the plesiotypic sister genera (Jacob and Glazaczow 1986).

It is difficult to discern what the evolutionary lineages are. The individual species are often known only from the original descriptions which are usually based solely on colour or size, characters which are variable and often unreliable. As well, descriptions are usually based on only one life stage. The obvious first step in any phylogenetic examination of Centroptilum and the entire subfamily would be to obtain better descriptions of the species involved.

This same lack of a sound taxonomic basis affects not only phylogenetic but also ecological research. The inadequacy of descriptions has resulted in a lack of keys to identify specimens. Therefore, researchers in North America have had to utilize the keys in Needham, Travers, and Hsu (1935) or in Burks (1953). The former reference has inadequate descriptions and is badly outdated while the latter reference covers only those species found in Illinois and surrounding states. These and other shortcomings have meant that up until 1984 Centroptilum infrequens McDunnough, C. rufostrigatum McDunnough, and C. quaesitum McDunnough were the only Centroptilum known to occur in Manitoba (Neave 1934; Flannagan and Flannagan 1982, 1984). Even for these three the individual life stages were poorly known. Prior to this work, the actual states of description of these species were:

SPECIES	NYMPH	SUBIMAGO	MALE IMAGO	FEMALE IMAGO
C. infrequens	unknown	unknown	unknown	poor
C. rufostrigatum	poor	unknown	good	poor
C. quaesitum	unknown	unknown	adequate	poor

It was clear that the known Manitoba species were in need of re-description. In addition, a large volume of unidentified material was known to represent several species not previously recorded in this province. It was not known whether these were new species or range extensions of previously described species.

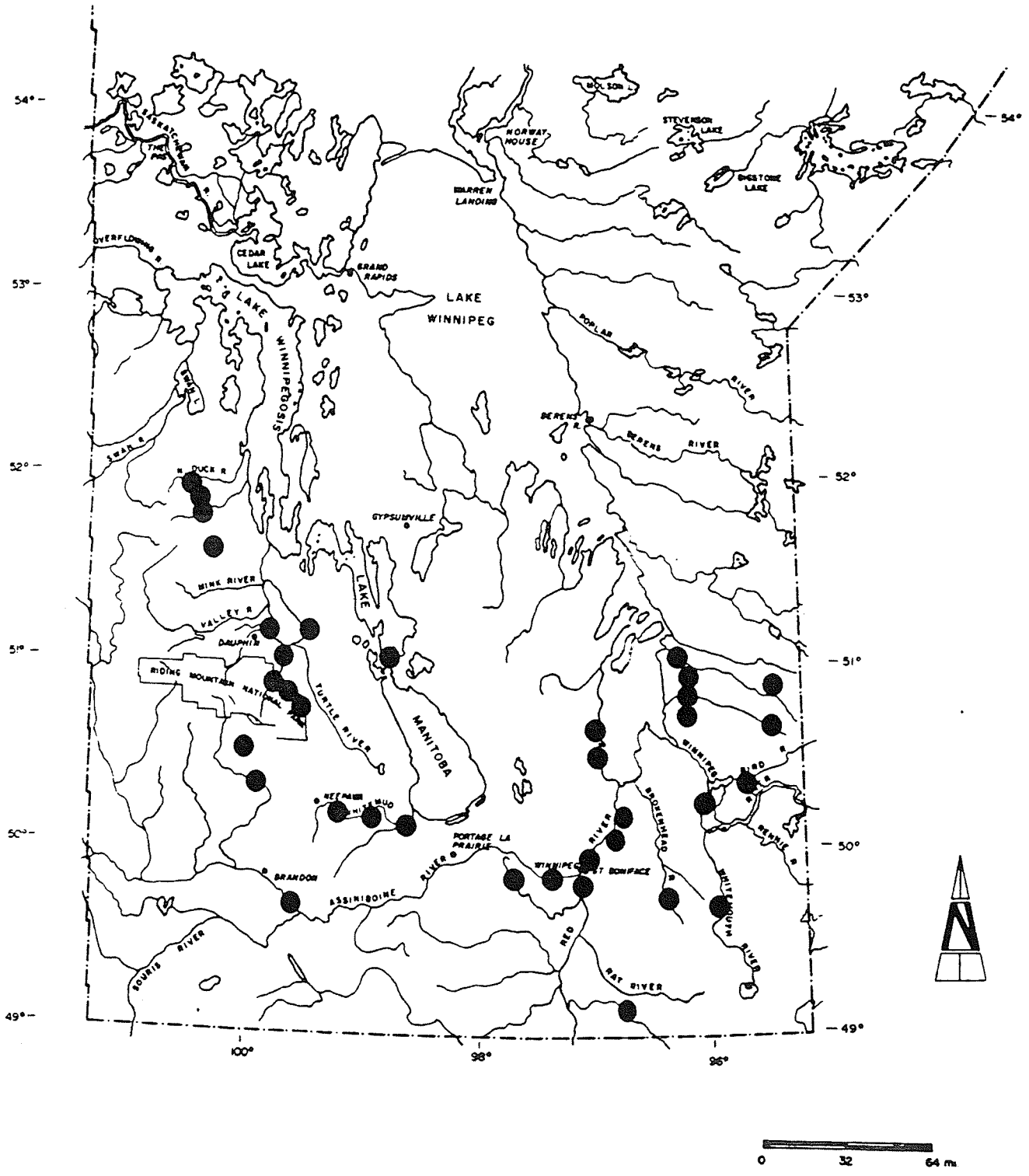
In an effort to clarify these unknowns, this study of Centroptilum in Manitoba was begun with five objectives: 1. identify and describe all life stages of Manitoba species, 2. provide a dichotomous key to identify all life stages, 3. compile museum and literature records to establish ranges, 4. determine evolutionary trends and phylogenetic relations within Manitoba species and with species known from other areas, and 5. attempt to reconstruct post-glacial dispersal patterns.

PART II. MATERIALS AND METHODS

a)Sample Sites and Rearing Methods

Nymphs were collected from streams, rivers, and lakes across southern Manitoba (Fig. 1). Nymphs were collected from the streams with a rectangular dip-net. "Kick-samples" yielded poor results. Sweeping the net rapidly through the water, over the substrate, and through submerged vegetation captured larger numbers of nymphs. Nymphs were sorted in the field. Immature nymphs and a representative sample of mature nymphs were preserved in 95% ethanol and later transferred to 70% ethanol. Most mature nymphs were transported back to the laboratory in the water in which they were captured. Mortality was lower if the nymphs were kept cool, but drastic changes in temperature increased mortality. Nymphs were reared to maturity in the lab in order to identify the various life stages of these insects. The nymphs were reared singly in one litre jars, half filled with stream or lake water. A stone or a few pebbles were placed into the jars as substrate. Vegetable based fish food was provided initially and the water was kept aerated with an air line. Each jar was covered with nylon mesh upon which the emerged subimago could land. Subimagines were less likely to drown if a small styrofoam cube was placed in the jar with them. Subimagines were placed in dry jars for their final moult. Imagines were allowed to mature for 24 hours so that colour would be fully developed when they were preserved.

Figure 1. Sites on Manitoba water bodies sampled for nymphs, 1985-88. All sites sampled at least twice.


54°
53°
52°
51°
50°
49°
100°
98°
96°
LAKE WINNIPEG
NORWAY HOUSE
STEVENSON LAKE
BIGSTONE LAKE
WARREN LANDING
CEDAR LAKE
GRAND RAPIDS
OVERFLOWING R.
WINNIPEGOSIS
SWAN R.
N. DUCK R.
GYPSUMVILLE
MINK RIVER
VALLEY R.
DAUPHIN
RIDING MOUNTAIN NATIONAL PARK
TURTLE RIVER
LAKE MANITOBA
BEERES R.
BERENS RIVER
POPLAR RIVER
BRANDON
ASSINIBOINE RIVER
PORTAGE LA PRAIRIE
WINNIPEG
ST. BONIFACE
RED RIVER
BOYNE R.
ROSEAU R.
WHITEMOUTH RIVER
SOURIS RIVER
RAT RIVER
0
32
64 mi

b)Museum Specimens

The following museums and individuals loaned specimens for this study. Voucher specimens will be deposited in these collections.

CNIC — Dr. R. Foottit, Canadian National Insect Collection, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, K1A OC6, CANADA.

FSCA — Dr. L. Berner, Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, 32622, U.S.A..

FWISL — Mr. J.F. Flannagan, Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, Manitoba, R3T 2N6, CANADA.

JBWM — Dr. R. Roughley, Department of Entomology, University of Manitoba, J.B. Wallis Museum of Entomology, Winnipeg, Manitoba, R3T 2N2, CANADA.

ROMC — Dr. G. Wiggins, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, CANADA.

UMIC — Drs. F. Harper and P. Harper, Université de Montréal, Département de Sciences biologiques, C.P. 6128, Succursale "A", Montréal, Québec, H3C 3J7, CANADA.

UWWO Dr. J. Ciborowski, University of Windsor, Department of Biology, Windsor, Ontario, N9B 3P4, CANADA.

ZSMG Dr. E.-G. Burmeister, Zoologische Staatssammlung, Münchhausenstr. 21, D-8000 Mnchen 60, FEDERAL REPUBLIC OF GERMANY.

Additional voucher specimens will be deposited in the following collections:

BMNH British Museum (Natural History), London, ENGLAND.

SBBC Dr. V. Landa, South Bohemian Biological Centre, Institute of Entomology, Branisovska 31, 37005 Ceske Budejovice, CZECHOSLOVAKIA.

UAMP Drs. R. Sowa and M. Kefferm̈ller, Uniwersytet im. Adama Mickiewicza, Instytut Biologii, Zaklad Zoologii Systematycznej, 61-701 Pozna, ul.Fredry 10, POLAND.

c)Preparation of Specimens

Some insects were pinned while others were preserved in either 70% alcohol or in Kahle's solution (Borror et al. 1981). Only imagines and mature nymphs were measured. Mature nymphs are here defined as those nymphs with darkened wing pads. Mayflies were measured using a bi-

nocular microscope with a callibrated eye piece graticule. Specimens being measured were laid as flat as possible. Specimens were occasionally held in place by crossed pins.

After measurements, nymphs and imagines were prepared for dissection and mounting by dehydrating through a series of increasing concentrations of ethyl alcohol to 100% ethanol. Specimens were then cleared and dissected in cedarwood oil and mounted on glass slides in Canada balsam. Prior to clearing, male genitalia and wings of either sex were removed. Male genitalia was heated but not boiled for 15 minutes in 10% potassium hydroxide solution and then placed for 10 minutes in glacial acetic acid before being cleared in cedarwood oil and mounted in Canada balsam. Wings were floated on to a glass slide then allowed to partially dry. A cover slip was taped securely over top and the slide allowed to dry completely. These techniques were modified from Burks (1953) and Mller-Liebenau (1969).

d)Taxonomic Format

Genera are described in alphabetical order. A description starts with the genus name and is followed by literature references. The literature references start with the original description of the genus followed by subsequent authors who wrote on that name. This is followed by a similar treatment of other generic names now considered invalid or synonymous to the valid name. The type species is named and the genus is then described. Both generic descriptions are divided into imaginal and nymphal descriptions. Both imaginal and nymphal descriptions are divided into diagnostic and constituent character

states. Diagnostic character states are apomorphic character states that in combination define the genus. Constituent character states are plesiomorphic character states that do not define the genus but are helpful in identifying specimens of that genus. The generic descriptions are followed by the descriptions of the species included in that genus.

The species descriptions follow a format similar to the genus descriptions. The species name is followed by the original description and subsequent descriptions of that species under that name. This is followed by descriptions of that species under other names. The literature review is followed by a list of types. All types are housed in the Canadian National Insect Collection, at the Biosystematics Research Centre, Ottawa, Ontario, Canada, and have all been examined by me.

The species descriptions are presented in following order: male imago, female imago, sub-imago, then nymph. Descriptions start with the total body length and general comments applicable to the entire body. This is followed by detailed description of head, thorax, and abdomen in turn.

Unless otherwise stated, n= number of specimens from which measurements were taken. All mearsurements are presented as means measured in millimeters followed in brackets by the observed range, unless otherwise stated. Total body length was measured from vertex of head to base of cerci. Leg segment lengths were measured along dorsal edge. Wing lengths were taken as the anterior edge of wing base to distal tip of wing.

Drawings were made using a Wild drawing tube and are taken from a particular specimen showing the typical form. Immature nymphs were taken into consideration for deciding on typical form and for qualitative descriptions. Drawings of nymphal labrum and labium are bisected with the left half showing the dorsal aspect and the right half showing the ventral aspect.

Descriptions are followed by a list of specimens examined. These are presented in alphabetical order by country then province or state. This does not include the type series which has already been listed.

Specimens examined are followed by field notes and a description of the known distribution. Field notes are qualitative descriptions of Manitoba collection sites along with some discussion of sites in the literature. Distribution is based on all specimens examined and records from the literature.

PART III. KEYS FOR IDENTIFICATION OF MANITOBA SPECIES

USE OF KEYS AND DEFINITION OF TERMS

Male is distinguishable from female in that male has approximately half of compound eye elongated into a turbinate eye whereas female has completely non-turbinate compound eye, male genitalia has the obvious paired forceps and penal plate (Fig. 4) while female genitalia has no external appendages.

For wing venation, I use the names proposed by Tillyard as discussed by Edmunds et al. (1976) (see Fig. 2). The abbreviations for veins discussed in this study are as follows:

C = costa

Sc = subcosta

R1, R2, R4+5 = radius 1, radius 2, radius 4+5

MA1, MA2 = medius anterior 1, medius anterior 2

MP1, MP2 = medius posterior 1, medius posterior 2

IMP = intercalary medius posterior

CuA = cubitus anterior

CuP = cubitus posterior

ICu1, ICu2 = intercalary cubitus 1,etc.

A1 = anal 1

MALE IMAGINES

1.- Penal plate with distal margin slightly to strongly concave, or round to conical, not truncate, with or without a large pointed process on the plate; segment III of forceps subequal to length of segment I (Figs. 4, 18, 27, and 37); abdominal terga VII to X brown or white, some specimens with pale red lateral patches.... .....Centroptilum (p. 22) 2

- Penal plate with distal margin round to truncate, without a process on the plate; segment III of forceps at most half length of segment I (Figs. 46, 59, and 68); abdominal terga VII to X predominantly reddish, or if brown then with paired red sub-lateral dashes on the posterior edge of terga I to III..... .....Pseudocentroptilum (p. 97) 5

2(1)- Penal plate with distal margin slightly to strongly concave, with a large pointed process on the plate (Fig. 4); hind wing with or without third longitudinal vein and with cross veins present (although they may be hard to see), costal process relatively stout or highly curved (Figs. 3 and 17).....3

- Penal plate with distal margin round to conical shape with at most a small slender process (Figs. 27 and 37); hind wing without third vein or cross veins, costal process thin and erect (Fig. 36).....4

3(2)- Hind wing wide with a third longitudinal vein or second vein branching distally, cross veins present, costal process stout and barely separated from wing margin (Fig. 3); fore wing IMP short,

about the same length as MP2 (Fig. 2); sternum IX with small rectangular brown patch mid-ventrally along the anterior margin.. .....C. bifurcatum p. 23

- Hind wing narrow to wide, some specimens with a small unattached vein at distal margin, some specimens with cross veins, costal process long and distinct but strongly curved (Fig. 17); IMP longer than MP2 (Fig. 16); without brown markings on sterna..... .....C. victoriae p. 44

4(2)- Process on penal plate very small, delicate, difficult to see (Fig. 27); marginal intercalaries reach less than half way to cross veins (Fig. 25); head light brown; abdominal terga VII to X opaque white.....C. album p. 61

- Penal plate without process (Fig. 37); marginal intercalaries reach at least half way to cross veins (Fig. 35); head dark brown to black; terga VII to X dark brown.....C. conturbatum p. 78

5(1)- Total body length less than 6.0 mm; mesothoracic wing length less than 6.0 mm; abdominal terga VII to X chestnut brown; red sub-lateral dashes on the posterior edge of abdominal terga I to at least III.....P. rufostrigatum p. 99

- Total body length greater than 6.5 mm; mesothoracic wing length greater than 7.0 mm; abdominal terga VII to X light brown with bright red shading; solid red-brown line on posterior edge of abdominal terga I to VIII.....6

6(5)- Hind wing thin and strap-like (Fig. 58); penal plate with distal margin truncate (Fig. 59); disc of turbinate eye bright orange when alive, dull orange in preserved specimens; abdominal terga I to VI semi-hyaline white.....P. infrequens p. 119

- Hind wing broad (Fig. 67); penal plate with distal margin semi-circular (Fig. 68); disc of turbinate eye bright yellow when alive, pale in preserved specimens; abdominal terga I to VI yellow-olive, not hyaline.....P. quaesitum p. 136

FEMALE IMAGINES

Note: Female imagines can not be consistently separated at the generic level.

1. - Hind wing costal process low and weakly separated from the wing (Fig.3); hind wing 0.9-1.4 mm long; ratio of fore wing length to hind wing length 5.0.....C. bifurcatum p. 23

- Hind wing costal process clearly separated from wing but can curve sharply towards wing (Fig. 17); hind wing less than 0.9 mm long, if longer then ratio of fore wing length to hind wing length more than 5.5.....2

2(1)- Hind wing with or without cross veins and spurious veins (Fig. 17); antenna yellow-tan basally, becoming hyaline distally; abdominal terga semi-hyaline with brown colour on posterior 2/3;

eggs, if present, clearly visible through terga.....
.....C. victoriae p. 44

- Hind wing without cross veins or spurious veins; if antenna is yellowish basally then is hyaline brown distally; abdominal terga can be semi-hyaline but never with brown colour on posterior 2/3 only; eggs if present only obscurely visible through terga.....3

3(2)- Total body length less than 6.5 mm; head light brown to brown or olive; antenna hyaline brown at least distally; ratio of length of fore wing to hind wing less than 6.5; hind wing with distal end a blunt point (Fig.26); costal process very thin and erect, straight in some specimens (Fig. 36 and 45).....4

- Total body length greater than 7.0 mm; head, at darkest, yellow-brown; antenna red-brown or smoky black; ratio of length of fore wing to hind wing greater than 7.5; hind wing with distal end rounded or if pointed, then costal process strongly curved (Figs. 45, 58, and 67).....6

4(3)- Fore wing with marginal intercalaries reaching at least half way to cross veins (Fig. 35); head brown; thorax light brown to brown, never white or light tan; abdominal terga dark brown dosally and white laterally, sharp delineation between these colours.....C. conturbatum p. 78

- Fore wing with marginal intercalaries reaching only a third of the way to the cross veins (Fig. 25); head light brown or olive; thorax light brown with white markings; abdominal terga variable, not as above.....5

5(4)- Head and pronotum light brown; abdominal terga dark brown laterally giving the appearance of a light mid-dorsal stripe.....
.....C. album p. 61

- Head olive-tan; pronotum opaque white; abdominal terga semi-hyaline with red-brown infusion.....P. rufostrigatum p. 99

6(3)- Antenna basally smoky or black becoming hyaline distally; hind wing ribbon-like and curved (Fig. 58); abdominal terga light brown and most specimens with scarlet mid-dorsal wedges forming a stripe.....P. infrequens p. 119

- Antenna basally opaque yellow and distally red-brown; hind wing wider and less curved than above (Fig. 67); abdominal terga white with red-brown posterior edge, if red is present it is in the shape of rounded "W's" and not wedges.....P. quaesitum p. 136

MATURE NYMPHS

1. - Abdominal terga I to VI or more with mid-dorsal pores (Figs. 5 and 19); mid-dorsal posterior edge of tergum IX lacking spines and in most specimens extending posteriorly as a rounded lobe; maxilla palpomeres II and III equal in length (Fig. 9); lateral spines of abdominal terga small or absent.....
.....Centroptilum (p. 22) 2

- Abdominal terga lacking pores, or pores on terga I or on I and VI only (Figs. 47, 60, and 69); mid-dorsal posterior edge of tergum IX with spines and not extended posteriorly; maxilla palpomere II

almost twice as long as III (Fig. 51); lateral spines of abdominal terga large.....Pseudocentroptilum (p. 97) 5

2(1)- Median terminal filament and cercus with dark band across middle segments; mid-dorsal posterior edge of tergum IX lacking spines but not expanded posteriorly; lateral spines absent or extremely small; maxilla with only one seta basal to biting teeth (Fig. 32).....C. album p. 61

- Median terminal filament and cercus without dark band across middle segments terminal segments can be darker; mid-dorsal posterior edge of tergum IX lacking spines and expanded posteriorly as a rounded lobe; small indistinct lateral spines on at least segments V III and IX; maxilla with two setae basal to biting teeth (Fig. 9).....3

3(2)- Wing pads without brown markings resembling veins; pattern on abdominal terga a series of unconnected paired rings, one on each side of mid-dorsal line (Fig. 5); maxilla with proximal row of five setae in an orderly line (Fig. 9); isolated group of two or three setae on inner edge of molar area of both mandibles (Fig. 7 and 8).....C. bifurcatum p. 23

- Wing pads with brown markings resembling veins; pattern on abdominal terga not as above; maxilla with proximal row of three to five setae in a disorderly array (Fig. 23); isolated group of two or three setae on inner edge of molar area of right mandible only (Fig. 22).....4

4(3)- Abdominal tergum VI black, contrasting sharply with near white terga on either side (Fig. 19); canines of left mandible fused along basal third or less (Fig. 21); second segment of labial palp with four setae in straight row (Fig. 24).....
.....C. victoriae p. 44

- Abdominal terga heavily patterned, tergum VI can be darkest but never bordered by near white terga (Fig. 38); canines of left mandible fused along basal half or more (Fig. 40); second segment of labial palp with five setae in a staggered row (Fig. 43).....
.....C. conturbatum p. 78

5(1)- Gills unilamellate with incompletely marked veins (Fig. 53); abdominal tergum VI with paired mid-dorsal pores (Fig. 47); canines of right mandible unfused (Fig. 50); maxilla with two setae basad to the palp (Fig. 51); posterior edge of sterna VII to IX with dark black line.....P. rufostrigatum p. 99

- Gills bilamellate on segments I to VI with veins unmarked or completely marked (Fig. 54); abdominal terga without paired mid-dorsal pores (Figs. 60 and 69); canines of right mandible fused for basal 3/4 (Fig. 63); maxilla without setae basad to the palp (Fig. 64); sterna can be marked but never with solid black line on posterior edges.....6

6(5)- Lateral spines restricted to abdominal segments VIII and IX; markings on prothorax resemble spirals (Fig. 60); wing pads lack markings resembling veins; secondary gill lamella largest on segment I (Fig. 54); nymph found in lotic habitats only.....
.....P. infrequens p. 119

- Lateral spines at least on segments IV to IX; markings on prothorax discontinuous, not resembling spirals (Fig. 69); wing pads with markings resembling veins; secondary gill lamella largest on segment IV or V (Fig. 55); nymph probably restricted to lentic habitats.....P. quaesitum p. 136

PART IV. SPECIES DESCRIPTIONS

Centroptilum Eaton

Centroptilum Eaton, A.E. 1869. Ent. Monthly Mag. 6: 131-132.
Keffermller, M., and R. Sowa. 1984. Pol. Pismo Ent. 54:
309-340 (*sensu stricto*)

Type Species: *Centroptilum luteolum* (Mller) by original designation

IMAGO

Diagnostic character states of imago include: hind wing of some species with pointed distal end, penal plate with distal margin conical and in some species upturned to resemble a concave margin, and pointed process between basal segments of forceps, secondarily lost in one species.

Constituent character states of imago include: fore wing with single marginal intercalaries, hind wing present, costal process present, hind wing with two or three longitudinal veins, terminal segment of male forceps long, and male forceps with inner margins of basal segments irregular.

NYMPH

Diagnostic character states of nymph include: distal group of maxillary setae reduced in number, prostheca of left mandible narrowed, prostheca of right mandible hightly narrowed, abdominal gills not highly asymmetrical, and gills with anterior margins serrate. Manitoba species further distinguished by canines of left mandible partially fused, pore-like spots on abdominal terga numerous, and tergum IX with mid-dorsal posterior projection.

Constituent characters of nymph include: maxilla palpomere III subequal to palpomere II, canines of right mandible divided to base, labial palpomere III with distal margin concave and inwardly expanded, hind wing pads present, tarsal claw with very fine double row of setae, gills on abdominal segments I to IX unilamellate, gills symmetrical and pointed in some species, lateral spines absent or small in size.

Centroptilum bifurcatum McDunnough

Centroptilum bifurcatum McDunnough 1924, Can. Ent. 56: p.96

McDunnough 1929, Can. Ent. 61: p. 171 (Male imago redescribed)

Holotype- Waterton Lakes, Alberta, Canada, 49°06'N 113°54'W (coll. J. McDunnough) (no. 677 CNIC): 23/VII/1923, male imago.

MALE IMAGO (n=6)

Total body length 5.8 (range 5.6-6.1).

a)Head

Turbinate eye orange and slightly divergent. Disc of turbinate eye broadly oval, width to length ratios range from 0.67 to 0.75. Stalk of eye distinctly paler with a brown ring around base. Stalk 0.25 mm tall. Non-turbinate eye and ocelli black. Antenna brown basally and hyaline distally, on some individuals antenna brown over entire length. Remainder of head light brown with dark brown on protruding ridges and vestigial mouthparts.

b)Thorax

Pronotum dark brown and unmarked. Mesonotum light tan anteriorly, laterally, and mid-dorsally. Paired dark brown sub-median stripes extend length of mesonotum, fusing posteriorly into a dark brown area. Metanotum light tan anterior to metascutellar hump and dark brown posterior to this hump. Prosternum and mesosternum pale tan ventrally, darkening near coxa. Metasternum dark brown.

Prothoracic leg semi-hyaline basally, becoming hyaline distally. Meso- and metathoracic legs hyaline throughout. Individual leg measurements variable (Table 1). Prothoracic leg 4.0 to 4.5 mm long. Protarsus five-segmented. Meso- and metathoracic legs and their component segments similar in length to each other (range 2.08 to 2.40). Femur longer than the tibia, but in individual specimens this may be reversed. Meso- and metatarsus four-segmented.

Table 1. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of *Centroptilum bifurcatum*. Prothoracic legs are divided by sex (n= 6 males and 6 females).

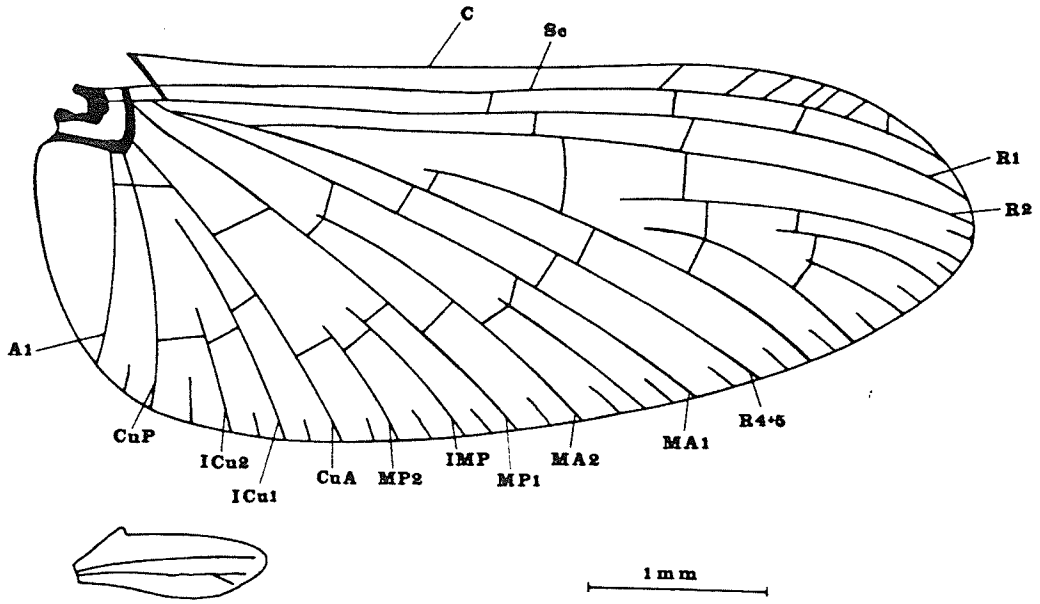
		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	1.17	1.42	0.14	0.62	0.52	0.30	0.19
PROTHORACIC	r	1.14-1.22	1.28-1.53	0.11-0.16	0.50-0.72	0.45-0.56	0.28-0.31	0.18-0.20
	:	2.0-2.6	2.6-2.8	0.2-0.4	1.1-1.3	1	0.5-0.6	0.3-0.4
FEMALE	x	0.89	0.83	0.25	0.13	0.08	0.19	-
PROTHORACIC	r	0.83-0.96	0.75-0.89	0.22-0.28	0.12-0.14	0.07-0.09	0.17-0.20	-
	:	10.4-11.9	9.4-11.1	2.8-3.5	1.6-1.8	1	2.1-2.5	-
	x	0.98	0.83	0.25	0.10	0.06	0.16	-
MESOTHORACIC	r	0.86-1.11	0.72-0.97	0.20-0.28	0.09-0.13	0.05-0.08	0.12-0.20	-
	:	13.2-20.6	9.0-18.2	2.9-5.6	1.1-2.5	1	2.0-3.8	-
	x	0.92	0.78	0.24	0.11	0.06	0.16	-
METATHORACIC	r	0.70-1.08	0.70-0.91	0.20-0.28	0.08-0.17	0.05-0.08	0.12-0.19	-
	:	10.5-21.6	8.6-18.2	2.5-6.6	1.1-2.2	1	1.6-3.8	-

Fore wing length 5.3 (range 5.1-5.8, n=5) and width 2.1 (range 1.9-2.3, n=5). Fore wing hyaline, brown basally and pterostigma clouded with white. Fore wing venation shown in Fig. 2. Number of cross veins variable. Wing with five to nine (median =6) cross veins between C and Sc. One to four cross veins between Sc and R1 and no intercalary present. Two or three cross veins between R1 and R2 and intercalary absent in some individuals. MA2 extends slightly past MA1/MP1 cross vein. IMP longer than MP2 and in some individuals extends as a fold to CuA/MP1 cross vein. ICu veins long with ICu1 almost reaching CuA/CuP cross vein. Small intercalary present basad to A1 in some individuals. Hind wing venation as in Fig. 3. Hind wing length 1.18 mm (range 1.16-1.25) and width 0.34 (range 0.31-0.41). Costal process stout but definitely hooked. Two veins in hind wing separate basally and in some individuals extend to wing margin. Shorter third vein either attached to second vein or free. Faint cross veins observable in some specimens under high magnification using phase contrast microscopy.

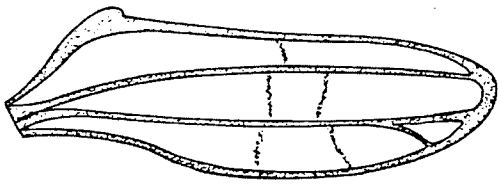
c)Abdomen

Sterna and terga I to VI hyaline white with yellowish tinge. Terga VII to X opaque chestnut brown, without markings but tergum X and posterior half of tergum IX considerably paler than terga VII, VIII, and anterior half of IX. Sterna VII to IX translucent yellow-tan. Sternum IX with small rectangular, mid-ventral brown patch at the anterior margin. Cercus hyaline white.

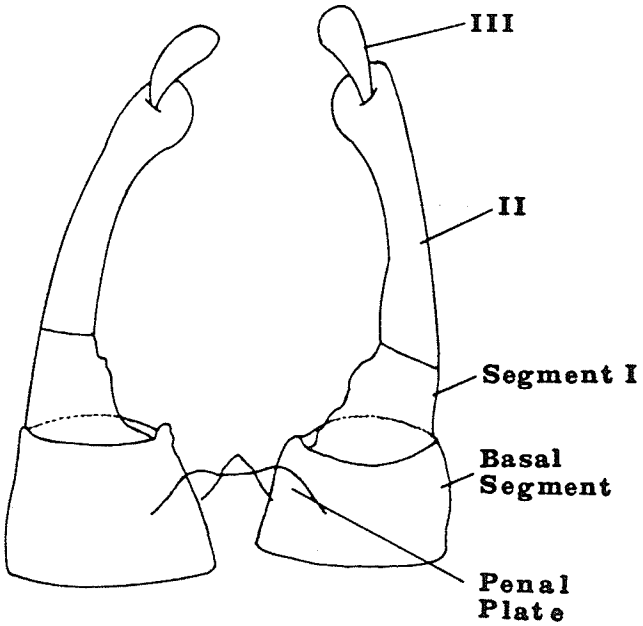
Figures 2-4. Structural features of Centroptilum bifurcatum McDunnough imago. 2)Mesothoracic and metathoracic wings. 3)Detail of metathoracic wings, showing range of variation. 4)Male genitalia, dorsal view.


C
Sc
R1
R2
A1
CuP
ICu2
ICu1
CuA
MP2
IMP
MP1
MA2
MA1
R4+5
1 mm

2


Costal
Process
0.5 mm

3


III
II
Segment I
Basal
Segment
Penal
Plate
0.1mm

4

Basal segments of forceps yellow-tan, broader than long (Fig. 4). Both with distinct tubercle along inner margin near joint with forceps segment I. Inner margin of basal segment diverging distally. Forceps segments I, II, and III hyaline. Segment I as long as but half as broad as basal segment. Segment I weakly fused to segment II and with distinct tubercle near this joint. Segment II twice as long as segment I and segment III 3/4 to sub-equal length of segment I. Segment III tear-drop shaped. Posterior edge of penal plate markedly concave, appearing semicircular in some specimens. This concavity not mentioned in original description but present in type series. Large pointed process on plate between basal segments.

No fresh specimens with complete cercus were obtained. Cercal length of pinned specimens 10.2 (range 8.7-11.2, n=56).

FEMALE IMAGO (n=6)

Body length 6.0 (range 5.5-6.5).

a)Head

Eye black. Antenna light brown basally becoming hyaline distally. Remainder of head opaque light tan with red-brown on raised edges of head.

b)Thorax

Pronotum opaque white with light brown spot laterally. Fine red-brown line along lateral and posterior edge. Mesonotum light olive

brown dorsally and opaque white laterally. Red highlights along edges. Metanotum opaque white anterior to metascutellar hump and dark olive brown posterior to metascutellar hump. All thoracic sterna hyaline with some light tan laterally.

Coxa opaque white. Remaining leg segments semi-hyaline tan. Measurements of legs and leg segments similar within individuals but highly variable among individuals (Table 1). Femur slightly longer than tibia. Protarsus slightly longer than meso- and metatarsus. Meso- and metatarsus about 3/4 length of tibia. Tarsomere I 2 to 3 times as long as tarsomere II.

Fore wing length 6.0 (range 5.4-6.4), width 2.3 (range 2.1-2.5). Fore wing colour and venation as in male imago. Hind wing as in male (Fig. 3). Length 1.1 (range 0.9-1.4) and width 0.3 (range 0.25-0.5).

c)Abdomen

Terga I to VII translucent light brown with paler or unmarked anterior edges. Terga I to VI with purplish spiracular blotches laterally. Terga VII to IX with lateral red patches. Terga IX and X opaque white, tergum VIII hyaline with white speckling. Sterna I to VII hyaline, with yellow eggs easily visible, and some red shading observable sub-laterally on posterior edges. Sternum VIII hyaline with opaque white speckling. Sternum IX and paraprocts opaque white. The opaque white and red shading retained in Kahle's solution but fades in alcohol to pale opaque tan. Cercus length 8.0 (range 7.7-8.4). Cercus semi-hyaline.

SUBIMAGO

Subimago similar to imago. Coloured areas paler while hyaline areas opaque grey or white. Wing venation as in imago. Cercus shorter than total body length. Forceps not fully expanded but process on penal plate easily visible.

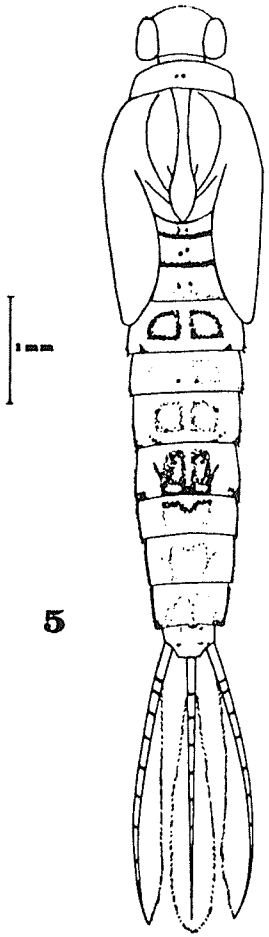
NYMPH (n=8)

Total body length 6.1 (range 5.5-6.9). Dorsal colour pattern as in Fig. 5.

a)Head

Head yellow-tan with light brown markings. Antenna hyaline brown, length 1.8 (range 1.6-2.1). Labrum as in Fig. 6. Arrangement and number of setae on labrum variable. Mandibles orange-brown distally fading to tan basally. Canines of left mandible fused for less than basal 1/3 of length (Fig. 7). Three projecting denticles on inner canine, four on outer canine. Prostheca well developed. Width of prostheca about one half of one canine. Fringe of setae extending from base of canines to base of "thumb" of molar area. Plane of molar area markedly depressed. Two isolated setae present on distal end of molar area. Canines of right mandible strongly divided, outer canine strongly bowed (Fig. 8). Five denticles on outer canine and three or four on inner canine. Prostheca very thin and almost needle-like. Fringe of setae extending from base of canines to molar area. Two rounded humps located on molar plane. First hump a semi-fused clump of

Figures 5-10. Structural features of Centroptilum bifurcatum McDunnough mature nymph. 5)Dorsal maculation. 6)Labrum. 7)Left mandible. 8)Right mandible. 9)Maxilla. 10)Labium.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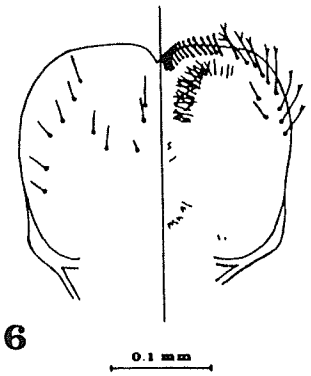
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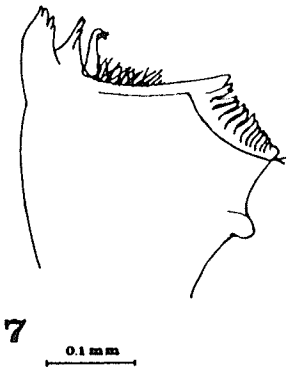
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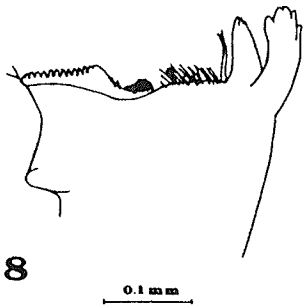
7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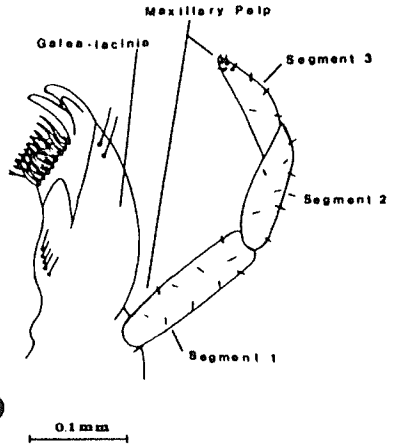
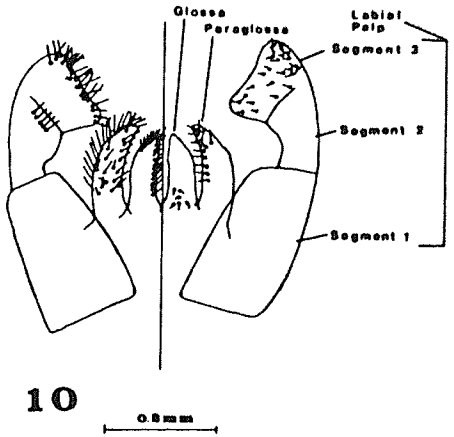

Maxillary Palp
Galea-lacinia
Segment 3
Segment 2
Segment 1
0.1 mm

9


Glossa
Paraglossa
Labial Palp
Segment 3
Segment 2
Segment 1
0.8 mm

10

setae in a shallow depression just before molar plane. Second hump a sclerotized projection on molar plane. This hump erodes with use and is therefore largest in newly moulted specimens. Remainder of molar area elevated above distal margin of mandible. Isolated clump of two or three setae present on distal end of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edge (Fig.9). Two rows of setae along anterior face of maxilla. One row of two setae distal, below level of biting teeth and another proximal row of five or six setae opposite palp. Maxillary palp longer than maxilla. Palp three-segmented and with many short spines. Palpomeres II and III subequal, each slightly shorter than palpomere I. Tip of palpomere III chisel-shaped, pointed when viewed from the side. Labium hairy (Fig. 10). Glossa marginally shorter than paraglossa. Dorsally, glossa with row of setae along inner and distal margin. Paraglossa with setae over whole dorsal surface. Ventrally, glossa with few scattered setae basally; paraglossa with scattered setae distally and row of setae along inner margin. Setae near edges can be on either side. Labial palp three-segmented but in some specimens division between palpomeres II and III difficult to discern. Palpomere I hairless, roughly rectangular. Palpomere II narrowest at base, expanding distally. Straight row of five short setae on dorsal side near distal end of palpomere II. Palpomere III truncate, broadly expanded and slightly concave. Setae widely scattered over ventral side, concentrated near the distal end on dorsal side.

b)Thorax

Lengths of pro-, meso-, and metathoracic leg segments variable (Table 2). All legs light tan with small dorsal brown area near distal end of femur. Femur with very small row of setae distally along dorsal margin. Tibia with arc of setae across dorsal margin near femoral joint. Thorax light tan to yellow-tan. Pronotum with light brown markings in sub-lateral position along anterior edge. Mesonotum unmarked. Wing pads semi-hyaline tan becoming black in final moults. Wing pads lacking markings resembling veins. Metanotum black along posterior edge. Paired mid-dorsal spots resembling pores on pronotum and metanotum. Sterna unmarked.

c)Abdomen

Terga light tan with brown markings (Fig. 5). Posterior tergal spines narrow and tall, evenly spaced with small gap between spines; only occasional small spines in between. Tergum with numerous semi-circular hollows. Mid-dorsal posterior edge of tergum IX produced posteriorly as rounded hump lacking spines. Paired mid-dorsal spots resembling pores on segments I, II, III, IV, and VI. Additional pairs of more lateral pores on segment V. Lateral spines very small, indistinct but numerous (Table 3). Sterna light tan and unmarked. Genital forceps of male visible in mature nymph as two small rounded extensions on the posterior edge of sternum IX. Gills on segments I to VII all unilamellate and broadly to slightly asymmetrical (Fig. 11). At least two most posterior pairs of gills minutely serrate along anterior edge. Some individuals with serrations on all gills. Median

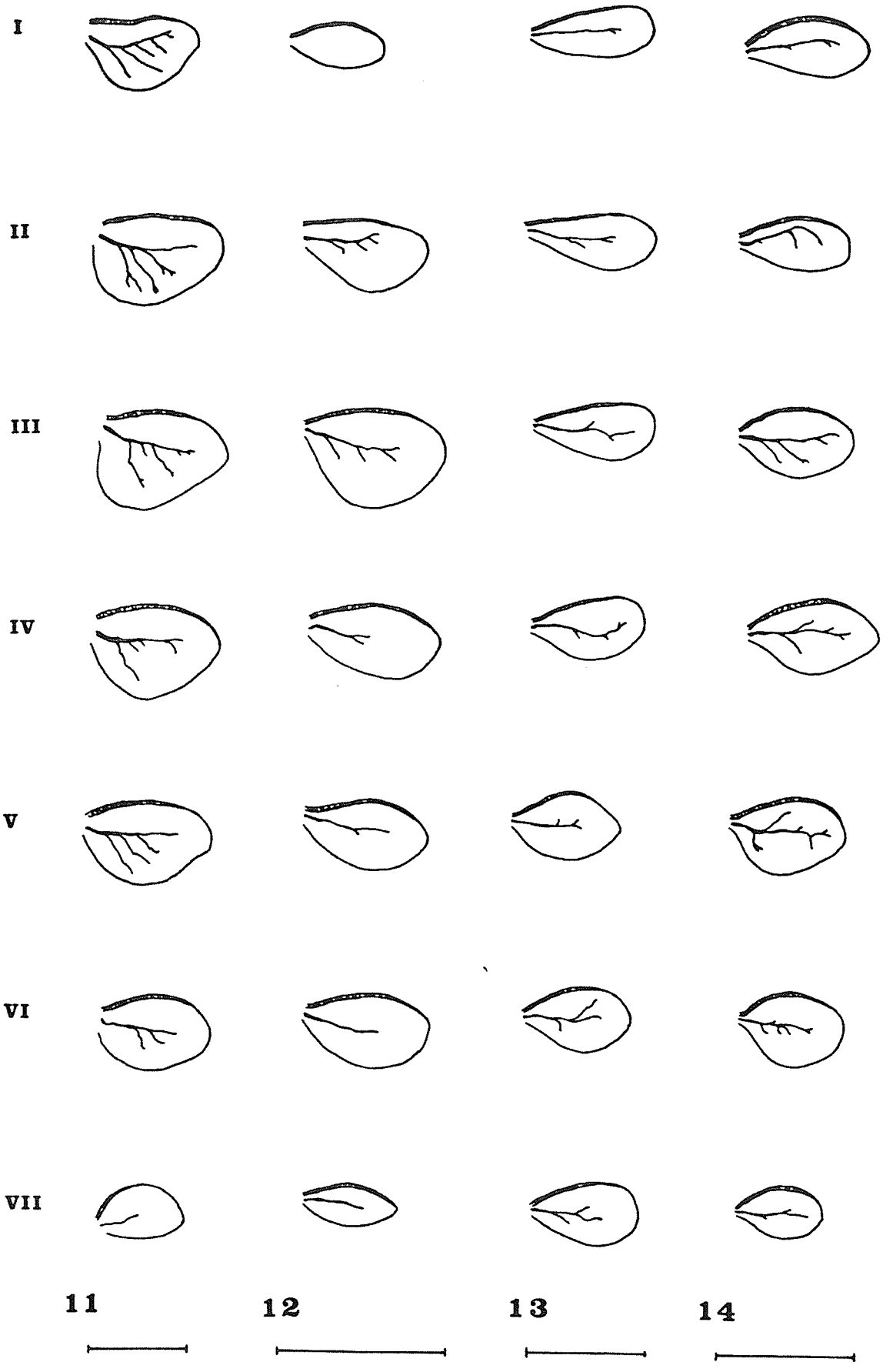
Table 2. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Centroptilum bifurcatum McDunnough (n=8).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	0.94	0.53	0.56	0.39
	r	0.84-1.03	0.44-0.63	0.47-0.63	0.36-0.44
	:	2.2-2.6	1.1-1.7	1.3-1.7	1
MESOTHORACIC	x	0.96	0.53	0.50	0.39
	r	0.84-1.16	0.47-0.59	0.44-0.56	0.31-0.50
	:	2.2-2.7	1.1-1.7	1.1-1.6	1
METATHORACIC	x	0.98	0.49	0.52	0.38
	r	0.87-1.09	0.41-0.56	0.47-0.56	0.31-0.44
	:	2.2-2.9	1.0-1.8	1.2-1.6	1

Table 3. Number of lateral spines observed on abdominal segments of mature nymphs.

ABDOMINAL	SPECIES						
SEGMENT	BIFURCATUM	VICTORIAE	ALBUM	CONTURBATUM	RUFOSTRIGATUM	INFREQUENS	QUAESITUM
I	0	0	0	0	0	0	0
II	0	0	0	0	0-3	0	0-2
III	0-1	0	0	0	0-5	0	0-2
IV	0-3	0	0	0	0-5	0	2-4
V	5-10	0	0-trace	0	3-8	0	4-5
VI	6-14	0	0-trace	0	6-8	0	6-8
VII	7-16	0	0-3	0	6-9	0	8-10
VIII	9-19	6-14	0-4	0-3	9-11	2-5	8-10
IX	10-17	8-14	0-3	0-8	7-11	5-7	11-14
X	0	0	0	0	0-trace	0	0

Figures 11-14. Abdominal gills of mature nymphs. Scale lines equal 0.5 mm. 11)Centroptilum bifurcatum McDunnough. 12)C. victoriae McDunnough. 13)C. album McDunnough. 14)C. conturbatum McDunnough.


I
II
III
IV
V
VI
VII
11
12
13
14

terminal filament length 2.5 (range 2.3-2.6) and cercus 2.6 (range 2.3-2.7). Cercus and median terminal filament hyaline brown with dark band every fourth intersegmental membrane. Distally all three tails darkened near tip. Without dark band across middle of tails.

SPECIMENS EXAMINED

CANADA

ALBERTA

Bearberry Creek, near Sundre, 51°48'N 114°40'W (coll. C.H. Young) (CNIC): 10/VIII/1926, 1 female imago.

Lethbridge, 49°42'N 112°47'W (coll. J.H. Pepper) (CNIC): 17/VII/1929, 5 male imagines; 30/VII/1929, 17 male imagines, 2 female imagines; 31/VII/1929, 7 male imagines, 1 female imago; 1/VIII/1929, 3 female imagines; 2/VIII/1929, 1 male imago, 5 female imagines; 3/VIII/1929, 1 male imago; 5/VIII/1929, 2 male imagines, 1 female imago; 13/VIII/1929, 1 male imago; 14/VIII/1929, 1 male imago, 5 female imagines; 15/VIII/1929, 3 male imagines; 7/VII/1930, 1 female imago; 8/VII/1930, 2 female imagines; 11/VII/1930, 2 female imagines; 28/VII/1930, 18 male imagines, 2 female imagines; 5/VIII/1930, 3 male imagines; 6/VIII/1930, 1 male imago, 14 female imagines. Belly River (coll. J. McDunnough) (CNIC): 15/VIII/1928, 6 male imagines, 1 female imago. St. Marys River (coll. J. McDunnough) (CNIC): 27/VII/1930, 1 male imago.

Medicine Hat, 50°03'N 110°41'W (coll. J.H. Pepper) (CNIC): 19/IX/1928, 1 male imago; 17/IX/1929, 53 male imagines; 18/IX/1929, 16 female imagines; 19/IX/1929, 11 male imagines, 1 female imago; 20/IX/1929, 1 male imago; 16/VI/1930, 1 female imago; 22/VII/1930, 1 female imago; 24/VII/1930, 1 male imago, 3 female imagines; 21/VIII/1930, 1 female imago. Ross Creek (coll. J.H. Pepper) (CNIC): 13/VII/1929, 5 female imagines. [South] Saskatchewan River (coll. J.H. Pepper) (CNIC): 9/VIII/1929, 1 female imago. Seven Persons Creek (coll. J.H. Pepper) (CNIC): 12/VI/1929, 28 male imagines; 17/VI/1930, 4 male imagines, 11 female imagines.

Milk River, 49°09'N 112°06'W (coll. J.H. Pepper) (CNIC): 18/VII/1929, 4 male imagines; 13/IX/1929, 10 male imagines; 10/VII/1930, 13 male imagines, 1 female imago; 18/VIII/1930, 1 male imago.

Pembina River, at Pembina River Provincial Park, Entwistle, 53°37'N 115°00'W (coll. J. Ciborowski) (UWWO): 28/VI/1979, 3 nymphs; 10/VIII/1979, 4 male imagines with nymphal exuviae, 5 female imagines with nymphal exuviae, and 5 nymphs.

Waterton Lakes, 49°06'N 113°54'W: 29/VIII/1926, 1 male imago (coll. N. Criddle); 9/VIII/1930, 1 male imago (coll. J.H. Pepper). At Cameron Creek, 17/VIII/1928, 1 male imago (coll. J. McDunnough). Middle, 19/VIII/1928, 2 male imagines (coll. J. McDunnough).

BRITISH COLUMBIA

Summerland, 49°39'N 119°33W, (coll. A.N. Gartrell) (CNIC):

9/VII/1933, 1 male imago; 18/VII/1933, 1 female imago; 8/VIII/1933, 1 female imago.

MANITOBA

Assiniboine River, site 1, at Highway 1, west of Winnipeg, 49°55'N 97°32'W, (coll. R.G. Lowen): 26/VIII/1985, 1 female subimago, 5 nymphs; 7/VII/1986, 3 nymphs; 28/VIII/1986, 9 nymphs, 3 nymphal exuviae; 10/IX/1986, 1 female imago with exuviae. Site 2, at Headingley, near Wescana Street, Winnipeg, 49°52'N 97°28'W (coll. R.G. Lowen): 10/IX/1986, 1 male imago, 2 female imagines with exuviae, 3 nymphal exuviae.

Ochre River, site 4, half way between the town of Ochre River and Dauphin Lake, 51°05'N 99°47'W: 10/VI/1986, 4 nymph, (coll. R.G. Lowen); 17/VI/1986, 7 nymphs, (coll. R.G. Lowen); 14/VII/1986, 1 male imago with exuviae, 1 female imago with exuvia, 13 nymphs, (coll. R.G. Lowen and S. Bernatski); 29/VII/1986, 1 nymph, (coll. R.G. Lowen); 8/VII/1987, 1 nymph, (coll. R.G. Lowen). Mouth of Ochre River, site 5, 51°07'N 99°46'W: 10/VI/1986, 6 nymphs, (coll. R.G. Lowen).

UNITED STATES OF AMERICA

WYOMING

Firehole River, Lower Geyser Basin, Yellowstone Park, 44°39'N 110°51'W (coll. J. McDunnough) (CNIC): 21/VII/1928, 12 female imagines; 22/VII/1928, 9 female imagines; 29/VII/1928, 1 female imago.

Upper Geyser Basin, Yellowstone Park, 44°29'N 110°49'W (coll. J. McDunnough) (CNIC): 27/VII/1928, 11 female imagines; 29/VII/1928, 8 female imagines.

DISTRIBUTION AND FIELD NOTES

In Manitoba, specimens were collected at two sites on each of two rivers. Both of these rivers are highly meandering prairie rivers with extensive agricultural development along their banks. The nymphs were common at both sites on the Assiniboine River which is a large turbid river, with thick clay and silt substrate. They were most common on submerged aquatic vegetation on the mud banks and were uncommon on submerged riparian vegetation. In the Ochre River, nymphs were only occasionally found. The Ochre River is a much smaller turbid stream but has a gravel and rock substrate. Nymphs were collected from early June to late September.

In addition to the specimens examined, Needham et al. (1935) record C. bifurcatum from Hollister and Tuttle, Idaho. Therefore all records of C. bifurcatum are in southwestern Canada and in northwestern United States, with the Manitoba records being the new eastern limits of the species (Fig. 15).

Centroptilum victoriae McDunnough

Centroptilum victoriae McDunnough 1938, Can. Ent. 70: p. 27.

Holotype- Inhabitants River, at Victoria Highway, Cape Breton Island, Nova Scotia, Canada, 45°46'N 61°20'W (coll. J. McDunnough) (no. 4288 CNIC): 19/VI/1936, male imago.

Paratypes- Inhabitants River, at Victoria Highway, Cape Breton Island, Nova Scotia, Canada, 45°46'N 61°20'W (coll. J. McDunnough) (CNIC): 19/VI/1936, 3 male imagines.

MALE IMAGO (n=8)

Total body length 4.1 (range 3.4-4.8).

a)Head

Turbinate eye orange, slightly divergent. Disc broadly oval with width to length ratio 0.67 to 0.75. Stalk much paler, 0.2 mm tall. Non-turbinate eye and ocelli black. Antenna brown basally, semi-hyaline distally. Head evenly brown which darkens on ridges.

b)Thorax

Dorsal half of thorax dark brown with a tendency to lighten laterally. Sternum pale tan with darker edges. Coxa brown. Leg yellowish semi-hyaline. Individual leg measurements variable

Figure 15. Known ranges of Centroptilum bifurcatum McDunnough and C. victoriae McDunnough.


C. bifurcatum
C. victoriae
NORTH AMERICA
0
500
MILES

(Table 4). Prothoracic leg just over 3.0 mm long. Tarsus five-segmented. Meso- and metathoracic legs and their component segments similar. Length over 1.7 mm. Tarsus four-segmented.

Fore wing length 4.0 (range 3.7-4.5) and width 1.5 (range 1.4-1.6). Fore wing hyaline with only slight brown colour basally. Pterostigma translucent white. Number of cross veins variable (Fig. 16). Wing with five to nine cross veins between C and Sc; 2 cross veins between Sc and R1 and between R1 and R2, in most specimens at a fixed location. Veins long. R3 reaches cross vein in middle of wing. MA2 vein reaches MA1/MP1 cross vein. IMP vein about as long as MP2. ICu veins short with ICu1 never reaching CuA/CuP cross vein. Hind wing length 0.74 (range 0.61-0.84) and width 0.21 (range 0.17-0.27). Shape of hind wing highly variable (Fig. 17). Wing tips broadly rounded to distinctly pointed with thicker and rounded wing tending to have a short third vein. Costal process strongly in-curved.

c)Abdomen

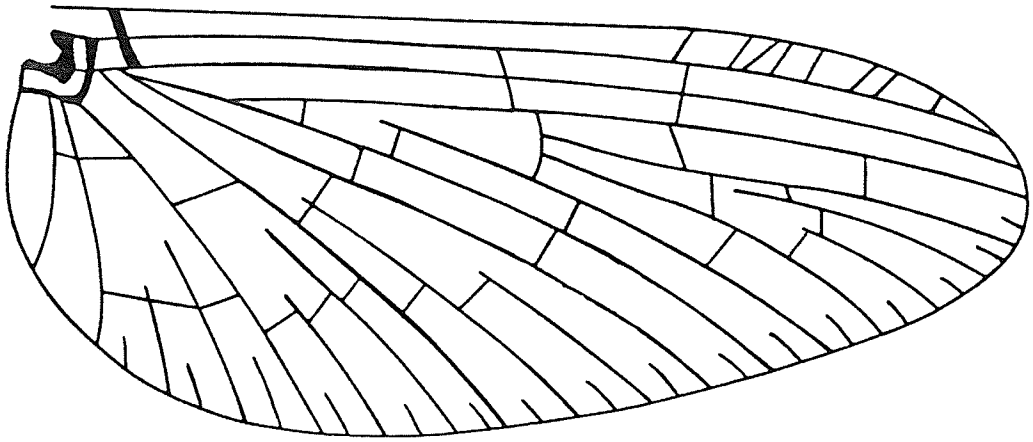
Terga I to II yellowish hyaline. Terga III to VI hyaline white without markings. Terga VII to X bright chestnut brown. Abdominal sternum I yellow hyalilne. Sterna II to VI hyaline white and unmarked. Sterna VII to IX opaque tan with alabster white markings. Cercus hyaline white. Cercal length 6.7 (range 6.1-7.5).

Basal segments of forceps tan coloured and broader than long (Fig. 18). Inner edges of basal segments nearly contiguous basally, diverging distally. Forceps segments I, II, and III hyaline white, variable width. Segment I approximately same length as basal segment,

Table 4. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in in imagines of *Centroptilum victoriae* McDunnough. Prothoracic legs are divided by sex (n= 8 males and 5 females).

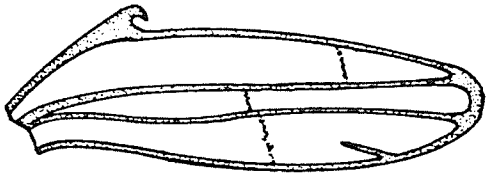
		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	0.80	1.12	0.07	0.44	0.36	0.20	0.15
PROTHORACIC	r	0.72-0.89	1.00-1.20	0.05-0.16	0.25-0.52	0.17-0.42	0.12-0.23	0.14-0.16
	:	1.9-2.3	2.7-3.0	0.1-0.2	1.2-1.3	1	0.5-0.6	0.3-0.4
FEMALE	x	0.68	0.72	0.21	0.12	0.06	0.15	-
PROTHORACIC	r	0.62-0.72	0.58-0.78	0.14-0.27	0.08-0.14	0.05-0.06	0.11-0.17	-
	:	11.7-13.4	11.6-13.0	2.8-4.5	1.6-2.3	1	2.2-2.8	-
	x	0.70	0.66	0.18	0.08	0.04	0.13	-
MESOTHORACIC	r	0.63-0.84	0.58-0.78	0.12-0.23	0.06-0.09	0.03-0.06	0.09-0.16	-
	:	11.0-24.0	10.4-22.3	2.3-7.3	1.3-2.7	1	2.1-5.3	-
	x	0.69	0.64	0.17	0.08	0.04	0.13	-
METATHORACIC	r	0.59-0.84	0.53-0.73	0.12-0.22	0.06-0.11	0.03-0.06	0.11-0.16	-
	:	9.8-24.3	8.8-22.3	2.5-5.7	1.2-2.7	1	1.8-5.3	-

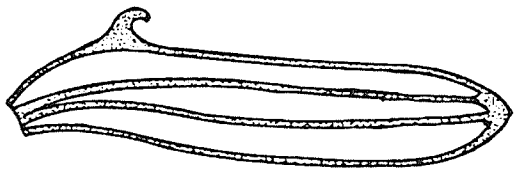
Figures 16-18. Structural features of Centroptilum victoriae McDunnough imago. 16)Mesothoracic and metathoracic wing. 17)Detail of metathoracic wings, showing range of variation. 18)Male genitalia, dorsal view.



16

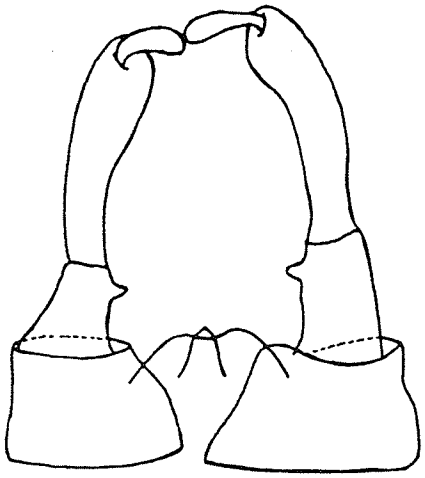
1 mm





17

0.5 mm



18

0.1 mm

distinct tubercle near distal margin. Segment II almost twice length of segment I. Segment II narrow basally, expanding distally. Segment III tear-drop shaped, subequal to segment I. Penal plate broad with a concave margin. Distinct process on penal plate.

FEMALE IMAGO (n=5)

Total body length 4.3 (range 3.6-5.5).

a)Head

Head and base of antenna light yellow-tan. Antenna hyaline distally. Eye and ocelli black.

b)Thorax

Pronotum yellow-tan with darker brown posterior and lateral edges. Mesonotum white dorsally, light tan dorso-laterally. All lateral ridges marked with brown. Metanotum white anterior of the metascutellar hump, dark brown posterior to hump. Thoracic sterna white with hyaline spots ventrad to coxa.

Leg hyaline white, segment lengths similar to the meta- and mesothoracic legs of male (Table 4). Fore wing length 4.6 (range 4.0-5.2), width 1.8 (range 1.6-2.1). Fore wing venation and colour as in male. Hind wing slightly narrower and coming to a sharper point than in male (Fig. 17). Length 0.77 (range 0.58-0.94) and width 0.19 (range 0.14-0.22). Costal process less curved than male.

c)Abdomen

Terga I to VI hyaline with brown on posterior 2/3 of each tergum. Eggs when present clearly visible through terga. Terga VII to X hyaline with red wash of colour. Broken black spiracular line on segments II to VIII. Sterna I to VIII semi-hyaline white, appearing yellow from eggs. Sternum IX mostly red wash on hyaline. Cercus hyaline white. Cercal length 5.6 (range 4.3-7.5).

SUBIMAGO

Only five subimagines were collected, three males and two females. Any specific comparisons with imagines could be misleading. In general, subimago similar to imago. Colour pattern similar but paler and more opaque in the subimago. Wing venation as in imago. Cercus shorter than total body length. Forceps not fully expanded but process on penal plate still easily visible.

NYMPH (n=26)

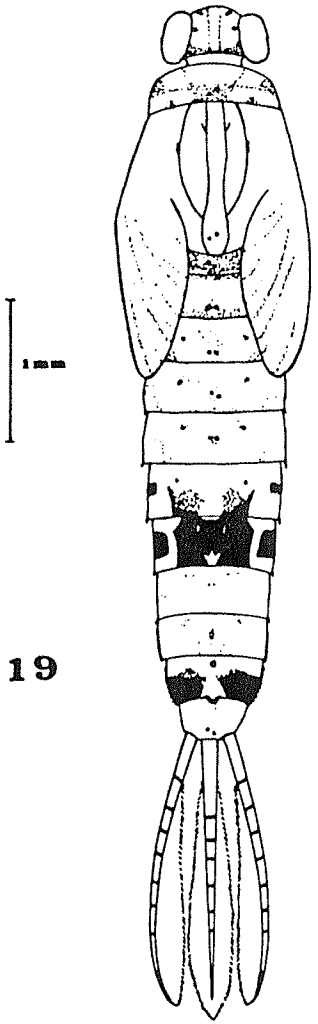
Total body length 5.1 (range 4.2-5.6). Dorsal colour pattern as in Fig. 19.

a)Head

Head light yellow-tan. Antenna unmarked hyaline tan. Antenna length 1.2 to 1.6 mm. Small light-coloured spot resembling a pore near each compound eye at narrowest point between eyes.

Labrum as in Fig. 20. Arrangement and number of setae on labrum variable. Mandibles orange-brown distally, hyaline brown basally. Canines of left mandible fused along basal third and strongly divergent distally (Fig. 21). Four denticles on each canine but worn canines lose distinction between denticles. Prostheca well developed but still less than half width of one canine. Fringe of setae extending almost entire length from prostheca to thumb of molar area. Molar area inclined basad. Canines of right mandible unfused, outer canine strongly bowed (Fig. 22). Four denticles on each canine with wear obliterating distinction between denticles. Prostheca very thin and spike-like. Fringe of setae extending half way from prostheca to molar area. Semi-fused hump of setae present near base of molar area closest to canines. Secondary hump in molar area never observed higher than molar teeth. Isolated group of two or three setae present on other end of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edge (Fig. 23). Two setae distal, below level of biting teeth, three or four setae in an irregular grouping proximal, opposite the palp. Maxillary palp with three subequal segments. Each palpomere bears relatively few very long setae, more dense on tip of palpomere III. Labium hairy (Fig. 24). Glossa slightly shorter than paraglossa. Group of small setae at base of glossa on ventral side. Row of setae along inner margin of glossa on ventral side and along outer margin on darsal side. These rows can appear to be on either side or exactly on edge. Ventral and dorsal sides of paraglossa with sparse long setae along inner margin. Long setae along outer edge mostly on dorsal side. Scattered short setae

Figures 19-24. Structural features of Centroptilum victoriae McDunnough mature nymph. 19)Dorsal maculation. 20)Labrum. 21)Left mandible. 22)Right mandible. 23)Maxilla. 24)Labium.



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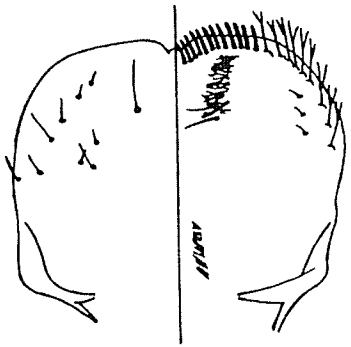

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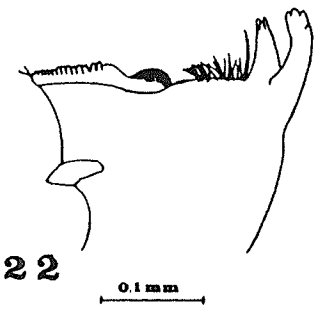

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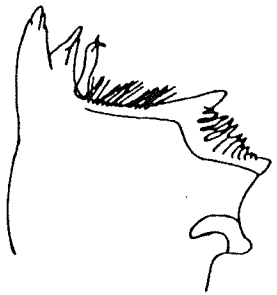

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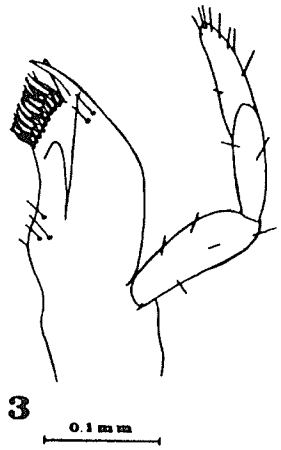

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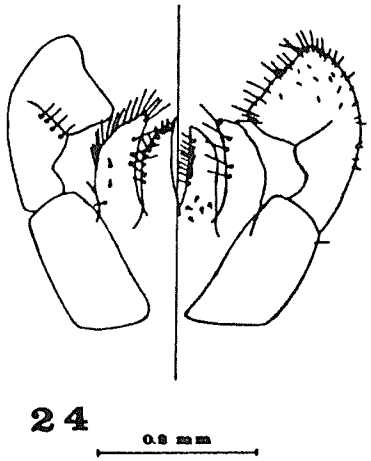


24

present on dorsal face of paraglossa. Labial palp three-segmented. Palpomere I rectangular, a few specimens with scattered setae along ventral side. Palpomere II narrow basally, expanding distally. Scattered setae on ventral side. Orderly row of four to six setae along distal margin of dorsal side. Palpomere III concave along distal margin with many setae on ventral side, few to no setae on dorsal side. Inner margin of palpomere III broadly expanded inwards.

b)Thorax

Comparative lengths of pro-, meso-, and metathoracic leg segments variable (Table 5). Leg light tan with dark brown spot near distal end of femur and smaller spot near proximal end of tibia. Tarsus and claw light brown with dark brown at tibial joint of tarsus. Distal end of femur with few scattered setae in a short row on dorsal margin. Wing pads with markings resembling veins (Fig. 19). Paired mid-dorsal pore-like spots on pronotum, mesonotum, and metanotum.

c)Abdomen

Posterior tergal spines very tall and narrow, evenly spaced with gaps and only occasional small spines in between. Terga with few scattered semi-circular hollows. Tergum IX produced posteriorly as mid-dorsal round hump lacking posterior spines. Paired mid-dorsal spots resembling pores on terga I, II, III, IV, and X. Second pair of more lateral pores on terga II, III, IV, V, VI, and IX. Lateral spines small and inconspicuous. Number of spines variable (Table 3). Genital forceps of male visible in mature nymphs as two small rounded

Table 5. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Centroptilum victoriae McDunnough (n=26).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	0.75	0.44	0.46	0.27
	r	0.62-0.97	0.36-0.50	0.39-0.53	0.23-0.33
	:	2.5-3.5	1.4-2.0	1.5-1.9	1
MESOTHORACIC	x	0.80	0.45	0.40	0.27
	r	0.67-0.94	0.36-0.56	0.34-0.47	0.23-0.33
	:	2.6-3.6	1.3-2.0	1.3-1.9	1
METATHORACIC	x	0.77	0.44	0.39	0.29
	r	0.64-0.91	0.33-0.55	0.34-0.47	0.22-0.42
	:	1.9-3.4	1.0-2.0	1.1-1.8	1

extensions on posterior edge of sternum IX. All gills unilamellate (Fig. 12) with some individuals having more pointed gills. Younger specimens have more pointed gills. At least two most posterior pairs of gills minutely serrated along anterior edge. Some individuals with serrations on all gills. Median terminal filament 1.5-2.0 mm long, cercus slightly longer at 1.6-2.3 mm. Cercus and median terminal filament similarly patterned with light tan ground colour and dark brown band every fourth segment. Terminal segments darkened in some individuals. Lateral fringes of cercus light brown to hyaline.

SPECIMENS EXAMINED

CANADA

MANITOBA

Cowan Creek, near the town of Cowan, 51°59'N 100°40'W, (coll. R.G. Lowen): 3/VI/1986, 5 nymphs; 12/VI/1986, 3 nymphs; 19/VI/1986, 4 nymphs; 24/VI/1986, 1 male subimago and exuvia, 1 female subimago and exuvia, 5 nymphs.

North Pine River, just upstream from Hwy. 10, 51°48'N 100°34'W: 21/VII/1985, 1 male subimago and exuvia, 3 nymphs, (coll. R.G. Lowen); 22/VII/1985, 1 female imago (coll. R.G. Lowen); 30/VII/1986, 4 nymphs (coll. S. Bernatski).

Ochre River, site 4, half way between the town of Ochre River and Daupin Lake, 51°05'N 99°47'W: 10/VI/1986, 1 male subimago and exuvia, 2 nymphs, (coll. R.G. Lowen); 17/VI/1986, 2 male subimagines with

exuviae, 30 nymphs and 1 exuvia (coll. R.G. Lowen); 10/VII/1986, 1 female imago with exuviae, (coll. R.G. Lowen); 14/VII/1986, 6 male imagines with exuviae, 3 female imagines with exuviae, 1 female subimago with exuvia, 58 nymphs (coll. S. Bernatski and R.G. Lowen); 22/VII/1986, 1 male imago with exuviae, 1 male subimago with exuvia, 1 female imago with exuviae, 15 nymphs and 1 exuvia (coll. S. Bernatski and R.G. Lowen); 29/VII/1986, 3 nymphs, (coll. R.G. Lowen); 8/VII/1987, 12 nymphs, (coll. R.G. Lowen); 9/VII/1987, 1 male imago with exuviae, 4 nymphs, (coll. R.G. Lowen). Mouth of Ochre River, site 5, 51°07'N 99°46'W: 10/VI/1986, 1 male subimago with exuvia, 55 nymphs and 1 exuvia, (coll. R.G. Lowen).

ONTARIO

Salem Creek, half way to the Canagagigue River, near Waterloo, 43°35'N 80°30'W (coll. L. LeSage) (UMIC): 18-27/VIII/1977, 1 male subimago, 1 female subimago.

DISTRIBUTION AND FIELD NOTES

This species was found in three Manitoba rivers. Cowan Creek is a small, spring fed stream with moderate agricultural development along either side. The substrate varies from sand to boulder with occasional mud banks. This stream retains unfrozen reaches year round. The North Pine River is a similar but larger river. Both rivers drain from the Duck Mountains and both have been stocked with brook charr. The North

Pine River has additionally been stocked with Rainbow trout. The Ochre River is as large as the North Pine River but is a more lowland river. The Ochre River has more agricultural development and carries a higher sediment load. In all three rivers, the species is most often found along gravel reaches near the deeper parts of the stream. Few nymphs were caught along the shore line. No nymphs were caught along the very fast or very slow parts of the streams. Nymphs were found on submerged vegetation if this was present along the gravel reaches otherwise the nymphs were found on top of the gravel. Nymphs were collected from early June to late July.

No specimens are reported from the literature, other than those examined for this study. The known distribution is therefore restricted to five sites in three provinces (Fig. 15). This is apparently an eastern species. Manitoba specimens represent the new western and northern limits of the species.

Centroptilum album McDunnough

Centroptilum album McDunnough 1926, Can. Ent. 58: p. 189.

McDunnough 1930, Can. Ent. 62: pp. 58-59. (describes nymph)

McDunnough 1932, Can. Ent. 64: p. 80. (redescribes male imago and nymph)

Holotype- Silver Creek, Orillia, Ontario, Canada, 44°37'N 79°25'W (coll. C.H. Curran) (no. 1790 CNIC): 13/VI/1925, male imago.

Allotype- Silver Creek, Orillia, Ontario, Canada, 44°37'N 79°25'W (coll. J. McDunnough) (CNIC): 11/VI/1925, female imago.

Paratypes- Silver Creek, Orillia, Ontario, Canada, 44°37'N 79°25'W (CNIC): 11/VI/1925, 3 female imagines (coll. C.H. Curran); 12/VI/1925, 3 male imagines, 2 female imagines (coll. C.H. Curran); 13/VI/1925, 6 male imagines, 9 female imagines (coll. C.H. Curran and J. McDunnough).

MALE IMAGO (n=4)

Total body length 4.4 (range 4.0-4.5).

a)Head

Antenna hyaline brown. Turbinate eye of living specimens orange-brown on disc, stalk lighter. Eye darker in alcohol preserved specimens. Disc relatively narrow, width to length ratio 0.50 to 0.67. Stalk 0.20-0.23 mm tall with dark brown rings around bases. Rest of head light brown, darker on raised edges.

b)Thorax

Pronotum brown without markings. Mesonotum and metanotum lighter, most species white dorsally, darkening to light brown laterally.

Sterna with mid-ventral white stripe, light tan laterally. Brown spot on coxa.

Leg hyaline-white, brownish basally. Individual leg measurements variable (Table 6). Prothoracic leg length 4.1. Tarsus five-segmented. Meso- and metathoracic legs with length 1.9. Length of component segments similar in each leg. Tarsus four-segmented.

Fore wing length 4.7 (range 4.1-5.0), width 1.7 (range 1.5-1.9). Fore wing hyaline, slightly yellow basally. Pterostigma translucent white. Venation of fore wing as in Fig. 25. Number and position of cross veins variable. Wing with four to nine cross veins between C and Sc. Two or three cross veins between Sc and R1 and always two cross veins between R1 and R2. MA2 extends past the MA1/MP1 cross vein. MP2 longer than IMP. ICu1 almost reaches CuA/CuP cross vein. Hind wing with venation as in Fig. 26. Length 0.66 (range 0.56-0.72) and width 0.15 (range 0.14-0.17). Distal tip of wing round or bluntly pointed. Costal process long, narrow, and only partially curved.

c)Abdomen

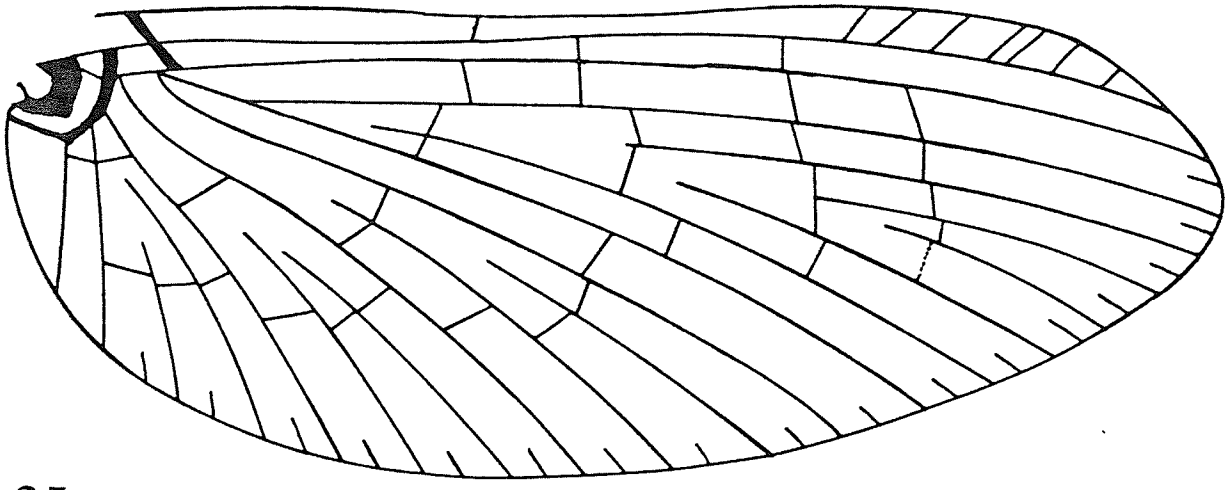
Terga I to V and anterior half of tergum VI hyaline white. Terga VII to X and posterior half of segment VI opaque white on a cream-coloured background. Sterna as terga except the opaque white more diffuse. Cercus hyaline white. Cercal length 8.2 (range 6.9-8.7).

Basal segments of forceps cream coloured and broader than long (Fig. 27). Basal segments nearly contiguous basally, diverging distally. Inner margin of basal segments highly irregular, in most specimens appearing as distinct tubercles. Forceps segments I, II, and III

Table 6. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of *Centroptilum album* McDunnough. Prothoracic legs are divided by sex (n= 4 males and 4 females).

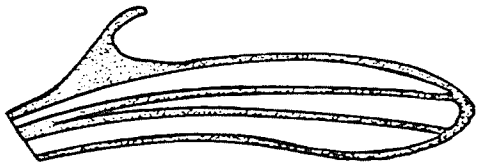
		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	0.94	1.37	0.05	0.66	0.54	0.38	0.14
PROTHORACIC	r	0.89-0.98	1.19-1.48	0.05-0.06	0.58-0.72	0.50-0.56	0.33-0.42	0.12-0.17
	:	1.7-1.8	2.4-2.7	0.09-0.11	1.2-1.3	1	0.7-0.8	0.2-0.3
FEMALE	x	0.69	0.65	0.19	0.12	0.07	0.15	-
PROTHORACIC	r	0.58-0.81	0.53-0.73	0.14-0.23	0.09-0.16	0.06-0.08	0.14-0.16	-
	:	8.4-10.1	8.8-9.1	2.3-2.9	1.5-2.0	1	2.0-2.3	-
	x	0.74	0.70	0.16	0.08	0.05	0.13	-
MESOTHORACIC	r	0.62-0.80	0.59-0.78	0.12-0.20	0.06-0.13	0.05-0.06	0.08-0.16	-
	:	12.2-15.6	11.0-15.6	2.5-3.8	1.2-2.1	1	1.6-2.8	-
	x	0.75	0.66	0.16	0.08	0.06	0.14	-
METATHORACIC	r	0.66-0.84	0.55-0.70	0.09-0.19	0.06-0.09	0.03-0.08	0.12-0.16	-
	:	8.6-16.8	8.0-13.2	2.1-3.8	1.0-2.0	1	1.4-4.2	-

Figures 25-27. Structural features of Centroptilum album McDunnough imago. 25)Mesothoracic and metathoracic wings. 26)Detail of metathoracic wings, showing range of variation. 27)Male genitalia, dorsal view.



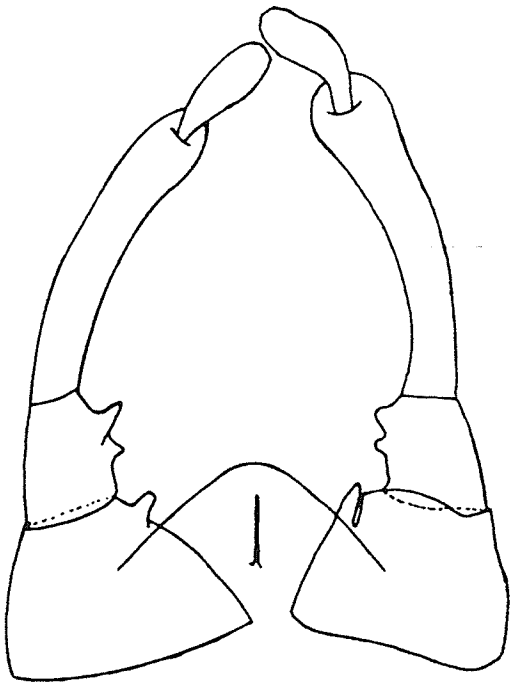
25

1 mm



26

0.5 mm



27

0.1 mm

hyaline white. Segments I, II, and III with variable width but relatively constant lengths. Segment I as long as basal segment but half as wide. Highly irregular inner margin can appear to be one or several tubercles. Segment I not fused to segment II. Segment II roughly three times as long as segment I. Narrowest in middle, expanding distally and proximally. Segment II incurved. Segment III tear-drop shaped, equal to or longer than segment I. Penal plate cream coloured with distal margin semi-circular, becoming cone-shaped in some individuals. A very small and narrow tubercle borne on penal plate between forceps. This tubercle probably not fully sclerotized as boiling in KOH solution destroys traces of it.

FEMALE IMAGO (n=5)

Total body length 4.7 (range 4.0-5.5).

a)Head

Eye black. Antenna hyaline brown. Head evenly light brown without markings.

b)Thorax

Pronotum tan-brown and unmarked. Mesonotum tan-brown with opaque white posterior edge. Metanotum brown anterior to metascutellar hump and opaque white on tan posterior to metascutellar hump. All sterna light brown and unmarked.

Coxa brown-black. All three pairs of legs resemble meso- and metathoracic legs of male (Table 6). Fore wing with length 4.8 (range 4.5-5.4) and width 1.7 (range 1.5-1.9). Wing venation as in male. Hind wing with length 0.71 (range 0.50-0.84) and width 0.16 (range 0.08-0.25). Somewhat narrower and more pointed than male hind wing (Fig. 26). Costal process less curved than in male.

c)Abdomen

Terga with mid-dorsal pairs of small black dashes and lateral patches of black-brown to red-brown; size of these patches decreases posteriorly. Patches give impression of a pale mid-dorsal stripe. Stripe accentuated on terga I to VI because of opaque light tan base colour. Terga VII to X hyaline but can still have lateral patches. Terga IX and X marked with opaque white patches. Sterna I to VIII with small, red-brown lateral patches. Sterna VI to VIII edged posteriorly with paired sub-ventral lines. Cercus hyaline white. Cercus within ranges observed for male.

SUBIMAGO

Only a few variously damaged specimens were available for study. In general, subimago has darker colours. Hyaline areas of imago grey or semi-hyaline in the subimago. Abdominal sterna of the female subimago hyaline with eggs clearly visible inside. Brown areas of imago more

diffuse in subimago. Abdominal pattern of female imago not exhibited in the subimago; an even brown colour present instead.

NYMPH (n=18)

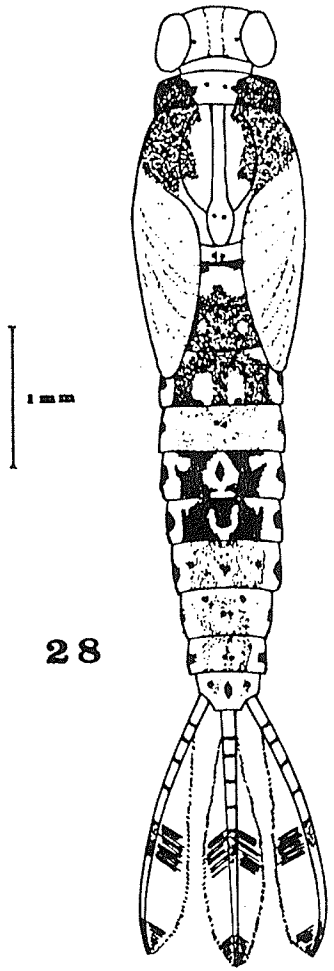
Total body length 5.1 (range 4.6-5.8). Dorsal colour pattern as in Fig. 28.

a)Head

Head light brown with mid-dorsal pair of stripes. Pore-like spot present near eye (Fig. 28). Antenna tan to hyaline; length 1.6 (range 1.4-1.7).

Labrum as in Fig. 29. Arrangement and number of setae on labrum variable. Mandibles orange-red distally, tan basally. Left mandible with canines fused over basal 1/3 or less (Fig. 30). Six denticles on outer canine, three on inner. Prostheca well developed, less than half as wide as one canine. Fringe of setae extending from base of canines to molar thumb. Right mandible with unfused canines, outer canine strongly bowed (Fig. 31). Prostheca a slender needle-like process. Fringe of setae extends from base of canines half way to molar area. Two rounded humps located on molar plane. First hump a semi-fused clump of setae located in a shallow depression just before the molar plane. Second hump a sclerotized projection on molar plane. This hump erodes with use and is therefore largest in newly moulted specimens. Rest of molar area elevated above distal margin of mandible. Distal

Figures 28-33. Structural features of Centroptilum album McDunnough mature nymphs. 28)Dorsal maculation. 29)Labrum. 30)Left mandible. 31)Right mandible. 32)Maxilla. 33)Labium.



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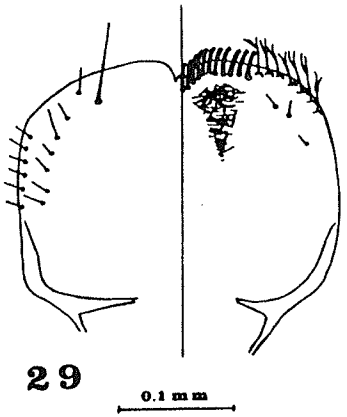

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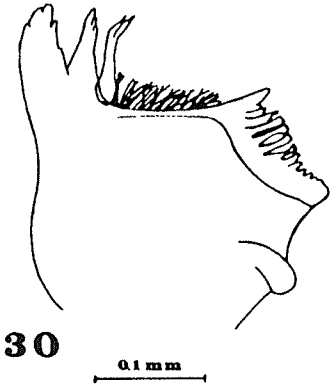

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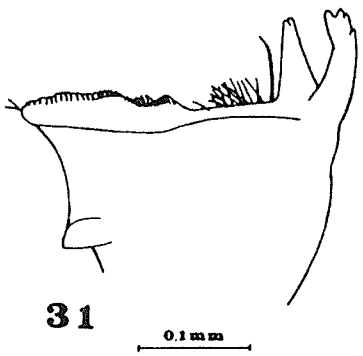

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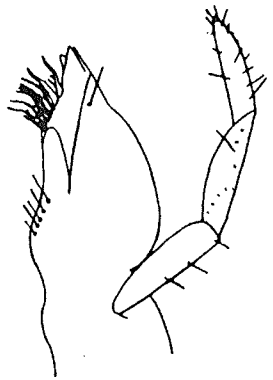

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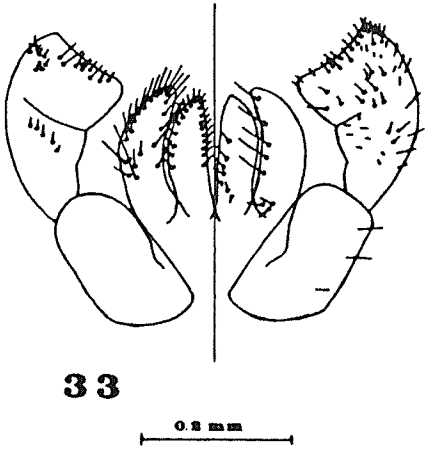


33

end of molar area with isolated clump of two or three setae. Maxilla with four biting teeth and a double row of setae extending along distal end (Fig. 32). Maxilla with one isolated seta near distal end below the biting teeth and a straight row of five setae more proximal in an area opposite the palp. Maxillary palp three-segmented; all palpomeres sub-equal. Palpomeres variously covered with both small and long setae, palpomere I with sparsest cover. Labium hairy (Fig. 33). Glossa shorter and straighter than paraglossa. Distal half of dorsal side of glossa with row of short setae along edge. Ventral side of glossa with few scattered setae along inner edge. Dorsal side of paraglossa with many long setae while setae on ventral side restricted to inner edge and base. Labial palp three-segmented, palpomere II weakly separated from palpomere III. Palpomere I rectangular with few scattered setae on ventral side. Palpomere II triangular, narrowest basally. Many setae ventrally, irregular row of five setae dorsally. Palpomere III very hairy ventrally, only in patches dorsally. Distal margin concave and slightly expanded inward.

b)Thorax

Thoracic terga dark brown laterally and white dorsally (Fig. 28). Sharp dividing line between these colours gives impression of a white mid-dorsal stripe. Paired mid-dorsal pores on tergum. Metanotum dark brown on posterior edge. Wingpads with hyaline brown markings resembling veins. Coxa light brown. Sterna hyaline to white. Leg tan to hyaline-brown. Femur with two dark brown patches dorsally, one distal of coxa and other proximal of tibia. Tibia with dorsal dark

brown patch near mid-length. Tarsus with dorsal dark brown patches at tibia and at claw. Claw brown, darker at tarsus. Relative leg segment lengths highly variable (Table 7). Tibia considerably longer or shorter than tarsus. Distal end of femur with few scattered hairs in a small row along dorsal edge. Tibia with distinct sub-proximal arc of setae across dorsal edge.

c)Abdomen

Posterior tergal spines short, wide, and rounded with little to no gap between spines. Terga with few scattered semi-circular hollows. Tergum IX lacking posterior tergal spines mid-dorsally and in some individuals this area projects posteriorly. Abdominal terga tan-brown, heavily marked with dark brown (Fig. 28). Male nymph on average lighter than female so that pattern can appear as series of dark circles with a dark dash inside. Tergum VI darkest in both sexes. Paired mid-dorsal pores on terga I, II, III, IV, VII, VIII, and IX. Additional lateral pores occur on terga VII, VIII, and X. Heavy patterning on at least sterna VII to IX. Paired mid-ventral pores also found on sterna II, VIII, and IX. Sternum VIII with two additional pairs of pores in a more lateral position. Some individuals lacking lateral spines but most have numerous very small spines (Table 3). Genital forceps of male visible as two small rounded extensions on posterior edge of sternum IX. Unilamellate gills on segments I to VII with simple venation (Fig. 13). Gills of segment I narrowest, progressively broader gills on more posterior segments. Gills fully rounded to sharply pointed. Gills usually slightly pointed. Earlier

Table 7. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Centroptilum album McDunnough (n=18).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	0.76	0.48	0.49	0.21
	r	0.64-0.89	0.41-0.55	0.42-0.53	0.14-0.25
	:	3.1-4.6	1.8-2.9	1.9-2.7	1
MESOTHORACIC	x	0.82	0.51	0.43	0.22
	r	0.77-0.91	0.47-0.55	0.39-0.47	0.19-0.27
	:	3.4-4.4	1.9-2.6	1.6-2.1	1
METATHORACIC	x	0.80	0.48	0.42	0.22
	r	0.69-0.89	0.39-0.55	0.37-0.47	0.20-0.25
	:	3.1-4.1	1.8-2.2	1.7-2.0	1

instars tend to have more sharply pointed gills. At least two most posterior pairs of gills with very minute spines along anterior edge. Cercus and median terminal filament tan hyaline with dark rings every fourth inter-segment. Dark brown band of segments in middle and at distal end. Cercal length 1.92 (range 1.78-2.03) (n=15). Median terminal filament length 1.77 (range 1.62-2.00) (n=17). Median terminal filament never longer than cercus.

SPECIMENS EXAMINED

CANADA

BRITISH COLUMBIA

Caltus Lake, (coll. J.K. Jacob) (CNIC): 15/X/1938, 1 female imago; 21/X/1938, 2 male imagines, 1 female imago.

Seton Lake, Lillooet, 50°42'N 121°56'W (coll. J. McDunnough) (CNIC): 28/V/1926, 1 female imago; 29/V/1926, 10 male imagines, 1 female imago; 30/V/1926, 17 male imagines, 1 female imago; 9/VI/1926, 1 male imago; 14/VI/1926, 3 male imagines.

MANITOBA

Churchill, 58°46'N 94°10'W (coll. W.J. Brown) (CNIC): 22/VII/1937, 1 male imago.

Cowan Creek, near Cowan, 51°59'N 100°40'W: 3/VI/1986, 6 nymphs (coll. S. Bernatski); 12/VI/1986, 65 nymphs and 3 exuviae (coll. S. Bernatski and R.G. Lowen); 19/VI/1986, 17 nymphs (coll. S. Bernatski

and R.G. Lowen); 24/VI/1986, 1 female subimago with exuvia, 11 nymphs and 1 exuvia (coll. S. Bernatski and R.G. Lowen); 10/VII/1986, 2 nymphs and 1 exuvia (coll. R.G. Lowen); 30/VII/1986, 4 male imagines with exuviae, 1 male subimago with exuvia, 3 female imagines with exuviae, 2 female subimagines with exuviae, 19 nymphs and 1 exuvia (coll. S. Bernatski and R.G. Lowen).

Ochre River, site 4, half way between the town of Ochre River and Dauphin Lake, 51°05'N 99°47'W, (coll. R.G. Lowen): 22/VII/1986, 1 female subimago with exuvia.

South Duck River, site 2, upstream from Hwy. 10, 51°52'N 100°37'W: 19/VI/1986, 2 nymphs, (coll. R.G. Lowen); 3/VII/1986, 1 male subimago with exuvia, 1 female imago with exuviae, 10 nymphs (coll. S. Bernatski and R.G. Lowen); 9/VII/1986, 1 nymph, (coll. R.G. Lowen); 10/VII/1986, 1 female imago with exuviae, (coll. R.G. Lowen); 23/VII/1986, 1 female subimago with exuvia, 7 nymphs, (coll. R.G. Lowen); 7/VIII/1986, 1 nymph, (coll. R. G. Lowen). Site 3, downstream from Hwy. 10, at power lines, 51°53'N 100°36'W, (coll. R.G. Lowen): 19/VI/1986, 5 nymphs; 9/VII/1986, 1 nymph.

NEW BRUNSWICK

Fredericton, 45°58'N 66°39'W (coll. J. McDunnough) (CNIC): 12/VI/1934, 1 male imago.

ONTARIO

Britannia, 45°22'N 75°48'W (coll. L.J. Milne) (CNIC): 15/VI/1931, 1 male imago.

Ottawa, at Ottawa Golf Club, 45°25'N 75°42'W (coll. J. McDunnough) (CNIC): 17/VI/1927, 3 male imagines; 24/VI/1927, 1 male imago.

Silver Creek, Orillia, 44°37'N 79°25'W (coll. C.H. Curran) (CNIC): 12/VI/1925, 2 female subimagines; 13/VI/1925, 1 female subimago; 29/VI/1926, 3 male imagines, 1 female subimago.

QUEBEC

Bradore Bay, 51°28'N 57°14'W (coll. W.J. Brown) (CNIC): 12/VII/1930, 3 male imagines; 14/VII/1930, 1 female imago; 26/VII/1929, 1 male imago; 31/VII/1930, 7 male imagines; 4/VIII/1930, 22 male imagines, 1 female imago; 6/VIII/1930, 1 male imago.

Chateauguay, 45°21'N 73°44'W (coll. F.P. Ide) (CNIC): 18/VI/1925, 1 male imago.

Knowlton, 45°13'N 72°31'W (coll. L.J. Milne) (CNIC): 2/VII/1930, 2 female imagines.

St. Anne, 48°27'N 71°04'W (coll. F.P. Ide) (CNIC): 24/VI/1925, 1 female imago.

Vaudreuil, 45°24'N 74°02'W (coll. G.S. Walley) (CNIC): 23/VI/1930, 13 male imagines; 25/VI/1930, 1 female imago.

DISTRIBUTION AND FIELD NOTES

In Manitoba, nymphs were collected from three streams, two of these, Ochre River and Cowan Creek, were described under previous sections. The third stream is the South Duck River and it is quite similar to but

slightly larger than Cowan Creek. The sites sampled on the South Duck River were subjected to flooding from nearby beaver dams and contained large amounts of mud and submerged vegetation. At all three rivers, nymphs were most often caught among the submerged riparian vegetation usually on muddy banks. The nymphs seemed to congregate in areas with at least a moderate current and occasionally in fast current areas. Nymphs were caught from early June till mid-August although specimens from British Columbia were labelled as caught in late May.

As well as the specimens examined as part of this study, this species is also recorded from North Carolina (Traver 1932) and from Bassin de la Rivire du Castor in northern Quebec (Harper and Harper 1981). In the literature this species was thought to be mostly eastern in distribution until Scudder (1975) examined the Canadian National Collection and published the records from British Columbia. These specimens were origially identified by J. McDunnough and upon examination of the British Columbia series, I concur with his identification. Therefore C. album has a trans-continental distribution and could very well be found in Alberta and Saskatchewan. The specimen from Churchill, Manitoba is the new northern record for the species (Fig. 34).

Figure 34. Known ranges of Centroptilum album McDunnough and C. conturbatum McDunnough.


● C. album
▲ C. conturbatum
NORTH AMERICA
0
500
MILES

Centroptilum conturbatum McDunnough

Centroptilum conturbatum McDunnough 1929, Can. Ent. 61: pp. 171-173.

Holotype- Cameron Lake, Waterton Lakes, Alberta, Canada, 49°06'N 113°54'W (coll. J. McDunnough) (no. 2985 CNIC): 20/VIII/1928, male imago.

Allotype- Cameron Lake, Waterton Lakes, Alberta, Canada, 49°06'N 113°54'W (coll. J. McDunnough) (CNIC): 20/VIII/1928, female imago.

Paratypes- Cameron Lake, Waterton Lakes, Alberta, Canada, 49°06'N 113°54'W (coll. J. McDunnough) (CNIC): 20/VIII/1928, 6 male imagines, 5 female imagines.

MALE IMAGO (n=8)

Total body length 4.7 (range 4.3-5.7).

a)Head

Most of head dark brown, almost black. Opaque white on vestigial mouthparts and two opaque white sub-dorsal stripes extending between the eyes. Antenna hyaline-brown with opaque white ring around the base. Disc of turbinate eye bright orange, narrow, width to length ratio 0.50 to 0.67. Stalk much paler, dark brown rings on basal portion. Stalk 0.23 mm tall.

b)Thorax

Pronotum unmarked dark brown. Mesonotum dark brown, edged posteriorly and at base of wing with opaque white. Metanotum dark brown, bordered on all sides with white, and with sublateral white spots. Prosternum dark brown, white rings around bases of leg. Mesosternum mostly dark brown, two sub-ventral white stripes and white ring around coxa. Metasternum similar to mesosternum but sub-ventral white stripes coalesce to form a single mid-ventral white stripe.

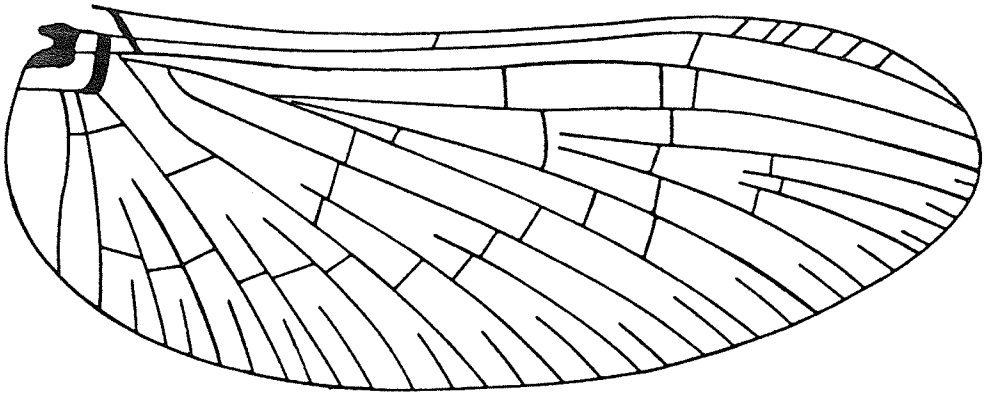
Leg hyaline white with brown coxa. Individual leg measurements variable (Table 8). Prothoracic leg 3.8 mm long. Tarsus five-segmented. Meso- and metathoracic legs 2.1 mm long. Femur usually longest leg segment but occasional individuals have tibia longer. Tarsus four-segmented. Claw similar on all legs.

Fore wing with length 4.8 (range 4.2-5.1) and width 1.8 (range 1.6-1.9). Fore wing hyaline, brown basally. Number of cross veins variable (Fig. 35). Four to nine cross veins between C and Sc. One to three (usually two) cross veins between Sc and R1 and between R1 and R2. Veins very long, especially intercalaries. R3 almost touches R2/R4+5 junction. MA2 extends past MA1/MP1 cross vein. IMP about equal in length to MP2. ICu1 slightly longer than ICu2. Hind wing as in Fig. 36. Length 0.82 (range 0.64-0.97); width 0.21 (range 0.17-0.27). Wing tips rounded; costal process strongly curved. Two veins extend length of wing, without cross veins.

Table 8. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of Centroptilum conturbatum McDunnough. Prothoracic legs are divided by sex (n= 8 males and 22 females).

		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	0.96	1.28	0.06	0.57	0.45	0.28	0.17
PROTHORACIC	r	0.89-1.06	1.14-1.44	0.03-0.12	0.30-0.73	0.25-0.61	0.23-0.34	0.14-0.19
	:	1.6-3.3	2.2-4.4	0.1-0.2	0.9-1.4	1	0.5-0.7	0.3-0.6
FEMALE	x	0.79	0.70	0.19	0.13	0.07	0.17	-
PROTHORACIC	r	0.69-0.94	0.59-0.91	0.16-0.23	0.11-0.17	0.05-0.08	0.11-0.20	-
	:	8.6-16.8	7.6-14.0	2.4-3.7	1.4-2.7	1	1.8-3.4	-
	x	0.88	0.72	0.19	0.10	0.06	0.17	-
MESOTHORACIC	r	0.67-1.08	0.62-0.89	0.14-0.25	0.08-0.16	0.05-0.08	0.12-0.22	-
	:	10.4-21.6	9.1-17.5	2.1-4.6	1.5-2.7	1	2.0-4.4	-
	x	0.89	0.73	0.17	0.10	0.06	0.17	-
METATHORACIC	r	0.75-1.02	0.61-0.87	0.11-0.23	0.08-0.13	0.03-0.08	0.14-0.19	-
	:	10.4-27.7	9.0-25.0	1.8-5.7	1.1-2.7	1	1.7-5.7	-

Figures 35-37. Structural features of Centroptilum conturbatum McDunnough imago. 35)Mesothoracic and metathoracic wings. 36)Detail of metathoracic wings, showing range of variation. 37)Male genitalia, dorsal view.



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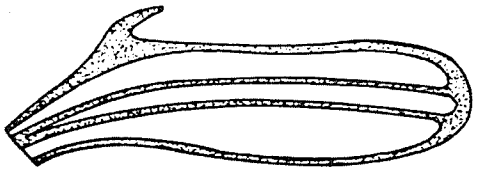
1 mm



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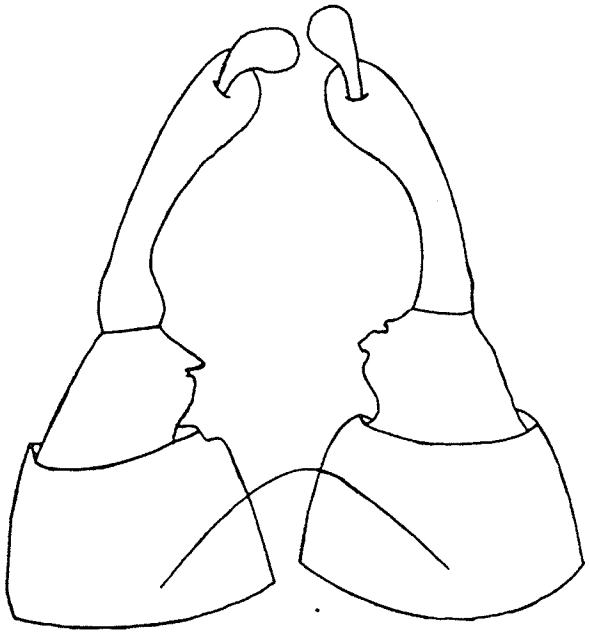
0.5 mm



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0.1 mm

c)Abdomen

Terga I and II semi-hyaline yellowish. Terga III to VI semi-hyaline white. Tergum VII opaque white with brown infusion. Terga VIII to X dark brown but lighter than thorax. In some individuals brown colour restricted to posterior 2/3 of tergum. Sterna I to VI hyaline-white. Sterna VII and VIII opaque-tan with hyaline sub-lateral lines. Sternum IX same colour as tergum IX. Cercus hyaline white. Cercal length 8.8 (range 7.8-10.1).

Basal segments of forceps brown and slightly broader than tall (Fig. 37). Irregularities along inner margins are common and can give appearance of tubercles. Forceps segments I, II, and III hyaline white. Segment I very hairy and about as long as wide. Very irregular inner margins with at least one distinct tubercle. Segment II strongly incurved and about twice as long as segment I. Segment III sub-equal to segment I. Penal plate brown, semi-circular to cone-shaped. No tubercle or process on penal plate.

FEMALE IMAGO (n=22)

Total body length 5.0 (range 4.1-6.3).

a)Head

Eye black. Head brown and unmarked. Some individuals with black markings along vestigial mouthparts. Antenna hyaline brown distally and opaque tan basally with brown markings.

b)Thorax

Pronotum light brown with red sub-dorsal spots. Mesonotum light brown dorsally with white along mid-dorsal anterior and posterior edges. Lighter brown laterally, some individuals strongly marked with opaque-white. Metanotum brown dorsally, hyaline laterally. Sterna opaque white mid-ventrally, clear hyaline laterally.

Leg resembles meso- and metathoracic legs of male (Table 8). Leg hyaline-white except for light brown meso- and metacoxa. Fore wing length 5.2 (range 4.6-6.2), width 1.8 (range 1.6-2.2) (n=18). Wing venation as in male but with occasional black markings in pterostigmal area. Hind wing length 0.82 (range 0.58-1.03) and width 0.20 (range 0.14-0.25). Similar shape as in male but costal process more erect and in most specimens not curved (Fig. 36).

c)Abdomen

Terga I to VI brown dorsally, semi-hyaline white laterally. In most individuals a sharp division between these colours. Terga VII to X similar but with narrow bands of red-brown mid-dorsally and posteriorly. Tergum X distinctly paler than other segments. Small red patches in posterior lateral positions of some individuals and can occur on any segment. Considerably darker brown in dried specimens. Sterna I to IX with narrow band of opaque-white mid-ventrally. Sternum I hyaline on anterior half and opaque-white on posterior half. Sterna II to VII semi-hyaline white which somewhat masks the eggs. Sterna VIII and IX translucent white with a brownish cast and with paired

sub-ventral hyaline lines. Cercus hyaline white. Cercus shorter than in male, length 6.8 (range 6.1-9.0).

SUBIMAGO

In general subimago resembles imago but colours more subdued. Reds and browns are paler or not yet expressed. Hyaline colours more opaque and an overall dark grey colour pervades.

NYMPH (n=18)

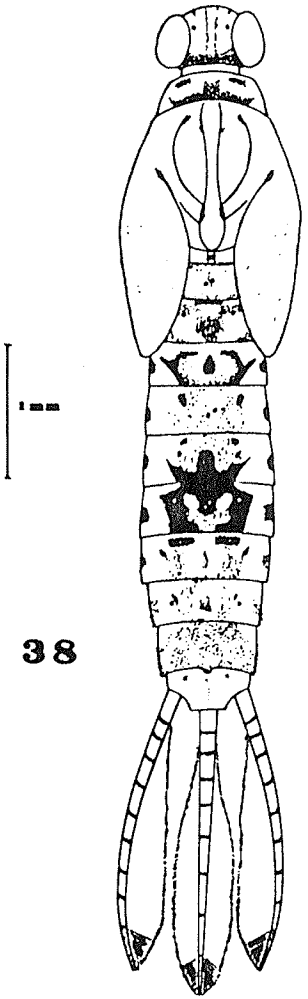
Total body length 5.4 (range 4.4-6.2). Dorsal colour pattern as in Fig. 38.

a)Head

Head brown with dark brown markings along posterior margin and in two sub-dorsal stripes. Pore-like spot located near eye. Antenna hyaline brown and 1.7 mm long (range 1.5-2.0).

Labrum as in Fig. 39. Arrangement and number of setae on labrum variable. Distal half of both mandibles orange-brown fading basally to same brown as rest of head. Canines of left mandible fused along basal half (Fig. 40). Three projecting denticles on inner canine and five on outer canine. Prostheca well developed, with at least three denticles. Width of prostheca less than 1/2 width of one canine. Fringe of setae extending from base of prostheca to base of molar thumb. Canines of right mandible completely divided (Fig. 41). Three denticles per

Figures 38-43. Structural features of Centroptilum conturbatum McDunnough mature nymph. 38)Dorsal maculation. 39)Labrum. 40)Left mandible. 41)Right mandible. 42)Maxilla. 43)Labium.



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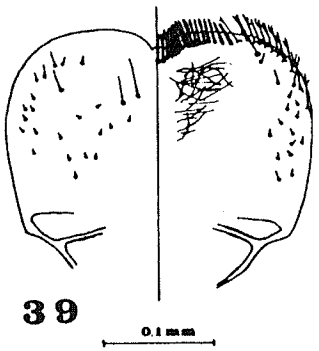

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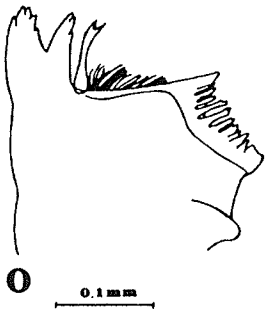

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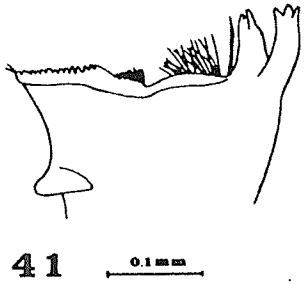

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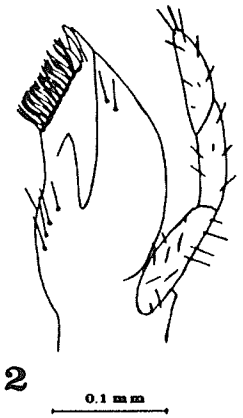

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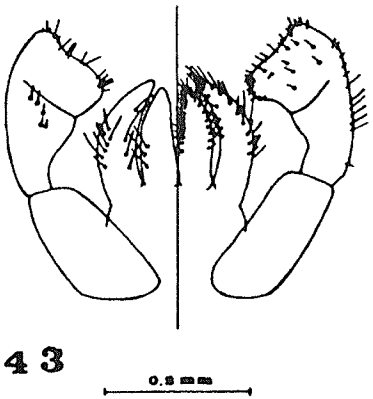


43

canine. Prostheca slender and spike-like. Fringe of setae extends from base of prostheca half way to molar area. Small hump of fused setae just before molar area. Secondary sclerotized hump on molar area itself. Second hump subject to wear. Rest of molar area flat. Isolated group of two or three setae on inner edge of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edge (Fig. 42). Distal group of two setae below level of biting teeth and proximal group of five setae in an irregular clump opposite palp. Maxillary palp slightly longer than maxilla. Palp three-segmented and covered with long setae. All palpomeres approximately equal in length. Labium hairy especially on glossa and paraglossa (Fig. 43). Glossa shorter and straighter than paraglossa. Ventral face of glossa with row of short setae along distal edge and along distal half of lateral edges. Ventral face of paraglossa with setae on distal half but setae longer and less restricted to edge. Dorsal face of glossa with a small clump of long setae located basally near outer edge. Dorsal face of paraglossa with a widely spaced row of long setae along inner margin and a small group of longer setae along outer edge. Labial palp three-segmented. Palpomere I rectangular and generally devoid of setae. Palpomere II narrowest at base and expanding distally. Palpomere II with distinct pattern of five setae dorsally and an irregular row of long setae ventrally along outer edge. Palpomere III truncate, wider than long. Distal edge concave with inner margin expanded in a rounded lobe. Dorsal setae on palpomere III restricted to near distal edge. Ventral side evenly covered with setae.

b)Thorax

Thoracic terga light brown to brown with scattered dark brown markings (Fig. 38). Pronotum with dark brown bands mid-dorsally and along posterior margin. Paired dark brown markings antero-laterally. Pair of pore-like spots present on either side of mid-dorsal line. Mesonotum light brown with only a few dark markings. Wing pads hyaline with brown hyaline markings resembling veins. Wing pads black in late instars. Metanotum with narrow brown markings along posterior edge and in two mid-dorsal lines. Pair of pore-like spots along these lines. Sterna light brown and unmarked.

Comparative leg segment lengths highly variable (Table 9). Leg semi-hyaline brown with dark brown dorsal markings. Coxa dark brown on prothorax but only brown or light brown on meso- and metathorax. Femur with dark brown patch just proximal to tibial joint and another distal to coxa. Tibia with brown patch along mid-length. Distal end of femur with a few scattered setae in small row along dorsal edge. Tibia with distinct sub-proximal arc of setae across dorsal edge. Tarsus with dark markings at each end. Claw darker than leg.

c)Abdomen

Terga light brown with brown to black markings (Fig. 38). Pattern stable but some individuals considerably lighter. Terga V and VI always darkest. Paired anterior dark patches on tergum VII. Terga with few scattered semi-circular hollows. Posterior tergal spines very tall and narrow, arranged in a non-contiguous row with occasional small spines in spaces. Posterior edge of tergum IX produced posteriorly

Table 9. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Centroptilum conturbatum McDunnough (n=18).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	0.84	0.52	0.54	0.28
	r	0.77-0.95	0.44-0.58	0.48-0.59	0.22-0.33
	:	2.5-3.7	1.6-2.3	1.6-2.3	1
MESOTHORACIC	x	0.88	0.51	0.48	0.30
	r	0.67-1.05	0.41-0.61	0.39-0.53	0.22-0.36
	:	2.0-4.3	1.2-2.4	1.2-2.2	1
METATHORACIC	x	0.90	0.54	0.48	0.30
	r	0.81-1.06	0.45-0.63	0.44-0.53	0.23-0.34
	:	2.5-3.5	1.4-2.1	1.4-2.0	1

into rounded hump lacking spines. Paired mid-dorsal pore-like spots found on terga I to VI and tergum VIII. Second pair of more lateral pores on terga II to VIII. Sterna light brown. Sterna I and II unmarked. Sterna III and IV with sub-lateral brown patches. Sterna V to VII with sub-lateral brown patches and with two pale brown patches along anterior edge. Sterna VIII and IX light, and unmarked. Lateral spines small, indistinct and variable in number (Table 3).
Unilamellate gills on segments I to VII (Fig. 14). At least two most posterior pairs of gills minutely serrated along anterior edge. Some individuals with serrations on all gills. Median terminal filament 1.9 to 2.4 mm long, always shorter than cerci which are 2.1 to 2.7 mm long. Cercus and median terminal filament hyaline brown with dark brown ring every fourth intersegment. Apical segments darker brown in some individuals.

SPECIMENS EXAMINED

CANADA

ALBERTA

Blairmore, 49°36'N 114°26'W (coll. J.H. Pepper) (CNIC): 28/VIII/1930, 1 male imago, 1 female imago.

Cameron Lake, Waterton Lakes, 49°06'N 113°54'W (coll. J. McDunnough) (CNIC): 20/VIII/1928, 1 male subimago.

BRITISH COLUMBIA

Cranbrook, 49°31'N 115°46'W: (coll. J.H. Pepper) (CNIC): 2/VIII/1930, 51 nymphs; 2/IX/1930, 19 male imagines, 15 female imagines.

Garnet Valley, Summerland, 49°39'N 119°33'W: 9/VI/1933, 1 male imago, 5 female imagines, 7 nymphs (coll. A.N. Gartrell and J. McDunnough) (CNIC); 13/VI/1933, 13 male imagines, 3 female imagines (coll. A.N. Gartrell) (CNIC); 17/VI/1933, 2 male imagines, 2 female imagines (coll. A.N. Gartrell) (CNIC); 2/VI/1934, 9 nymphs (coll. A.N. Gartrell) (CNIC); 4/VI/1934, 1 female imago (coll. A.N. Gartrell) (CNIC); 5/VI/1934, 1 male imago (coll. A.N. Gartrell) (CNIC); 2 nymphal exuviae labelled 536 R 387 and 536 R 389, Subimago 5/VI/1934, Adult 7/VI/1934, (coll. A.N. Gartrell) (CNIC).

Hope Mountains, 6000', 49°22'N 121°27'W (coll. A.N. Gartrell) (CNIC): 4/VIII/1932, 7 female imagines; 25/VIII/1932, 11 nymphs.

Jesmond, 51°16'N 120°58'W (coll. J.K. Jacob) (CNIC): 23/VIII/1937, 1 female imago.

MANITOBA

Cowan Creek, site 3, downstream from Duck Mountain Provincial Forest, 51°50'N 100°40'W, (coll. R.G. Lowen): 10/VII/1986, 2 female imagines with exuviae, 6 nymphs. Site 5, near Cowan, 51°59'N 100°40'W: 3/VI/1986, 1 nymph (coll. S. Bernatski); 10/VII/1986, 9 nymphs, (coll. R.G. Lowen).

Ochre River, site 4, half way between Ochre River and Dauphin Lake, 51°05'N 99°47'W, (coll. R.G. Lowen): 14/VII/1986, 2 nymphs.

South Duck River, site 1, just inside boundary of Duck Mountain Provincial Park, 51°52'N 100°40'W, (coll. R.G. Lowen): 10/VII/1986, 6 male imagines with exuviae, 1 male sub-imagine with exuvia, 13 female imagines with exuviae, 3 female subimagines with exuviae, 29 nymphs. Site 2, upstream from Hwy. 10, 51°52'N 100°37'W: 19/VI/1986, 1 male imago with exuviae, 1 male subimago with exuvia, 3 female imagines with exuviae, 27 nymphs; 3/VII/1986, 2 male imagines with exuviae, 5 female imagines with exuviae, 3 female subimagines with exuviae, 16 nymphs; 7/VII/1986, 1 female imago with exuviae; 23/VII/1986, 1 female imago with exuviae, 5 nymphs; 7/VIII/1986, 1 nymph. Site 3, downstream from Hwy. 10, at power lines, 51°53'N 100°36'W, (coll. S. Bernatski): 19/VI/1986, 17 nymphs.

DISTRIBUTION AND FIELD NOTES

The Manitoba specimens were collected at Cowan Creek, Ochre River, and South Duck River. All of these rivers have been described in previous sections. All previous records of this species are from high altitude mountainous areas. The Manitoba sites represent a low altitude record for the species. Even in Manitoba, this species is more common in upstream sites, especially in areas with cold water springs. On the South Duck River, the species was most common nearer the head-waters and was rare in beaver dam areas. The Ochre River is the warmest of the three rivers and only two nymphs were found there in spite of intense collecting. Within a given reach, the nymphs were

most often located on submerged riparian vegetation. In Manitoba, nymphs were found from early June to early August.

As well as the specimens examined, the species has been reported from Moose, Wyoming and Waddell Creek, California (Needham et al. 1935). The species is clearly western in distribution with the Manitoba sites representing the eastern and northern limits of the range (Fig. 34). The distribution is quite similar to but more montane than that of C. bifurcatum. The two species probably have different post-glacial histories. This will be examined in greater detail in later sections.

Pseudocentroptilum Bogoescu

Pseudocentroptilum Bogoescu, C.D. 1947. Bull. Sect. Sci. Acad. Roum. 29: 602-604

Keffermller, M., and R. Sowa. 1984. Pol. Pismo Ent. 54: 309-340

Cloeoptilum Kazlauskas, R.S. 1969. Trudy XIII Mezhdunarod. Ent. Kongressa, Moskva, 2-9 avgusta 1968, Leningrad, 3: 337-338 (invalid formal description)

Type Species: Pseudocentroptilum motasi Bogoescu, by original designation.

IMAGO

Diagnostic characters of imago include: male genital forceps with distal segment small and forceps with shelf-like division between basal segment and segment I.

Constituent characters of imago include: fore wing with single marginal intercalaries, hind wing present, costal process present, hind wing with two or three longitudinal veins, penal plate with distal margin round or truncate, and no process between basal segments of forceps.

NYMPH

Diagnostic characters of nymph include: maxillary palpomere III half as long as palpomere II and weakly separated, canines of left mandible fused for more than half of length, gills without serrations, lateral spines on at least abdominal terga VIII and IX, and lateral spines large.

Constituent characters of nymph include: canines of right mandibles fused for two-thirds length or less, hind wing pads present, gills unilamellate or bilamellate, gills distinctly asymmetric, few or no pore-like spots on abdominal terga, no mid-dorsal posterior projection of tergum IX.

Pseudocentroptilum rufostrigatum(McDunnough) comb. nov.

Centroptilum rufostrigatum McDunnough 1924, Can. Ent. 56: pp. 95-96.

Needham, Travers, and Hsu 1935, Mayflies of North America: p. 717 (redescribes male imago).

Burks 1953, Bull. Illinois Nat. Hist. Surv. 26: p. 120 (describes female imago).

Centroptilum bistrigatum Daggy 1945, Ann. Ent. Soc. Am. 38: p. 389 (describes nymph).

Holotype- Aweme, Manitoba, Canada, 49°43'N 99°38'W (coll. R.M. White) (no. 676 CNIC): 30/IX/1923, male imago.

Paratypes- Aweme, Manitoba, Canada, 49°43'N 99°38'W (CNIC): 8/IX/1923, 2 male imagines (coll. N. Criddle); 30/IX/1923, 10 male imagines (coll. R.M. White). Treesbank, Manitoba, Canada, 49°38'N 99°38'W (CNIC): 22/IX/1923, 1 male imago (coll. R.M. White).

MALE IMAGO (n=4)

Total body length 4.7 (range 4.1-5.8).

a)Head

Disc of turbinate eye light orange with brown rings along edge. Approximately 0.50 times as wide as long. Stalk paler, 0.20 mm tall.

Non-turbinate eye and ocelli black. Antenna hyaline brown throughout. Most of head chestnut brown, paler on vestigial mouthparts.

b)Thorax

Thoracic terga darker brown than head, slightly paler mid-dorsally. Sterna dark brown. In some individuals sterna paler than terga with white patch mid-ventrally on metasternum.

Leg white semi-hyaline, basally opaque. Leg segment lengths variable (Table 10). Prothoracic leg 3.7 mm long. Protarsus five-segmented. Meso- and metathoracic legs subequal, over 2.1 mm long. Tarsus four-segmented. Fore wing length 4.4 (range 4.0-4.9), width 1.7 (range 1.5-1.9). Fore wing hyaline, basally brown (Fig. 44). Five to seven cross veins between C and Sc, two or three between Sc and R1 and between R1 and R2. Vein length variable. MA2 does not extend past MA1/MP1 cross veins. IMP extends to MP1/CuA cross vein. Vein lying in between R3 and R4+5 extends almost to junction of R2 and R4+5. Hind wing as in Fig. 45. Length 0.81 (range 0.69-0.91), width 0.14 (range 0.11-0.16). Wing tip comes to a rounded point or broadly rounded. Costal process either strongly rounded or highly erect. Two veins extend length of wing, without cross veins.

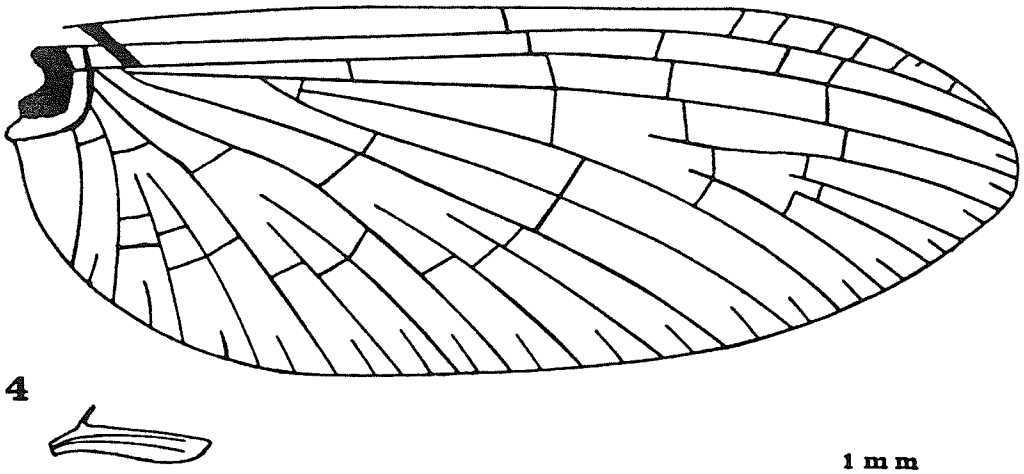
c)Abdomen

Terga I to VI hyaline with broken black spiracular line along lateral margin. Terga VII to X evenly chestnut brown, similar to head. Paired red dashes lying sub-dorsally along posterior margin of at least terga I to III and in some individuals extending through to tergum X.

Table 10. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of *Pseudocentroptilum rufostrigatum* (McDunnough). Prothoracic legs are divided by sex (n= 4 males and 6 females).

		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	0.90	1.20	0.05	0.66	0.45	0.23	0.17
PROTHORACIC	r	0.83-0.94	1.12-1.30	0.04-0.06	0.61-0.69	0.42-0.47	0.22-0.25	0.16-0.19
	:	1.8-2.2	2.4-2.8	0.1	1.4-1.5	1	0.5	0.3-0.4
FEMALE	x	0.83	0.83	0.33	0.17	0.07	0.17	-
PROTHORACIC	r	0.78-0.89	0.78-0.86	0.31-0.38	0.16-0.19	0.06-0.08	0.16-0.17	-
	:	9.7-13.3	9.7-14.3	3.9-6.2	2.0-2.7	1	2.0-2.8	-
	x	0.84	0.73	0.32	0.12	0.05	0.16	-
MESOTHORACIC	r	0.75-1.05	0.62-0.83	0.27-0.37	0.11-0.13	0.03-0.06	0.14-0.16	-
	:	15.0-27.7	12.5-27.7	5.2-10.0	1.8-4.3	1	2.3-5.3	-
	x	0.84	0.70	0.26	0.11	0.05	0.15	-
METATHORACIC	r	0.64-1.03	0.55-0.84	0.09-0.35	0.06-0.14	0.03-0.06	0.12-0.17	-
	:	12.8-22.0	12.5-18.3	3.0-7.0	1.2-2.8	1	2.5-4.2	-

Figures 44-46. Structural features of Pseudocentroptilum rufostrigatum (McDunnough) imago. 44)Mesothoracic and metathoracic wings. 45)Detail of metathoracic wings, showing range of variation. 46)Male genitalia, dorsal view.



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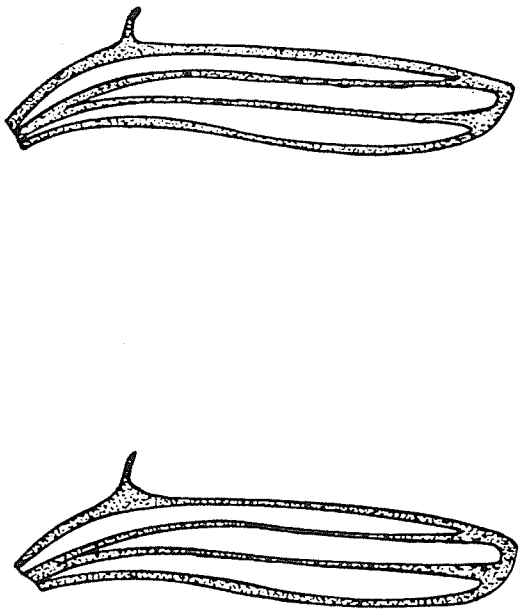
1 mm



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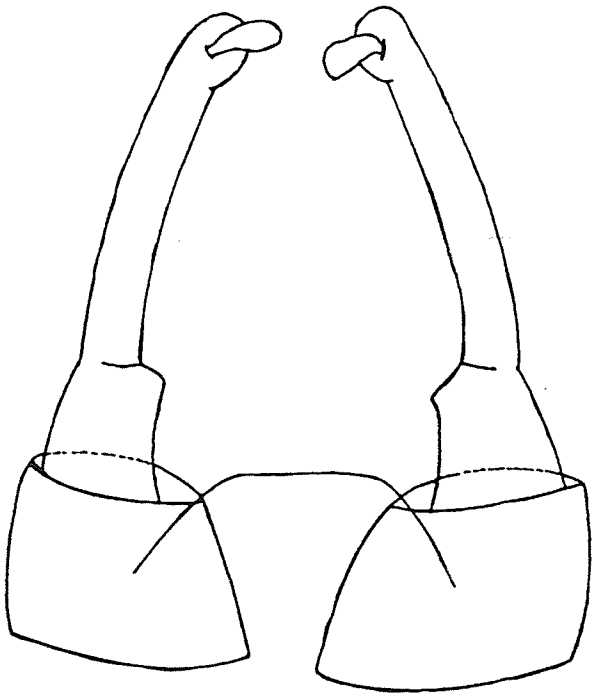
0.5 mm



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0.1 mm

Sterna I and II semi-hyaline white with yellowish cast. Sterna III to VI hyaline, unmarked. Sterna VII to IX opaque white with brownish cast. Cercus hyaline white. Cercal length 7.7 (range 6.1-8.6).

Basal segments of forceps tan. Near contiguous basally, diverging distally (Fig. 46). Smooth inner margin, shelf-like division with segments I. Segments I to III semi-hyaline white. Segment I slightly shorter than basal segment, approximately half as wide. Shelf-like divisions between segments I and II. Segment II 2.5 to 3.0 times as long as segment I, about half as wide. Segment III tear-drop shaped, about half as long as segment I. Penal plate tan and trapezoidal. No process on penal plate.

FEMALE IMAGO (n=6)

Total body length 5.0 (range 4.2-6.0). Colour of these females is the most variable of any of the Manitoba species.

a)Head

Head olive-tan, in some specimens alabaster white laterally and dorsally. Antenna hyaline brown distally, olive-tan basally. Eye black with greenish sheen, quickly fades to black when preserved.

b)Thorax

Pronotum opaque white dorsally, tan sub-dorsally, opaque white laterally. Mesonotum opaque white with mid-dorsal tan area. Pronotum and mesonotum tan throughout in some individuals. Metanotum alabaster

white anterior to and on metascutellar hump. Tan posterior to meta-scutellar hump. Prosternum opaque white mid-ventrally becoming hyaline laterally. Mesosternum semi-hyaline white throughout. Metasternum tan.

Leg tan distally, hyaline white basally. All three pairs of legs resemble meso- and metathoracic legs of male (Table 10). Fore wing length 5.3 (range 4.9-5.7), width 2.1 (range 1.9-2.2). Fore wing hyaline to semi-hyaline. Venation as in male. Hind wing length 0.87 (range 0.72-0.94), width 0.16 (range 0.12-0.19). Shape and venation as in male.

c)Abdomen

Terga I to VIII semi-hyaline tan to chestnut brown. Some individuals with eggs visible through terga. Terga IX and X alabaster white in lighter specimens, opaque tan in darker forms. Distinctive hyaline markings on these segments as follows: tergum IX with hyaline mid-dorsal and sub-lateral stripes, tergum X with "M" shaped hyaline marking with base on posterior edge and with small dome-shaped hyaline marking mid-dorsally on posterior edge. Sub-lateral red marks on posterior edge of anterior-most segments, up to tergum IX. These marks variable; very bright, very pale, or totally absent. Broken black spiracular line and purple-black tracheal veins present. Cercus semi-hyaline. Cercal length 7.7 (range 6.9-8.2).

SUBIMAGO

Subimago resembles imago. Colours more subdued with browns and reds barely noticeable, hyalines opaque. Posterior red marks on abdominal terga still noticeable, at least in male. Wing steel-grey. Hind wing venation and shape as in imago, most consistent means of identifying subimago.

NYMPH (n=5)

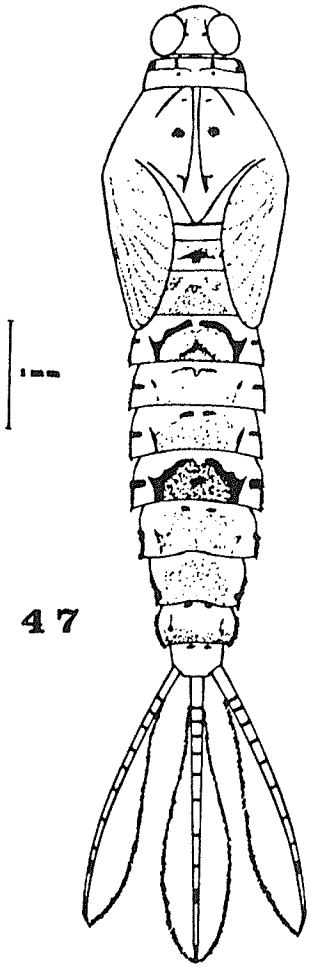
Total body length 6.1 (range 5.2-6.5). Dorsal colour pattern as in Fig. 47.

a)Head

Head tan or brown. Antenna semi-hyaline and easily broken even in living specimens. Arc of setae around the dorso-anterior half of base of antenna. Pore-like spot beside dorsal margin of eye.

Labrum as in Fig. 48. Arrangement and number of setae on labrum variable. Mandible orange brown distally, fading to tan basally. Canines of left mandible fused for basal 1/2 of length (Fig. 49). Three denticles on each canine. Prostheca well developed, about 1/2 width of one canine. Fringe of setae extending from base of canines to base of molar thumb. Plane of molar area markedly depressed. Canines of right mandible completely divided and with outer canine strongly curved (Fig. 50). Three denticles on each canine. Prostheca thin but not needle-like. Fringe of setae extending from base of canines almost to molar area. Two rounded humps located on molar plane. First hump a

Figures 47-52. Structural features of Pseudocentroptilum rufostrigatum (McDunnough) mature nymph. 47)Dorsal maculation. 48)Labrum. 49)Left mandible. 50)Right mandible. 51)Maxilla. 52)Labium.



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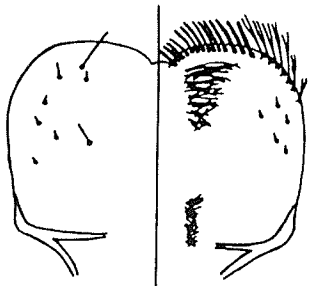

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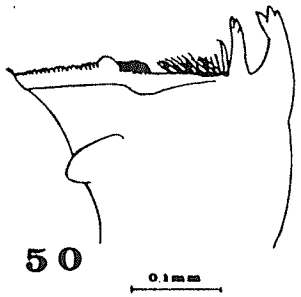

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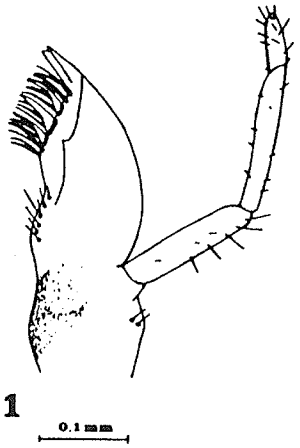

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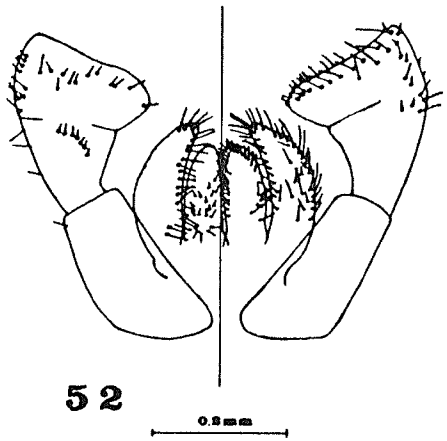


52

semi-fused clump of cerci located in a shallow depression just before the molar plane. Second hump a sclerotized projection on the molar plane. This hump erodes with use and is therefore largest in newly moulted specimens. Rest of molar area elevated above distal margin of mandible. Isolated clump of two or three setae present on distal end of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edge (Fig. 51). No group of setae basad to the biting teeth but there is a proximal group of seven setae opposite the palp. An additional group of two setae just basad to palp. Dark brown area directly opposite base of palp. Maxillary palp longer than galea-lacinia. Palp three-segmented with numerous short spines. Palpomeres I and II sub-equal. Palpomere I with several long setae in addition to short spines. Palpomere III about 1/3 length of palpomere II, weakly separated from it. Labium hairy (Fig. 52). Glossa shorter than paraglossa. Dorsal face of glossa with numerous short setae over basal 2/3. Ventral face of glossa with row of setae along distal and inner margin as well as a group of setae along outer edge. Dorsal face of paraglossa with row of setae along distal and inner margin. Ventral face with row of long setae along all edges and scattered singly throughout. Labial palp three-segmented. Palpomere I almost rectangular, setae present on some individuals. Palpomere II sub-triangular, narrowest at base, only weakly separated from palpomere III. Some individuals with long setae along outer edge of palpomere II and always has arc of seven setae on dorsal face near distal edge. Palpomere III truncate, some individuals with concave distal margin. Inner margin slightly expanded inwards into a rounded

lobe. Many short setae along outer margin. Very many setae at distal margin of ventral face and near but not at distal margin of dorsal face.

b)Thorax

Dorsal colour pattern as in Fig. 47. Paired subdorsal spots resembling pores on pronotum. Comparative lengths of leg segments variable (Table 11). Leg light tan with small dark brown spot near distal end of femur. Femur with distinct arc of long setae near distal margin and along dorsal edge. Tibia with distinct sub-proximal arc of long setae mostly along dorsal edge but bending slightly across edge. Wing pads semi-hyaline tan becoming black in final moults. No markings on wing pads.

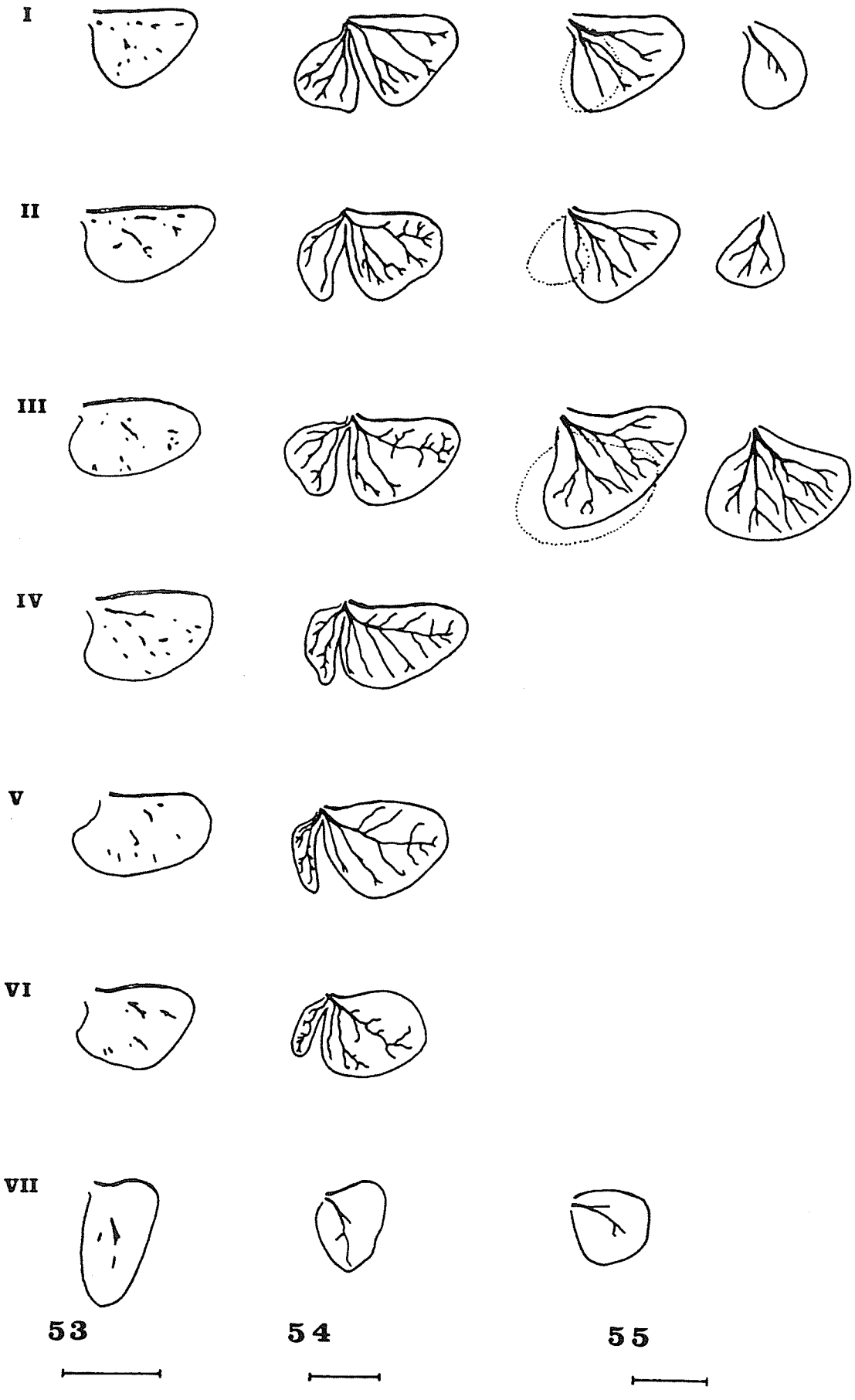
c)Abdomen

Posterior tergal spines very long and narrow but unevenly spaced, interspersed with many smaller spines in staggered rows. All terga with numerous semi-circular hollows. Paired mid-dorsal spots resembling pores on segment VI. Lateral spines large and variable in number (Table 3). Segment X with thin hair-like spines occasionally present. Genital forceps of male visible in mature nymph as two small rounded extensions on posterior edge of sternum IX. Unilamellate gills on segments I to VII broadly asymmetrical (Fig. 53). Gills semi-hyaline whitish with veins marked black in isolated sections giving impression of spotted gills. Gills lack serrations. Median terminal filament length 2.4 (range 2.2-2.8). All three with dark

Table 11. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Pseudocentroptilum rufostriqatum (McDunnough) (n=4).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	0.97	0.59	0.59	0.43
	r	0.92-1.13	0.52-0.67	0.56-0.69	0.39-0.47
	:	2.0-2.9	1.1-1.7	1.2-1.8	1
MESOTHORACIC	x	1.08	0.59	0.59	0.48
	r	0.94-1.30	0.52-0.75	0.53-0.67	0.47-0.49
	:	2.0-2.7	1.2-1.6	1.2-1.4	1
METATHORACIC	x	1.04	0.53	0.57	0.47
	r	0.95-1.22	0.44-0.70	0.50-0.67	0.41-0.50
	:	1.9-2.5	0.9-1.5	1.0-1.4	1

Figures 53-55. Abdominal gills of mature nymphs. Scale lines equal 0.5 mm. 53)Pseudocentroptilum rufostrigatum (McDunnough). 54)P. infrequens (McDunnough). 55)P. quaesitum (McDunnough).


I
II
III
IV
V
VI
VII
53
54
55

bands every fourth intersegment.

SPECIMENS EXAMINED

CANADA

MANITOBA

Aweme, 49°43'N 99°38'W (CNIC): 9/VII/1984, 1 male imago, 1 female imago (coll. N. Criddle); 18/VIII/1924, 1 male imago (coll. R.M. White); 19/IX/1924, 1 male imago (coll. R.M. White).

Darlingford, 49°13'N 98°34'W (coll. N. Criddle) (CNIC): 6/VII/1924, 5 male imagines.

Marchand, 49°27'N 96°22'W (coll. N. Criddle) (CNIC): 25/VII/1928, 2 male imagines.

North Pine River, just upstream from Hwy. 10, 51°48'N 100°34'W (coll. R.G. Lowen): 21/VII/1985, 1 nymph.

Ochre River, site 4, half way between Ochre River and Dauphin Lake, 51°05'N 99°47'W (1984 specimens collected for Dauphin Lake Rehabilitation Project, Freshwater Institute, Winnipeg) (all 1984 specimens FWISL): 9/VII/1984, 1 male imago; 11/VII/1984, 1 male imago, 5 male subimagines, 1 female imago, 5 female subimagines; 13/VII/1984, 1 male imago, 2 male subimagines, 1 female imago, 3 female subimagines; 1/VIII/1984, 3 female imagines, 2 female subimagines; 8/VIII/1984, 1 female imago; 10/VIII/1984, 1 male imago; 13/VIII/1984, 1 male imago, 1 female imago; 5/IX/1984, 1 female imago; 14/VII/1986, 1 nymph and 1 exuvia (coll. R.G. Lowen); 22/VII/1986, 2

nymphs (S. Bernatski coll.); 29/VII/1986, 3 nymphs (coll. R.G. Lowen); 2/VIII/1986, 1 female subimago with exuvia (coll. R.G. Lowen); 6/VIII/1986, 1 female imago with exuvia, 1 nymph (coll. R.G. Lowen); 3/IX/1986, 1 nymph and 2 exuviae (coll. R.G. Lowen); 24/IX/1986, 3 nymphs (coll. R.G. Lowen); 9/VII/1987, 4 nymphal exuviae (coll. R.G. Lowen).

NEW BRUNSWICK

Fredericton, 45°58'N 66°39'W (coll. W.S. Brown) (no. 114 CNIC): 16/VII/1928, 6 male imagines, 24 female imagines.

ONTARIO

Walsh, 42°44'N 80°22'W (coll. G.S. Walley) (CNIC): 10/VII/1925, 1 male imago.

DISTRIBUTION AND FIELD NOTES

In Manitoba, nymphs were collected in the North Pine River and in the Ochre River. These sites have been previously described. Nymphs were rare and I had to rely heavily on adults caught in emergence traps. Nymphs were not found in the smaller streams and adults have all been caught near a large or medium sized river. This is consistent with most records for the species in the literature.

Specimens not examined by me have been reported from Manitoba, Minnesota, Wisconsin, Michigan, northern Quebec, Pennsylvania,

Kentucky, Illinois, and Maryland. In Manitoba the species has also been reported from the Rouseau River (Friesen et al. 1980; Flannagan and Flannagan 1982). Daggy (1945) reported the species as widespread in Minnesota and abundant on the Mississippi River. Burks (1953) reported the species as being known from Wisconsin and observed specimens from Kankakee and Oakwood, Illinois. In Michigan, the species is reported from the Au Sable River in Crawford County (Leonard and Leonard 1962). In northern Quebec, the species was found in Bassin de la Rivire du Castor (Harper and Harper 1981). In Kentucky, specimens were found in Morgan's Creek, Meade County (Minshall 1967) and in Pennsylvania they were found in White Clay Creek (Sweeney and Vannote 1978). Finally, two specimens have been collected from Harpers Ferry, Maryland (Needham et al. 1935). The total distribution is therefore northeastern United States and southeastern Canada (Fig. 56). The North Pine River is the new western limit of the species.

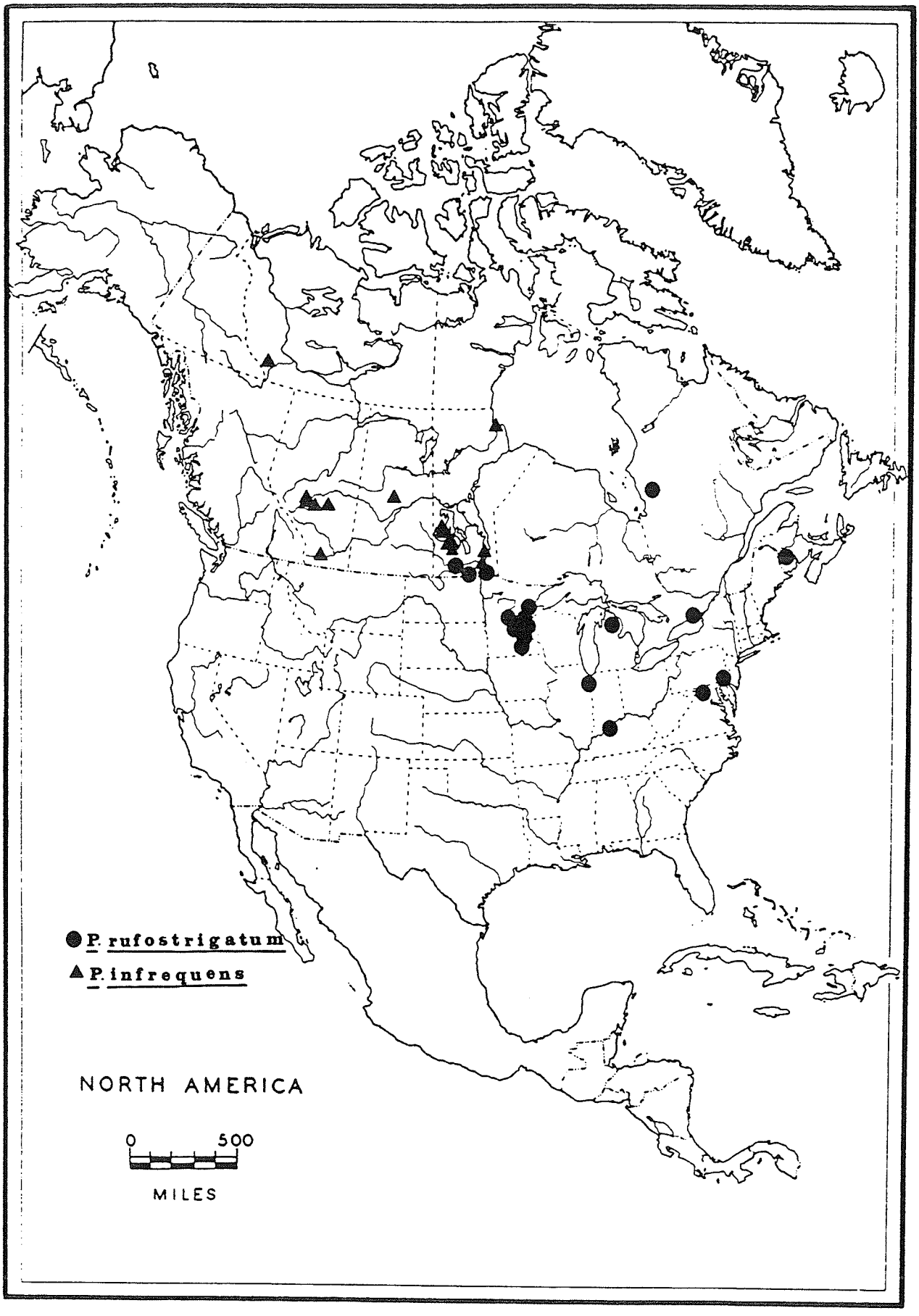
Pseudocentroptilum infrequens (McDunnough) comb. nov.

Centroptilum infrequens McDunnough 1924, Can. Ent. 56: 98.

McDunnough 1931, Can. Ent. 63: 87 (in discussion of C. quaesitum).

Holotype- Winnipeg Beach, Manitoba, Canada, 50°30'N 97°57'W (coll. J. Hunter) (no. 695 CNIC): 10/VII/1923, female imago.

Figure 56. Known ranges of Pseudocentroptilum rufostrigatum (McDunnough) and P. infrequens (McDunnough).


P. rufostrigatum
P. infrequens
NORTH AMERICA
0
500
MILES

MALE IMAGO (n=24)

Total body length 8.5 (range 7.3-10.0).

a)Head

Turbinate eye bright orange, slightly divergent. Disc of turbinate eye broadly oval, 0.67 to 0.75 as wide as long. Stalk of eye paler, 0.4 to 0.5 mm tall. Non-turbinate eye and ocelli black. Antenna smoky at base, translucent distally. Rest of head yellow-white to yellow-brown, red on vestigial mouth parts of some individuals.

b)Thorax

Pronotum unmarked creamy-tan. Mesonotum and metanotum light brown laterally and paler dorsally, in some individuals an opaque white mid-dorsal stripe. Entire thorax with terga reddish along lateral margins. Some individuals lack red. Thoracic sterna pale tan to opaque white, coxa slightly darker.

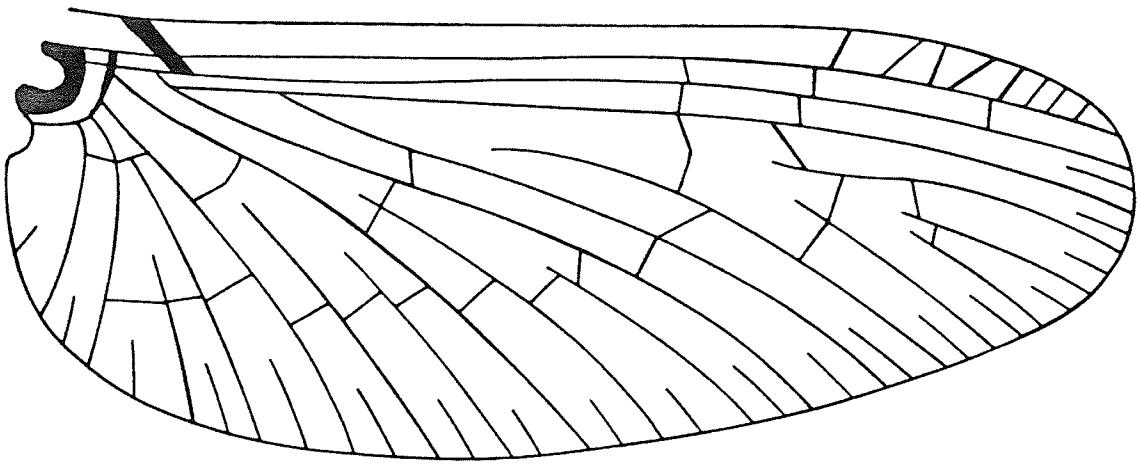
Leg hyaline white distally, yellowish proximally. Individual leg measurements highly variable (Table 12). Prothoracic leg 7.0 to 7.5 mm long. Protarsus five-segmented. Meso- and metathoracic legs near 4 mm length. Tarsi four-segmented.

Fore wing length 9.0 (range 8.1-10.3), equal to or longer than body length. Fore wing hyaline, basally yellow. Pterostigma translucent white, no clearing on cross veins. Wing about 3 times longer than wide (Fig. 57). Length 9.0 (range 8.1-10.3), width 3.2 (range 2.9-3.6).

Table 12. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of *Pseudocentroptilum infrequens* (McDunnough). Prothoracic legs are divided by sex (n= 24 males and 25 females).

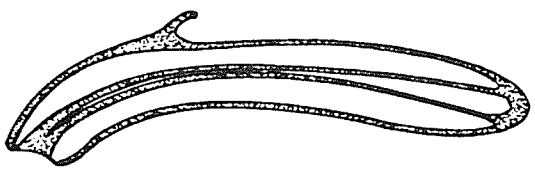
		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	2.14	2.19	0.10	1.24	0.90	0.48	0.31
PROTHORACIC	r	1.88-2.40	2.00-2.36	0.08-0.12	0.90-1.80	0.84-0.96	0.44-0.56	0.28-0.34
	:	2.1-2.7	2.1-2.8	0.1	1.0-2.2	1	0.5-0.6	0.3-0.4
FEMALE	x	2.06	1.45	0.60	0.32	0.15	0.32	-
PROTHORACIC	r	1.80-2.24	1.20-1.74	0.50-0.72	0.28-0.36	0.10-0.16	0.28-0.40	-
	:	12.0-19.4	8.6-17.2	3.7-6.4	1.9-3.2	1	1.8-3.5	-
	x	1.72	1.23	0.51	0.22	0.10	0.27	-
MESOTHORACIC	r	1.36-2.16	1.12-1.30	0.46-0.62	0.18-0.26	0.08-0.12	0.24-0.30	-
	:	12.3-26.4	10.3-16.2	4.8-7.7	1.9-3.2	1	2.3-3.7	-
	x	1.83	1.29	0.50	0.21	0.09	0.28	-
METATHORACIC	r	1.44-2.28	1.14-1.52	0.44-0.60	0.19-0.24	0.06-0.10	0.24-0.36	-
	:	15.8-27.0	11.8-19.3	4.4-7.2	2.1-3.5	1	2.5-3.9	-

Figures 57-59. Structural features of Pseudocentroptilum infrequens (McDunnough) imago. 57)Mesothoracic and metathoracic wings. 58)Detail of metathoracic wings, showing range of variation. 59)Male genitalia, dorsal view.



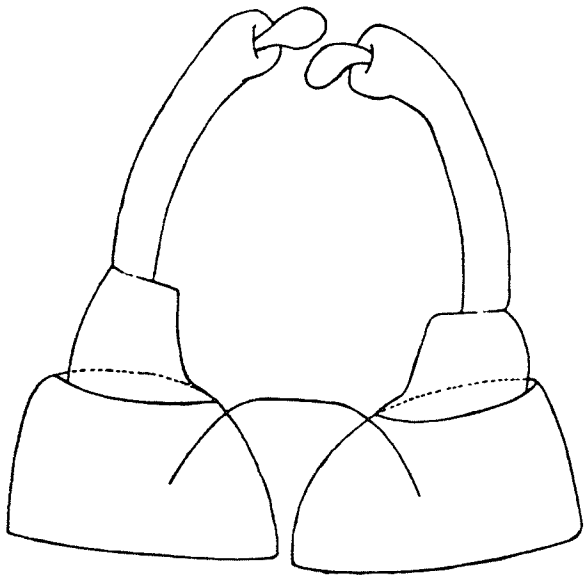
57

1 mm



58

0.5 mm



59

0.1 mm

Number of cross veins variable. Four to sixteen cross veins between C and Sc (median =7). One to four cross veins between Sc and R1, an intercalary present in some individuals. Two to four cross veins between R1 and R2, an intercalary present in most individuals. MA2 reaches at least MA1/MP1 cross vein, extending past in most individuals. MP2 longer than IMP and in some individuals both extend as folds to the CuA/MP1 cross veins. Individuals with these folds have MA2 extending past MA1/MP1 cross vein and a higher number of cross veins in pterostigmal area. Small intercalary present basad to A1 in some individuals. Hind wing as in Fig. 58. Length 0.95 (range 0.70-1.30). Width not highly variable, ratio of length to width varies from 5.0 to 8.5. Costal process long and curved, begins after basal third of wing length. Two veins on hind wing can be separate over entire length or fused up to just before costal process.

c)Abdomen

Posterior margin of terga I to VIII with solid red-brown line. Terga I to VI semi-hyaline. Tergum I with red markings dorso-posteriorly. Terga VII to X, and in some individuals half of VI, light brown with a dorsal scarlet stripe or a series of red wedges, widest posteriorly. Note that this red colour varies considerably and can be entirely absent or only present as a red wash. Scarlet colour, when present, is an infusion rather than a pattern. Broken black spiracular line present in some individuals. Sterna I to VI semi-hyaline, unmarked. Sterna VII to X opaque tan to opaque white, reddish markings

laterally in some individuals. Cercus hyaline white. Cercal length 14.0 (range 11.0-17.0).

Basal segments of forceps tan and broader than long (Fig. 59). Basal segments near contiguous basally but diverging distally. Forceps segments I, II, and III hyaline white. Segment I as long as basal segment but half as wide. Segment I weakly separated from segment II, with a distinct shelf between them. Segment II narrowest basally, expanding slightly distally. Segment II three times length of segment I and strongly curving inwards. Segment III tear-drop shaped, clearly separated from segment II. Segment III about half length of segment I. Penal plate opaque tan with a red brown posterior edge, truncated with rounded edges.

FEMALE IMAGO (n=25)

Total body length 9.5 (range 7.7-10.9) (n=19).

a)Head

Head colouration as in male, most specimens with more red than male. In some individuals two red stripes extend posteriorly from ocelli. Antenna smoky at base, translucent distally.

b)Thorax

Thorax light brown. Pronotum of some individuals with red dorsally. Edges of mesonotum and metanotum opaque white. Posterior edge of metathorax opaque white with red anterior of white patch. Leg colour

as in male. Leg resembles meso- and meta-thoracic legs of male (Table 12). Fore wing with length 10.0 (range 9.5-11.0). Wing venation as in male. Hind wing as in male. Length 1.1 (range 0.7-1.3).

c)Abdomen

Abdomen markedly different from male. Terga tan or light brown. Posterior edge of terga I to VII black. Terga VIII to X with bright scarlet overlay, some individuals with sub-dorsal hyaline areas in sub-dorsal pairs. Terga I to VII with bright red dorsal stripe or series of unconnected red wedges with the widest part on posterior edge of tergum. As in the male, red colour can be absent or present only as red wash and is an infusion of colour rather than a pattern. Red is never completely absent except in alcohol-preserved specimens. Sterna I to VII hyaline, unmarked, with eggs clearly visible. Sterna VIII and IX translucent white with red tinges, in some individuals marked with opaque white. Cercus hyaline white and slightly longer than male.

SUBIMAGO (n=16)

Colours of head and thorax much as in imago except that hyaline areas of imago are semi-hyaline or opaque white in sub-imago. Male coloured as follows: posterior margins of terga black; terga I to VI opaque light brown or white in some individuals; terga VII to X light brown or brown with slight or no red markings; sterna I to IX opaque white with no other markings; cercus and forceps white. Female coloured as in imago except hyaline and sub-hyaline areas of imago are

opaque white in subimago. Red abdominal stripe absent in most specimens.

NYMPH (n=52)

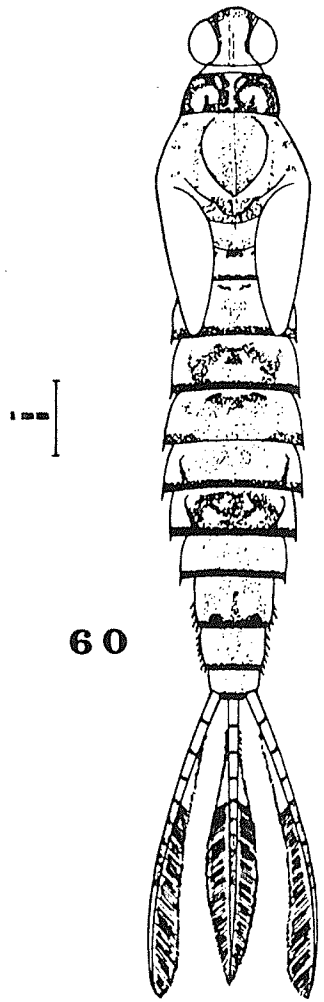
Total body length 9.2 (range 8.0-10.5). Dorsal colour pattern as in Fig. 60.

a)Head

Head light brown with dark band bordering dorsal half of compound eye. Antenna semi-hyaline, 2.0-2.5 mm long. Arc of numerous short setae surrounding the dorso-anterior half of base of antenna.

Labrum with black basal edge (Fig. 61). Arrangement and number of setae on labrum variable. Distal half of both mandibles orange-brown semi-hyaline brown basally. Canines of left mandible almost totally fused (Fig. 62). Four projecting denticles on each canine. Prostheca well developed, with five denticles. Width of prostheca equal to 1/4 width of fused canines. Tuft of setae extending for 1/2 distance from base of canines to molar area. Large molar thumb. Canines of right mandible slightly divided, fused for 3/4 length (Fig. 63). Three denticles per canine, prostheca with four denticles. Prostheca slender, being only 1/8 width of fused canines. Tuft of setae extending half way from base of canines to molar area. Plane of molar area parallel to but slightly raised above level of distal edge of mandibles. Secondary tuft of partially fused setae present around edge of molar area closest to canines. Isolated group of two or three setae

Figures 60-65. Structural features of Pseudocentroptilum infrequens (McDunnough) mature nymph. 60)Dorsal maculation. 61)Labrum. 62)Left mandible. 63)Right mandible. 64)Maxilla. 65)Labium.



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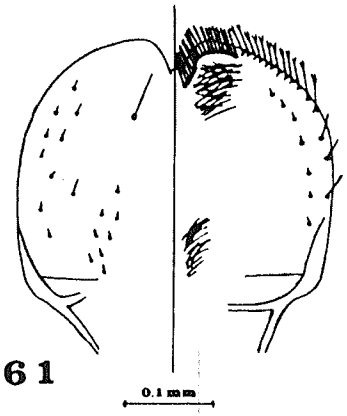

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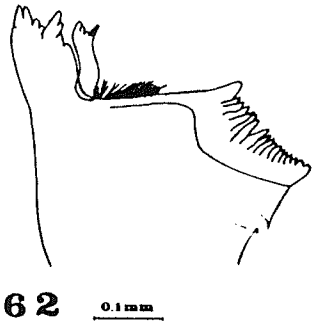
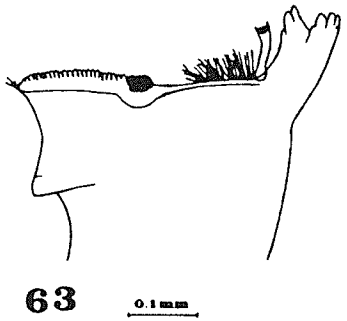


62



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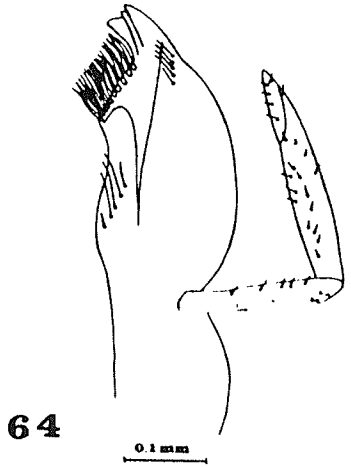
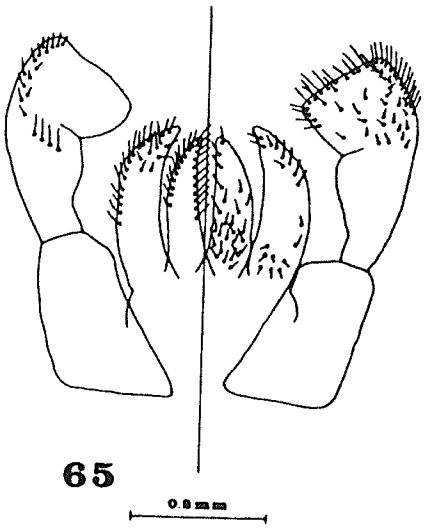


64



65

present on other end of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edge (Fig. 64). Distal group of five setae below level of biting teeth and proximal group of five setae opposite palp. Maxillary palp slightly longer than galea-lacinia. Palp three-segmented with numerous spines. Palpomeres I and II sub-equal, palpomere III 1/2 or less length of palpomere II. Palpomere III partially fused to II. Labium hairy especially glossa and paraglossa (Fig. 65). Glossa slightly shorter than paraglossa. Dorsal face of glossa with row of setae along distal edges. Ventral face with dense cluster of setae at proximal half and scattered setae distally. Dorsal face of paraglossa with row of setae along outer edge and scattered setae at distal tip. Ventral face with broken row of setae along outer edge. Labial palp three-segmented but palpomere II partially fused to palpomere III. Palpomere II narrowest basally, expanding distally. Dorsal face of palpomere II with straight row of five short setae near distal end. Palpomere III truncate but not broadly expanded and only slightly excavated. Palpomere III with staggered row of setae along outer edge of dorsal face. Ventral face with row of setae along outer and distal edge as well as scattered setae over surface.

b)Thorax

Thoracic terga light brown with dark brown or black markings (Fig. 60). Pronotum consistently with pattern resembling paired spirals. Sterna white to pale brown. Wing pads off-white to light brown, without markings. Comparative lengths of leg segments highly variable

(Table 13); legs similar in colour. Coxa dark brown or black, femur light tan with dorsal dark patch near each end. Femur with subapical, but poorly defined row of long, fine setae. Tibia and tarsus brown with pale patch where they join. Tibia with subproximal row of long setae and long dorsal row of setae. Small unornamented spine subtends the tarsus. Claw brown with dark patch at tarsal joint and with few, extremely small setae along surface.

c)Abdomen

Terga light brown, posterior margins black, with dark brown or black dorsal pattern (Fig. 60). Pattern darkest on segments II, III, V, and VI. Posterior tergal spines very long and narrow, evenly spaced with gaps and one small spine in between. Occasionally even smaller spines between small and long spines. Terga with numerous semi-circular hollows. Lateral spines large and variable in number (Table 3). Sterna white to light tan with lateral patches of brown. Sternum IX evenly brown. Brown stripe along anterior edge of sterna III to VIII or at least VI to VIII. Genital forceps of male visible in mature nymph as two small rounded extensions on posterior edge of sternum IX. Gills hyaline white with dark brown or black veins. Gills on segments I to VII, bilamellate on segments I to VI, unilamellate on segment VII (Fig. 54). Secondary lamella largest on segment I, decreasing in size posteriorly. Gills lack serration. Paraprocts tan with dark spines. Median terminal filament 3.5-4.0 mm long, cercus slightly longer, (3.7-4.5 mm). All three light brown with dark brown segment every fourth inter-segmental membrane. Band of dark segments across middle

Table 13. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Pseudocentroptilum infrequens (McDunnough) (n=52).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	2.17	0.95	1.04	0.49
	r	2.04-2.36	0.85-1.14	0.96-1.08	0.42-0.56
	:	3.8-5.4	1.6-2.7	1.9-2.5	1
MESOTHORACIC	x	2.03	0.99	0.97	0.53
	r	1.74-2.32	0.90-1.08	0.92-1.00	0.40-0.64
	:	2.9-5.1	1.6-2.5	1.6-2.3	1
METATHORACIC	x	2.05	0.92	0.87	0.56
	r	1.88-2.20	0.84-0.98	0.78-0.94	0.48-0.62
	:	3.2-4.5	1.7-2.0	1.5-2.0	1

of cercus and median terminal filament. Lateral fringes of setae light brown in basal half and dark brown over distal half.

SPECIMENS EXAMINED

CANADA

ALBERTA

Battle River, Hwy. 21 at campground north of New Norway, 52°57'N 112°58'W (coll. L.D. Corkum): 15/VI/1979, 5 nymphs.

Lethbridge, 49°42'N 112°50'W (coll. J.H. Pepper) (CNIC): 15/VIII/1929, 1 female imago; 8/VII/1930, 1 female imago.

Medicine River, Hwy. 766 just north of Eckville, 52°57'N 114°22'W (coll. L.D. Corkum): 14/VI/1979, 5 nymphs.

Pembina River, just north of Lodgepole, 53°08'N 115°19'W (coll. J. Ciborowski): no date, 3 nymphs. At Pembina River Provincial Park, Entwistle, 53°38'N 114°59'W (coll. J. Ciborowski): 28/VI/1979, 22 nymphs; 14/VII/1979, 1 male subimago, 2 female subimagines, 3 nymphal exuviae.

MANITOBA

Churchill, 58°46'N 94°10'W (coll. W.J. Brown) (CNIC): 1/VIII/1937, 1 male imago.

Cowan Creek, near Cowan, 51°59'N 100°40'W (coll. R.G. Lowen): 3/VI/1986, 3 nymphs; 24/VI/1986, 2 male imagines with exuviae, 3 female imagines with exuviae, 19 nymphs; 10/VII/1986, 1 female imago

with exuviae; 30/VII/1986, 2 female imagines with exuviae, 2 female subimagines with exuviae, 1 gyandromorph imago with exuviae, 3 nymphs.

Little Ochre River, just inside boundary of Riding Mountain National Park, 50°56'N 99°47'W (coll. R.G. Lowen): 15/VII/1985, 1 male imago with exuviae, 1 male subimago with exuvia, 1 female subimago with exuvia; 17/VII/1985, 1 female imago with exuviae, 1 female subimago with exuvia; 19/VII/1985, 2 male imagines with exuviae, 2 female imagines with exuviae, 2 female subimagines with exuviae, 2 nymphs; 24/VII/1985, 3 male imagines with exuviae, 1 male subimago with exuvia, 4 female imagines with exuviae, 1 female subimago with exuvia, 22 nymphs; 26/VII/1985, 1 male imago with exuviae, 1 female imago with exuviae, 1 female subimago with exuvia, 10 nymphs; 6/VIII/1985, 2 male imagines with exuviae, 1 male subimago with exuvia, 1 female imago with exuviae; 2/VII/1986, 6 nymphs.

North Pine River, by Hwy. 10 bridge, 51°48'N 100°34'W (coll. R.G. Lowen): 9/VII/1986, 1 nymph; 30/VII/1986, 4 nymphs.

Ochre River, site 4, half way between Ochre River and Dauphin Lake, 51°05'N 99°47'W (coll. R.G. Lowen): 17/VI/1986, 6 nymphs; 14/VII/1986, 4 nymphs; 22/VII/1986, 1 female imago with exuviae; 29/VII/1986, 3 nymphs; 3/IX/1986, 1 nymph. Site 5, at mouth of Ochre River, 51°07'N 99°46'W (coll. R.G. Lowen): 10/VI/1986, 2 nymphs.

South Duck River, by Hwy. 10 bridge, 51°53'N 100°37'W (coll. R.G. Lowen): 30/VII/1985, 1 male imago with exuviae, 1 female imago with exuviae; 9/VII/1986, 6 nymphs. Site 1, just inside boundary of Duck Mountain Provincial Park, 51°52'N 100°40'W (coll. R.G. Lowen): 10/VII/1986, 1 female imago with exuviae, 1 nymph. Site 2, upstream

from Hwy. 10, 51°52'N 100°37'W (coll. R.G. Lowen): 19/VI/1986, 17 nymphs; 3/VII/1986, 9 male imagines with exuviae, 7 female imagines with exuviae, 1 nymph; 7/VII/1986, 1 female imago with exuviae; 9/VII/1986, 2 male imagines with exuviae, 1 female imago with exuviae, 2 nymphs; 23/VII/1986, 1 male imago with exuviae, 1 male subimago with exuvia, 41 nymphs; 7/VIII/1986, 4 male imagines with exuviae, 5 male subimagines with exuviae, 7 female imagines with exuviae, 6 female subimagines with exuviae, 68 nymphs. Site 3, downstream from Hwy. 10, at power lines, 51°53'N 100°36'W (coll. R.G. Lowen): 3/VII/1986, 39 nymphs.

Wilson Creek, just inside Riding Mountain National Park, 50°43'N 99°33'W (coll. R.G. Lowen): 24/VII/1985, 1 nymph; 26/VII/1985, 1 male imago with exuviae, 1 female imago with exuviae; 7/VIII/1985, 1 female imago with exuviae.

NORTHWEST TERRITORIES

Nahanni River, Nahanni National Park, 61°35'N 125°20'W (coll. R. Wickstrom): no date, 1 male subimago (FWISL).

SASKATCHEWAN

Lavallee Lake, Prince Albert National Park, 54°18'N 106°34'W (coll. unknown): 30/VII/1929, 1 female imago (ROMC).

DISTRIBUTION AND FIELD NOTES

In Manitoba, nymphs of P. infrequens were caught at Cowan Creek, South Duck River, North Pine River, Ochre River, Little Ochre River, and Wilson Creek. Most of these sites have already been described in previous sections. Little Ochre River and Wilson Creek are small spring fed streams with a loose shale substrate interspersed with large boulders. The sites sampled are in Riding Mountain National Park and are therefore pristine. During drought the streams can be reduced to a series of pools with only hyporheic flow. P. infrequens was the only Centroptilum or Pseudocentroptilum species caught at either site and it was often caught in large numbers. The species has not yet been caught in any large river in Manitoba. It is usually found in quiet backwaters or on the downstream face of large boulders. P. infrequens seems to be associated with the same areas of a stream where members of the family Gerridae (Hemiptera) congregate. The gerrids provide a good visual cue when searching for P. infrequens. Nymphs were observed in the water from early June to mid September.

There are no records of this species other than those specimens examined as part of this study. The distribution of the species is in northern and western Canada (Fig. 56) (Flannagan and Flannagan 1982). No specimens have been previously reported for Saskatchewan and the Northwest Territories. The single specimen from the Northwest Territories represents the new northern and western limits of the species.

Pseudocentroptilum quaesitum (McDunnough) comb. nov.

Centroptilum quaesitum McDunnough 1931, Can. Ent. 63: 87.

Burks 1953, Bull. Illinois Nat. Hist. Surv. 26: 120-121 (redescribes male imago).

Holotype- Seven Persons Creek, Medicine Hat, Alberta, Canada, 50°03'N 110°40'W (coll. J.H. Pepper) (no. 3279 CNIC): 17/VI/1930, male imago with subimaginal exuvia.

Allotype- Seven Persons Creek, Medicine Hat, Alberta, Canada, 50°03'N 110°40'W (coll. J.H. Pepper) (CNIC): 17/VI/1930, female imago with subimaginal exuvia.

Paratypes- Seven Persons Creek, Medicine Hat, Alberta, Canada, 50°03'N 110°40'W (coll. J.H. Pepper) (CNIC): 12/VI/1930, 1 male imago; 17/VI/1930, 2 male imagines, 3 female imagines.

MALE IMAGO (n=1)

Aside from pinned specimens, only one male imago was examined. This was a specimen reared from a nymph. As pinned specimens could not be accurately measured, all quantitative measurements except for wing venation are taken from the one fresh specimen. Total body length 6.8 mm.

a)Head

Head yellow-tan. Antenna opaque yellow basally, hyaline red- brown distally. Disc of turbinate eye bright yellow, ratio of width of disc to length is 0.75. Stalk light orange to tan and 0.41 mm tall. Nonturbinate eye and ocelli black.

b)Thorax

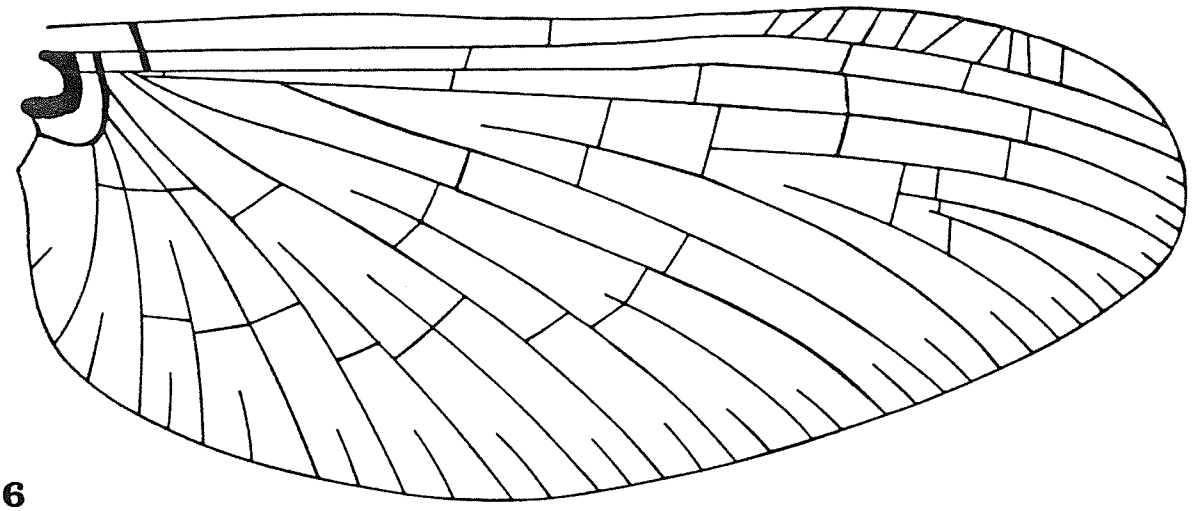
Pronotum red-brown with opaque white mid-dorsal area. Mesonotum opaque white, olive-tan dorsally. Metanotum olive-tan, alabaster white stripe extending laterally through metascutellar hump. Dried specimens reddish anterior of this stripe and paler posterior of this stripe. Prosternum yellow-brown, meso- and metasternum yellow white. Sterna tinged reddish in dried specimens. Coxa olive-tan. Leg semi-hyaline yellow. Leg measurements see Table 14. Prothoracic leg 6.7 mm long. Tarsus five-segmented. Meso- and metathoracic legs near 3.8 mm long. Tarsus four-segmented.

Fore wing 8.2 mm long and 3.4 mm wide. Fore wing yellow basally. Pterostigma semi-hyaline white. Six to eleven cross veins between C and Sc, two to four between Sc and R1 and between R1 and R2 (Fig. 66). MA2 extends past MA1/MP1 cross vein. MP2 longer than IMP. ICu1 very long, extending to base of wing. Hind wing 1.19 mm long and 0.28 mm wide (Fig. 67). Costal process narrow and very curved or partially erect.

Table 14. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments in imagines of Pseudocentroptilum guaesitum (McDunnough). Prothoracic legs are divided by sex (n= 1 male imago and 1 female subimago).

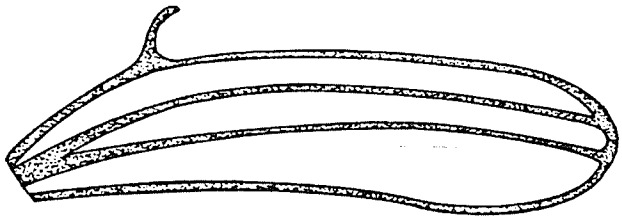
		FEMUR	TIBIA	TARSUS 1	TARSUS 2	TARSUS 3	TARSUS 4	TARSUS 5
MALE	x	1.88	2.12	0.08	0.94	0.81	0.53	0.28
PROTHORACIC	r	-	-	-	-	-	-	-
	:	2.3	2.6	0.1	1.2	1	0.7	0.3
FEMALE	x	1.31	1.28	0.41	0.30	0.14	0.28	-
PROTHORACIC	r	-	-	-	-	-	-	-
	:	9.4	9.1	2.9	2.1	1	2.0	-
	x	1.54	1.18	0.41	0.25	0.11	0.29	-
MESOTHORACIC	r	1.44-1.64	1.14-1.22	0.41	0.23-0.27	0.09-0.13	0.28-0.30	-
	:	13.1-16.0	9.6-12.7	3.3-4.6	2.2-2.6	1	2.4-3.1	-
	x	1.57	1.24	0.39	0.24	0.10	0.28	-
METATHORACIC	r	1.52-1.62	1.17-1.31	0.31-0.47	0.22-0.25	0.09-0.11	0.27-0.30	-
	:	14.8-16.7	10.6-14.6	2.8-5.2	2.3-2.4	1	2.7-3.0	-

Figures 66-68. Structural features of Pseudocentroptilum quaesitum (McDunnough) imago. 66)Mesothoracic and metathoracic wings. 67)Detail of metathoracic wings, showing range of variation. 68)Male genitalia, dorsal view.



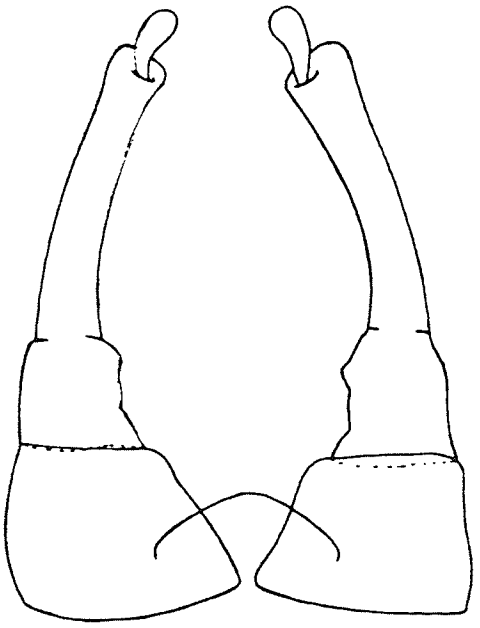
66

1 mm



67

0.5 mm



68

0.1 mm

c)Abdomen

Terga I to VI yellow-olive. Posterior margin of tergum I red-brown. Each of terga II to IX with scarlet marking resembling a round edged "W" with its base on posterior edge. Terga VII to IX opaque white with hyaline mid-dorsal stripe and hyaline oval sub-dorsal lines. Tergum X yellow-olive with opaque mid-dorsal white stripe and two lateral white stripes originating from centre of anterior edge and diverging posteriorly. Small scarlet patch at junction of white lines. Many dried specimens have this pattern obscured into generalised dorsal red area with narrow pale lateral area. Sternum I opaque yellow-tan. Sterna II to VI semi-opaque yellow-tan. Sterna VII and VIII opaque white with large paired sub-dorsal hyaline spots anteriorly; small paired sub-dorsal hyaline spots posteriorly. Sternum IX yellow-tan, two large opaque white spots sub-dorsally. Cercus hyaline white. Cercus 15.4 mm.

Basal segments of forceps semi-hyaline yellow, slightly broader than long (Fig. 68). Near contiguous basally but diverging distally. Forceps segments I, II, and III hyaline white when fresh but red-brown in dried specimens. Shelf-like division between basal segments and segment I and between segments I and II. Segment I 3/4 as long as basal segment. Segment II 2 1/2 times as long as segment I. Segment III tear-drop shaped and roughly 1/2 as long as segment I. Penal plate olive-yellow and semi-circular.

FEMALE IMAGO

No fresh female imagines were observed. The following colour descriptions were taken from pinned material in the Canadian National Collection.

a)Head

Most of head yellow-tan as in male. Eye black. Antenna opaque yellow basally, red-brown distally.

b)Thorax

Pronotum unmarked light brown. Mesonotum olive-white. Metanotum olive-white anterior of metascutellar hump, white posterior of hump. All sterna semi-hyaline white. Leg hyaline yellow-brown. Wing slightly yellowish basally; pterostigma whitish. Venation as in male.

c)Abdomen

Posterior margin of terga I to X red-brown. Terga I to VI white with slight mid-dorsal red-brown shading. Terga VII to X opaque white with pale hint of red "W's" observed in male. Each of sterna I to VI hyaline white on anterior half and opaque white on posterior half. Terga VII to IX opaque white with sub-dorsal hyaline lines.

SUBIMAGO

No male subimago and only one female subimago were observed. This specimen had died before the colours darkened so that little colour

characteristics could be determined. Remnant markings of the scarlet W's were observed as a series of dark pigmented spots. Colour scheme probably similar to pinned imago.

Total body length 9.2 mm. Cerci missing at time of capture. Wing steely-grey with short fringes along posterior edge. Fore wing 8.5 mm long, 3.1 mm wide. Six cross veins between C and Sc. Three cross veins between Sc and R1, two between R1 and R2. Hind wing as in male imago except for colour and fringes. Hind wing 1.06 mm long and 0.25 mm wide. Length of leg segments as in Table 14.

NYMPH (n=2)

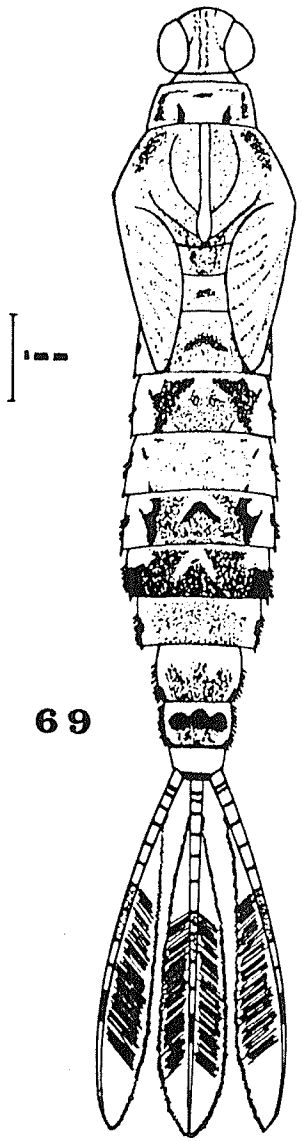
Two mature male nymphs and one immature nymph were observed. Observed body lengths were 9.3 and 7.9 mm for the mature nymphs. Dorsal colour pattern as in Fig. 69.

a)Head

Head light brown with darker markings around the eye and in two sub-dorsal stripes. Antenna hyaline brown, 3.6-2.7 mm long.

Labrum as in Fig. 70. Mandibles dark orange- brown distally, light brown basally. Canines of left mandible almost totally fused (Fig. 71). Four denticles on inner canine, three on outer. Prostheca well developed with five denticles. Width of prostheca greater than 1/4 width of fused canines. Setae extend from base of canines halfway to molar area. Molar area strongly tilted basad. Canines of right mandible slightly divided (Fig. 72), fused for more than 3/4 of length.

Figures 69-74. Structural features of Pseudocentroptilum quaesitum (McDunnough) mature nymph. 69)Dorsal maculation. 70)Labrum. 71)Left mandible. 72)Right mandible. 73)Maxilla. 74)Labium.



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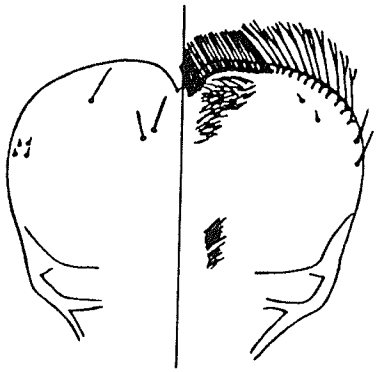

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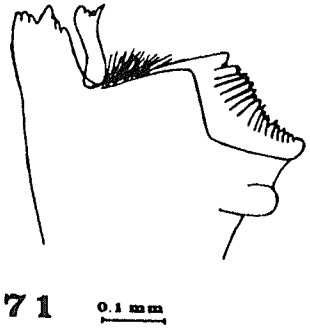

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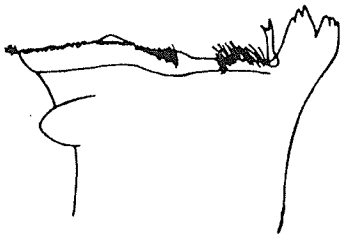

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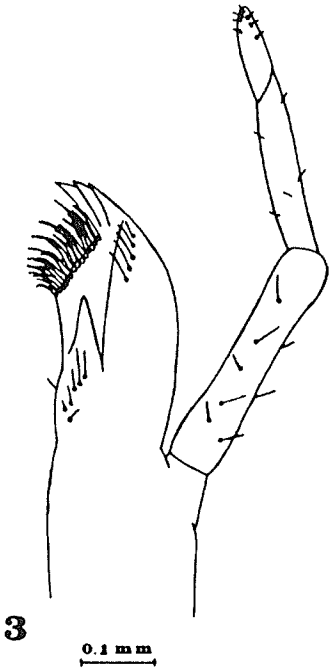

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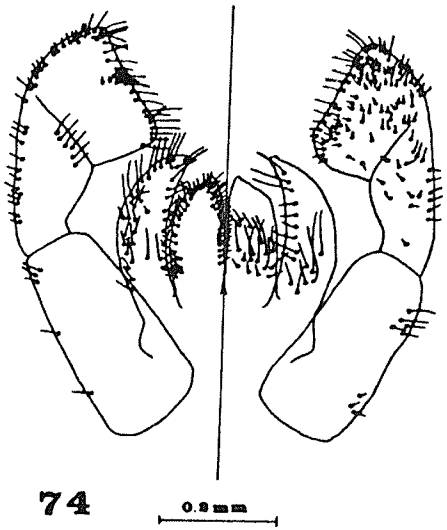

74

Three denticles on each canine. Prostheca narrow, approximately 1/2 width of left prostheca. Fringe of setae extends from base of canines half way to molar area, deflecting downwards to form a curved arc. Two rounded humps located on molar plane. First hump a semi-fused clump of cerci located in a shallow depression just before the molar plane. Second hump a sclerotized projection on molar plane. This hump erodes with use and is therefore largest in newly moulted specimens. Rest of molar area elevated above distal margin of mandible. Isolated clump of five or six setae on distal end of molar area. Maxilla with four widely spaced biting teeth and double row of setae along distal edges (Fig. 73). Distal group of five setae below level of biting teeth and proximal group of six or seven setae opposite the palp. Maxillary palp slightly longer than galea-lacinia. Palp three-segmented with short spines distally and longer spines proximally. Palpomere II about 2/3 as long as palpomere I. Palpomere III about 1/2 as long as palpomere II. Labium hairy (Fig. 74). Glossa shorter than paraglossa. Glossa with row of short setae along entire dorsal margin and group of long setae at mid-length ventrally. Dorsal face of paraglossa with double row of long setae along outer edge and single row along inner edge and with two or three scattered setae basally. Ventral face of paraglossa with row of very long setae along inner edge and staggered row along mid-ventral face. Labial palp three-segmented. Palpomere I rectangular with scattered setae along outer edge. Palpomere II triangular, narrowest at base. Numerous setae scattered over ventral surface, few setae on outer margin of dorsal side. Seven setae arranged in a staggered arc near the distal margin of dorsal side.

Palpomere III truncated and slightly concave. Numerous setae on ventral surface, setae restricted to distal and outer dorsal margins.

b)Thorax

Comparative lengths of leg segments variable (Table 15). Leg light tan, brown spot near distal end of femur and at basal end of tibia. Tibia, tarsus, and claw light brown; in some individuals darkening near joints. Distal end of femur with row of long setae along and across dorsal edge. Tibia with distinct sub-proximal row of long setae along dorsal edge and arcing across edge. Wing pads semi-hyaline tan colour becoming black in final moults. Wing pads with dark brown markings resembling veins (Fig. 69).

c)Abdomen

Dorsal colour pattern as in Fig. 69. Posterior tergal spines very long and narrow, evenly spaced with gaps and one or two very small spines in between. Lateral spines large and variable in number (Table 3). Genital forceps of male visible in mature nymph as two small rounded extensions on posterior edge of sternum IX. Bilamellate gills on segments I to VI and unilamellate gills on segment VII. Most gills were heavily damaged and only those illustrated in Fig. 55 were sufficiently intact to allow drawing. Median terminal filament 3.7 mm long and cercus 4.0 mm long. Cercus and median terminal filament hyaline brown with dark band every fourth intersegmental membrane. Dark band of segments about 3/4 of the way from the base. Cercus and median terminal filament unmarked distal to this band.

Table 15. Mean lengths (x), observed ranges (r) (mm), and within leg ratios (:) of leg segments of mature nymphs of Pseudocentroptilum quaesitum (McDunnough) (n=2).

		FEMUR	TIBIA	TARSUS	CLAW
PROTHORACIC	x	1.57	0.87	0.98	0.49
	r	1.56-1.58	0.86-0.88	0.92-1.04	0.47-0.51
	:	3.1-3.3	1.7-1.8	2.0-2.1	1
MESOTHORACIC	x	1.51	0.86	0.90	0.56
	r	1.48-1.54	0.84-0.88	0.81-0.99	0.40-0.64
	:	2.9-5.1	1.6-2.5	1.6-2.3	1
METATHORACIC	x	1.47	0.86	0.91	0.59
	r	1.42-1.52	0.85-0.87	0.84-0.98	0.55-0.63
	:	2.4-2.6	1.3-1.5	1.5-1.6	1

SPECIMENS EXAMINED

CANADA

ALBERTA

Bearberry Creek, near Sundre, 51°48'N 114°40'W (coll. C.H. Young) (CNIC): 24/VIII/1926, female imago.

Nordegg, 52°28'N 116°03'W (coll. J. McDunnough) (CNIC): 6/VII/1921, 1 female imago; 11/VII/1921, 1 female imago.

Seven Persons Creek, Medicine Hat, 50°03'N 110°40'W (coll. J.H. Pepper) (CNIC): 17/VI/1930, 1 female imago.

BRITISH COLUMBIA

Okanagan Landing, 50°12'N 119°28'W (coll. A.N. Gartrell) (CNIC): 12/VII/1933, 1 female imago.

MANITOBA

Berens River, 52°22'N 97°02'W (coll. W.J. Brown) (CNIC): 9/VII/1938, 1 male imago.

Churchill, 58°46'N 94°10'W (coll. W.J. Brown) (CNIC): 31/VII/1937, 1 female imago.

Douglas Lake, (coll. E. Criddle) (CNIC): 30/VII/1924, 1 female imago.

Unnamed pot-hole lake, west of Hwy. 270, 5 km south of Hwy. 45, near Erickson, 50°25'N 99°58'W: 6/VIII/1985, 1 nymph (coll. J. Mathias and K. Rose); 23/IX/1986, 1 male imago with exuviae, 1 female subimago, 2 nymphs (coll. R.G. Lowen).

DISTRIBUTION AND FIELD NOTES

This species is unusual in that except for the Alberta specimens, nymphs were only found in lakes and adults were all found near lakes. These lakes range in size from small prairie pot-hole lakes to Lake Winnipeg, which by surface area is the 13th largest lake in the world. The pot-hole lake I sampled is in a highly agricultural area and had little to no drainage. The nymphs were most often found in the reed beds that lined the shore. Nymphs were caught from late July till late September but since imagines were caught before July in other areas, they might be present much earlier than this.

As well as the specimens examined here the species is also recorded from Cairo, Illinois (Burks 1953) and from Gull Bay and Warren's Landing on Lake Winnipeg, Manitoba (Neave 1934). Aside from the single Illinois record, the species is only known from western Canada (Fig. 75). The previously unpublished records from British Columbia and from Churchill, Manitoba represent respectively, the new western and northern limits of the species.

Figure 75. Known range of Pseudocentroptilum quaesitum (McDunnough).


● P. quaesitum
NORTH AMERICA
0
500
MILES

PART V. DISCUSSION

a)Descriptions and keys.

Prior to 1984, three species were known to occur in Manitoba. These three species were inadequately described (see text table p. 3). Four additional species were collected in the Province, of which the nymph and subimago of Centroptilum bifurcatum, C. victoriae, and C. conturbatum, and the female imago of C. bifurcatum and C. victoriae were not previously described. These descriptions of previously unknown or poorly known life stages mean that the seven Manitoba species are now at least adequately described. The status of current descriptions compared to their previous status is shown in the following text table. In this table, "poor" means that the description could apply to several species and that identification could only be made by comparison with the type series. "Adequate" means that the description would identify some members of a population, and "good" means that the description would suffice to identify most members of a population.

SPECIES		NYMPH	SUBIMAGO	MALE IMAGO	FEMALE IMAGO
C. bifurcatum	old	unknown	unknown	good	unknown
	now	good	good	good	good
C. victoriae	old	unknown	unknown	adequate	unknown
	now	good	good	good	good
C. album	old	good	poor	good	adequate
	now	good	adequate	good	good
C. conturbatum	old	unknown	unknown	adequate	poor
	now	good	adequate	good	good
P. rufostrigatum	old	poor	unknown	good	poor
	now	good	adequate	good	good
P. infrequens	old	unknown	unknown	unknown	poor
	now	good	good	good	good
P. quaesitum	old	unknown	unknown	adequate	poor
	now	good	adequate	adequate	adequate

All seven Manitoba species have strong variability in the characters previously used to define species. Colour characteristics are perhaps the prime example of this. The diagnostic dorsal stripe on the abdomens of female P. infrequens can be a bright scarlet stripe or only a series of pale reddish areas. The paired bright red spots on the terga of P. rufostrigatum can be completely absent in the female. The posterior abdominal tergites on male of C. album can be tinged with brown, especially in alcohol-preserved specimens. Nymphs of most species vary from near white to black. The pattern rather than the intensity should be used as a means of identification.

Even characters previously thought not to vary, have been found to do so. For example, the hind wing of C. victoriae can be indistinguishable from C. bifurcatum or can strongly resemble that of C. conturbatum. Variation is not always illustrated but the range of variation is discussed in the text.

The keys have been written specifically for Manitoba species and the majority of specimens key out correctly. Specimens from outside Manitoba were examined in order to determine if geographic variation existed. In no case was geographic variation found that would cause species to be incorrectly identified.

b)Nomenclature and the phenetic classification of the genera.

Phenetic classification is the grouping of individuals into taxa on the basis of overall similarity (Wiley 1981). The original definitions of the genera in the subfamily Cloeoninae were based on overall similarity of their component species and are therefore phenetically classified. Species were placed in the genus Centroptilum if the imago had single marginal intercalaries and hind wings. Species with single marginal intercalaries but which lacked hind wings were placed in the genus Cloeon. As more species were described, new genera were erected to include species that seemed to have apomorphic character states. This splitting off of derived groups has resulted in uncertain limits to the genus Centroptilum. Nomenclatural examinations of this genus have progressed in two directions.

One group of researchers emphasizes the similarities between the old genera and has suggested extensive synonymies (Burks 1953; Edmunds et al. 1976). The genera Centroptilum sensu stricto and Pseudocentroptilum share close affinities with Cloeon Leach and Procloeon Bengston respectively. Species of Cloeon and Procloeon lack hind wings and the genera were thought to be sister taxa. The reduction and loss of hind wings however, has occurred independently in the Baetis Leach/Pseudocloeon Klapalek lineage (Landa and Soldn 1985) and could therefore have independently occurred more than once within the subfamily. Soldn and Thomas (1985) described a new species, Centroptilum dimorphicum. The nymph and male imago would place this species in Centroptilum, but the adult female lacked hind wings and therefore would be assigned to Cloeon. Jacob and Glazaczow (1986) argue that in order to properly reflect the phyletic affinities within the classification system, the closest relatives of species without hind wings will be among species which have hind wings. They propose that Procloeon is the sister taxon to Pseudocentroptilum. Waltz and McCafferty (in press and personal communication) consider Pseudocentroptilum to be polyphyletic and most of the species to be synonymous with Procloeon. They described a new species, Procloeon tatualis Waltz and McCafferty (1985), which previously would have been assigned to Centroptilum. I reject synonymizing Pseudocentroptilum with Procloeon or Centroptilum with Cloeon until it can be shown that there is a paraphyletic relationship among their component species. Jacob and Glazaczow (1986) acknowledge that Pseudocentroptilum is

probably polyphyletic and assigne two species from it to their new genus Pseudocentroptiloides.

It has been suggested that Procloeon is a junior synonym of Cloeon because of the unreliability of characters previously used to seperate these genera (Burks 1953; Edmunds et al. 1976; and others). Gillies (1980), working with newly discovered nymphs of African Cloeon and Procloeon, concluded that the only valid character distinguishing these genera is that Procloeon nymphs have unilamellate gills where Cloeon nymphs have bilamellate gills. Although Gillies did not propose a formal synonymy, he suggested that Procloeon was at best a sub-genus of Cloeon. Edmunds et al. (1976) even questioned whether Centroptilum sensu lato should be considered separate from Cloeon sensu lato. The only noteworthy difference between the groups is the absence of hind wings in Cloeon and their presence in Centroptilum. If presence or absence of hind wings is no longer a valid distinction then the difference between Cloeon and Centroptilum is obscured.

The second group of researchers has attempted to account for the differences between species groups within the existing genera and have therefore erected several new genera. Kazlauskas (1969) noted the differences between Centroptilum luteolum (Mller), the type species of the genus, and the other European species of Centroptilum. He proposed the genus Cloeoptilum to encompass the species other than the type species but because he did not include a type species the name must be considered invalid (Hubbard 1979; Keffermller and Sowa 1984).

Keffermller and Sowa (1984) reviewed the Central European species of Centroptilum and agreed with Kazlauskas' division of the genus but concluded that if Cloeoptilum was a valid name, it would be a junior synonym of Pseudocentroptilum Bogoescu (1947). Bogoescu created this genus for the species P. motasi, because it had a third longitudinal vein and numerous cross veins in the hind wings. These characters were inadequate to separate the genus from other genera and it was synonymized with Centroptilum (Keffermller, in Keffermller and Sowa 1984). Since it was the first generic name given to a species in Kazlauskas' Cloeoptilum group, Keffermller and Sowa (1984) resurrected and redefined Pseudocentroptilum as those species formerly assigned to Centroptilum that were similar to P. motasi and different from C. luteolum. A problem arose in that although they defined Pseudocentroptilum in a very broad context they included in it only the type species, P. motasi. They suggested that other species could be included in this genus but did not formally transfer them. Consequently, the majority of European species are still technically in Centroptilum although the name Pseudocentroptilum is often used (eg. Jacob and Glazaczow 1986).

The Manitoba species are phenetically divisible into two groups. Group A contains P. quaesitum and P. infrequens. Group B consists of C. bifurcatum, C. victoriae, C. conturbatum, and C. album. Pseudocentroptilum rufostrigatum has characteristics in common with both groups. I will examine these groups in greater detail before I attempt to place them in particular genera.

Group A, in common with all baetids, can be diagnosed most easily in the nymphal stage. The nymph of this group has bilamellate gills on segments I to VI, the maxilla palpomere III about 1/2 as long as palpomere II, a row of five setae on the maxilla just basad to the biting teeth, the canines of the left mandible completely fused, the canines of the right mandible fused at least 2/3 of the way, a well developed right prostheca, an arc of well developed setae near the distal end of the femur, large and numerous lateral spines, no pore-like spots on the terga, and no posterior projection of tergum IX. The imagines are more difficult to typify: the male forceps have a short terminal segment, a strong shelf-like division between forceps segments I and II, and both male and female have red as the dominant colour on the abdominal terga (note that this varies and can quickly fade in alcohol-preserved specimens).

Group B is also easier to diagnose in the nymphal stage. The nymph of this group has unilamellate gills with serrate anterior edges, maxilla palpomeres II and III of sub-equal length, two or fewer setae on maxilla just basal to the biting teeth, canines of the left mandible never more than 2/3 fused, canines of the right mandible completely unfused, very narrow right prostheca, a poorly developed distal arc of setae on the femur, very small or absent lateral spines, many circular markings resembling pores arranged in species specific patterns, and the posterior edge of terga IX produced posteriorly into a small round hump lacking spines. The imago is difficult to typify. The male forceps have a relatively long terminal segment while segment I and the basal segments tend to be strongly tuberculate or at least project

inwards to some degree. Red colouring can be present on some individuals but never very bright and never as the dominant colour.

Pseudocentroptilum rufostrigatum holds a position intermediate between groups A and B and could be placed in either group. The imago resembles group A in that the male genitalia has a short terminal segment, a shelf-like division between segments I and II, and the terga of the male imago and many of the females have distinctive bright red markings. The nymph resembles group A in that it has gills with smooth edges, maxilla palpomere III about 1/2 as long as palpomere II, a right prostheca that is narrow but not as narrow as group B, a well developed femoral arc of setae, large lateral spines present on most segments, and no posterior projection of tergum IX. The nymph resembles group B in that it has no row of setae just basal of the biting teeth of the maxilla, the left canines fused for only 1/2 their length, completely unfused right canines, few pore-like circular markings, and unilamellate gills.

c)Polarity of character states.

A phenetic classification system can be misleading in that species with a great many plesiomorphic character states would be grouped together even though they are in different phylogenetic lineages. A researcher attempting to create a phylogenetic classification tries to group taxa along evolutionary lines. In order for a classification system to reflect this phylogeny, species in any taxon must have a more recent common ancestor with each other than they have with a species in

another taxon (Hennig 1965, 1966; Wiley 1981). To find out if this is so it must be determined which species have the apomorphic character states. A character is any aspect of an organism (eg. claw), while a character state is the form the character takes (eg. claw long or claw short). The polarity of a series of character states is the determination of which character states are primitive or plesiotypic and which are derived or apotypic and can be thought of as the order in which the charater states evolved. Organisms that share apomorphic character states are assumed to have a more recent common ancestor than organisms which do not have the apomorphic character states.

The determination of which character states are apomorphic is accomplished by comparing the range of character states to those present in an out-group (Hennig 1965, 1966). An out-group is a monophyletic taxon which is a sister taxon to the group of interest. The character state that both groups have in common is taken as the plesiomorphic state. If the out-group lacks the character, or does not have a character state in common, then the state present in the most plesiomorphic member (based on other characters) of the group being examined is taken as the plesiomorphic state.

The genus Centroptilum has been split into several genera of uncertain phylogenetic position. To insure that the species here examined are monophyletic relative to the out-group, the genus Callibaetis is taken as the out-group. Callibaetis species have enough autapomorphies that they have long been considered a monophyletic group. In addition, species of Callibaetis are thought to be the plesiomorphic sister taxon to the rest of the Cloeoninae together

(Check 1982; Landa and Soldn 1985). A summary of the character states for the seven Manitoba species is given in Table 16.

Character 1. Length to width ratio of hind wing.

The length to width ratio varies from 3.5 to 6.7. The hind wings of the entire family are reduced relative to the rest of the order. Callibaetis species tend to have less reduced wings than the rest of the family. Since lower ratios mean wider wings, they are taken as plesiotypic.

Wide wings, such as those in Callibaetis, tend to have greater than two longitudinal veins, and numerous cross veins. Narrower hind wings, such as those in Centroptilum tend to have only two longitudinal veins and few or no cross veins. A narrow hind wing can therefore be taken as an indicater of apotypic wing venation.

Character 2. Shape of distal tip of hind wing.

The distal end of the hind wing can be either round or broadly pointed (Figs. 36 and 58). The shape appears to be independent of the degree of narrowing since round and pointed distal ends occur in both wide and narrow hind wings. Pointed hind wings do not occur in Callibaetis and are rare in the rest of the sub-family so that pointed is taken to be the apotypic state.

Table 16. Character states of Manitoba species of Centroptilum and Pseudocentroptilum.

See text for further explanation.

CHARACTER	SPECIES						
	BIFURCATUM	VICTORIAE	ALBUM	CONTURBATUM	RUFOSTRIGATUM	INFREQUENS	QUAESITUM
1. Hind wing length:width	3.5	3.5	4.4	3.8	5.8	6.7	4.3
2. Hind wing shape of tip	round	round to pointed	pointed	pointed	pointed	round	round
3. Length meta-tarsus II:III	1.1-2.2	1.2-2.7	1.0-2.0	1.1-2.7	1.2-2.8	2.0-3.5	2.3-2.4
4. Penal plate shape	round to concave	concave	round to conical	round to conical	truncate	truncate	round
5. Penal plate process	large	large	small	absent	absent	absent	absent
6. Forceps segment III	long	long	long	long	short	short	short
7. Arc of setae on labial palp	few setae orderly	few setae orderly	few setae disorderly	few setae disorderly	many setae disorderly	few setae orderly	many setae disorderly

Table 16. Continued

CHARACTER	SPECIES						
	BIFURCATUM	VICTORIAE	ALBUM	CONTURBATUM	RUFOSTRIGATUM	INFREQUENS	QUAESITUM
8. Maxillary palp segment III	long	long	long	long	short	short	short
9. Distal group of maxilla setae	2	2	1	2	0	5	5
10. Proximal group of maxilla setae	5	3	4	5	6	5	6
11. Fusion of left canine	0.33	0.50	0.33	0.66	0.66	1.00	1.00
12. Fusion of right canine	0.00	0.00	0.00	0.00	0.00	0.66	0.66
13. Width of left prostheca	middle	middle	middle	middle	wide	wide	wide
14. Width of right prostheca	very narrow	very narrow	very narrow	very narrow	narrow	middle	middle

Table 16. Continued

CHARACTER	SPECIES						
	BIFURCATUM	VICTORIAE	ALBUM	CONTURBATUM	RUFOSTRIGATUM	INFREQUENS	QUAESITUM
15. Gill lamella	unilamellate	unilamellate	unilamellate	unilamellate	unilamellate	bilamellate	bilamellate
16. Gill serrations	serrate	serrate	serrate	serrate	smooth	smooth	smooth
17. Lateral spines	small	small	small to absent	small	large	large	large
18. Pore-like spots	many	many	many	many	some	none	none
19. Projection on terga IX	yes	yes	trace	yes	none	none	none
20. Metatarsus:claw lengths	1.2-1.6	1.1-1.8	1.7-2.2	1.4-2.0	1.0-1.4	1.5-2.0	1.5-1.6

Character 3. Ratio of length of metatarsus II to metatarsus III.

Tables 1, 4, 6, 8, 10, 12, and 14 contain the mean lengths and ranges of the leg segments of Manitoba species. Ratios of leg segment lengths have considerable intra-specific variation and overlap. Their value in phylogenetic studies is therefore minimal. This ratio has some use in separating group A from group B only at the extremes of the observed ratios. Callibaetis nymphs have tarsal segments that are closer to being the same length than is evident here, so that the higher ranges of ratios are taken to be apotypic.

The particular character of length of metatarsus II to metatarsus III has been used to define genera. I have attempted to include this character for comparison purposes with other studies. As negative evidence, my work is in agreement with Gillies (1980), who discussed the relative lengths of metatarsal segments 2 and 3 as a means of separating the related baetid genera of Cloeon and Procloeon. He concluded that these relative lengths were inconsistent and of little value in differentiating the genera.

Character 4. Shape of distal margin of penal plate.

This character can occur in three different states: semi-circular becoming cone-like in some individuals (Fig. 37), a truncated trapezoid (Fig.59), or with a concave distal margin (Fig.18). The concave margin state appears, on close examination to have evolved directly from a semi-circular or cone-like shape since the concave margin appears to be a modified semi-circle with the distal most end folded dorsally. Whether the semi-circle shape arose from the trapezoidal shape or vice

versa is difficult to determine. Penal plates do occur in some species of Callibaetis but are much smaller and represent a different character state. These small penal plates tend to have truncated distal margins and therefore somewhat resemble the trapezoid state. For this reason I will assume that trapezoidal is the plesiotypic state, although both states could have arisen independently.

Character 5. Penal plate process.

The pointed process on the penal plate can be either absent, large and obvious, or small and membranous (Figs. 18 and 27). Since no species of Callibaetis has this process, the absence is taken as plesiotypic. The small process may have arisen from reduction of the large process or the small process may have been enlarged into the large process. Since the out-group provides no basis for comparison, this must be decided relative to the other characters and will be discussed later.

Character 6. Length of forceps segment III.

Segment III of the forceps can be either long and subequal to the basal segment or short and about half as long as the basal segment (Figs. 18 and 59). Segment III in Callibaetis is large; I will therefore take large as the plesiotypic state.

Character 7. Arc of setae on labial palp.

On the distal margin of labial palpomere II, there is a row of setae of variable number that can be arrayed in a straight line or in a

disorderly row. Callibaetis nymphs have very many setae in a disorderly row, which is taken to be the plesiotypic state. The two, perhaps independent, evolutionary trends involving a reduction in number and a straightening of the row of setae.

Character 8. Length of maxillary palpomere III.

There are two states of this character. Palpomere III can be equal in length to (Fig. 9), or about 1/2 as long as palpomere II (Fig. 51). All species of Callibaetis lack palpomere III and so other information is needed to decide which is the plesiotypic state. There are signs of fusion of palpomeres II and III in P. infrequens. In addition, the families Siphlonuridae and Metretopodidae are closely related to the family Baetidae and tend to have the palpomeres of equal length (Needham et al. 1935; Edmunds 1984) so I will consider a long palpomere III as plesiotypic.

Characters 9 and 10. Distal and proximal groups of maxilla setae.

There are two rows of setae on each maxilla. One is distal, just below the biting teeth and consists of five, two, one, or zero setae. The other is proximal, just opposite the maxillary palp and consists of three to six setae. Most Callibaetis species have very numerous setae in these locations (Check 1982) so numerous setae are taken to be plesiomorphic.

Characters 11 and 12. Fusion of left and right canines.

Canines of both mandibles are fused to various degrees. The left mandible can be either 1/3, 1/2, 2/3, or completely fused (Figs. 7, 21, 49, and 62). The right mandible is either just over 2/3 or not at all fused (Figs. 8 and 63). Increased fusion is taken to be apotypic since fully divided canines are prevalent throughout the Order.

Characters 13 and 14. Widths of left and right prostheca.

The left prostheca is either wide or of moderate development. In comparison, the right prostheca ranges in width from moderate developement, through narrow, to very narrow which is almost needle-like in shape. Prostheca of both mandibles is well developed in Callibaetis and other genera of the family. This is taken as a reduction series with wide as the plesiotypic state.

Character 15. Secondary gill lamella.

The gills are either unilamellate or bilamellate on gills I to VI. Gills of Callibaetis are either unilamellate, bilamellate, or trilamellate. The secondary lamella in Callibaetis is ventral while that of the species I examined are dorsal so that the bilamellate gills of Callibaetis are of a different type and the unilamellate gill is the only state that the species I examined have in common with the out-group. Unilamellate gills are taken as plesiotypic.

Character 16. Gill serrations.

This character occurs in two states: serrate, or smooth anterior margins. Callibaetis nymphs have smooth-margined gills. The Manitoba species with smooth-margined gills have highly asymmetric gills (Figs. 53-55). This is more like the condition in Callibaetis. Other genera with serrate gills have a narrowed gill (eg. Baetis). It appears that serrate gills are connected with the reduction in gill size and therefore smooth edges are taken as plesiotypic.

Character 17. Lateral spines.

Lateral spines can be either large, small, or absent. Spined lateral margins occur in most genera of the subfamily Cloeoninae but many genera, including Callibaetis, lack spines. Gillies (personal communication) believes that the presence of spines along the lateral margins of the terga is a derived character state only present in the Centroptilum-Cloeon lineage. I will therefore consider the absence of spines as plesiotypic with the evolutionary trend being to increase the size of the spines.

Character 18. Pore-like spots on terga.

Pore-like spots on the terga are either absent, present in small number, or numerous. Pore-like spots occur in several species within the Cloeoninae but these spots have not been described as being numerous (Keffermller and Sowa 1984; and others). It seems that numerous spots is only found among Nearctic species. Some Callibaetis and some Baetis species that I examined have two spots on the most

anterior segments. Therefore, the plesiotypic state is only a few such spots with one group evolving numerous spots and the other group losing all such spots.

Character 19. Posterior projection on tergum IX.

The posterior edge of tergum IX can be straight with an uninterupted row of posterior spines or it can project posteriorly in the form of a rounded hump lacking spines. This hump is not known to occur in any other species of Ephemeroptera and so is probably a derived state. Centrotptilum album has, at most, a very small such hump but it always lacks posterior spines at this point.

Character 20. Ratio of length of metatarsus to claw.

Mean lengths and observed ranges of leg segments of Manitoba nymphs in are presented in Tables 2, 5, 7, 9, 11, 13, and 15. The ratio of the length of the metatarsus to the length of the claw has been used to separate some species of Centroptilum (Berner and Pescador 1988). This ratio is therefore used as a character. Callibaetis nymphs have long slender claws but Edmunds et al. (1976) in their discussion of the taxonomy of Cloeon decided that the primitive species of Centroptilum had short claws and unilamellate gills and that claws lengthened and gills developed a dorsal flap as adaptations to life in slow waters. If this is so, the value of these two characters in a phylogenetic analysis would be minimal. If lengthening of claws and doubling of gills was a wide spread common reaction to similar environmental pressures then the shared derived character states could have come from

parallel evolution. Fortunately the two characters appear to be have arisen indipendently since it is the Manitoba species with single gills that have the relatively longest claws. Since Callibaetis nymphs are all slow water species and have long claws and since non-Cloeoninae baetids usually have short claws, I will consider short claws plesiotypic.

d)Manitoba species groups and their phylogenetic relationships.

A final goal of most phylogenetic studies is the creation of a phylogenetic tree in which the species are grouped by common descent. In reality the phylogenetic tree is a hypothesis based on available data and the same data might lead to several phylogenetic trees. A phylogenetic tree based on only a few species of a group is based on a low amount of data and might therefore lead to questionable results. It is for this reason that I have not constructed a phylogenetic tree for the seven Manitoba species. I have attempted to group the species into phylogenetic units but I am fully aware that further research on a greater number of species might widen, narrow, or remove these groupings.

Pseudocentroptilum infrequens and P. quaesitum are closely related species. These two species share five apomorphic character states that are absent in the other five Manitoba species. These five character states are: 3. high ratio of length of metatarsus II to metatarsus III, 11. left canine completely fused, 12. right canine mostly fused, 15. gills I to VI bilamellate, and 18. an absence of pore-like spots on

the nymphal terga. These two species vary in only three of all the characters listed. Pseudocentroptilum quaesitum has a semi-circular penal plate, relatively wide hind wings, and six setae on the proximinal group on the maxilla while P. infrequens has a trapezoidal penal plate, very narrow hind wings, and five setae on the proximal group on the maxilla.

Pseudocentroptilum rufostrigatum is intermediate on the basis of overall similarity but if only apotypic character states are considered, P. rufostrigatum forms a natural group with P. infrequens and P. quaesitum. These three species share three apotypic character states that the others do not possess. These are: 6. segment III of the male forceps relatively short compared to basal segment, 8. maxilla palpomere III about 1/2 the length of palpomere II, and 17. large lateral spines on nymphal abdomen. In Four other characters from Table 16 Pseudocentroptilum rufostrigatum has the more plesiotypic state while one or both of the other two species has the more derived state. These characters are: 7. the arc of setae on the labial palp, 11. the degree of fusion in the canines of the left mandible, 12. the degree of fusion in the canines of the right mandible, and 18. the presence of pore-like spots on P. rufostrigatum. Pseudocentroptilum rufostrigatum differs from P. quaesitum and P. infrequens in four of the characters listed. Pseudocentroptilum rufostrigatum has a pointed hind wing, no distal group of setae on the maxilla, a small prostheca on the right mandible, and nymphal claw almost equal to the tarsus in length.

The four species of group B apparently form a monophyletic group. In five of the characters evaluated they share apotypic states that the

other three Manitoba species lack. These five character states are: 13. prostheca on the left mandible slightly reduced, 14. prostheca on the right mandible highly reduced, 16. gills with serrate margins, 18. multiple pore-like spots on terga, and 19. at least a trace of a posterior projection on abdominal tergum IX. In addition, group B shares apotypic character states in four characters that also occur in group A. These character states are: 4. the imaginal penal plate semi-circular to cone-like, 7. the arc of setae on the labial palps are few in number, 9. the distal group of setae on the maxilla are two or fewer in number, and 10. the proximal group of setae on the maxilla are five or fewer in number. These four characters are evidence that group B is monophyletic but they are weaker evidence since the apotypic character states also occur in members of group A. Based on consideration of all of the above evidence, I conclude that the group B species form a monophyletic group relative to group A.

The relationships within group B are harder to determine. Centroptilum bifurcatum and C. victoriae have the penal plate with the end turned upwards into an apparently concave margin. This is the most derived state of this character and so is good evidence that these two species are closely related. In addition, they have the apotypic state in the labial arc of setae and the nymphal claw length/tarsal length ratio, but this is weaker evidence since these states are also present among the members of group A. Centroptilum bifurcatum and C. victoriae differ from each other in only three of the characters examined. Centroptilum bifurcatum has five setae in the proximal group on the maxilla, the canines on the left mandible fused for only 1/3 of their

length, and a hind wing that does not have a pointed distal margin. Centroptilum victoriae has three setae in the proximal group on the maxilla, the canines on the left mandible fused for 1/2 their length, and a hind wing that in some individuals has a pointed distal margin. One can safely say that these two species are closely related since these differences are minor while at least one of the similarities is unique.

Centroptilum album and C. conturbatum can also be said to form a natural group, although the evidence is weaker. The reduced number of setae in the proximal group on the maxilla is evidence for a relationship between C. album and C. victoriae but I have shown that C. victoriae is most closely related to C. bifurcatum. A reduction in the number of setae would look similar even if it evolved independently. This character is therefore not very strong evidence. The higher degree of fusion of the canines on the left mandible and the slightly higher ratio of nymphal claw to tarsus is evidence that C. conturbatum is more closely related to C. victoriae and C. bifurcatum than to C. album but the differences are not large and since both of these character states occur in group A they can not be considered strong characters. Finally, two characters are evidence that C. album is more closely related to C. conturbatum than to any other Manitoba species. These characters are: 1. elongation of the hind wing and therefore no third longitudinal veins, and 2. hind wing with distal end rounded. Both these characters have low weight since they have evolved several times, but there is a qualitative similarity in their hind wings that is not present in C. bifurcatum and C. victoriae. The

hind wings of C. album and C. conturbatum lack the third longitudinal vein and have a very erect costal process. Both of these characters appear to be derived and within the context of group B it is evidence that C. album and C. conturbatum are more closely related to each other than either is to C. bifurcatum and C. victoriae. This evidence is not conclusive and since these species show a great number of autapomorphies, it would perhaps be more accurate to say that C. album and C. conturbatum are less distantly related to each other than either is to C. bifurcatum and C. victoriae.

An interesting point of this arrangement of group B is that C. conturbatum lacks a penal plate process. Centoptilum conturbatum is a generally derived member of group B and C. album has the smallest process of the group. If this grouping is correct, the penal plate process either evolved twice or it is secondarily lost in C. conturbatum. It is more parsimonious to conclude that C. conturbatum has secondarily lost this process and that the penal process of C. album is a reduced form of the state in C. bifurcatum and C. victoriae.

e)Generic placement of Nearctic species.

The two groupings of Manitoba species relate roughly to the Palaearctic groups as defined by Kazlauskas (1969) and Keffermller and Sowa (1984). Group A clearly belongs in the Pseudocentroptilum as defined in Keffermller and Sowa (1984) and group B has similarities with the genus Centroptilum sensu stricto. To determine whether Manitoba species actually belong in these genera, comparisons must be made between the Manitoba species and the type species of the genera.

The type species of Pseudocentroptilum is P. motasi Bogoescu. The male of this species is unknown and the nymph described in Keffermller and Sowa (1984) may not be P. motasi. Comparisons among nymphs are based on this nymph and comparisons among male imagines are based on characters common to males in other species assigned to Pseudocentroptilum as well as to a subimago dissected out of the inconclusively identified nymph. The shortcomings of this are obvious but we are left with no option until the immatures of the type species are better known. Group A and P. motasi share the following plesiotypic character states: 2. the hind wing is blunt at the ends or at least highly rounded, 4. the penal plate is truncated or semi-circular but never cone-shaped, 5. there is no process between the basal segments of the forceps, 16. the gills end bluntly and are highly asymmetric and the first pair of gills are relatively large. They also share the following apotypic character states: 8. maxillary palpomere III is about half as long as palpomere II and in P. infrequens is partially fused, 11. and 12. canines of both mandibles are highly fused, 15. gill pairs I to VI are bilamellate, and 17. lateral spines are large and obvious. On this information, it appears that P. motasi is more closely related to P. infrequens and P. quaesitum than to any other Manitoba species.

The type species for Centroptilum is C. luteolum (Mller) which has a large pointed process on the penal plate and the presence of small lateral spines. This is evidence for a close relationship with group B but in other characters it appears to be a hightly derived member of group B. Centroptilum luteolum has a very narrow hind wing which comes

to a sharp point. Centroptilum conturbatum and C. album have narrow hind wings that occasionally come to a definite point. Centroptilum luteolum has a highly cone-shaped penal plate whereas C. conturbatum and C. album have a semi-circular penal plate that comes to a blunt cone. Centroptilum luteolum has symmetrical gills that come to a sharp point and the first pair is narrower than the succeeding pairs. Centroptilum victoriae, C. album, and C. conturbatum also have symmetrical gills with the first pair more narrow than the others and in some individuals these gills come to a distinct point.

The above comparisons strongly support the idea that group B species are congeneric with C. luteolum but members of group B also possess several autapomorphies. This means that group B could be considered a distinct sub-genus within Centroptilum. Each member of group B has the following character states that C. luteolum does not possess: canines of left mandible at least partially fused, multitude of pore-like spots on nymphal terga, anterior margins of gills serrate, and mid-dorsal posterior margin of nymphal tergum IX lacking spines and produced posteriorly.

It is evident that group A fits the definition of Pseudocentroptilum sensu Kefferml1er and Sowa (1984) and is clearly distinct from C. luteolum. Group B is monophyletic and more closely related to C. luteolum than to group A, yet members of group B contain many plesiotypic character states in common with Pseudocentroptilum. These states include: hind wing blunt at end or rounded, penal plate semi-circular and without a process, gills asymmetrical and blunt,

numerous, albeit small, lateral spines, and canines of mandibles partially fused.

Working strictly from published descriptions, other Nearctic species can be compared to Manitoba species. The typical Pseudocentroptilum-type of male genitalia consists of a small terminal forceps segment, a shelf-like division between forceps segments I and II, and a round to truncate distal margin of the penal plate. Published descriptions of the following species have this type of genitalia: Centroptilum bellum McDunnough (1924, 1930), C. fragile McDunnough (1923), C. rivulare Traver and C. venosum Traver (Needham et al. 1935). The nymphs of C. fragile and C. venosum are unknown but the nymph of C. bellum has bilamellate gills on segments I to VI and the nymph of C. rivulare has bilamellate gills on segment I (McDunnough 1930; Needham et al. 1935). Centroptilum viridocularis Berner (1940) has a truncate penal plate with a small forceps segment III, and a nymph with large lateral spines and a small maxillary palpomere III. A nymph with unilamellate gills and a similar ventral colour pattern could mean that this species is related to P. rufostrigatum. I have not seen specimens of these species but predict that they will conform to the genus Pseudocentroptilum.

Typical Centroptilum-type male genitalia have a long terminal segment, a round to conical distal margin of the penal plate, and a process between the basal segments. Centroptilum selanderorum Edmunds (1954) and C. semirufum McDunnough (1926, 1929) have a distinct process between the basal segments. In addition, C. selanderorum has a penal plate with a concave distal margin. These species are probably members

of Centroptilum sensu stricto and C. selanderorum is probably closely related to C. bifurcatum and C. victoriae. Centroptilum asperatum Traver has a penal plate with a concave distal margin but it lacks a process. Centroptilum elsa Traver has a conical penal plate (Needham et al. 1935). These last two species might also be members of Centroptilum sensu stricto.

Centroptilum convexum Ide (1930) was distinguished from C. album by having a pink lateral margin on tergum IX, a wider hind wing, and greater development of the tubercle on the second forceps joint. In the Royal Ontario Museum, Toronto, there is a large series of pinned imagines of C. convexum that were collected and identified by Ide. Not all of the males in this series possess a pink lateral margin on tergum IX, and the hind wings and forceps tubercle were within the ranges observed for Manitoba C. album. In addition, females of this series are indistinguishable from females of Manitoba C. album. I strongly suspect that C. convexum is a junior synonym of C. album but have not seen the types of C. convexum.

f)Post-glacial dispersal.

Southwestern to west-central Manitoba represents a meeting point between eastern and western faunas (Scudder 1979; and others). So it is not surprising that the species studied here have predominantly eastern or predominantly western distributions. The eastern species present are P. rufostrigatum and C. victoriae. The western species are C. bifurcatum, C. conturbatum, P. infrequens, and P. quaesitum. In addition, C. album has a trans-continental distribution. Among the

western species, C. bifurcatum and C. conturbatum have a southwestern distribution, while P. infrequens has a northwestern distribution, and P. quaesitum is western but associated with the Mississippi drainage. In the case of the eastern species, the range of C. victoriae is too poorly known but P. rufostrigatum is clearly eastern and associated with the Mississippi River draingage system.

As has been shown for other taxa, these distributions are probably a reflection of the geological history of North America (Ross et al. 1967; Scudder 1979; Flannagan and Flannagan 1982). All of Manitoba and most of Canada was covered by the Laurentide ice sheet during the Wisconsin glaciation (Flint 1971). Since this would have eliminated the biota present before glaciation, any organism currently in Manitoba must have come from elsewhere during or after the retreat of the ice. There are four major unglaciated areas that could have served as refugia. These are: western and montane United States, central to western United States and parts of Alberta, eastern United States, and the Bering land bridge and its surrounding areas (Beringia). Any one or combination of these could have served as refugia for species now in the province.

It has been pointed out that adult mayflies have poor powers of dispersal and that it is unlikely that they could extend their range without a direct water connection (Lehmkuhl 1972; Flannagan and Flannagan 1982). This means that colonization of Manitoba was not possible until the province was both deglaciated and the ice masses between Manitoba and the refugia retreated. In addition, water bodies immediately surrounding glaciers may be inhospitable to many species

because of suspended particles in the water (Ross et al. 1967). Colonization of Manitoba from the refugia would therefore follow in the order that viable water connections between Manitoba and the refugia occurred. Thus by reviewing the history of deglaciation and the current distributions of the insects we should be able to determine how and when they entered the province.

The Laurentide ice sheet consisted of the Keewatin sector and the Labradorean sector. In the Canadian prairies, the Keewatin sector covered western Manitoba, Saskatchewan, and most of Alberta while the Labradorean sector covered eastern and most of northern Manitoba (Prest et al. 1987). The Laurentide ice sheet began retreating about 12,000 to 15,000 years before the present (BP) but the two sectors retreated at different rates (Flint 1971). At about 14,000 BP, southern Alberta and Saskatchewan were free of ice while Manitoba was still covered by the Labradorean sector. This means that the Saskatchewan and Milk Rivers were blocked by the ice and therefore flowed south into the Missouri River (Clayton 1983). At about 13,000 BP the ice had retreated enough to expose most of the Red River valley (Clayton 1983). Since drainage to the east and north were blocked by ice, glacial Lake Agassiz formed. This lake lasted some 5,000 years and at this stage drained south into the Mississippi River. About 11,000 to 12,000 B.P. the ice retreated from northern Ontario. Lake Agassiz is thought to have then drained eastward into Lake Superior (Teller and Thorleifson 1983). At around 10,000 to 11,000 BP, a slight advancement of the ice in northern Saskatchewan and northern Ontario resulted in the eastern connection being blocked. This raised the level of Lake Agassiz and

possibly allowed a connection between the headwaters of the Athabasca River and the watershed of northern Lake Agassiz (Elson 1967). The extent of this connection is unclear but it certainly provided the first viable link between Beringia and Lake Agassiz. The southern outlet of Lake Agassiz was also reconnected at this time. Between 9000 and 8000 BP a series of advances and retreats of the ice resulted in alternate southwards and eastwards drainage of Lake Agassiz before settling into an eastern drainage (Elson 1967; Clayton 1983). Sometime between 6,000 and 7,000 BP the ice had receded enough that the lake finally drained north into Hudson Bay.

If we examine the two southwestern species, C. bifurcatum and C. conturbatum, we see that they have similar distributions (Figs. 15 and 34). They may have entered Manitoba in the same way at perhaps roughly the same time. This type of distribution is typical of the Montane-Saskatchewan route as defined by Flannagan and Flannagan (1982). Entry into Manitoba by this means occurred in two stages. First, the species entered the Saskatchewan River from the Missouri during the early pre-Lake Agassiz time period. Around 13,000 BP, further retreat of the ice allowed the Saskatchewan River to flow directly into Manitoba as it does to this day. Neither of these species has yet been found in the Missouri River. Centroptilum conturbatum is a cold water species so it probably no longer occurs in the Missouri. Centroptilum bifurcatum is a big river species so if this species used the Montane-Saskatchewan route, I would expect it to eventually be found in the Missouri River.

The current distribution of P. quaesitum could have arisen from two possible post-glacial dispersal routes (Fig. 75). The species could have survived glaciation in the Missouri-Mississippi River basin and used a Montane-Saskatchewan route into the province. Alternatively, the species could have entered Manitoba when Lake Agassiz drained south into the Mississippi River. This is the South Agassiz route of Flannagan and Flannagan (1982). This latter route is less likely, however. The British Columbia records of this species are in a Pacific drainage basin which was no longer connected to the Hudson Bay drainage when Lake Agassiz drained southward. This species probably followed a Montane- Saskatchewan route and secondarily entered the Mississippi River from either the Missouri River or from Lake Agassiz.

Pseudocentroptilum infrequens is also mainly western and its distribution could have resulted from a Montane-Saskatchewan route of entry into Manitoba but the species is also found in the North-West Territories. This new northern record could mean the species survived in the Beringia refugia and entered Manitoba through the Mackenzie-Athabaska River systems. This is the West Agassiz route of Flannagan and Flannagan (1982) and was open some time between 10,000 and 9,000 BP. Although either route is possible, the West Agassiz route is more likely since this is a large and colourful species, and if present, would probably have been collected on the west coast or in the Missouri River. However, it is rarely collected anywhere in its range and may yet be found in these areas.

The distribution of the eastern species, C. victoriae is poorly known (Fig.15). Its mode of entry into Manitoba might be similar to

that of P. rufostrigatum. Pseudocentroptilum rufostrigatum has been widely collected throughout northeastern North America (Fig. 56). Both species either gained access to Manitoba from the east or gained access to the east via Manitoba from the south. As stated earlier, eastward drainage of Lake Agassiz occurred continuously for some time between 12,000 and 10,000 BP and again sporadically between 9,000 and the final drainage of Lake Agassiz. Since P. rufostrigatum is found in northern areas of Quebec and Manitoba, it might be expected to do well in the Mackenzie River system. It has not yet been found there, suggesting that the species entered Manitoba sometime after the connection between Lake Agassiz and the Mackenzie River system was broken. Thus original entry into Manitoba probably occurred sometime after 9,000 BP, when the series of advances and retreats of the ice sheet resulted in alternate eastward and southward drainage of Lake Agassiz. At this time, either refugia could have been colonized from the other. An eastern refugium seems more likely since the species is more widely distributed eastwards.

Finally there is the distribution of C. album which is transcontinental (Fig. 34). This distribution is typical of that produced by the South Transcontinental migration route of Flannagan and Flannagan (1982). Insects that used this route are thought to have preceded the glacier southwards and then followed it north as the ice retreated. East-west dispersal is thought to have occurred along margin lakes and streams. Therefore this species could have been one of the first to enter the province.

PART VI. CONCLUSIONS

The Manitoba fauna consists of seven species in two groups. Group A consists of Pseudocentroptilum rufostrigatum, P. quaesitum, and P. infrequens. Group B consists of Centroptilum bifurcatum, C. victoriae, C. album, and C. conturbatum. It is not acceptable to include group B with group A as Pseudocentroptilum since this would result in a genus with a paraphyletic relationship to C. luteolum. It is inconvenient to raise group A or group B to a separate genus since this would result in three genera with a tremendous number of overlapping character states. Any key couplet that discriminates among these genera would be so full of exceptions as to be virtually useless. A more useful taxonomic treatment that would still be phylogenetically correct, would be to include group B with C. luteolum as Centroptilum sensu stricto and to include group A with the European genus Pseudocentroptilum.

I conclude that the Manitoban species support assignment of the Manitoba species into two genera and that group A species are congeneric with at least some European members of the genus Pseudocentroptilum Bogoescu. I recommend that the three group A species be included in the genus Pseudocentroptilum until such time that the phylogenetic relationships among the Palearctic types is better understood. The proper names of these species would therefore be as follows: Pseudocentroptilum infrequens (McDunnough), P. quaesitum

(McDunnough), and P. rufostrigatum (McDunnough). I further conclude that the four group B species are congeneric with C. luteolum. They might represent a distinct subgenus. The proper names of these species is conserved as follows: Centroptilum album McDunnough, C. bifurcatum McDunnough, C. conturbatum McDunnough, and C. victoriae McDunnough.

Pseudocentroptilum infrequens and P. quaesitum are in the same species group as the European species P. pennulatum Eaton and P. nemorale Eaton (Keffermller and Sowa 1984). Pseudocentroptilum rufostrigatum does not fit closely with any central European species groups and is the first recorded Pseudocentroptilum species to have unilamellate gills. Centroptilum luteolum and two undescribed European species apparently form a species group separate from the Manitoba species (Keffermller and Sowa 1984) which as mentioned might represent a distinct subgenus.

In the species descriptions section, many life stages are described for the first time and more detail is provided on those stages that were previously known. This has allowed the construction of dichotomous keys. The keys will allow identification of all specimens within Manitoba. The seven Manitoba species represent all species of Centroptilum and Pseudocentroptilum known to occur in western and northern Canada. Geographic variation was not greater than intraspecific variation. Specimens from outside Manitoba will probably be identified correctly in the key.

Geographic distribution is attributable to dispersal out of glacial refugia. Distributions are here arranged into the groups defined by Flannagan and Flannagan (1982): C. album has a South Transcontinental

distribution, C. victoriae and P. rufostrigatum have an East Agassiz distribution, P. infrequens has a West Agassiz distribution, and C. bifurcatum, C. conturbatum, and P. quaesitum have a Saskatchewan-Montane distribution.

However, there are still shortcomings in this study. The examination of the evolutionary trends within the genera is heavily influenced by our understanding of the out-group, the genus Callibaetis. This genus is found in North and South America. The North American species have been reviewed (Check 1982) but the South American species are poorly known. This genus is thought to be the sister taxon to the rest of the sub-family but its members possess several apotypies which at least superficially are similar to those of members of Pseudocentroptilum. Callibaetis nymphs have bilamellate and some species trilamellate gills and maxillary palps with only two palpomeres. A phylogenetic study of this genus might clarify the evolutionary trends examined as part of this study.

Another major problem is the difficulty in distinguishing between the genera with hind wings and those without. A phylogenetic study of the Cloeon and Procloeon species is needed in order to define the generic limits and to settle questions of their possible synonymy with Centroptilum and Pseudocentroptilum.

The shortcomings of this study can be resolved through further phylogenetic research. Care must be taken that we do not base all of our conclusions on regional fauna. Final decisions on the taxonomy of a genus with a nearly world-wide distribution cannot be made on the basis of a small number of North American and Central European species.

The results of this study should be considered tentative until a more extensive study is completed.

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