

THE UNIVERSITY OF KANSAS SCIENCE BULLETIN

VOL. XLVII

PAGES 71-115

APRIL 14, 1967

No. 3

A Review of the Subfamily Cylindrotominae in North America (Diptera: Tipulidae)¹

By

FENJA BRODO

INTRODUCTION

The Cylindrotominae are the smallest subfamily of the Tipulidae. Members of the group are not commonly collected and are therefore unlikely to appear in general insect collections. Literary references are scattered, with no all-inclusive keys existing to the North American species.

The purpose of this paper is to redescribe the North American species of Cylindrotominae, to construct comprehensive illustrated keys for their identification, to describe and illustrate representative immature stages, and to bring together the pertinent literature about this group.

There is still a difference of opinion concerning the taxonomic rank of this group. Schiner (1864) first recognized these flies as forming a natural taxon, Limnobinae Cylindrotomaeformes, within the tribe Limnobina. Later workers (Brunetti, Needham) retained Cylindrotomini as a tribe of the Limoniinae (Limnobiinae). Others (Kertész, Peus) have considered them as a distinct family. Alexander, Rogers and Takahashi relegate them to a subfamily of the Tipulidae. This latter classification is adopted here.

One North American species of Cylindrotominae was described (from Europe) by Linnaeus (1758), four were described by Osten Sacken in 1865, one by Johnson (1912), and the last to be described were *Phalacrocera occidentalis* and *P. vancouverensis* by Alexander (1927a, b). Immature stages of *Phalacrocera replicata* (from Europe) were first described by De Geer (1773); Cameron (1918) described the larva and pupa of *Cylindrotoma distinctissima americana* (as *C. splendens*), and Alexander (1914b) described the immature stages of *Liogma nodicornis*. The descriptions of the

¹ Contribution No. 1341 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

larva and pupa of *Triogma exsculpta* and of the pupa of *Phalacrocer tipulina* are included in this paper. The immatures of *Cylindrotoma tarsalis* and *Phalacrocer occidentalis* are still unknown.

After comparing the North American cylindrotomines with those of Europe and Asia (by the examination of some European specimens as well as the literature), I suspect that the genera are ill-defined, as suggested by Alexander (1949), and further study of the subfamily on a world-wide basis may result in the lowering of some of the genera to subgeneric level.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr. George W. Byers who suggested this study, made much of the material available and advised and encouraged me. To Dr. Charles D. Michener I extend my thanks for his friendly advice and interest. Thanks are due Dr. C. P. Alexander, Amherst, Massachusetts, for his graciousness in loaning me valuable specimens, and to Dr. J. R. Vockeroth, Entomology Research Institute, Canada Department of Agriculture, for descriptions and drawings of the holotype of *P. vancouverensis* and for the loan of many European and American specimens from the Canadian National Collection. I wish also to thank Dr. T. E. Moore, University of Michigan, Dr. P. J. Darlington, Jr., Museum of Comparative Zoology, Harvard University, and Dr. Selwyn Roback, Academy of Natural Sciences of Philadelphia, for the loan of additional specimens.

METHODS AND MATERIALS

Adult specimens either pinned or preserved in alcohol were used for most of this study. Wherever possible, the genitalia of at least one male and one female of each species were boiled for a few minutes in a weak solution of KOH, washed, and placed in glycerine, permitting detailed study with magnifications as high as 54X. The genitalia were eventually placed in microvials pinned under the respective specimens.

All measurements were taken with an ocular grid and are therefore rough, serving only to indicate the general size range of the structures in question. Body length refers to the distance between the vertex of the head (disregarding antennae) to the tip of the abdomen, regardless of the curvature of the body. Wing length is the straight-line measurement from point of attachment to tip.

KEY TO THE SUBFAMILIES OF TIPULIDAE IN NORTH AMERICA (ADULTS) (modified from Alexander, 1942)

1. Terminal segment of maxillary palpus elongate, whip-like; nasus usually distinct; antennae usually with 13 segments; vein Cu_1 deflected at m-cu, the latter at or close to fork of M_{3+4} ; body size usually large. *Tipulinae*

Terminal segment of maxillary palpus short; no distinct nasus; antennae usually with either 14 or 16 segments; vein Cu_1 straight, not deflected at m-cu, the latter placed far before fork of M_{3+4} , usually at or close to fork of M ; body size usually small or medium. 2

2. Male: aedeagus tripartite (Figs. 1-8), often extruded in dried specimens (Figs. 9-20); female: cerci short, broad (Figs. 21-27); mesonotal suture distinct only in median third of thorax, fading out laterally (Fig. 28); wings not patterned except for pale stigma. *Cylindrotominae*

Male: aedeagus having one or two openings; female: cerci elongate, pointed; mesonotal suture distinctly "V-shaped," characteristic of the family; wings often patterned. *Limoniinae*

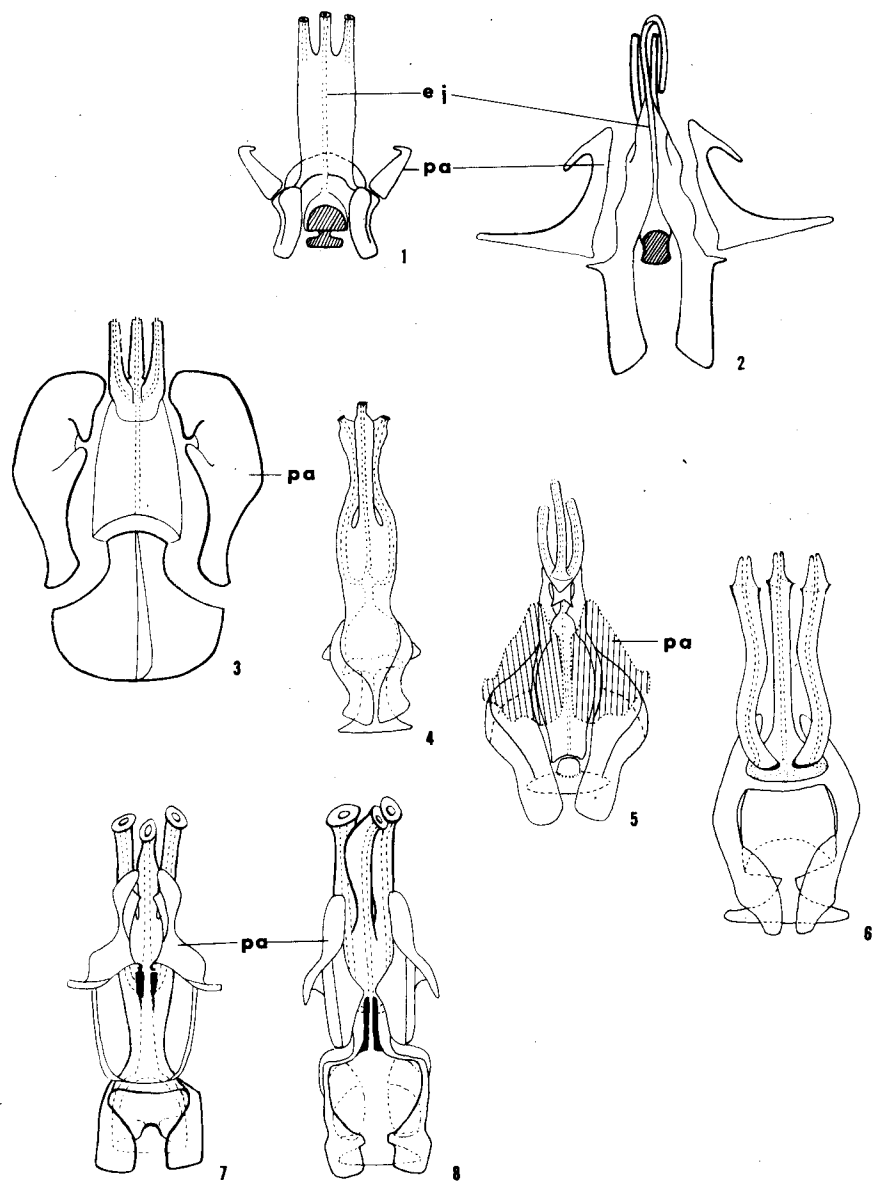
SUBFAMILY CYLINDROTOMINAE ALEXANDER

Limnobinae Cylindrotomaeformes Schiner, 1864: 560-563.
Cylindrotomaeformia Osten Sacken, 1865: 234-342.
Cylindrotomina Osten Sacken, 1869: 289-308; 1897: 362-366.
Cylindrotomini Scudder, 1894: 189.
Erucaeformia Bengtsson, 1897: 1-102.
Cylindrotomidae Kertész, 1902: Peus, 1952: 1-77; Takahashi, 1960: 81-91.
Cyttaromini Meunier, 1915: 229-230.
Cylindrotominae Alexander, 1914a: 603-605; 1919c: 926-928; 1920: 959-974; 1927a: 1-16; 1942: 292-296.

This is a curious little subfamily of the Tipulidae comprising 46 species in nine genera. In contrast to the widespread and diverse distribution of the majority of crane flies, the Cylindrotominae are, in general, sparsely scattered over the Holarctic Region, although they also include 14 species in four genera extending southward into the Oriental and Neotropical regions. They usually occur in small, scattered populations in wooded situations at high altitudes, where conditions are typically cool.

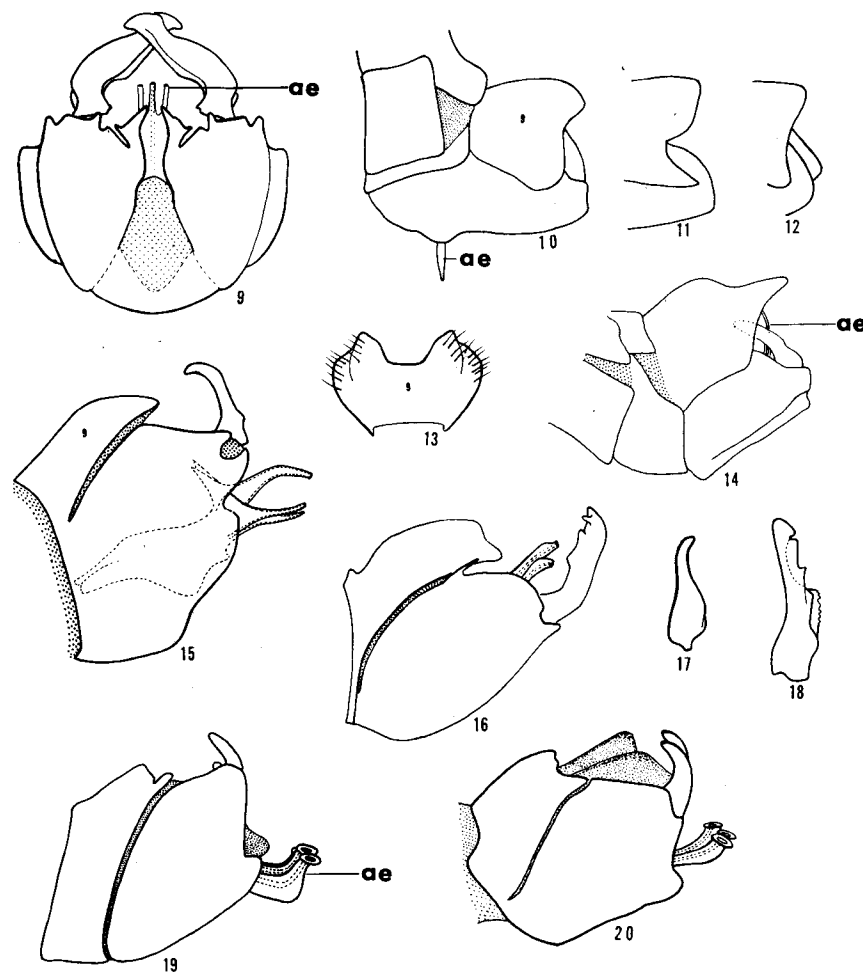
The genera within this subfamily cannot yet be satisfactorily placed in any kind of evolutionary sequence. However, they do fall neatly into two tribes, Cylindrotomini and Stibadocerini, on the basis of the much longer antennae in the latter, as well as several other morphological characters.

The Stibadocerini appear to be the more specialized group morphologically, but their ecology and biology are very inadequately known. The scanty data accompanying specimens indicate that these flies are usually found near small waterfalls and mountain streams at altitudes of 3,000 to 11,000 ft. The combined range of the 14 species of Stibadocerini extends along the southern border of the distribution range of the Cylindrotomini, with nine of these species concentrated in the Oriental Region. All these species (as far as the records indicate) occur at high altitudes where conditions are very similar to those of North America and Europe. Three species are found in the Australian Region (one each in New Guinea, New South Wales and Tasmania), and one isolated species is found in the mountains of Patagonia in southern Chile.



FIGS. 1-8. Aedeagus and accompanying structures, dorsal aspect. ej—ejaculatory duct; pa—paraphyses (gonapophyses, of most authors). Fig. 1. *Cylindrotoma distinctissima americana*. Fig. 2. *Cylindrotoma tarsalis*. Fig. 3. *Phalacrocera replicata* (=neoxena). Fig. 4. *Phalacrocera tipulina*. Fig. 5. *Phalacrocera vancouverensis*. Fig. 6. *Liogma nodicornis*. Fig. 7. *Triogma exculpta*.

The Cylindrotomini consist of 32 species arranged in five genera (see Peus, 1952; Alexander, 1956b). Only eight of these, representing four genera, occur in North America: *Cylindrotoma tarsalis*, *C. distinctissima americana*, *Phalacrocera replicata* (=neoxena of other authors), *P. occidentalis*, *P. tipulina*, *P. vancouverensis*, *Liogma nodicornis*, and *Triogma exculpta*. The



FIGS. 9-20. Hypopygia of males. ae—acedeagus; 9—ninth sternum. Fig. 9. *Cylindrotoma distinctissima americana*, ventral aspect. Fig. 10. *Cylindrotoma distinctissima americana*, left lateral aspect. Fig. 11. *Cylindrotoma distinctissima borealis*, left lateral aspect. Fig. 12. *Cylindrotoma distinctissima americana*, left lateral aspect. Fig. 13. *Cylindrotoma distinctissima americana*, ninth tergum. Fig. 14. *Cylindrotoma tarsalis*, left lateral aspect. Fig. 15. *Phalacrocera tipulina*, left lateral aspect, showing position and outline of aedeagus. Fig. 16. *Phalacrocera replicata* (=neoxena), left lateral aspect. Fig. 17. *Phalacrocera occidentalis*, left dististyle, outer aspect. Fig. 18. *Phalacrocera vancouverensis*, left dististyle, outer aspect. Fig. 19. *Liogma nodicornis*, left lateral aspect. Fig. 20. *Triogma exculpta*, left lateral aspect.

richest cyclindrotomine fauna is in the Orient (China, Japan and India), where there are nine species of *Cylindrotoma*, three *Phalacrocer*a, seven *Liogma*, two *Triogma* and two *Diogma*. The European species are *Cylindrotoma d. distinctissima*, *C. d. alpestris*, *C. d. borealis*, *Phalacrocer*a *replicata*, *Diogma glabrata* and *Triogma trisulcata*.

GEOLOGICAL RECORD

The earliest information concerning the geological history of the Tipulidae comes from the Mesozoic; however, this is rather inconclusive, and it is not until the lower Tertiary that undisputed tipuline forms occur. In the North American Eocene (such as the White River and Green River beds) and in the Oligocene (the Florissant shales, etc.), there is evidence of an extraordinary development of the Cylindrotominae. In the White River basin they almost dominate the known crane fly fauna, in sharp contrast to their paucity and irregular distribution within the fauna of today.

Many fossil finds have been erroneously placed in this subfamily, but the only fossil genus now generally accepted as belonging to the Cylindrotominae is *Cyttaromyia*, with *Cyttaromyia fenestrata* Scudder (1877) the type species. This genus is extraordinarily similar to the modern genus *Cylindrotoma*, which is also confined to the Holarctic and is distinguished from the former only by having an additional crossvein in cell R_5 forming another closed cell in the wing. *Cylindrotoma* specimens having this additional crossvein are occasionally found (Fig. 46). Cockerell (1920) described a new species from the Eocene (White River, Colorado) which appeared to lack this vein, and he therefore placed it with question in the genus *Cylindrotoma* as *C. veterana*.

Of the five genera in this holarctic group, it is generally accepted that *Cylindrotoma* is probably the most advanced genus, although a form very similar to this genus is postulated as having given rise to the other four genera (Alexander, 1927a).

Fossil record of North American Cylindrotominae to date:

From the Eocene:

Cyttaromyia fenestrata Scudder, 1877, White River, Utah.

C. fuscula (Cockerell 1920, as *Asilopsis*), White River, Colorado.

C. reclusa Cockerell, 1924, Green River, Colorado.

? (*Cylindrotoma*) *veterana* Cockerell, 1920, Roan Mountain, Colorado.

From the Oligocene:

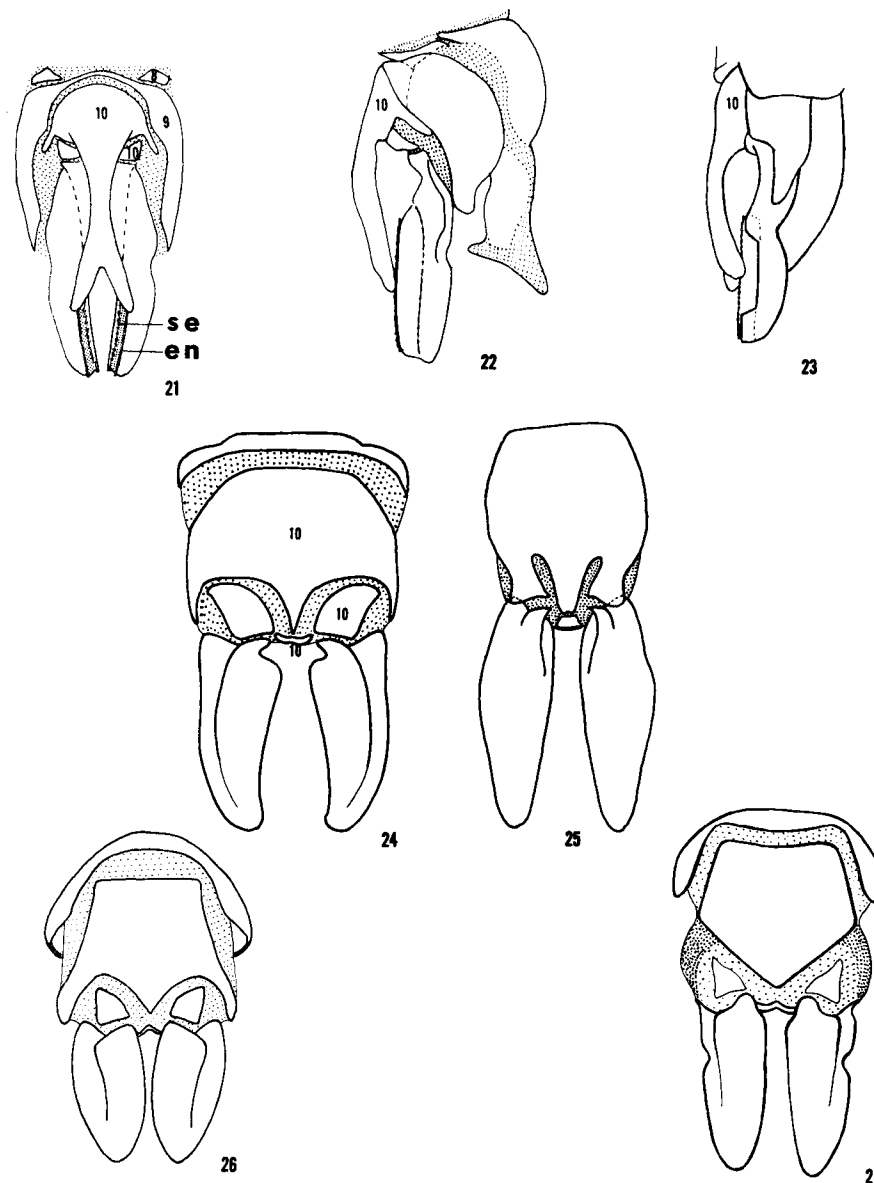
Cyttaromyia cancellata Scudder, 1894, Florissant, Colorado.

C. clathrata Scudder, 1894, Florissant, Colorado.

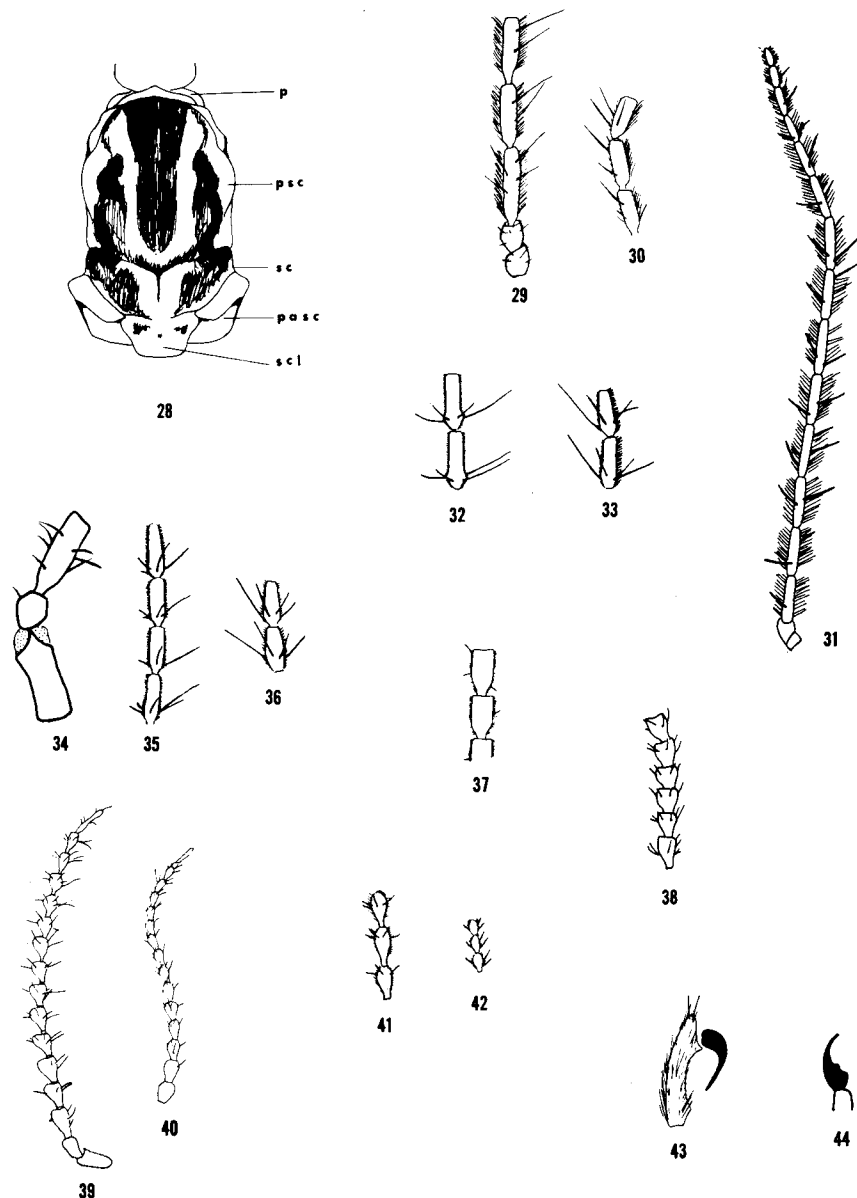
C. oligocena Scudder, 1894, Florissant, Colorado.

C. princetoniana Scudder, 1894, Florissant, Colorado.

The above species seem to be most closely related to North American species of *Cylindrotoma*.



FIGS. 21-27. Female terminalia. 9—ninth tergum; 10—tenth tergum; en—entire edge; se—serrated edge. Fig. 21. *Cylindrotoma distinctissima americana*, dorsal aspect. Fig. 22. *Cylindrotoma distinctissima americana*, right lateral aspect. Fig. 23. *Cylindrotoma tarsalis*, right lateral aspect. Fig. 24. *Phalacrocer tipulina*, dorsal aspect. Fig. 25. *Phalacrocer replicata* (= *neoxema*), dorsal aspect. Fig. 26. *Liogma nodicornis*, dorsal aspect. Fig. 27. *Triogma exsculpta*, dorsal aspect.



FIGS. 28-44. Structural details of Cylindrotominae. p—pronotum; pasc—parascutellum; psc—prescutum; sc—scutum; scl—scutellum. Fig. 28. *Cylindrotoma tarsalis*, thorax, dorsal aspect. Fig. 29. *Cylindrotoma distinctissima americana*, male, scape, pedicel and three flagellar segments. Fig. 30. *Cylindrotoma distinctissima americana*, female, three typical flagellar segments. Fig. 31. *Cylindrotoma tarsalis*, male antenna. Fig. 32. *Phalacrocera occidentalis*, male, 2 typical flagellar segments. Fig. 33. *Phalacrocera occidentalis*, female, 2 typical flagellar segments. Fig. 34. *Phalacrocera tipulina*, male, scape, pedicel and first flagellar segment. Fig. 35.

It is curious that no Cylindrotominae have been found in the lower Oligocene Baltic Amber of Europe. According to paleoecologists, the Baltic region in the lower Oligocene was covered with *Pinus succinifera*, an amber-producing pine growing on very mountainous terrain cut by rushing mountain streams. This was a humid and densely shaded environment, judging by the total lack of any specimens requiring arid or sunny conditions and the presence of Trichoptera and other insects which thrive in cool, damp situations. The dipterous fauna in the Baltic amber most closely resembles that which now inhabits eastern North America between 32° and 40° latitude (Alexander, 1931).

TRIBE CYLINDROTOMINI

Diagnosis: The Cylindrotomini (which include all North American species of the subfamily Cylindrotominae) are characterized by medium body size (8-16 mm) and legs which are considerably shorter than those of Limoniinae of equivalent body size. The wings are slightly suffused with brown and sometimes have in addition a pale oval stigma but never possess any other kind of pattern. The antennae are 16-segmented. The thorax has at least a faint indication of 3 broad longitudinal stripes, giving a characteristic pattern to this group of flies. The mesonotal suture is curved instead of "V-shaped" and does not extend beyond the median prescutal stripe. The male hypopygium is broad and bears only 1 pair of dististyles. The aedeagus divides into 3 tubes distally and is often found protruding in dried specimens. The female terminalia are short and broad in contrast to the much longer and more slender external genital apparatus found in most species of the other 2 subfamilies. The blade-like cerci are dorsal to and partly overlap the hypovalves.

Description: Antennae 16-segmented, longer in male than in female; scape with small, toothlike lateral projection (Fig. 34); palpi 5-segmented, last segment sometimes lengthened, often almost as long as first 4 combined but never exceeding these segments in length; clypeus short, with apical tuft of hairs but no "nasus"; first cervical sclerite very tiny or apparently absent; second cervical sclerite large, quadrate.

Pronotum typically divided into 3 areas by two longitudinal furrows, anteriorly a ridge, medially a more or less raised crest, posteriorly a ridge split and flattened medially. Pretergite glabrous, generally paler than rest of thorax; mesonotum with 3 more or less distinct broad longitudinal stripes,

Phalacrocera tipulina, male, 4 typical flagellar segments. Fig. 36. *Phalacrocera tipulina*, female, 2 typical flagellar segments. Fig. 37. *Phalacrocera replicata* (=neoxena), male, 2 typical flagellar segments. Fig. 38. *Phalacrocera vancouverensis*, male, 6 typical flagellar segments. Fig. 39. *Liogma nodicornis*, male antenna. Fig. 40. *Liogma nodicornis*, female antenna. Fig. 41. *Triogma exsculpta*, male, 3 typical flagellar segments. Fig. 42. *Triogma exsculpta*, female, 3 typical flagellar segments. Fig. 43. *Phalacrocera tipulina*, male, tarsal segment and tarsal claw. Fig. 44. *Phalacrocera vancouverensis*, male, tarsal claw.

median stripe extending from pronotum to mesonotal suture, lateral stripes commencing slightly below median stripe, swelling outwards on scutum, narrowing, almost merging behind mesonotal suture; mesonotal suture curved behind median stripe, fading out laterally (Fig. 28) (in *Cylindrotoma* apparently continuing forward along sides of median stripe); anterior edges of scutum raised, more or less giving impression of continuation of mesonotal suture across thorax.

Wings pale brown due to microscopic brown hairs; veins darker brown, costa and distal branches of radius and media bearing brown macrotrichia, other veins bare; pale, oval stigma usually present. Subcosta ending unbranched before stigma or joining costa or radius, or dividing, Sc_1 ending in costal cell, Sc_2 turning posteriorly (Fig. 49, Sc_{2A}) to join R_1 for a short length, then anteriorly (Sc_{2B}) to join costa; branches of Sc often fragmented. Radius with 2 or 3 branches reaching costa; tip of R_{1+2} usually obliterated, R_2 considered to have fused with R_1 just beyond area of stigma, often present only as a very short, almost obliterated crossvein (Fig. 53); R_3 and R_{4+5} reaching costa independently. Three or 4 branches of media reaching costa: M_1 and M_2 not separated in *Liogma* and *Triogma*; M_3 and M_4 not separated in *Phalacrocer* *replicata*, *P. tipulina* and *P. vancouverensis*. Cubitus straight, not bent at junction of m-cu, but sharply curved distally, joining wing margin perpendicularly. Two anal veins, as characteristic of the family.

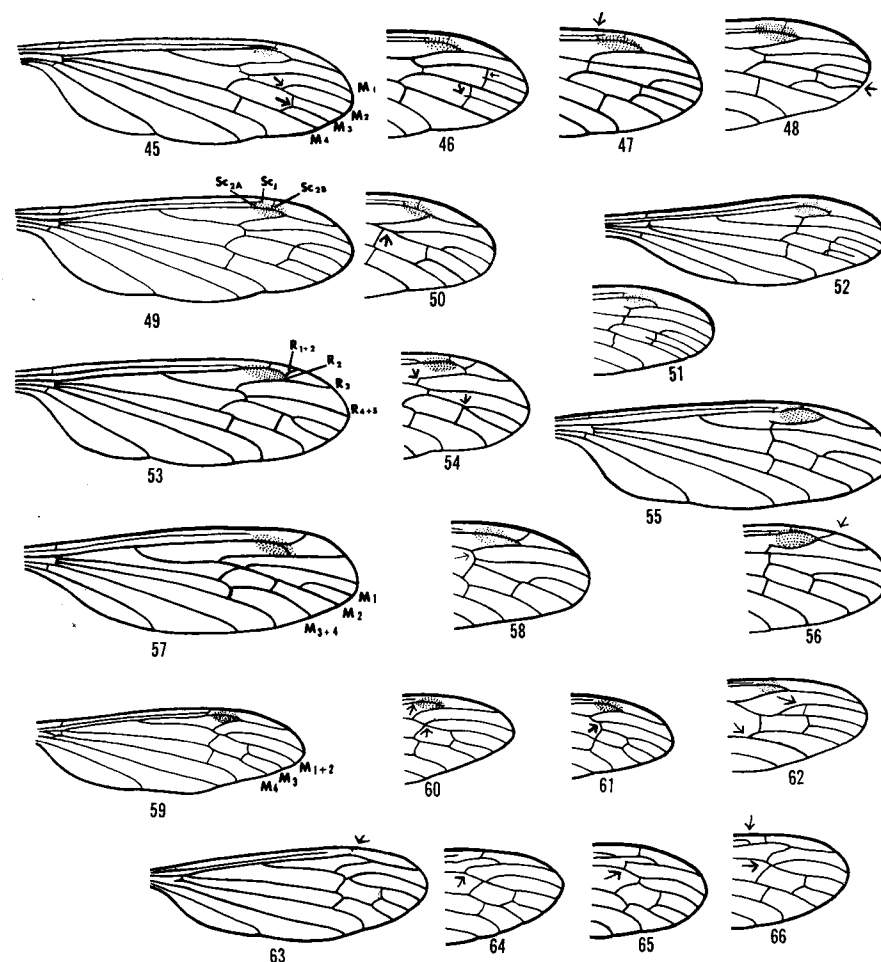
Abdomen long, broad posteriorly, more slender and darker anteriorly. Ninth tergum variously lobed or notched. Basistyles large, broad, indistinctly separated medially by membranous region; single pair of dististyles, simple or armed with small projections. Aedeagus² tripartite distally (bipartite in the European *Diogma*) enclosing 3 ejaculatory ducts (lateral ducts in *Cylindrotoma* apparently vestigial). Various shaped sclerotized plates closely associated with basal end of aedeagus (lacking in *Phalacrocer* *occidentalis* and *Cylindrotoma tarsalis*, but probably represented by basal developments of aedeagus in the latter). Paraphyses (Figs. 1, 2, 3, 5, 7, 8) 2 variable sclerites on either side of or above aedeagus.

FEMALE terminalia: Ovipositor short, broad; cerci broad, flat, entire or with serrated dorsal edge; hypovalves lightly sclerotized, fused to eighth sternum or separated by thin membranous region. Tenth tergum fragmented: large flat sclerite with median and often with two lateral projections caudally (in *Cylindrotoma* median projection much prolonged and forked distally),

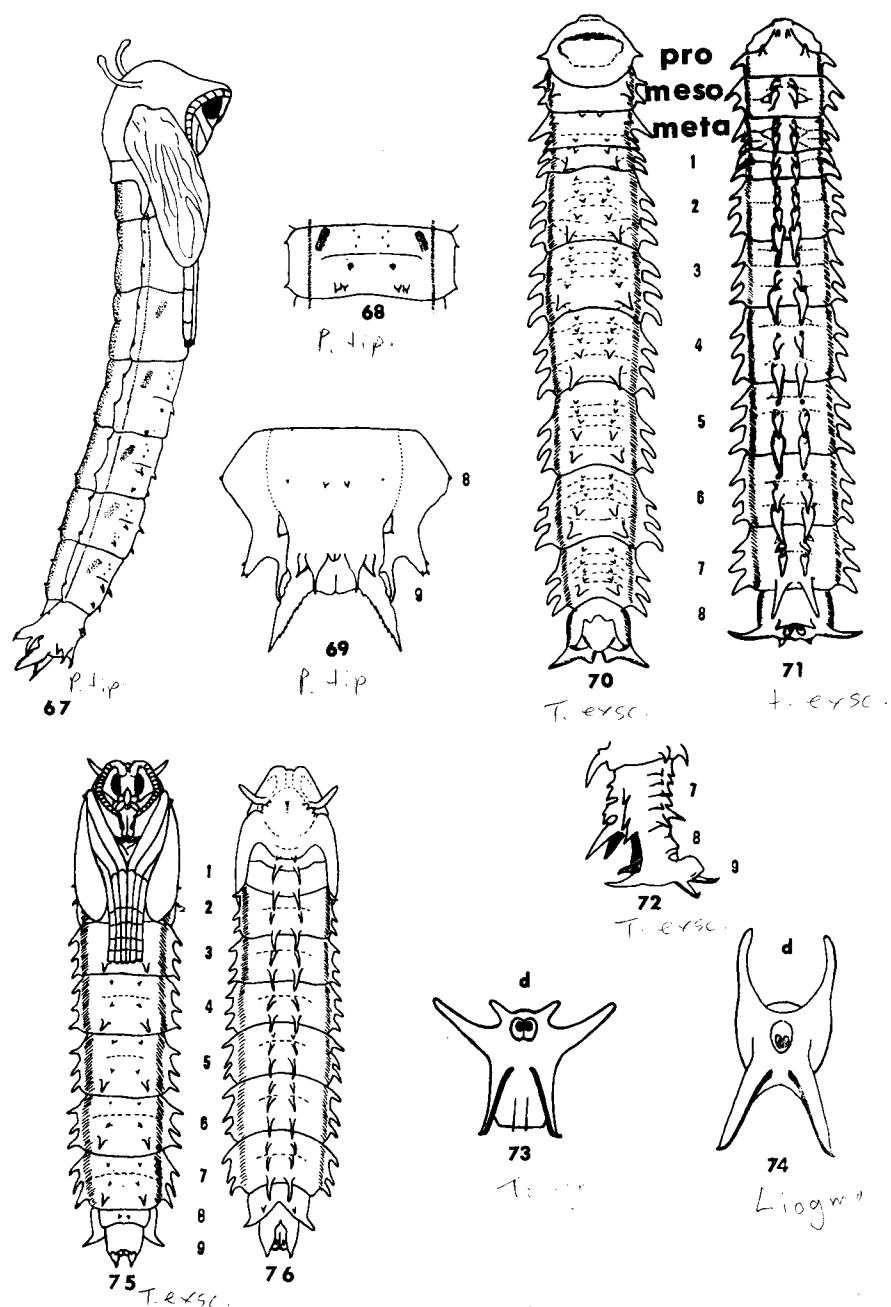
²The morphology of the aedeagus and its accompanying structures is confusing. Snodgrass (1904), studying the hypopygium of *Phalacrocer tipulina*, concluded that the penis (aedeagus) might actually represent a fusion of the penis and its guard (adminiculum). The aedeagus of *P. tipulina* has a bifurcate, dorsal, sclerotized prolongation, reminiscent of the adminicular rods of *Dolichopeza* (see Byers, 1961).

2 small sclerites on either side (attached in *Phalacrocer replicata* and *Triogma trisulcata* of Europe), and narrow sclerite between bases of cerci. Three sclerotized spermathecae visible in cleared specimens.

One suspects that the cylindrotomine genera are ill-defined when noting the striking similarity between *Triogma* and *Liogma*, both of which genera include only one North American and one European species. The insecure taxonomic position of *Phalacrocer occidentalis*, which has been shifted between *Phalacrocer* and *Cylindrotoma*, testifies to the inadequate definition of



Figs. 45-66. Wings of Cylindrotominae. M—media; R—radius; Sc—subcosta; arrows—call attention to variations in venation. Figs. 45-48. *Cylindrotoma distinctissima americana*. Figs. 49-50. *Cylindrotoma tarsalis*. Figs. 51-52. *Phalacrocer occidentalis*. Figs. 53-54. *Phalacrocer replicata* (= *neoxena*). Figs. 55-56. *Phalacrocer tipulina*. Figs. 57-58. *Phalacrocer vancouverensis* (58=holotype). Figs. 59-62. *Liogma nodicornis*. Figs. 63-66. *Triogma exsculpta*.



Figs. 67-76. Figures showing immature stages. d—dorsal aspect; 1, 2, 3 etc.—refer to abdominal segments. Fig. 67. *Phalacrocer tipulina*, pupa, right lateral aspect. Fig. 68. *Phalacrocer tipulina*, pupa, ventral aspect of typical abdominal segment. Fig. 69. *Phalacrocer*.

these two genera. A world-wide study of this group with particular emphasis on the more diverse Asian species should lead to a better delineation of the genera.

KEY TO THE GENERA OF CYLINDROTOMINAE OF NORTH AMERICA (adults)

1. Stout, dark flies, distinctly rugose or punctate on head and thorax. *Triogma*
- Slender bodied flies without such punctations. 2
2. Thoracic dorsum with whitish or yellowish-grey pubescence; pleurae pubescent, dull black or brown. *Phalacrocer*
- At least part of thorax pale yellow, 3 more or less distinct black stripes on prescutum, thorax dull or shiny but not pubescent. 3
3. Shiny mahogany-brown or black stripes on prescutum; 3 branches of media reaching wing margin (Fig. 59); cerci smooth, rounded blades (Fig. 26); antennae nodulose, almost cordate in male (Fig. 39). *Liogma*
- Dull brown or black stripes on thorax; 4 branches of media reaching wing margin (Fig. 45); cerci with serrated edges dorsally (Figs. 21, 22, 23); antennal segments cylindrical (Figs. 29, 30). *Cylindrotoma*

The following keys to the larvae and to the pupae are provisional since the immatures of several species remain unknown. The diagnosis of *Phalacrocer* is based on the characteristics of *P. replicata*, *P. tipulina* and *P. vancouverensis*. The immature stages of *P. occidentalis* are not known. The diagnosis of *Cylindrotoma* is based solely on *C. distinctissima* subspecies since the immatures of *C. tarsalis* are not known.

KEY TO THE LARVAE OF CYLINDROTOMINAE OF NORTH AMERICA (modified from Alexander, 1927a)

1. Body appendages very long, filiform and dichotomously branched dorsally. *Phalacrocer*
- Body appendages short. 2
2. Dorsal appendages simple, in a single median row on abdominal segments 3-7; terrestrial on spermatophytic plants. *Cylindrotoma*
- Dorsal appendages in pairs with teeth or with small protuberances anteriorly. 3

tipulina, pupa, ventral aspect of posterior segments. Fig. 70. *Triogma exsculpta*, larva, ventral aspect. Thoracic segments indicated as pro, meso, meta. Fig. 71. *Triogma exsculpta*, larva, dorsal aspect. Fig. 72. *Triogma exsculpta*, larva, right lateral aspect of posterior segments. Fig. 73. *Triogma exsculpta*, spiracular disk of larva. Fig. 74. *Liogma nodicornis*, spiracular disk of larva (redrawn from Alexander, 1920). Fig. 75. *Triogma exsculpta*, female pupa, ventral aspect. Fig. 76. *Triogma exsculpta*, female pupa, dorsal aspect.

3. Two pairs of processes on spiracular disks (Fig. 74); dark, oblique, lateral marks on abdominal terga. *Liogma*
 Three pairs of processes on spiracular disks (Fig. 73); abdominal segments brown dorsally, whitish at edges. *Triogma*

KEY TO THE PUPAE OF CYLINDROTOMINAE OF NORTH AMERICA

(modified from Alexander, 1927a)

1. Abdominal terga 3 to 7 without processes or lobes. 2
 Abdominal terga 3 to 7 with lobes on each segment. 3
 2. Abdominal sterna bearing small spines; mesonotal³ respiratory horns elongate, directed backwards (Figs. 67, 68). *Phalacrocer*
 Abdominal segments unarmed; mesonotal respiratory horns small, directed slightly forward. *Cylindrotoma*
 3. Two of 3 pairs of lobes on each abdominal tergum (Fig. 76). *Triogma*
 A single pair of long slender lobes on each abdominal tergum. *Liogma*

Cylindrotoma Macquart

Cylindrotoma Macquart, 1834: 107; Walker, 1856: 268-337; Schiner, 1863: 217-226; Osten Sacken, 1865: 234-237; Alexander, 1920: 927; 1942: 294; Peus, 1952: 67.
 Type: *Limnobia distinctissima* Meigen.

Diagnosis: *Cylindrotomini* with 3 dull, dark brown or black stripes on pale yellowish prescutum. Four branches of media reaching wing margin. Female cerci distinctly serrate dorsally, partially covered by distal branches of median prolongation of tenth tergum.

Description: Head smooth, bare, very light to dark brown; scape short, round; flagellar segments cylindrical; no hairs anteriorly on pronotum; pretergites pale yellow; mesonotum hairless, pale yellow, often dusky anteriorly, with 3 dark longitudinal stripes on prescutum; mesonotal suture apparently "U-shaped", flanking median stripe, slightly raised edges of scutum giving only faint indication of continuation of mesonotal suture across thorax; scutum partially divided by longitudinal suture; scutellar sutures clearly defined; pleural sclerites pale yellow, black areas on anepisternum, postepisternum, and pleurotergite; mesepisternum with transverse suture; longitudinal suture on pleurotergite; wings faintly suffused with brown, oval stigma slightly darker; Sc₁ fading just before stigma, Sc₂ weakly indicated or absent; radius with two branches (R₃ and R₄₊₅) reaching costa; r-m usually present (occasionally lacking in one or both wings); 4 branches of media present, M₁ branching at distal edge of discal cell, M₃ together with short medial cross-

³ Byers (1961: 769) noted that the breathing horns of the Tipulidae are mesothoracic not prothoracic as propounded in the literature. I have verified this for the *Cylindrotominae*.

vein forming distal edge of cell; tibial spurs small, indistinct, close together, covered with appressed microscopic hairs; tarsal claws small, slender. Abdomen varying from dark to light brown, lighter median longitudinal band on dorsum and venter; distal edge of each segment pale.

MALE terminalia: Eighth tergum narrow, entire or partially divided dorsally by narrow membranous area; ninth tergum large, squarish, rectangularly notched medially, produced into 2 lateral lobes distally; aedeagus with three tubes, only middle tube showing complete ejaculatory duct leading to semen pump.

FEMALE terminalia: Eighth tergum not continuous, reduced to 2 narrow lateral sclerites; ninth tergum produced into 2 large lateral areas narrowly joined anteriorly and dorsally; tenth tergum elongate, divaricate distally, with 2 small lateral projections near base, 2 triangular fragments in membrane between tenth tergum and cerci; cerci broad, dorsal margins serrate.

KEY TO ADULTS OF NORTH AMERICAN SPECIES OF CYLINDROTOMA

1. Male with flattened, gently curved aedeagus, aedeagal tubes short, of equal length (Figs. 1, 9); 2 dorsal edges on each female cercus, outer edge entire, inner edge serrate (Figs. 21, 22); tarsal segments brown, slightly darker distally. *distinctissima americana*
 Males with broadly curved aedeagus, aedeagal tubes elongated, middle tube considerably longer than lateral tubes (Figs. 2, 14); 2 dorsal edges on female cercus as in *C. distinctissima americana*, but the outer non-serrated edge vestigial, represented only by anterior and posterior vestiges joined basally (Fig. 23); second and third tarsal segments abruptly paler than distal segments. *tarsalis*

Cylindrotoma distinctissima americana Osten Sacken

(Figs. 1, 9, 10, 13, 21, 22, 29, 30, 40-48, 77)

Limnobia distinctissima Meigen, 1818: 131.⁴
Cylindrotoma distinctissima; Macquart, 1834: 107.
Cylindrotoma brevicornis Zetterstedt, 1838: 846.
Cylindrotoma americana Osten Sacken, 1865: 236-237; Alexander, 1942: 294.
Cylindrotoma splendens Doane, 1900: 197, pl. 8, fig. 21 (wing); Cameron, 1918: 67-89; Alexander, 1920: 708-710, 967-969, pl. 84 (larva and pupa); 1927, pl. 1, fig. C (wing), fig. 8 (female genitalia), fig. 9 (male genitalia). (New synonymy.)
Cylindrotoma juncta Coquillett, 1900: 401.
Cylindrotoma pallescens Alexander, 1930: 280.
Cylindrotoma splendens pallescens Alexander, 1954: 42. (New synonymy.)
Cylindrotoma distinctissima americana; Alexander, 1956a: 177.

There is much confusion concerning the taxonomic extent of this species. Osten Sacken (1865) characterized *americana* from eastern North America by its three black thoracic stripes, the central stripe being longitudinally divided by a thin yellow line (Fig. 28). He concluded with the observation: "The European *C. distinctissima* seems to be very like *americana* in its color-

⁴ Only the basic references to the European *C. d. distinctissima* have been cited.

ing." In 1900, Doane described a western species, *C. splendens*, having black thoracic stripes; no mention was made of a median yellow dividing line on the prescutum, but he noticed three distinct dark spots on the pleurae and minor variations in the radial and medial fields of the wing. My study of *splendens* and *americana* revealed that the thin yellow stripe along the midline of the thorax occurs occasionally in both groups of flies and that both exhibit the same pleural markings.

In 1930 Alexander described *pallescentis*, which he differentiated from *splendens* by its much paler and rufous appearance. Later, in 1954, he came to the conclusion that *pallescentis* was merely a subspecies of *splendens*. I was able to compare several hundred specimens ranging in the west from Unalaska, Alaska, southward to Colorado and in the east from Nova Scotia southward to New York and westward to Michigan (see Fig. 77). It soon became apparent that coloration is of little use taxonomically, as the same sort of variation exists throughout, and the same held true for slight differences observed occasionally in wing venation. The details of the genitalia are virtually identical throughout. Despite the geographic division of these specimens into eastern and western populations, I consider them to represent one species. There is insufficient evidence or justification for the retention of subspecies within this group.

In a relatively recent paper, Alexander (1956) gave his opinion that *americana* is merely a subspecies of the European *distinctissima*. I am indebted to the Canadian National Collection for the loan of 11 specimens of *distinctissima* from Sweden and the opportunity to compare these in the minutest detail with representative specimens of *americana* from all parts of its range. In almost every structural detail, including those of the genitalia in both sexes, no differences could be found. The Swedish specimens, however, lacked the very pale and rufous form characteristic of some of the American populations, but this may simply be a function of the smaller sample size in the former. Peus (1952) distinguished three subspecies of the European *distinctissima*, and with the help of his drawings and descriptions I was able to differentiate the *americana* group by the shape of the posterior edge of the ninth tergum in the male (Figs. 10-12). Unfortunately this character is of limited use as the exact shape of the tergum is often difficult to determine, due to distortion in drying of the insects.

Diagnosis: Males of this species have a flattened, slightly curved aedeagus, divided distally into 3 short tubes of equal length. Females have a pair of cutting edges dorsally on each cercus, the outer edge smooth, the inner edge serrate. All tarsal segments are brown, but the fourth and fifth are slightly darker.

Description: MALE: Body length 10-12 mm; wing length 8-10 mm. Head pale yellow, dark spot behind antennae, almost square in dorsal profile,

slight indentation behind eyes; no pubescence on head, several light hairs posteriorly; palpi, labium, and labrum medium to dark brown, membranous areas lighter; clypeus medium brown, irregularly fringed with hairs, narrow laterally (slightly broader than in *tarsalis*), defined by deep, horizontal fronto-clypeal suture; antennal bases raised anteriorly, close together, narrow furrow between them widening and fading out behind scapes; scape short, brown, lighter apically, slightly longer medially but lacking distinct tooth-like projection; pedicel slightly broader than scape; flagellum dark brown with cylindrical segments densely covered with erect hairs as long as width of segments proper; 2 to 4 longer darker hairs on each segment, those more dorsal slightly longer (Fig. 29); eyes not protruding but accented by slight indentation behind; ommatidia small (smaller than in *tarsalis*), black; first cervical sclerite small, narrow; second cervical large, squarish, dark brown.

Pronotum pale yellow to brown, anterior edge slightly curved, broader and higher medially creating depression behind; 2 more or less fused basal spots on postscutellum; halteres dark on knobs, stems lighter, fringed with hairs; coxae pale, inner distal edge black; femora, tibiae brown; tarsi brown, apical segments slightly darker. M_{1+2} branching near distal edge of discal cell.

Terminalia of male: Ninth tergum broad, slightly produced laterally into broad conical lobes (Fig. 13); dististyles heavily sclerotized, haired, broad, with denser tufts of hairs basally, narrower ridged shaft widening anteriorly into round concave head (Fig. 9); aedeagus a flattened, slightly curved blade, divided distally into 3 short tubes of equal length, basally supported by a ventral sclerite and a sclerite on each side (Fig. 1); paraphyses small, slender sclerites lying transversely in membrane between aedeagus and basistyles.

FEMALE: As for male, except for following characteristics: thoracic stripes never attaining dark brown-black characteristic of many males; flagellar segments (Fig. 30) shorter than in male, covered with shorter hairs, several longer hairs dorsally. **Terminalia** (Figs. 21, 22): Cerci broad flat blades bearing two dorsal cutting edges, separated by narrow sclerotized trough, outer edge smooth, inner edge serrate; ventral edges of cerci sinuous; tenth sternum 2 lightly sclerotized plates with hairs, lying in membrane ventral to cerci; hypovalves membranous and narrowly cleft at tips; 3 identical, spherical, heavily sclerotized spermathecae.

Variation: Variation in amount and distribution of pigments has been the sole basis for differentiating the western group *pallescentis* from *splendens* and from *americana* as noted above. Among the specimens which I have studied, three from Nova Scotia (Baddeck, 6 July 1928, D. M. Bates) in addition to 19 from Colorado (Kenosha Pass, 20 June-10 July, 1919) were mottled light orange on the thorax, with the longitudinal stripes barely distinguishable from the background, thus fitting the description of *pallescentis*.

The eastern specimens, with the exception of the paler ones from Nova Scotia, had distinct dark stripes (but females never attained the full black of some of the males), and the western specimens from Washington and Oregon varied from almost white to very black. Occasionally fully pigmented specimens of both the eastern and western populations show the yellow dividing line down the middle of the thorax. A series from Klamath Falls, Oregon, 23 June 1959 (G. W. Byers), was intermediate in coloration, containing mostly pale brown specimens and several darker males. Strikingly similar variation in pigmentation has been studied in other insects (Ross, 1956), and experiments have shown that varying humidity and temperature caused the production of different amounts of carotinoids and melanins. Apparently this is a basic physiological reaction, the effects of which are masked in many insects by other pigments or by structural colors.

The wings also exhibit much variation (Figs. 45-48). Traces of Sc_2 are variable, M_{1+2} may divide before or beyond the distal edge of the discal cell, and parts of the media or radius may be weak or almost obliterated. Short spurs are often present, particularly on branches of the media, and one specimen was found with an extra crossvein in cell R_5 , creating another closed cell, as in the fossil genus *Cyttaromyia*.

Larva: Living specimens are light chlorophyll green with 2 narrow, pale brown longitudinal lines on dorsum, extending from the posterior end, above spiracles anteriorly, becoming more expanded and diffuse on the fore part of the body. Preserved specimens are brown to light yellow, the longitudinal lines remaining visible. Dorsal processes are simple, in a single median row on abdominal segments three to seven.

Pupa: The live pupa is green. Preserved specimens are pale yellowish. The small mesonotal breathing horns are directed slightly forwards.

Detailed descriptions of larvae and pupae were given by Cameron (1918), Alexander (1920) and Peus (1952).

Ecology: The life history of this species is well-known, having been described in detail by Cameron (1918) and summarized by Alexander (1920). The females have a unique ovipositor equipped with two sawlike blades, enabling them to make incisions in the upper epidermis of leaves of small land plants upon which their larvae will later feed. In the western range of this species, the larvae have been found in rich woodlands, feeding on *Allium*, *Anemone*, *Trautvetteria*, *Stellaria*, and *Viola*. The larvae cease feeding after one molt, hibernate among fallen dead leaves, and finish feeding and molting in the following spring. Females emerge in large numbers before males are seen. Dr. George W. Byers observed near Anchorage, Alaska, on 28 June and 3 July, that this species was locally very abundant in cow parsnip (*Heracleum*) thickets in deep shade and that the adults rest on the

upper surface of the leaves or hang from the edge with wings outspread. They were also taken in Klamath County, Oregon, in a swale where *Smilacina sessilifolia* was a common plant.

Cylindrotoma distinctissima americana occurs in northern regions at relatively high elevations. In Colorado, the southernmost tip of its known range, it has been collected at 10,000 ft.; in Oregon and Washington at 3,000-4,000 ft.; up to 7,000 ft. in Montana and British Columbia; 5,000 ft. in New Hampshire; and almost at sea level in Unalaska, Alaska, and Nova Scotia.

Flight records: 6 May-31 Aug.

Distribution (Fig. 77): ALASKA: Admiralty Island, 23 June-26 Aug.; Cascade (15 mi. SE of Anchorage), 28 June -3 July; Cold Bay (163° W 55° N, on tundra), 26-27 July; Igiak Bay, 17 July; Kenai Peninsula (22 mi. N of Seward), 1 July; Unalaska, 24 Aug.; Virgin Bay, (Prince William Sound), 26 June. ALBERTA: 39 mi. SSE of Valley View, 10 July; Waterton Lakes National Park, 23-24 June. BRITISH COLUMBIA: Vancouver District, Squamish Diamond Head Trail (3200-4000 ft.), 5-19 Aug.; Caribou District, Lillooet, Mt. McLean (7200 ft.), 12 June; Kootenay District, Mt. Revelstoke, 26-30 Aug.; Nanaimo District, Vancouver Is.: Forbidden Plateau, Victoria, Westholme, 10 May-18 Aug. COLORADO: Grand Co., Ute

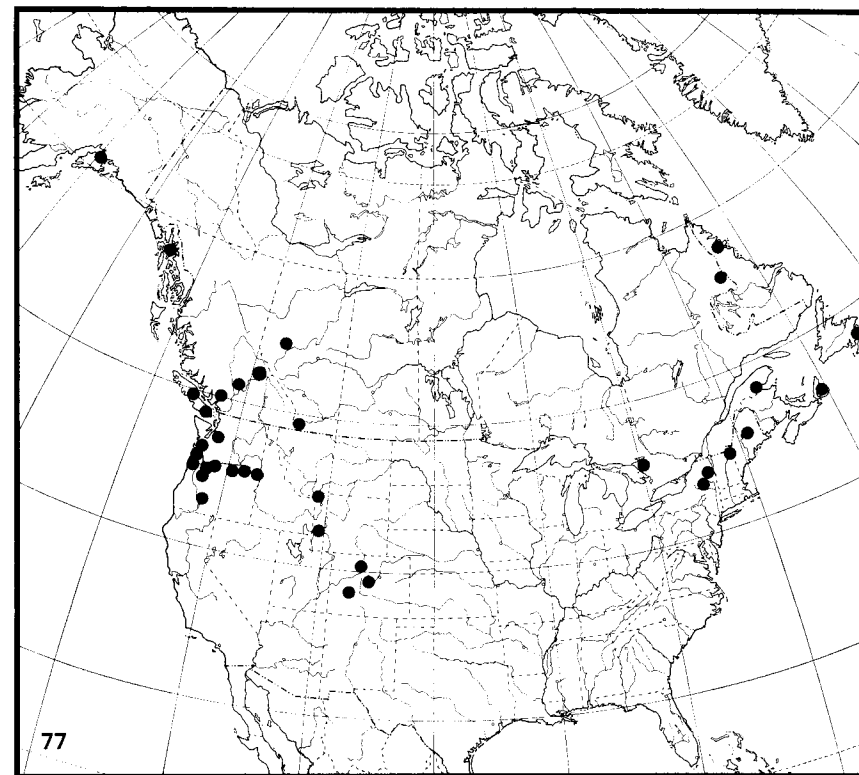


FIG. 77. Range of *Cylindrotoma distinctissima americana*. Each spot represents one or more collections within a county or at a locality.

USNMAL McKinlay N.P. (now Denali), Bear River L. 160°15' W 56°03' N.
CANADA VT AK Hwy. Teelin Lake. BC. Spring AK Hwy mile 35

Pass (Williams Fork Range, 10,500 ft.), 16 July; Gunnison Co., Gothic (9500-10,000 ft.), 16 July; Park Co., Kenosha Pass (10,000 ft.), 20 June-10 July. LABRADOR: Nutak, 26 July. MAINE: Piscataquis Co., Capens, 11 July. NEW BRUNSWICK: (no further data). NEW-FOUNDLAND: Bonavista North and South Districts, Terra Nova National Park, 8 July. NEW HAMPSHIRE: Coos Co., Bretton Woods, Glen House, Mount Washington, Lake of the Clouds (5000 ft.), Tuckerman's Ravine (5400 ft.), White Mts., 28 June-31 Aug. NEW YORK: Essex Co., Mt. Marcy, 21-28 July; Fulton Co., Gloversville, 17 June. NOVA SCOTIA: Victoria Co., Baddeck, 6 July. ONTARIO: Parry Sound Co., Burks Falls, Sand Lake, 5-14 Aug. OREGON: Clackamas Co., Still Creek, 16 July; Clatsop Co., Saddle Mt. (Boyer Station), 6 May-18 June; Hood River Co., Cascades (Mt. Hood, Hood River Meadows, 4800 ft.), 17 July-8 Aug.; Klamath Co., SE edge of Crater Lake National Park (4350 ft.), Crater Lake (6200 ft.), Odell Lake (4760 ft.), 23 June-2 Aug.; Linn Co., Big Meadows, North Santiam, 3 Aug.; Morrow Co., Castle Rock, Sourgrass Creek, 13-17 May; Umatilla Co., Blue Mt., Spring Creek (3900 ft.), Little Antone Creek (4100 ft.), Little Phillips Creek (3800 ft.), 5 June-3 July; Wallowa Co., Wallowa Creek (4635 ft.), above Lazy T Ranch (5500 ft.), Lostine Valley Guard Station (4900 ft.), 29 June-17 July; Yamhill Co., High Heaven, 4 May. PENNSYLVANIA: (no further data). QUEBEC: Bonaventure Co., Escuminac, 2-31 July; Indian House Lake (56° 08' N Lat., 64° 44' W Long.), 18 July. WASHINGTON: Pierce Co., Cayuse Pass (Mt. Rainier, 4650 ft.), Nisqually Glacier Trail (4000 ft.), Wonderland Trail (above White River, 4900-5000 ft.), 23 July-1 Aug.; Pacific Co., Ilwaco, 5 May. WYOMING: Lincoln Co., Jenny Lake (6780 ft.), Leigh Lake (6870 ft.), 3-12 July; Yellowstone National Park (Northeast Entrance 7200 ft.), Obsidian Creek (7300 ft.), 24-27 June.
Schefferville, 17 July 1961

Types: *C. americana* Osten Sacken, two male syntypes (one with broken abdomen), White Mountains, New Hampshire, end of June, 1836 (no. 10237, Museum of Comparative Zoology, Harvard University).

C. splendens Doane, three male syntypes, Unalaska, Alaska, 24 Aug. 1897 (Kincaid) (no. 7,051, U.S. National Museum).

C. juncta Coquillett, female holotype, Virgin Bay, Prince William Sound, Alaska, 26 June (no. 5,204, U.S. National Museum).

C. pallescens Alexander, female holotype, Ute Pass, Williams Fork Range, Grand Co., Colorado, 10,500 ft., 16 July 1929 (C. F. Clagg), (C. P. Alexander Collection, Amherst, Massachusetts).

Cylindrotoma tarsalis Johnson

(Figs. 2, 14, 23, 28, 31, 49, 50, 78)

Cylindrotoma tarsalis Johnson, 1912: 2, fig. 4 (wing); Alexander, 1919c: 963, plate 30, fig. 7 (wing); 1927a: plate I, fig. 1 (wing); 1942: 294, fig. 8 (antenna), fig. G (wing).
Cylindrotoma ? anomala Johnson, 1912: 2-3, fig. 3 (wing).

Diagnosis: In the male the aedeagus is strongly curved, and its median tube is greatly prolonged. The female has a serrated dorsal edge on each cercus, lateral to which lie anterior and posterior vestiges of a smooth edge. The second and third tarsal segments are abruptly lighter than the other leg segments.

Description: MALE: Body length 8-9 mm; wing length 7-9 mm. Head dark brown dorsally, lighter ventrally and laterally, grayish pollinose with fine light hairs posteriorly, broadly oval in dorsal profile, no indentation behind eyes; palpi, labium, labrum medium brown, membranous areas lighter; clypeus light brown, irregularly fringed with hairs, delineated by arched

frontoclypeal suture; clypeus narrow laterally (narrower than in *C. d. americana*); antennal bases raised slightly and somewhat further apart than in *americana*, separated by narrow dark brown sclerotized strip; scape and pedicel of equal length, pale yellow or brown; broad tooth on scape; flagellum (Fig. 31) brown, cylindrical segments densely covered with erect hairs the length of diameter of segments, 2 to 4 longer hairs dorsally on flagellar segments, none ventrally; head oval in dorsal aspect, with eyes forming rounded ends ommatidia larger than in *americana*, appearing grayish white within black network; first cervical sclerite small, narrow; second large, approximately square.

Pronotum hairless, pale to dark brown, anterior edge slightly curved, broader and higher medially, creating depression behind; pale brown spot on postscutellum; halteres dark on knobs, stems lighter and fringed with hairs; coxae pale, inner distal edge black; femora, tibiae brown; first, fourth, fifth tarsal segments brown, second and third abruptly lighter. M_{1+2} branching close to distal edge of discal cell.

Terminalia of male: Ninth tergum with 2 narrow lobes (Fig. 14); dististyles sclerotized, simple structures narrowing and curving distally, fewer hairs than in *americana*; median tube of aedeagus much prolonged, curved dorsally; baso-lateral portions of aedeagus much produced on either side; paraphyses large sclerotized "C-shaped" structures on either side of aedeagus (Fig. 2).

FEMALE: Only 2 females seen. Similar to male except for usual sexual dimorphism. Head slightly indented behind eyes; flagellar segments shorter than in male, first 2 segments broadly joined, others showing small basal "neck" region; segments clothed with short hairs, less dense than in male, appressed rather than erect; several longer, darker hairs on dorsal surface of segments. Terminalia (Fig. 23): Cerci broad, flat; serrate dorsal edge on each cercus lateral to which lie anterior and posterior vestiges of smooth blade joined basally, entire central portion of blade apparently never developed; ventral edges of cerci straight; hypovalves membranous at tips, cleft somewhat more deeply than in *americana*; (tenth sternum and spermathecae not observed due to insufficient material).

Variation: The same differences in the amount and quality of pigmentation exist here (at least in the males) as in *C. d. americana*. Occasionally the crossvein r-m is obliterated.

Immature stages: Not seen.

Ecology: These flies apparently frequent the same sort of habitats as *C. d. americana*. They are found at high altitudes, in Hudsonian and high Canadian zones, in small, widely scattered populations, flying from May to September. The adults can be swept from rank vegetation shaded by trees in close proximity to water. The females have serrated edges on their cerci;

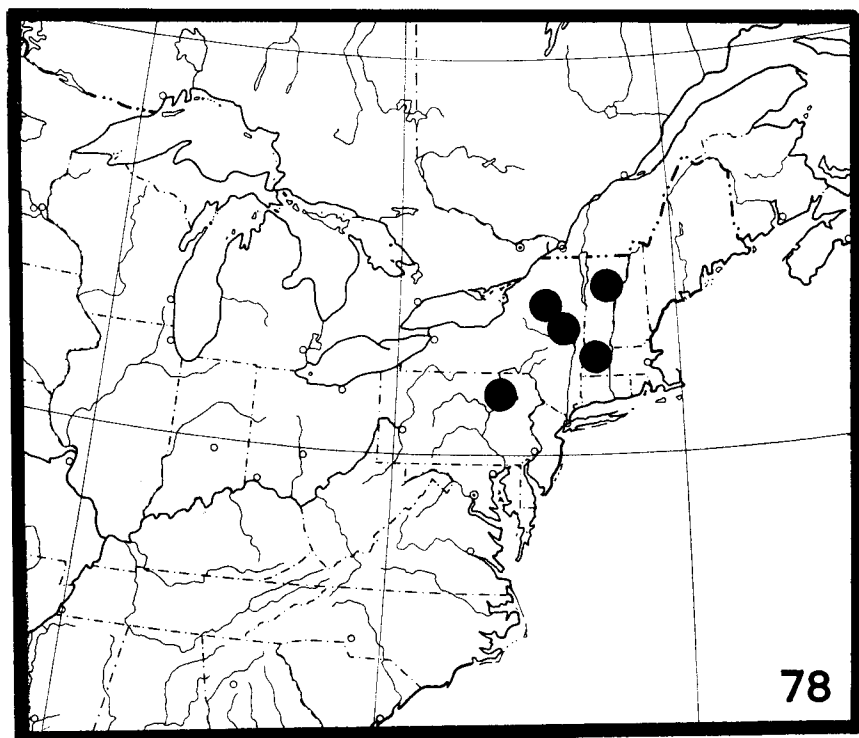


FIG. 78. Range of *Cylindrotoma tarsalis*. Each spot represents one or more collections within a county or at a locality.

thus in this species the eggs are probably laid in incisions of the epidermis of food plant leaves in much the same manner as by *C. d. americana*.

Flight records: 30 May-12 Sept.

Distribution (Fig. 78): CONNECTICUT: Litchfield Co., Norfolk, 12 June-12 Sept. NEW BRUNSWICK: (no further data). NEW YORK: Fulton Co., Bleeker (Woodsworth's Lake, 1650 ft.), Gloversville, 9 June-19 Aug.; Herkimer Co., Indian Castle, 13 June. PENNSYLVANIA: Lycoming Co., 30 May. VERMONT: Lamoille Co., Stowe, 15-24 June.

Types: Male holotype, 6 male paratypes, Woodsworth's Lake, Bleeker, New York, 19 Aug. 1909, (no. 7480, Museum of Comparative Zoology, Harvard University); 7 male paratypes, same data (C. P. Alexander collection, Amherst, Massachusetts).

C. ? anomala Johnson. Female holotype, Woodsworth's Lake, Bleeker, New York, 1 Aug. 1909, (no. 7481, Museum of Comparative Zoology, Harvard University).

Phalacrocer Schiner

Phalacrocer Schiner, 1863: 224; Alexander, 1927a: 9-10; 1942: 292-293; Peus, 1952: 64.

Type: *Tipula replicata* Linnaeus, 1758 (= *Limnobia nudicornis* Schummel, 1829).

Schiner established this genus on the basis of the presence of R_{1+2} and the sparsely haired flagellar segments. However, neither of these characters is useful, even when only the Palearctic species are considered. The four North American species, *Phalacrocer occidentalis*, *tipulina*, *replicata* (= *neoxena*) and *vancouverensis*, form a reasonably homogeneous group, but characters employed in this paper are probably of limited use on a world-wide basis.

Diagnosis: This genus may be recognized by the light pubescence on a black or dark brown head and thorax, almost obscuring the 3 mesonotal stripes, which are only faintly outlined by a thicker pubescence. Either 3 or 4 branches of the media reach the wing margin. The tenth tergum in the female is not greatly elongated and extends only to the base of the cerci. The cerci do not have a serrated dorsal edge.

Description: Head smooth, black or dark brown, covered with whitish or yellowish pubescence; scape longest antennal segment; flagellar segments cylindrical or subcylindrical, sparsely haired or densely covered with extremely short erect hairs; pronotum haired; pretergites pale yellow to brown; mesonotum black, pubescent, pubescence thickest along longitudinal lines delimiting thoracic stripes; pleural sclerites black or dark brown; scutellar suture usually indistinct; transverse suture on mesepisternum; longitudinal suture on pleurotergite; wings faintly suffused with brown, oval stigma barely darker; Sc_1 and Sc_2 usually present; radius with 2 or 3 branches reaching wing margin; r-m present; 3 or 4 branches of media reaching wing margin; if only 3, M_{3+4} not branching but continuing directly to wing margin; if 4, pattern as for *Cylindrotoma*. Tibial spurs large, strongly curved and divergent, haired, tips bare; tarsal claws larger than those of *Cylindrotoma*.

MALE terminalia: Eighth tergum entire, narrow; ninth tergum large, squarish, notching at distal edge variable; lateral lobes variable; aedeagus with 3 slender tubes each sheathing an ejaculatory duct.

FEMALE terminalia: Eighth tergum narrow, may be reduced to 2 lateral sclerites; ninth tergum narrow, not produced laterally, tenth tergum variable but never prolonged and forked over cerci; cerci broad, flat, with no distinct serrated edge but occasionally several microscopic, irregularly formed teeth distally.

KEY TO ADULTS OF NORTH AMERICAN SPECIES OF PHALACROCERA

1. Pronotum with distinct transverse crest in center; R_{1+2} present. 2
Pronotum almost flat except for shallow horizontal furrow; tip of R_{1+2} usually atrophied. 3
2. Flagellar segments covered with dense coat of short erect hairs, with a few longer irregularly placed hairs (Fig. 32); mesonotal suture broad, shiny brown. *replicata*

probably does have dense short hairs - 2007

Flagellar segments with verticils, not covered with short dense hairs (Fig. 38); mesonotal suture narrow, dull and darker than rest of thorax. *vancouverensis*

3. Three branches of media present (Fig. 55); median aedeagal tube strongly arched dorsally, lateral tubes parallel and close together (Fig. 15); pronotum glabrous. *tipulina*

Four branches of media present (Fig. 51); 3 aedeagal tubes short, straight and parallel (Fig. 3); pronotum pollinose. *occidentalis*

***Phalacrocer* *occidentalis* Alexander**

(Figs. 3, 17, 32, 33, 51, 52, 79)

Phalacrocer *occidentalis* Alexander, 1927a: 10.

Cylindrotoma *occidentalis* Alexander, 1954: 41-42.

This species is of particular interest because it resembles both *Phalacrocer* and *Cylindrotoma*. Alexander (1954) placed *occidentalis* in *Cylindrotoma* because it has four branches of the media, although he later (Alexander, 1965) listed this species in *Phalacrocer*. I am recognizing *Phalacrocer* *occidentalis* because this species seems to resemble the genus *Phalacrocer* more closely in the following respects: The thorax is blackish with a grayish-yellow pubescence. (*Cylindrotoma* species have three distinct black prescutal stripes on a pale thorax.) The mesonotal suture does not flank the median stripe. The longest antennal segment is the scape, and the whorl of hairs on the basal enlargement of the flagellar segments most closely resembles that of *P. tipulina*. The pronotum is flat like that of *P. tipulina*, lacking the median crest of *Cylindrotoma*. The cerci of the female are simple rounded blades, lacking the serrated edge found in *Cylindrotoma*, and the ninth tergum is not prolonged nor divaricate distally. Lastly, the tibial spurs are long and slender, characteristic of *Phalacrocer*. Except for characters of the male genitalia, this species most closely resembles *P. tipulina*.

Diagnosis: This species is black with grayish-yellow pubescence on the head and thorax. The pronotum is broad, flat and pollinose. Four branches of the media reach the wing margin. The semen pump and its apodemes and paraphyses are extremely large in comparison to the three very small tubes of the aedeagus.

Description: MALE: Body length 12 mm; wing length 8-10 mm. Head dorsally black with whitish pubescence, ventrally dark brown glabrous; dorsal profile subtriangular, no indentation behind eyes, eyes confluent with head contour; palpi, labial segments dusky brown, haired, membranous region lighter brown; labrum shiny brown; clypeus dusky brown, pubescent, broad and flat, bearded distally, lateral portions long, at least two-thirds length of anterior region; frontoclypeal suture deep, horizontal; antennae about 5 mm, dusky brown, bases not raised anteriorly; scape longest, broadest segment, lateral teeth narrow; pedicel globular; flagellar segments sub-

cylindrical, covered with extremely short, erect hairs, whorl of longer hairs on enlargement near base of each segment (Fig. 32); first cervical sclerite not seen (insufficient material), second large, black, convex.

Pronotum almost flat, dark brown with yellowish pubescence, short erect hairs anteriorly, shallow furrow bisecting it horizontally; pretergite pale yellow to brown. Mesonotum black with yellowish pubescence; 3 stripes indicated vaguely by denser pubescence in longitudinal furrows flanking region of stripes; narrow line of lighter pubescence longitudinally bisecting mesonotum; mesonotal suture small, almost straight, glabrous brown, scutum black, pubescent, pubescence whiter at scutal suture; scutellum very pale, pubescent, with 2 shiny brown pits anterolaterally; postscutellum with 2 black basal areas, whitish pubescence medially; pleurites light brown to black, pubescent, membranes dusky; pleurotergal suture and suture between anepisternum and preepisternum lacking.

Coxae dark brown, pubescent; trochanters lighter, edged with black distally; femora, tibiae, tarsal segments brown, darker distally; tibial spurs long, diverging, clothed with short brown appressed hairs, darker and bare distally; last tarsal segment cylindrical, claws long, slender and broadly curved, only slightly widened at base. Knobs of halteres dusky black, stems lighter, edged with hairs.

Wings (Figs. 51, 52) pale brown, stigma slightly darker, oval; Sc₁ fading out just before stigma, Sc_{2A} and Sc_{2B} absent or merely suggested by presence of pale lines in wing; 2 branches of radius (R₃ and R₄₊₅) reaching wing margin, (a very small portion of R₁₊₂ found on 1 specimen); r-m in line with radial crossvein, joining media near proximal corner of discal cell; 4 branches of media reaching wing margin; M₁₊₂ branching at or just beyond distal edge of discal cell, M₃₊₄ branching at posterior distal edge of discal cell; short medial crossvein plus section of M₃ form distal edge of discal cell.

Abdomen dark brown to black, posterior segments bordered anteriorly by a colorless band. Terminalia of male (Figs. 3, 17): Ninth tergum with rounded notch medially on distal edge; basistyles without lateral projections; dististyles simple narrow structures, slightly widened at base, yellowish, blackened distally, covered with short fine hairs; aedeagus with 3 short, parallel tubes, large, broad semen pump, but no basal sclerites; paraphyses large, "mitten-shaped" (Fig. 3).

FEMALE: Differs from male in the following characters: antennae shorter (2.5 mm), flagellar segments shorter (Fig. 33), cylindrical, without basal enlargements, clothed with erect hairs slightly longer than in male, whorl of longer hairs basally. Terminalia: (Character of ninth tergum not observed on the one dried specimen); tenth tergum a large sclerite with 3 distal projections, two small triangular sclerites in membrane between projections;

cerci short, broad, haired structures, rounded distally; hypovalves weakly sclerotized, incompletely fused to ninth sternum, narrowly notched and membranous distally.

This description is based on only two specimens, a male and a female, borrowed from Dr. C. P. Alexander, Amherst, Massachusetts.

Immature stages: Not seen.

Ecology: This species has been found in highest, humid Transition or low Canadian life zones in Washington State at 2,800 ft., and at 4,475 ft. in Oregon. Individuals were found in high alpine meadows overgrown with grasses and sedges in the vicinity of a stream. The characteristic plants in this region were clumps of scrubby willow, *Veratrum viride*, *Habenaria*, *Caltha leptosepala*, *Pedicularis groenlandica surrecta*, *Dodecatheon* and alpine fir, mountain hemlock and pines along streams (see Alexander, 1949).

Flight records: 10 June-8 Aug.

Distribution (Fig. 79): OREGON: Hood River Co., Cascades, (Hood River Meadows, Mt. Hood, 4475 ft.), 17 July-8 Aug. WASHINGTON: Pierce Co., Longmire Springs (Mt. Rainier, 2800 ft.), 10 June, 17 July.

Type: Male holotype, Longmire Springs, Mt. Rainer, Washington, 10 June 1917 (H. G. Dyar), (C. P. Alexander collection, Amherst Massachusetts).

Phalacrocer replicata (Linnaeus)

(Figs. 4, 16, 25, 37, 53, 79)

Tipula replicata Linnaeus, 1758: 587.⁵

Limnobia nudicornis Schummel, 1829: 122.

Tipula brevisrostris Zetterstedt, 1838: 844.

Phalacrocer replicata; Schiner, 1863: 224; Grünberg, 1910: 33-35, fig. 33 (antenna), fig. 34 (male terminalia), fig. 35 (female terminalia), fig. 36 (wing); Peus, 1952: 1-77, fig. 2 (head), fig. 4 (thorax), fig. 10 (wings), fig. 17 (tarsal claws), fig. 18 (female terminalia), fig. 23, 29 (male terminalia), fig. 33, 36, 37a, 39, 40, 41, 42, 43, 47, 50 (larvae), fig. 52, 56a, 57a (pupae), fig. 61 (eggs).

Phalacrocer neoxena Alexander 1914a: 603-604, pl. 25, fig. 10 (wing); 1919: 30, fig. 9 (wing); 1927a: pl. 2, fig. 6 (wing); 1942: 293, 295, fig. 33, E (wing).

A comparison of American specimens of *neoxena* with five Swedish specimens of *replicata* indicates that only one species is involved. Alexander (1914a) noted a similarity between these two groups but also pointed out several differences such as color, variations in the radial-medial crossvein and differences in the male genitalia. However, my material afforded detailed comparisons, including comparable preparations of the genitalia of both sexes, and I found approximately the same range of variation in both populations, albeit my European sample was considerably smaller and limited in geographic range.

Diagnosis: This is one of the more robust species in the subfamily. It is black with grayish pubescence on the head and whitish yellow pubescence

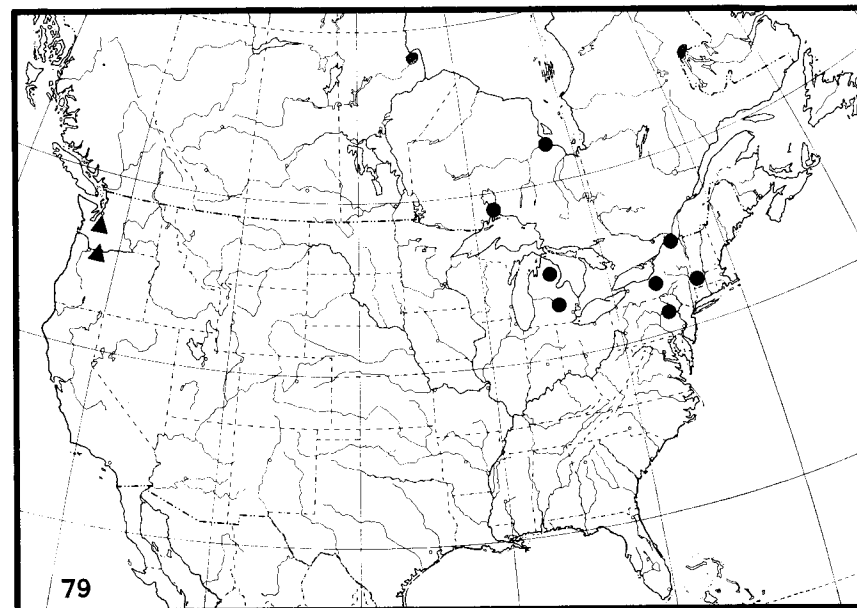


FIG. 79. Ranges of *Phalacrocer occidentalis* (triangles) and *Phalacrocer replicata* (circles). Each spot represents one or more collections within a county or at a locality.

on the thorax. The pronotum is pollinose with dark crest in the center, accented by a furrow behind and flanked by 2 dark spots on either side. Three branches of the media and 3 of the radius reach the wing margin. The 3 aedeagal tubes are long and slender in comparison to the semen pump and its apodemes. The flagellar segments have several long, scattered hairs in addition to a dense covering of very short hairs. The mesonotal suture is broad and shiny brown.

Description: MALE: Body length 12-15 mm; wing length 10-11 mm. Head black, grayish pubescence particularly evident laterally and bordering eyes, several light hairs posteriorly; dorsal profile broadly rectangular with short, narrow "neck", slight indentation behind eyes; labium, labrum, and palpi medium brown, clypeus brown, broadest and most densely haired distally, slight horizontal distal groove giving impression of broad rim; lateral expansion of clypeus somewhat less than two-thirds its length; frontoclypeal suture strongly arched, obscured by coloration; antennae (Fig. 37) about 4.0 mm, dark brown, bases not raised but separated by dark narrow groove; scape subcylindrical, slightly widened apically, about length of first few flagellar segments, lateral teeth broadly triangular; pedicel globular; flagellar segments subcylindrical, each gently tapered proximally, truncate apically, covered with very short, dense, erect hairs with several sparse, irregularly

⁵ Only the basic European references to this species are given.

placed longer hairs; first cervical sclerite brown, small, squarish; second cervical sclerite larger, rectangular, anterior corner narrowly prolonged.

Pronotum broad, almost flat, dark brown with grayish pubescence; short row of erect hairs anteriorly, raised crest in center accentuated by furrow behind, flanked by dark spot on either side; pretergite pale yellow. Mesonotum black, smooth, with whitish yellow pubescence; pubescence thicker along 2 longitudinal furrows, lighter along narrow mid-line; mesonotal suture curved, polished brown, extending to longitudinal furrows; scutum black, pubescent; scutal suture obliterated basally; scutellum brown, pubescent, finely pitted, with 2 larger pits anteriorly; postscutellum light yellow, smooth, with narrow ridge along mid-line; pleurites with minute white hairs, no discernible suture between the anepisternum and postepisternum; pleurotergal suture also lacking.

Coxae, trochanters pale; femora, tibiae, tarsi uniformly darker brown, heavily haired; tibial spurs stout, sharply pointed, covered with appressed hairs, tips bare and black; tarsal claws sharply curved, brown with black tips. Halteres with light brown knobs, stems lighter, edged with hairs.

Wings (Figs. 53, 54) strongly suffused with brown, stigma prominent, oval; Sc_1 fading out before reaching stigma; Sc_1+Sc_{2A} usually reaching radius, presence of Sc_{2B} variable; 3 branches of radius reaching margin: R_{1+2} , R_3 and R_{4+5} ; r-m present, or occasionally almost obliterated; 3 branches of media reaching margin: M_{1+2} branching just beyond discal cell, therefore cell M_1 petiolate, single crossvein closing cell distally; M_{3+4} not branching, curving slightly at margin.

Abdomen brown, with darker median longitudinal streak on dorsum and venter. Terminalia of male (Figs. 4, 16): Eighth tergum entire; ninth tergum with round medial notch; basistyles with narrow fingerlike projections laterally; dististyles mostly hairy, bare at tips, longitudinal central ridge broader distally, small sclerotized lobe and notch on outer edge, broad concavity basally, aedeagus with three long slender tubes, each enclosing ejaculatory duct, tubes narrowed at tips, close together, outer pair more curved and slightly shorter than median tube; 1 small basal sclerite enveloping semen pump region of aedeagus; paraphyses (not shown in figure) long, curved, arms attached to inner sclerotized edges of basistyles; fleshy anal segment often visible in dried specimens.

FEMALE: As in male except for following characters: antennae shorter (2.5mm), dark brown, scape cylindrical; flagellar segments small, subcylindrical; covered with minute hairs, several longer hairs on each segment, shorter, stiffer ones ventrally. Terminalia (Fig. 25): Ninth tergum broad; tenth tergum large with 3 distal extensions plus a small sclerite between cercal bases; cerci broad, entire; hypovalves deeply notched distally, fused with broader eighth sternum, thin projection distally on dorsal edge.

Larva: Distinctly greenish when alive. "Body covered with numerous, elongate, trachea-bearing filaments, the posterior pair on dorsal segments deeply forked, the others simple. Spiracular disk with dorsal pair of lobes formed by rudimentary posterior branch of branched filaments of eighth abdominal segments" (Alexander, 1927a).

Pupa: "[Mesonotal] breathing horns long, almost straight. Dorsal abdominal segments with tubercles, those of sixth and eighth segments enlarged into spinous hooks; 2 pointed tubercles on seventh sternite" (Alexander, 1927a).

More complete descriptions of larvae and pupae are given by Alexander (1920).

Ecology: Rogers (1942) reports this species is "locally common to abundant about the moss and *Myriophyllum* choked pools of unshaded seepage marshes". They are often taken around the "margins of grass-sedge-fern marshes" but never found in association with *Sphagnum*.

Flight records: 12 May-30 June.

Distribution (Fig. 79): MASSACHUSETTS: Berkshire Co., Mt. Greylock, 15 June. MICHIGAN: Livingston Co., E. S. George Reserve, Honey Creek, Putnam Twp., 12-20 May; Oscoda Co., 18 June. NEW YORK: Cayuga Co., North Fairhaven, 17 May. ONTARIO: Thunder Bay Co., Nipigon, 17 June; Cochrane Co., Fort Albany (James Bay), 10 June. PENNSYLVANIA: Luzerne Co., Hazleton, 30 June. QUEBEC: Huntingdon Co., Hemmingford, 23-27 June. *churchill*
July 7, 1912
Schafferville

Ont. Bells Corners

Types: *P. neoxena* Alexander. Male holotype, Nipigon, Thunder Bay County, Ontario, 17 June 1913 (Dr. E. M. Walker). Female allotype and one male paratype no. 1 same data as holotype; no. 2, male, type locality, 18 June 1913; no. 3, female, North Fairhaven, Cayuga Co., N. Y., 17 May 1913. (Type and paratype no. 1 in University of Toronto collection; paratype no. 2 in C. P. Alexander collection, Amherst, Massachusetts.) *collected in Fontinalis hypnoides in Churchill, 29*

Phalacrocer a tipulina Osten Sacken

(Figs. 5, 15, 24, 34-36, 43, 55, 56, 67-69, 80)

Phalacrocer a tipulina Osten Sacken, 1865: 241-242; Needham, 1908: pl. 11, fig. 2 (wing); Alexander, 1914a: pl. 25, fig. 11 (wing); 1919: pl. 30, fig. 8 (wing), text fig. 125 J (male antenna); 1920: 961; 1942: 293; Dickinson, 1932: 210, fig. 112 (wing).

Diagnosis: This species is dark brown to black with a tawny pubescence. The pronotum is broad, flat and glabrous. Two branches of the radius and 3 branches of the media reach the wing margin. The 3 long, slender aedeagal tubes are readily visible, the median tube arched over the parallel lateral tubes, with the tips of all 3 converging.

Description: MALE: Body length 10-14 mm; wing length 8-11 mm. Head dorsally dark brown to black, with tawny pubescence, several light hairs posteriorly; dorsal profile triangular, narrow "neck" with 2 or 3 encircling ridges, no indentation behind eyes; palpi, labial segments dark brown, hairy; labrum and surrounding membranes orange-brown, clypeus darker brown, relatively large, rectangular, distally bearded, giving appearance of short

nasus, lateral expanse about half of frontal length; fronto-clypeal suture horizontal, groove-like; antennae 3.5-4.5 mm, dusky brown, bases not raised (or only slightly so); scape longest segment, cylindrical, irregularly haired, often secondarily grooved or ringed, lateral teeth narrow (Fig. 34); pedicel globular, pubescent, with several long scattered hairs; flagellum (Fig. 35) slightly narrower than scape, segments sub-cylindrical, covered with short dense hairs, whorl of longer hairs on slight proximal enlargement, last segment attenuated medially, 4 hairs at tip; first cervical sclerite brown, small, narrow; second cervical sclerite large, rectangular, anterior corner medially prolonged.

Pronotum broad, flat, narrowed anteriorly, shiny brown except for narrow band of pubescence anteriorly before shallow groove; more distinct groove before paler pretergites. Mesonotum black with yellowish pubescence, pubescence thickest on longitudinal furrows, narrow bare line often dividing mesonotum longitudinally; mesonotal suture a polished brown shallow curve widening to shiny brown pits at longitudinal furrows; scutum black, pubescent; scutal suture indistinct or absent; scutellum brown, pubescent, with 2 pits anteriorly; postscutellum smooth, brown, whitish pubescence medially; pleurites brown, thickly pubescent, suture present between anepisternum and postepisternum; pleurotergal suture lacking.

Coxae, trochanters light brown; femora, tibiae, tarsi darker, thickest and darkest apically, covered with hairs; tibial spurs long, diverging, with short appressed hairs, bare at tips; last tarsal segment concave ventrally (Fig. 43); tarsal claws almost length of preceding segment, slender, strongly curved, several short teeth basally. Halteres brown at knobs, stems lighter, edged with hairs.

Wings (Figs. 55, 56) strongly suffused with brown, stigma darker, oval; Sc_1 fading out before stigma, Sc_{2A} present, Sc_{2B} variable; 2 branches of radius reaching costa, R_3 and R_{4+5} ; r-m always present, usually touching radial crossvein and joining media close to proximal end of discal cell; 3 branches of media reaching wing margin: M_{1+2} forming rectangular edge of discal cell, cell M_1 usually petiolate; M_{3+4} not dividing, curving slightly at margin.

Abdomen dark brown, segments edged distally by darker band next to outer colorless band. Terminalia of male (Figs. 5, 15): Eighth tergum entire; ninth tergum rectangular, with narrow medial notch (smaller than in *replicata*); basistyles without lateral projections; dististyles haired at least basally, bare at tips, slender, curved and tapering distally; aedeagus with 3 long narrow tapered tubes, each enclosing ejaculatory duct, median tube arched over parallel lateral tubes, sclerotized bifurcate projection at juncture of three tubes; large basal sclerite enveloping basal half of aedeagus; paraphyses (Fig. 5), triangular plates dorsal to aedeagus.

FEMALE: As in male except for following characters: antennae (Fig. 36) considerably shorter than in male (2-2.5 mm), flagellar segments shorter, basal enlargement more pronounced, short hairs less dense; tarsal claws shorter, broader basally not strongly curved, lacking teeth. Abdomen broader than in male. Terminalia (Fig. 24): Ninth tergum a narrow sclerotized ring; tenth tergum of 4 sections: large sclerite with 3 short distal extensions, 2 small triangular sclerites in membrane between extensions, small narrow sclerite between and just anterior to cercal bases; cerci short, broad, with rounded caudal edges, smooth lateral edges; hypovalves weakly sclerotized, deeply notched at tip, thin projection distally on dorsal edge.

Variation: The tip of R_{1+2} is occasionally present on one or both wings, confusing this species with *P. replicata*. A pair of slender horny outgrowths of the pronotum were found on two specimens of approximately 300 studied. Another specimen had only one horn with no indication of its mate on the other side of the pronotum. This is probably nothing more than an anomaly.

Larva: Not seen.

Pupa (Figs. 67-69): Only pupal skins were available for study. Specimens were light brown, wing pads and leg sheaths darker, darker brown stripe on dorsal mid-line, pair of small spots laterally on venter of each segment.

Length 13.5 mm; width 3 mm. Cephalic part of head broad, without spines or lobes. Prothorax lacking processes. Mesothorax broad, irregular, with a slender pair of curved breathing horns anteriorly, devoid of other processes. Broad wing sheaths extending down two-thirds of second abdominal segment. Metanotum devoid of spines; haltere sheaths lying alongside first abdominal segment, partially covered by wing sheaths. Leg sheaths extending almost to end of third abdominal sternum. First abdominal segment short, without processes. Abdominal segments 2 to 8 as follows: 4 pairs of spots dorsally, posterior 2 bearing short hair on small prominence; ventrally (Fig. 68) with 2 oval spots antero-laterally, 3 pairs of tiny spots medially, a thin transverse division behind which lies a roundish spot on each side of mid-line, and more posteriorly, a pair of small spines on each side; laterally produced into a broadly bi-lobed flange, a pigmented spot at each tip. Eighth segment with a broad lateral flange, a small pigmented spot at broadest portion on each side; 4 small spines ventrally, middle 2 larger; posteriorly, 2 rounded processes, each tipped with a small hair. Ninth segment terminating in several lobes: dorsal pair of lobes longest, 2 rows of spines dorsally; 6 ventral lobes, middle lobe smallest; deeply bilobed lateral process, outermost lobes broader, tipped with 3 small hairs.

This pupa is quite similar to that of *P. replicata*, differing only in the absence of a pair of terminal processes on the dorsum of the sixth abdominal segment and on the seventh abdominal sternum.

Ecology: This species is not as difficult to find as are most *Cylindrotominae*. It occurs in or near sphagnum bogs in northern or mountainous locali-

Poste de la Baleine

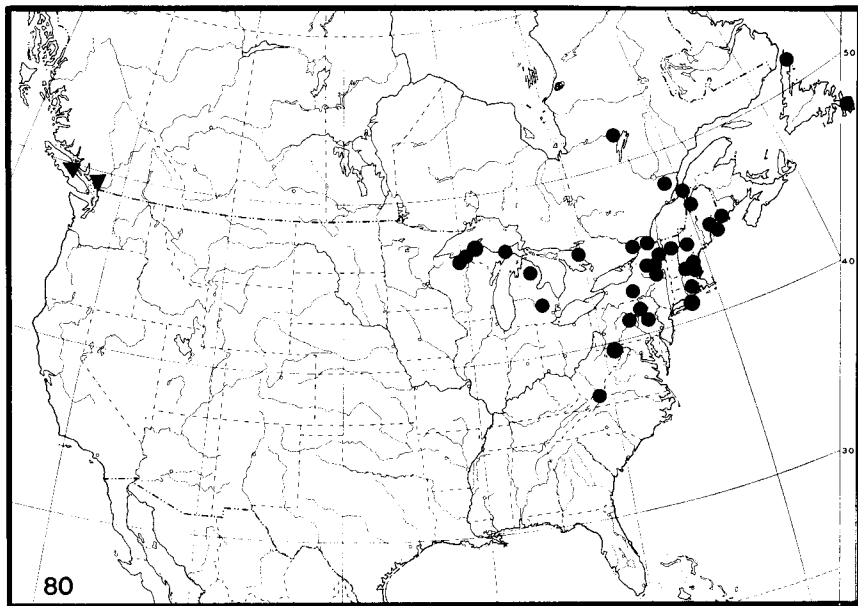


FIG. 80. Ranges of *Phalacrocer vancouverensis* (inverted triangles) and *Phalacrocer tipulina* (circles). Each spot represents one or more collections within a county or at a locality.

ties. Good series have been taken in Michigan (J. S. Rogers) and Pennsylvania (G. W. Byers). Byers recorded in his field notes (Centre County, Pennsylvania) taking these flies "in low-hanging branches of alder and hemlock along the edges of a marsh and in clumps of *Carex*. Several mating pairs were collected. The female supports or suspends the male or both may cling to adjacent leaves of *Carex* for support. The flies hang up with wings outspread and may let hind legs hang free." A live male pupa and several male skins were found in low hummocks of *Sphagnum*. Wing remains of this species have been found in the pitcher plant, *Sarracenia purpurea* (see Alexander, 1920).

Flight records: 9 May-6 Sept.

Distribution (Fig. 80): CONNECTICUT: Windham Co., Putnam, 15 June; (?) Co., Manic Lake, 8-9 June. MAINE: Aroostook Co., Ninemile (near Lac Frontière, Quebec), 2 June; Hancock Co., Bar Harbor, Mt. Desert, 4-23 July; Penobscot Co., Bangor, May-July; Washington Co., Machias, May-July. MARYLAND: Garrett Co., Cranesville Pine Swamp, 18 June. MASSACHUSETTS: Essex Co., Beverly, 3 June. MICHIGAN: Gogebic Co., 15 June-16 Aug.; Houghton Co., 20 June; Livingston Co., 12 May; Oscoda Co., 19-25 June; Schoolcraft Co., Floodwood, 20 July-14 Aug. NEWFOUNDLAND: Avalon Peninsula, Cochrane Pond (450 ft.), Mackinson's, St. John's (Karwood Cabins, along shore of Neville's Pond), Cataracts of North Harbor River near Colinet, 22-30 June; White Bay District, St. Anthony, 2 July. NEW HAMPSHIRE: Cheshire Co., Mt. Monadnock area, May-July; Coos Co., White Mountains, May-July; Rockingham Co., Hampton area, May-July. NEW YORK: Essex Co., Ausable Lakes, Hampton, Lake Tear of the Clouds, Mt. Marcy, 10-30 July; Fulton Co., near Sacandaga Park, Canada Lake (1600 ft.), 18 June-10 July; Hamilton Co., Lake Pleasant, 20-21 June; Herkimer Co., Old Forge, July-3 Aug.; Suffolk Co., Riverhead, 2 June; Tompkins Co.,

Ringwood Hollow, 3 July. ONTARIO: Carlton Co., Mer Bleu, Hawthorne, Ottawa, 20 May-6 Sept.; Georgian Bay, 13 July. PENNSYLVANIA: Centre Co., Bear Meadows (1820 ft.), 25-26 June; Luzerne Co., Hazelton, 19 May-4 June; Sullivan Co., 27 June. QUEBEC: Huntingdon Co., Covey Hill, Hemmingford, 27 June-13 July; Kamouraska Co., Andreville, 25-31 June; Laurentides Park, 24 June-16 Aug.; large bog 2 mi. N Lake Mistassini, Rupert River, 10 June-13 July. VERMONT: Lamouille Co., Stowe, 24 June. VIRGINIA: Giles Co., Hawthorne, Little Stony Creek, Mountain Lake, 29 May-21 June. WISCONSIN: Vilas Co., July. * Poste de la Baleine

Types: Two syntypes (male and female), White Mountains, New Hampshire. (no. 10238, Museum of Comparative Zoology, Harvard University.)

Phalacrocer vancouverensis Alexander

(Figs. 6, 18, 38, 44, 57, 58, 80)

Phalacrocer vancouverensis Alexander, 1927b: 189-190; Spencer: 1930: 15-16.

Diagnosis: This species is dark brown and robust, with whitish pubescence on the head and golden pubescence on the thorax. The pronotum has a prominent transverse crest. Three branches of the radius and 3 of the media reach the wing margin. The flagellar segments have verticils. The mesonotal suture is narrow, dull and darker than the rest of the thorax.

Description: MALE: Body length 12-13 mm; wing length 10-12.6 mm. Head dark brown to black, with whitish pollinosity of short hairs, most dense ventrally and around eyes, several brown hairs on vertex; dorsal profile of head broadly rectangular, with short narrow "neck" region; labium, labrum, and palpi brown, membranes yellowish; clypeus large, trapezoidal, brown-black, with whitish pubescence, several brown hairs distally, lateral extensions narrow; fronto-clypeal suture broad, horizontal (not as well defined as in *tipulina*); antennae dark brown, scape longest segment, cylindrical, bearing scattered hairs, lateral tooth obscured on available specimens; pedicel globular, with scattered hairs; flagellar segments (Fig. 38) subglobular, slightly longer than pedicel, slightly produced ventrally, bare except for whorl of short dark hairs on each segment; first cervical sclerite brown, small, narrow; second large, rectangular, its curved edge without narrow anterior prolongation.

Pronotum dusky black, broad, with prominent transverse crest, bordered anteriorly with erect hairs; pretergites brown. Mesonotum dull black, with golden pubescence; longitudinal furrows barely suggested by slightly heavier pubescence, no median longitudinal line on thorax; mesonotal suture dull brown, narrow, slightly curved, visible only behind median stripe of thorax; scutum dark brown; scutal suture distinct; postscutellum and pleurites dull brown with light grayish pollinosity, membranes dusky beige; suture present between anepisternum and postepisternum; pleural suture lacking.

Coxae, trochanters obscure yellow; femora brownish yellow, lighter basally, tips widened and dark brown; tibiae, basitarsi light brown, tips narrowly darkened; other segments of tarsi dark brown; tibial spurs lighter brown, black tipped, conspicuous; tarsal claws (Fig. 44) sharply curved, with

BC, Kamloops, 10 mi. N of, Modoc Lake, 18.VI.1973 Teshu
9th 7 dististyle
sharp point
may be a vein

small bump near broad base. Knobs of halteres dark brown, stems dusky yellow, haired.

Wings (Figs. 57, 58) strongly suffused with brown, stigma barely discernible; Sc_1 fading out before stigma, no evidence of Sc_2 ; 3 branches of radius reaching costa: R_{1+2} , R_3 , R_{4+5} ; R_{1+2} very short, sharply diverging from R_3 ; r-m in line with base of discal cell; 3 branches of media reaching margin; M_{1+2} branching just beyond edge of discal cell, cell M_1 petiolate. M_{3+4} not branching, slightly curved at margin.

Abdomen dark brown, segments edged distally by narrow colorless bands. Terminalia (Figs. 6, 18): Character of eighth and ninth terga obscured in specimen examined (on slide). Dististyles irregularly shaped, with flat rounded head, a notch and a small tooth along inner edge, several small teeth along outer of broad basal region; 3 tubes of aedeagus on same plane, outer two curved, inner straight, each narrowed distally; basal sclerites "H-shaped," lying dorsal to aedeagus; paraphyses long, narrow sclerites attached to inner sclerotized edges of basistyles (not shown in figure). Holotype differs in the following characters: antennae slightly shorter than in male, scape and flagellar segments oval to subcylindrical, not produced at all ventrally nor truncate apically; last segment elongate, nearly twice length of penultimate; each segment with a whorl of hairs; terminal segment elongate, relatively long, conspicuous. Wing of holotype possesses r-m crossvein. (Probably this character is quite variable in *vancouverensis*.) Abdomen light yellowish brown, with conspicuous black median stripe on dorsum and venter; first segment darkened, pruinose; caudal margins of segments narrowly pale. Terminalia (observations incomplete due to insufficient material): Base of cerci obscured by rather large, distally pointed hairy tenth tergum. Tips of cerci subacute, caudal margins roughened, almost serrulate. Hypovalues deeply notched.

Immature stages: Not seen. The larva is bright green and has bifurcated filamentous dorsal and lateral processes (Spencer, 1930).

Ecology: Spencer (1930) observed that the larva was green and resembled the stems of the pond weed *Nitella*, to which it was clinging. Its movements were sluggish, barely perceptible. The long bifurcated dorsal and lateral "gills" were very slowly waved back and forth. After pupation, the last larval skin remained loosely attached to the pond weed and the pupa floated at an angle of 30° to the water surface.

Flight records: 10 April-9 Aug.

Distribution (Fig. 80): BRITISH COLUMBIA: Vancouver Island, Forbidden Plateau, 9 Aug.; Vancouver District, Vancouver, 10 April.

Type: Female holotype, Vancouver, 10 April 1922 (W. B. Anderson), in (Canadian Nat. Collection). Male allotype (genitalia on slide), Forbidden Plateau, Vancouver, British Columbia, 9 Aug. 1950; (in Museum of Zoology, University of Michigan, Ann Arbor).

♂ AK Liberty Falls, 16.VI.53, W.C. Frohne (USNM) Liberty Falls, Kenny L. $61^\circ 37' 17'' N$
 $144^\circ 32' 42'' W$

Liogma Osten Sacken

Liogma Osten Sacken, 1869: 298; Peus, 1952: 66.

Type: *Triogma nodicornis* Osten Sacken.

Liogma is a poorly defined genus represented by only one species in North America. It shows many striking similarities to *Triogma* in wing venation and genitalia, yet superficially these genera are quite dissimilar.

Diagnosis: This genus is distinguished by having strongly nodulose, almost cordate antennal segments which are much more pronounced in the male than in the female. The prescutal stripes are shiny black.

Description: Head shiny black, with fine light hairs laterally and posteriorly; scape long, cylindrical; flagellar segments nodulose or cordate; pronotum bare; pretergites pale yellow; prescutum pale yellow with 3 shiny black stripes; mesonotal suture a shiny brown curve ending in small pits on either side of median stripe; scutum divided longitudinally by distinct suture; scutellar sutures obscured in dark brown, spindle-shaped pits; pleural sclerites pale yellow, brown-black areas on anepisternum, postepisternum; pleurotergite brown-black, wrinkled; wings suffused with brown, stigma oval, very pale; Sc_1 fading before stigma; Sc_{2A} present, Sc_{2B} obliterated; 2 branches of radius reaching margin (R_3 and R_{4+5}); r-m obliterated by fusion of R_{4+5} with M_{1+2} at corner of or before discal cell; 3 branches of media reaching wing margin (M_{1+2} , M_3 , M_4); medial crossvein plus part of M_3 closing discal cell distally; tibial spurs very short, stout, haired; tarsal claws long, slender, broadly curved. Abdomen dark brown, distal edge of each segment colorless.

MALE terminalia: Eighth tergum entire; ninth tergum squarish, produced into 2 conical projections distally; aedeagus with 3 tubes each enclosing ejaculatory duct leading from semen pump.

FEMALE terminalia: Ninth tergum very narrow; tenth tergum divided into 4 sclerites: large median sclerite, pair of triangular lateral sclerites, one narrow anterior sclerite; cerci short, broad, not distinctly serrate.

Liogma nodicornis (Osten Sacken)

(Figs. 7, 19, 26, 39, 40, 59-62, 74, 81)

Triogma nodicornis Osten Sacken, 1865: 239-240.

Cylindrotoma nodicornis Osten Sacken, 1869: 301.

Liogma nodicornis Osten Sacken, 1869: 298; Alexander, 1914b: 105-118; 1927a: 10-11.

Liogma nodicornis flaveola Alexander, 1919b: 195.

Diagnosis: This species is intermediate in length between *Cylindrotoma* and *Phalacrocer*. The thorax is pale yellow with shiny black or dark brown stripes. The antennal segments are strongly nodulose or cordate.

Description: **MALE**: Body length 9-12 mm; wing length 8.5-9.5 mm. Head shiny black, broadly oval, tapering behind eyes; labium, labrum medium brown, haired distally; palpi darker brown; membranous areas tawny; cly-

peus dark brown, short, narrow, convex, with long hairs distally extending over labial segments; fronto-clypeal suture arched; antennal bases close together, separated by narrow incision-like groove; scape long, cylindrical, slightly narrower than flagellum and roughly twice the length of 1 flagellar segment, bearing several hairs; lateral teeth not pronounced; pedicel sub-ovate; most flagellar segments expanded ventrally (Fig. 39), distal segments sub-ovate, last segment attenuated, slender; dense, erect, short hairs covering each flagellar segment, verticillate, dorsal bristles longer.

Pronotum pale yellow to dark brown in center, anterior region reduced, prominent narrow transverse crest near mid-length; pretergites pale yellow with short erect hairs; prescutal stripes shiny black, median stripe divided posteriorly by short narrow longitudinal furrow; scutellum light brown; postscutellum shiny brown posteriorly, paler and wrinkled anteriorly. Halteres dusky, lighter at base of stem; thick row of hairs on anterior edge.

Coxae brown, trochanters light yellow, edged with black; femora, tibiae very pale, brown at tips, covered with short, stout hairs, each in small brown spot; tarsi dark brown, hairs long.

Terminalia (Figs. 7, 19): Dististyles light brown, slender, widened at base, covered with short hairs except for bare tips, denser hairs along inner edges; aedeagus branching into three tubes beyond junction of ejaculatory ducts, outer tubes slightly more curved than median tube; ventral side of each tube prolonged distally, tips flattened; basal sclerite apparently fused to aedeagus and joined to paraphyses by a long narrow extension on each side; paraphyses irregular sclerites (Fig. 7) lying dorsal to aedeagus; anal segment lightly sclerotized.

FEMALE: Differs from male in the following: antennae (Fig. 40) somewhat shorter, pedicel and flagellar segments nodulose, not cordate, verticils shorter than in male. Terminalia (Fig. 26): Large median sclerite of tenth tergum with three sharp points on caudal margin. Cerci with very small irregular terminal teeth; hypovalves short, broadly notched distally, fused to slightly broader eighth sternum.

Variation: Considerable variation has been noted in the extent of color on the mesothorax. The black mesonotal stripes may merge anteriorly or be distinct along their entire length. The background color varies from very pale to quite dusky yellow. Pleural sclerites and postnotum are very pale in some specimens. Wing variations include the occasional presence of r-m, occasional absence of Sc_{2A} and m-cu joining M before, beyond or at the base of the discal cell. One specimen was found with an additional crossvein in cell R₅ (Fig. 62).

Larva: Living specimens are light green. Numerous slender lobes covering body are darker. Preserved specimens are pale whitish-yellow with dark oblique marks laterally on abdominal segments. Tuberculate paired processes

on abdominal terga each bearing a small sharp tooth anteriorly near base.

Pupa: Living pupae are light yellow to brown (probably depending upon age). Preserved specimens are brownish with an interrupted dark longitudinal line along either side of the middle of the dorsum. Each abdominal segment bears a single dorsal pair of slender lobes.

Detailed descriptions of the immature stages are presented by Alexander (1914).

Ecology: The adults of this species are relatively abundant although quite local in distribution. They are very sluggish flyers and may be swept from rank vegetation in cool, shaded, or partially shaded woodlands, in tamarack and sumac swamps, and along wooded margins of marshes. The Alberta specimens were collected at the edge of spruce and tamarack "muskeg" (Alexander, 1927c). Immature stages of these flies have been found feeding on *Mnium punctatum*, *Hypnum cupressiforme* and related species of mosses, and in shallow pools.

Flight records: 7 May-28 July.

Distribution (Fig. 81): ALBERTA: Bilby (30 mi. W. of Edmonton), 19 June. CONNECTICUT: Fairfield Co., Redding, 2 June; Hartford Co., Grandby, W. Grandby, Hartland, 8-9 June; Litchfield Co., Cornwall Bridge, Kent Falls, Norfolk, Riverton, 31 May-13 June; New Haven Co., Hamden, 2 June. DISTRICT OF COLUMBIA: Washington (no date). GEORGIA: Union Co., Neel Gap, 22 May. ILLINOIS: Carroll Co., Savanna, 15 June. INDIANA: Jefferson Co., 25-27 May; Owen Co., McCormick's Creek State Park, 6 June; Parke Co., Turkey Run State Park, 28 May-11 June. MAINE: Franklin Co., Rangeley Lakes, June-July; Hancock Co., Mt. Desert area, 7 June-4 July; Penobscot Co., Bangor, Ellsworth, Orono, 8 June-July; Piscataquis Co., Capens (Moosehead Lake area), June-July; Washington Co., Machias, 25 July. MANITOBA: Portage la Prairie Distr., Aweme, 25 May-16 June; Souris Distr., Ninette, 12 June. MARYLAND: Montgomery Co., Glen Echo; Prince Georges Co., Beltsville, Bowie, 29-31 May. MASSACHUSETTS: Berkshire Co., Mt. Greylock, N. Adams, 14-18 June; Hampshire Co., Amherst, 3-16 June; Worcester Co., Petersham, June. MICHIGAN: Clinton Co., Beulah, Cusino, Rose Lake, 24 May-27 June; Crawford Co., 4 June; Delta Co., 11 June; Ionia Co., Ionia, 31 May; Iron Co., 13 June; Keweenaw Co., Copper Harbor, 19 June; Houghton Co., 20 June; Lake Co., 8 June; Livingston Co., E. S. George Reserve, 26 May-27 June; Mackinac Co., 7 June-5 July; Marquette Co., Huron Mts., 13-15 June; Newaygo Co., 21 July; Oakland Co., 20 May; Ogemaw Co., Rifle River area, 3-10 June; Ontonagon Co., 18 June; Oscoda Co., 14-15 June; Roscommon Co., 4 June; Schoolcraft Co., 8 June-5 July; Washtenaw Co., Ann Arbor, Cascade Glen, 28 May-10 June. MINNESOTA: St. Louis Co., Eagle Nest, 4 June. NEW BRUNSWICK: Charlotte Co., Waweig, 23 May. NEWFOUNDLAND: Bonavista North and Bonavista South Dists., Middle Brook, Southwest River near Lethbridge, Terra Nova Nat'l Pk., 3-6 July. NEW HAMPSHIRE: Cheshire Co., Jaffrey, Mt. Monadnock, 19 June; Coos Co., Bretton Woods, Randolph, White Mountains, May-July; Grafton Co., Franconia, Hanover, June-July. NEW JERSEY: Essex Co., Orange Mts., West Orange, June; (?) Co., Hemlock Falls, May. NEW YORK: Erie Co., Hamburg, 28 May-20 June; Essex Co., Mt. Marcy, Heart Lake (2150 ft.), 29 June; Fulton Co., Canada Lake, Gloversville, Johnstown, Sacandaga Park, Vanderburgs, 15-27 June; Hamilton Co., Lake Pleasant, 20 June; Herkimer Co., Indian Castle, 9 June; Onondaga Co., Green Lake; Orange Co., Bear Mt., 31 May; Brookview, 7 June; Tompkins Co., North Lansing, Ithaca, 1-14 June; Washington Co., Hampton (no date); Westchester Co., Dobbs Ferry, Tarrytown, 9 June; (?) Co., Misake, 20 June. NORTH CAROLINA: Buncombe Co., Swannanoa, 23 May; Burke Co., Linville Falls (3250 ft.), 3-10 June; Haywood Co., Black Mt., Mt. Pisgah (3000 ft.), 28 May; Jackson Co., Cashiers (3800 ft.), 12 June; Macon Co., Highlands (4000 ft.), Van Hook Glade (3800 ft.), Nantahala Gorge, May-June; Swain Co., Great Smoky Mountains National Park, Forney Ridge trail (6000-6300 ft.), 18 June; Transylvania Co., Camp Toxoway (3200 ft.), 9-10 June; Wake Co., Raleigh, May; Yancey Co., Mt. Mitchell Game Refuge (3100 ft.), 22 May-9 June; (?) Co., Conestee Falls, 12 June. NOVA SCOTIA: Kings Co., Kentville, 4 July; Victoria Co., Baddeck, 6-27 July. OHIO: Hocking Co., Goodhope Twp., 20 May-6 June, Wayne Co., Wooster, 13 May. ONTARIO: Carleton Co., Britannia Bay, Ottawa, 1-12 June; Cochrane Co., Fort Albany (James Bay), 15-19 June; Kent Co., Bothwell, 13 June;

a A. Macan Co.
June 13, 1974

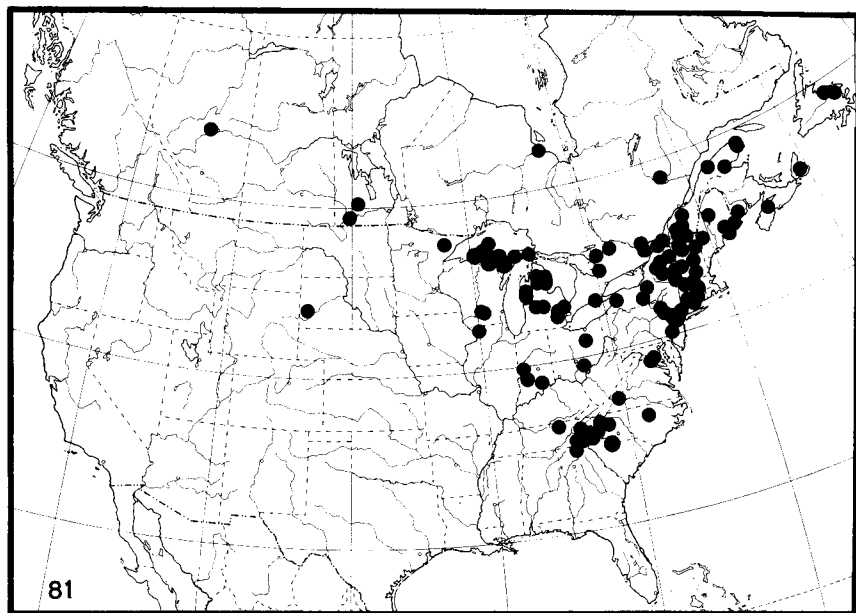


FIG. 81. Range of *Liogma nodicornis*. Each spot represents one or more collections within a county or at a locality.

Nipissing Co., Algonquin Pk., 3 June-7 July; Norfolk Co., Normandale, Simcoe, 9-20 June; Parry Sound Co., Burks Falls, Kearney, Sand Lake, 29 June-16 July; Simcoe Co., Orillia, 28 June-2 July; (?) Co., Fishers Glen, 2 July. PENNSYLVANIA: Carbon Co., Palmerton, 10 June; Luzerne Co., Hazleton, 22 May-26 June; Philadelphia Co., Roxborough, 7 June. QUEBEC: Bonaventure Co., Escuminac, 2-31 July; Brome Co., Knowlton, 14-29 June; Gaspé East Co., Gaspé, 26 June-28 July; Gaspé West Co., Anse Pleureuse, Mt. Lyall (1500 ft.), 27 June-29 July; Gatineau Co., Hull, Meach Lake, 28 May-21 June; Huntingdon Co., Covey Hill, 17 June; Lake St. John West Co., Mistassini, (?) June-20 July; Matane Co., Metis-sur-mer, 26 June-29 July; Megantic Co., 6-16 July; Richmond Co., Stoke Centre, 26 June; Shefford Co., Abbotsford, 17 June; Stanstead Co., Georgeville, 14-19 June; Terrebonne Co., Montreal, (?) June. SOUTH CAROLINA: Spartanburg Co., Spartanburg, 13 May. SOUTH DAKOTA: Pennington Co., Harney Peak (6700 ft.), 15 July. TENNESSEE: Great Smoky Mountains National Park, Siler's trail (6000-6500 ft.), Indian Gap (5300-5500 ft.), Anakeesta Ridge (4500 ft.), Leconte Lodge (6400 ft.), Greenbrier, Brushy Mt. trail (3500 ft.), 7 May-15 June; Green Co., Camp Creek, 7 May; Scott Co., 29 May. VERMONT: Bennington Co., Manchester, 6 June; Franklin Co., St. Albans, 19 June; Washington Co., Montpelier, 25 June. VIRGINIA: Alexandria Co., Glencarllyn, 7 June; Arlington Co., Chain Bridge, 28 May; Fairfax Co., Dead Run, Falls Church, Great Falls, 19 May-18 June; Giles Co., Kire, Little Stoney Creek, Mountain Lake, 27 May-17 June. WISCONSIN: Dane Co., May-June; Sauk Co., 28 May.

Types: 8 syntypes (5 males, 1 female, 2 broken), Washington, D. C., Dobbs Ferry, New York; White Mountains, New Hampshire; Illinois; New Jersey (no. 10236, Museum of Comparative Zoology, Harvard University). One male paratype, New Jersey, May (in Academy of Natural Sciences of Philadelphia).

Liogma nodicornis flaveola Alexander, male holotype, Great Falls, Virginia, 19 May 1915; allotype, Great Falls, Virginia, 7 June 1915 (in C. P. Alexander collection, Amherst, Massachusetts).

Triogma Schiner

Triogma Schiner, 1863: 223; Osten Sacken, 1865: 237-241.

Type: *Limnobia trisulcata* Schummel.

This is a very small genus consisting of four known species with only one from North America. Peus (1952) places the two Oriental species of *Triogma* (*nimbipennis* Alexander, *kuwanai* Alexander) "incertae sedis" pending more detailed studies, particularly of the genitalia. Thus this genus is actually based on only two species (*trisulcata* of Europe and *exsculpta* of North America).

Diagnosis: A heavily rugose and pitted head and thorax and dull dark coloration distinguishes this genus in North America.

Description: Head bare, dull dark brown, pitted; scape long, cylindrical; flagellar segments subcylindrical; pronotum bare; pretergites glabrous, dark brown; prescutum concolorous dark brown to black, two longitudinal series of pits trisecting mesothorax; mesonotal suture pitted, ending at and joining with longitudinal rows of pits; scutal suture pitted; scutellar sutures obscured by two deep pits; all pleural sclerites dark brown to black, pitted; wings strongly suffused with brown, stigma absent; Sc_1 extending to juncture of Sc_{2A} with radius; Sc_{2B} usually present; 2 branches of radius reaching margin (R_3 and R_{4+5}); r-m usually obliterated by short fusion of R_{4+5} with M_{1+2} at corner of discal cell; three branches of media reaching wing margin: M_{1+2} not dividing, forming basal and anterior edges of discal cell; M_{3+4} at posterior edge of cell, branching, M_3 and M_4 attaining margin independently; medial crossvein plus part of M_3 closing cell distally; tibial spurs short, prominent, haired; tarsal claws short, broad, abruptly curved distally. Abdomen dull dark brown, posterior edge of each segment pale.

MALE terminalia: Eighth tergum entire; ninth tergum squarish, 2 small broad caudal projections laterally; aedeagus with 3 tubes, each enclosing an ejaculatory duct leading from semen pump.

FEMALE terminalia: Ninth tergum very narrow; tenth tergum divided into four sclerites: large median pentagonal sclerite, 2 small triangular sclerites, 1 on each side, one narrow anterior sclerite; cerci short, broad, not serrate.

Triogma exsculpta Osten Sacken

(Figs. 8, 20, 27, 41, 42, 63-66, 70-73, 75, 76, 82)

Triogma exsculpta Osten Sacken, 1865: 239; 1869: 304-305.

Triogma exsculpta [sic]; Alexander, 1919: 926; 1920: 974; 1927: 11; 1942: 296; Rogers, 1942: 77.

Diagnosis: *Triogma exsculpta* is the stockiest and darkest species in this subfamily. It is dull dark brown to black with characteristic pits or punctations on both the head and the thorax.

Description: *MALE*: Body length 7-8 mm; wing length 7-8 mm. Head dull dark brown, subspherical, rugose; labium, palpi dark brown, haired;

labrum dark brown, glabrous; membranes around mouth parts dusky; clypeus very short, dark, convex, not extended laterally, with small hairs distally; fronto-clypeal suture arched; antennal bases very close together; scape cylindrical, longest and broadest segment, sparsely haired, bearing small tooth on each side, inner tooth broader than outer tooth; pedicel subglobular, sparsely haired; flagellar segments subcylindrical, covered with long erect hairs, verticils in an uneven whorl.

Pronotum dark brown to black, a shiny brown furrow separating anterior pitted ridge from shiny, lighter posterior portion; prescutum black, with tawny pubescence, trisected by 2 longitudinal rows of deep pits, a secondary row of pits along mid-line; scutum, scutellum black with tawny pubescence; postscutellum smooth, with 2 black spots posteriorly, anteriorly lighter, wrinkled, longitudinally divided by shallow furrow; pleural membranes dusky orange-brown. Stems of halteres pubescent, dusky yellow, knobs darker.

Coxae blackish, pubescent; trochanters lighter, pubescent, sparsely haired; femora, tibiae, tarsi light brown, haired, segments progressively more haired distally.

Terminalia (Figs. 8, 20): Dististyles short, simple, curved, haired, but tips bare; aedeagus branching into 3 tubes beyond junction of ejaculatory ducts, middle tube more curved than lateral tubes; ventral side of each tube slightly prolonged distally (less pronounced than in *Liogma*), tips flattened; basal sclerite apparently fused to aedeagus; paraphyses irregular sclerites lying dorsal to aedeagus (Fig. 8); anal segment lightly sclerotized.

FEMALE: Differs from male in the following: antennae (Fig. 42) shorter, flagellar segments subspherical, almost moniliform, hairs extremely short, verticils just below mid-length of each segment. Terminalia (Fig. 27): Cerci flat, broad, smoothly rounded, notched laterally; hypovalves short, broadly notched posteriorly, narrower than and fused to eighth sternum.

Variation: This species is quite uniform; however, variations in wing venation are found, e.g., the absence or only traces of Sc_2 and of the tip of Sc_1 , occasional presence of r-m; also, the position of m-cu is quite variable, and the medial crossvein is often lacking.

Larva (Figs. 70-73): Only preserved specimens have been studied. This larva is distinguished by having short, paired tergal and sternal lobes, no distinct color pattern and 3 pairs of lobes (2 large, 1 small) surrounding spiracular disk.

Length 16 mm; width 3 mm. Head completely retractile into prothorax, the latter having neither hairs nor bristles. Numerous conical lobes cover larva. Prothorax with 2 pairs of short, simple, dorsal lobes, anterior pair smaller and closer together than posterior pair; 1 pair of lateral lobes; no ventral lobes. Mesothorax with 2 pairs of dorsal lobes, posterior pair slightly

larger, lobes with a small anterior protuberance at base; 2 pairs of simple lobes on each side. Metathorax dorsally as for mesothorax; 3 simple lobes on each side and 3 pairs of ventral lobes, second pair largest, placed further apart. Dorsal abdominal lobes as follows: first abdominal segment with 2 pairs of lobes, each with an anterior protuberance; 4 pairs of lobes on segments 2 to 7, first pair very small (largest on second segment, becoming progressively smaller towards posterior end of larva), second pair of lobes slightly larger, third pair with two dorsal tooth-like protuberances, fourth pair longest, with one dorsal "tooth". Lateral abdominal lobes simple; first abdominal segment with two on each side; second to seventh abdominal segments with 3 on each side. Ventral lobes simple, conical projections, arranged in pairs, posterior pair largest: 2 pairs on first abdominal, 5 pairs on second to seventh abdominal segments. Probably 3 or 4 segments involved in caudal region of larva. Spiracular disk (Fig. 66) small, the 2 rounded spiracles situated side by side, inclined toward each other; 3 pairs of lobes surrounding spiracle, a small median dorsal pair, a longer dorso-lateral pair, and a ventral pair with a conspicuous black line on inner surface of each lobe, tip ending in a sharp recurved hook. Ventral surface of terminal segment with protuberances (Fig. 67).

Triogma exsculpta larvae closely resemble those of *Liogma nodicornis* but differ from the latter by having no color pattern, a hairless pronotum, and an additional small pair of dorsal lobes on the spiracular disk.

Pupa (Figs. 75, 76): Only preserved female specimens have been studied. This pupa is distinguished by having no color pattern and by 2 short, dorsal pairs of lobes on each segment, each with a very small, basal protuberance.

Length 12 mm; width 3 mm. Cephalic part of head flat, broad, without lobes. Prothorax without processes. Mesonotal breathing horns small, directed dorsad and laterad, terminal half bent cephalad. Mesonotum with two small slender lobes caudally; broad wing sheaths laterally reaching posterior margin of second abdominal segment. Metanotum with 2 pairs of simple lobes, anterior pair very small, posterior pair longer; lateral haltere sheaths lying alongside first abdominal segment, obscured by wing sheaths. Leg sheaths ending just before posterior margin of third abdominal sternum. First abdominal segment short, 2 pairs of dorsal processes posteriorly, each with small sharp tooth basally; no ventral nor lateral processes. Abdominal segments 2 to 7 with 3 pairs of dorsal processes, anterior pair small, simple (not always figured, obscured by posterior pair of processes of preceding segment), middle pair longer, bearing 2 sharp spines anteriorly, posterior pair largest, 2 teeth anteriorly; laterally 3 simple lobes on each side; ventrally 3 pairs of short simple spines, anteriormost pair extremely tiny. Eighth abdominal segment smaller than seventh, terminating in lateral lobes, with a small medial pair of spines on dorsum and on venter. Ninth abdominal segment narrower than eighth,

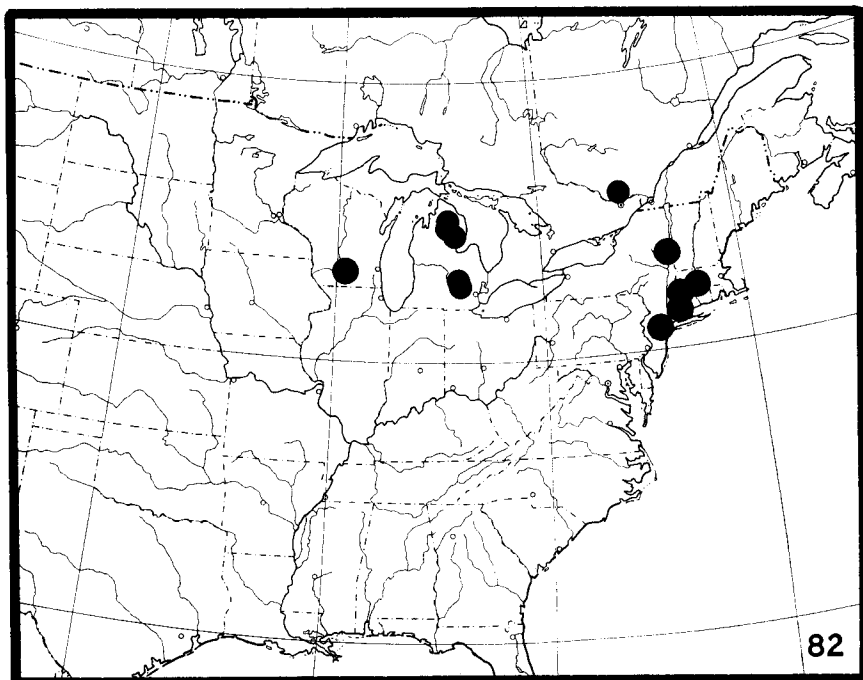


FIG. 82. Range of *Triogma exsculpta*. Each spot represents one or more collections within a county or at a locality.

terminating dorso-laterally in a pair of lobes, between which the developing female cerci can be seen in mature specimens.

This pupa closely resembles that of *Liogma nodicornis* but may be differentiated from the latter by having no dorsal pattern and by having 3 pairs of dorsal lobes on all but the first abdominal tergum.

Ecology: Rogers (1942) reported *Triogma exsculpta* as very local yet numerous in quite limited areas. The flies may be found in seepage areas and along short marshy spring rills and are often found in wet mossy meadows where there is no woody vegetation. The larvae and pupae have been collected on the aquatic moss *Fontinalis antipyretica*, and they have been found on floating mosses of small marsh pools.

Flight records: 20 April-19 June.

Distribution (Fig. 82): CONNECTICUT: Fairfield Co., Stamford, 15 May, Litchfield Co., Norfolk, 9 June. MASSACHUSETTS: Hampshire Co., Amherst, 20 April-25 May. MICHIGAN: Arenac Co., 25 May; Crawford Co., Branch of Big Creek, 23 May-19 June; Livingston Co., E. S. George Reserve, Honey Creek, Putnam Twp., 15-20 May; Otsego Co., 24 May; Washtenaw Co., 15 May. NEW HAMPSHIRE: (no further data). NEW JERSEY: Essex Co., Waverly, May. NEW YORK: Washington Co., Hampton, 20 May. PENNSYLVANIA: (no further data). QUEBEC: Gatineau Co., Hull, 17 May. WISCONSIN: Dane Co., 10 May.

Types: Female holotype, Pennsylvania, (ANSP Type no. 6058, Academy of Natural Sciences, Philadelphia).

LITERATURE CITED

BIBLIOGRAPHY

- ALEXANDER, C. P. 1913. Report on a collection of Japanese crane-flies (Tipulidae). Canadian Ent. 45(10):313-322.
- . 1914a. New or little-known crane-flies from the United States and Canada, Tipulidae. Proc. Acad. Nat. Sci. Philadelphia 66:579-606.
- . 1914b. Biology of the North American crane-flies (Tipulidae, Diptera). II. *Liogma nodicornis* Osten Sacken. Pomona Jour. Ent. and Zool. 6:105-120.
- . 1919a. Undescribed species of Japanese crane-flies (Tipulidae, Diptera). Ann Ent. Soc. Amer. 12:327-348.
- . 1919b. New Nearctic crane-flies (Tipulidae, Diptera). Part VIII. Canadian Ent. 51: 191-199.
- . 1919c. The crane-flies of New York. Part I. Distribution and taxonomy of the adult flies. Cornell Univ. Agr. Exp. Sta. Memoir 25:766-993, plates XXX-LV.
- . 1920. The crane-flies of New York. Part II. Biology and phylogeny. Cornell Univ. Agr. Exp. Sta. Memoir 38:695-1133, plates XII-XCVII.
- . 1922. Undescribed crane-flies (Tanyderidae, Tipulidae) in the South Australian Museum. Rec. South Australian Museum 2:250-251.
- . 1924. New or little-known crane-flies from northern Japan (Tipulidae, Diptera). Philippine Jour. Sci., 24(5):531-611.
- . 1927a. Cylindrotominae. Genera Insectorum. 187:1-16, plates I, II.
- . 1927b. New Nearctic crane-flies (Tipulidae, Diptera). Part XII. Canadian Ent. 59(8): 184-193.
- . 1927c. Records and descriptions of crane-flies from Alberta (Tipulidae, Diptera). Canadian Ent. 59(8):214-225.
- . 1930. New or insufficiently-known crane-flies from the Nearctic Region (Tipulidae, Diptera). Part II. Bull. Brooklyn Ent. Soc. 25(5):276-282.
- . 1931. Crane-flies of the Baltic Amber (Diptera). Bernstein-Forschungen (Amber Studies), Vol. 2, ed. by K. Andree. Berlin and Leipzig: Gruyter and Co. 135 pp., illus.
- . 1932. New or little known Tipulidae from the Philippines (Diptera). Part XIII. Philippine Jour. Sci. 47(1):163-195.
- . 1933. Records and descriptions of Japanese Tipulidae (Diptera). Philippine Jour. Sci. 51(2):216-219.
- . 1940. Records and descriptions of North American crane-flies (Diptera). Part I. Tipuloidea of the Great Smoky Mountains National Park, Tennessee. Amer. Midland Nat. 24(3):602-644.
- . 1941. Records and descriptions of North American crane-flies (Diptera). Part II. Tipuloidea of mountainous western North Carolina. Amer. Midland Nat. 26(2): 281-319.
- . 1942. Family Tipulidae. In, The Diptera or true flies of Connecticut. Conn. State Geol. and Nat. Hist. Survey, Bull. 64:196-509.
- . 1943a. Records and descriptions of North American crane-flies (Diptera). Part III. Tipuloidea of the Upper Gunnison Valley, Colorado. Amer. Midland Nat. 29(1): 147-179.
- . 1943b. Records and descriptions of North American crane-flies (Diptera). Part IV. Tipuloidea of the Yellowstone National Park. Amer. Midland Nat. 30(3):718-764.
- . 1945. Records and descriptions of North American crane-flies (Diptera). Part V. Tipuloidea of the Grand Teton National Park and Teton National Forest, Wyoming. Amer. Midland Nat. 33(2):391-439.
- . 1949. Records and descriptions of North American crane-flies. Part VIII. Tipuloidea of Washington. Amer. Midland Nat. 42(2):257-333.
- . 1954. Records and descriptions of North American crane-flies (Diptera). Part IX. Tipuloidea of Oregon, I. Amer. Midland Nat. 51(1):1-86.
- . 1956a. Undescribed species of crane-flies from the eastern United States and Canada (Diptera, Tipulidae). Part XII. Ent. News 67:177-185.
- . 1956b. Undescribed species of crane-flies from the Himalaya Mountains (Tipulidae, Diptera), I. Jour. New York Ent. Soc. 64:137-147.
- . 1965. Family Tipulidae, p. 16-90. In, A catalog of the Diptera of America north of Mexico. Agriculture handbook No. 276. Agriculture Research Service, U.S. Dept. Agr., Washington.

- , AND W. L. McATEE. 1920. Diptera of the Superfamily Tipuloidea found in the District of Columbia. Proc. U.S. Nat. Mus. 58(2344):385-435.
- BENGTTSSON, S. 1897. Till kännedom om larven af *Phalacrocer replicata* (Lin.) Acta Reg. Soc. Physiogr. Lund. 8:1-117, 4 plates.
- BRIMLEY, C. S. 1938. Insects of North Carolina. North Carolina Dept. Agr., Div. of Ent., Raleigh. 560 pp.
- BRUNETTI, E. 1912. Diptera Nematocera (excluding Chironomidae and Culicidae). In, The fauna of British India, as one volume in a series. London, Taylor and Francis. 581 pp., 12 plates.
- BYERS, G. W. 1961. The crane fly genus *Dolichopeza* in North America. Univ. Kansas Sci. Bull. 42(6):665-924.
- CAMERON, A. E. 1918. Life-history of the leaf-eating crane fly *Cylindrotoma splendens* Doane. Ann. Ent. Soc. Amer. 11:67-89.
- COCKERELL, T. D. A. 1920. Eocene insects from the Rocky Mountains. Proc. U.S. Nat. Mus. Washington 57(2313):233-260.
- COQUILLETT, D. W. 1900. Papers from the Harriman Alaska expedition. Entomological results (3). Proc. Washington Acad. Sci. 2:389-464.
- DICKINSON, W. E. 1932. The crane-flies of Wisconsin. Bull. of the Public Museum of the City of Milwaukee 8(2):139-260.
- DOANE, R. W. 1900. New North American Tipulidae. Jour. New York Ent. Soc. 8:182-198.
- ENDERLEIN, G. 1912. Studien über die Tipuliden, Limoniiden, Cylindrotomiden und Ptychopteriden. Zool. Jahrb. Syst. 32:83-85.
- GRÜNBERG, K. 1910. Diptera, Zweiflügler, Part I. Die Süßwasserfauna Deutschlands 2A:1-312.
- HENNIG, W. 1950. Die Larvenformen der Dipteren. Part II. Berlin: Akademie-Verlag, 458 pp., 10 plates.
- JOHNSON, C. W. 1912. New North American Diptera. Psyche 19(1):1-5.
- KERTÉSZ, C. 1902. Catalogus dipterorum hucusque descriptorum. Vol. II. Cecidomyiidae, Tipulidae, etc. Leipzig. 359 pp.
- LEONARD, M. D. 1928. A list of insects of New York. Cornell Univ. Agr. Exp. Sta. Memoir 101:1-1121 (Tipuloidea, pp. 688-701).
- LINNAEUS, C. 1758. Systema Naturae. Editio decima, reformata, Tomus I. Laurentii Salvii, Holmiae. 824 pp.
- MACGINITIE, H. D. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Institute of Washington. Washington iii + 198 pp.
- MACQUART, P. J. M. 1834. Histoire naturelle des insectes. Diptères. I Tom. Paris, Librairie Encyclopedique de Roret, 578 pp., 12 plates.
- MEIGEN, J. W. 1818. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. 1:1-269.
- MEUNIER, F. 1906. Monographie des Tipulidae et des Dixidae de l'ambre de la Baltique. Ann. Sci. Nat., Zool. (9)4:349-403.
- . 1915. 9. Über einige fossile Insekten aus den Braunkohlenschichten (Aquitaniens) von Rott im Siebengebirge. Zeitschr. Deutschen Geo. Ges. 67:219-230.
- NEEDHAM, J. G. 1908. Report of the entomologic field station conducted at Old Forge, New York, in the summer of 1905. 23rd Rept. of the State Entomologist, 1907:156-248, 15 figs.
- OSTEN SACKEN, C. R. 1865. Description of some new genera and species of North American *Limnobia*. Part I. Proc. Ent. Soc. Philadelphia 4:224-242.
- . 1869. Monographs of the Diptera of North America. Part IV. Smithsonian Misc. Coll. 8(219):1-345, 4 plates, 7 figs.
- . 1878. Catalogue of described Diptera of North America. Second edition. Smithsonian Misc. Coll. 16(270):1-276.
- . 1887. Studies on Tipulidae. Part 2. Review of the published genera of the *Tipulidae brevipalpi*. Berliner Ent. Zeitschr. 31:163-242.
- . 1897. Remarks on the literature of the earlier stages of the Cylindrotomina, a section of Tipulidae. Trans. Ent. Soc. London 1897:362-366.
- PEUS, F. 1952. Cylindrotomidae. In, Lindner, Erwin. Die Fliegen der palaarktischen Region. Lfg. 169(17):1-80, 2 plates, 83 figs.
- ROGERS, J. S. 1918. Collection of Tipulidae from Schoolcraft Co., Michigan. Occ. Papers Mus. Zool. Univ. Michigan 55:1-4.
- . 1930. The summer crane-fly fauna of the Cumberland Plateau in Tennessee. Occ. Papers Mus. Zool. Univ. Michigan 215:1-50, 5 plates.
- . 1942. The crane-flies (Tipulidae) of the George Reserve, Michigan. Univ. Mich. Mus. Zool. Misc. Publ. 53:1-128, 8 plates.

- ROSS, H. H. 1956. A textbook of entomology. 2nd edition. New York, John Wiley & Sons, Inc., xi + 519 pp., 402 figs.
- SCHINER, I. R. 1863. Vorläufiger Commentar zum dipterologischen Theile der "Fauna austriaca." V. Wiener Ent. Monatschr. 7:217-226.
- . 1864. Fauna austriaca. Die Fliegen. 2:1-658.
- SCHUMMEL, T. E. 1829. Beschreibung der in Schesien einheimischen arten einiger dipteren-gattungen. I. *Limnobia*. Beitr. z. Ent. (Breslau): 97-201.
- SCUDDER, S. H. 1877. The first discovered traces of fossil insects in the American tertiaries. Bull. U.S. Geol. Surv. Terr. 3(4):741-762.
- . 1894. Tertiary Tipulidae, with special reference to those of Florissant Colorado. Proc. Amer. Philos. Soc. 32:163-245.
- SNODGRASS, R. E. 1904. The hypopygium of the Tipulidae. Trans. Amer. Ent. Soc. 30:179-235.
- . 1957. A revised interpretation of the external reproductive organs of male insects. Smithsonian Misc. Collections 135(6):1-60.
- SPENCER, G. J. 1930. Notes on *Phalacrocer* species, an aquatic crane fly (Diptera, Tipulidae). Proc. Ent. Soc. British Columbia 27:15-16.
- TAKAHASHI, M. 1960. A review of Japanese Cylindrotominae (Diptera, Tipulidae). Trans. Shikoku Ent. Soc. 6(6-7):81-91.
- WALKER, F. 1856. Insecta Britannica. Diptera III:268-337.
- ZETTERSTEDT, J. W. 1838. Insecta Lapponica descripta. Lipsiae, Voss. Dipt.:477-868.

- * Miall, F. R. S. & R. Shelford.
xv The structure and life-history of *Phalacrocer replicata*.
- * De Geer
Mém. Hist. Ins., vi p. 351, pl. xx