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A REVISION OF THE GENUS PRIONOCERA AND THE PHYLOGENY OF
THE FAMILY TIPULIDAE (DIPTERA)

by

Fenja Blank Brodo, B.S., M.A.

A thesis submitted to the Faculty of
Graduate Studies, and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario
16 August 1984

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The undersigned hereby recommend to the Faculty of
Graduate Studies and Research acceptance of this thesis,
submitted by Fenja Blank Brodo, B.S., M.A.,
in partial fulfilment of the requirements
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9 October 1984

ABSTRACT

In this taxonomic revision of the genus Prionocera, five species, all from North America, are described as new: byrssi, cryptica, elliptica, naskapi and woodorum.

Eleven names are placed in synonymy: absentiva

Mannheims, broweriana Alexander, fulvicauda Alexander, gracilistyla Alexander, lackschewitzi Mannheims,

lapponica Tjeder, oslari Dietz, primoveris Alexander,

proxima Lackschewitz, rostellata Doane, and uinticola

Alexander. Prionocera hybrida is removed from the genus

Prionocera and is placed in synonymy with Tipula

(Angarotipula) illustris Doane. Two names are considered

nomina dubia: bergrothi Williston and parrii Kirby.

These changes result in 20 species being recognized, 4

which are known only from the Palearctic, 10 from the

Nearctic and 6 which have a Holarctic distribution.

A phylogeny of the genus Prionocera is presented.

Synapomorphous characters which define four species groups are given, and the ground plan of the genus is discussed.

In order to answer the question of the phylogenetic position of the genus Prionocera within the subfamily Tipulinae, a cladistic analysis was done on the family Tipulidae. It is suggested that Prionocera is most closely related to the genus Tipula.

Synapomorphies of the Cylindrotominae and Tipulinae suggest that these are sister groups and together form a sister group of the rest of the crane flies - the Limoniinae. Analysis of characters indicates that the most primitive crane flies are in the Hexatomini (Limoniinae) and that the other four tribes of this subfamily have evolved from hexatomine-like ancestors.

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A revision of a holarctic group such as this one depends upon the cooperation of many curators. I wish to acknowledge with thanks the individuals and their institutions listed below for the loan of specimens. Most of the abbreviations (in parentheses) are taken from Heppner & Lamas (1982), and are used in the text when referring to specimens studied. The exceptions are ALAK, CAL, MPUL, ROM and SUBC which were not included in the aforementioned list, and CMNH, MSU, SEM and UMMZ which are, I believe, too well established to be changed.

(ALAK) University of Alaska, Fairbanks, Alaska; Dr. G.S.

MacLean.

(AMNH) American Museum of Natural History, New York, N.Y.; Dr. P. Wygodzinsky.

(ANSP) Academy of Natural Sciences, Philadelphia, Pa.; Dr. C. Dunn.

(BMNH) British Museum (Natural History), London, England; Dr. P. Cranston, Dr. K.G.V. Smith.

- (CAL) University of Calgary, Calgary, Alta.; Dr. G. Pritchard.
- (CAS) California Academy of Sciences, San Francisco, Ca.; Dr. P.H. Arnaud, Jr.
- (CMNH) Carnegie Museum of Natural History, Pittsburgh, Pa.; Dr. C. W. Young.
- (CNC) Canadian National Collection, Biosystematics Research Institute, Ottawa, Ont.; Dr. H.J. Teskey.
- (FEM) Frost Entomological Museum, Pennsylvania State University, University Park, Pa.; Dr. Ke Chung Kim.
- (MAKB) Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (B.R.D.); Dr. H. Ulrich.
- (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; Ms. M. Thayer, Dr. M. Hathaway, Dr. C. Vogt.
- (MPM) Milwaukee Public Museum, Milwaukee, Wisc.; Dr. G. Noonan.
- (MPUL) Musée Provancher, Université Laval, Québec, P.Q.; Dr. J.M. Perron.
- (MSU) Michigan State University, East Lansing, Mich.; Dr. R.L. Fischer.
- (NRS) Naturhistoriska Riksmuseet, Stockholm, Sweden; Dr. P. Lindskog, Dr. P. I. Persson.
- (NSMH) Nova Scotia Museum, Halifax, Nova Scotia; Mr. B.

Wright.

(OSU) Ohio State University, Columbus, Ohio; Dr. C.A.

Triplehorn.

(ROM) Royal Ontario Museum, Toronto, Ont.; Dr. G.B.

Wiggins.

(SEM) Snow Entomological Museum, University of Kansas,

Lawrence, Ks.; Dr. G.W. Byers, S. Teale.

(SUBC) Spencer Entomological Museum, University of

British Columbia, Vancouver, B.C.; Mr. S.G.

Cannings.

(UMMZ) University of Michigan, Museum of Zoology, Ann

Arbor, Mich.; Dr. T.E. Moore.

(UMSP) University of Minnesota, St. Paul, Minn.; Dr. P.

Clausen.

(UNH) University of New Hampshire, Durham, N.H.; Dr. J.F.

Burger.

(USNM) United States National Museum of Natural History,

Washington, D.C.; Dr. W.N. Mathis.

(WSU) James Entomological Collection, Washington State

University, Pullman, Washington; Dr. R. Zuck.

(ZMH) Zoological Museum of the University, Helsinki,

Finland; Dr. B. Lindeberg.

(ZMHB) Museum für Naturkunde der Humboldt Universität,

East Berlin, Germany (D.D.R.); Dr. H. Schumann.

(ZMLS) Zoological Museum, Lund, Sweden; Dr. R.

Danielsson, Dr. B. Tjeder.

(ZMUB) Zoological Museum, University of Bergen, Norway;

Dr. L.G. Jensen.

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Several northern expeditions mounted by the Department of Agriculture, Ottawa, Canada, resulted in the collection of over 1,600 unidentified Prionocera which formed the basis for this study. In order to add to this and the other borrowed material, field work was carried out in the summers of 1977, 1978, 1979 and 1981. I thank the following individuals and their institutions for accommodations and logistical support.

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PART I

A REVISION OF THE GENUS PRIONOCERA

INTRODUCTION

The northern nearctic insect fauna is still not very well known (Danks, 1979), but the crane fly family, Tipulidae, is one of the better known groups with relatively few species remaining to be described (McAlpine, 1979). When I began this study, over 1,600 unidentified Prionocera, the fruits of several northern collecting expeditions, were in the Canadian National Collection, Ottawa. Most of these specimens were impossible to identify or even to sort to species groups with any degree of certainty. Fifteen "species" of Prionocera had been described from North America and 13 from Eurasia. Three monographs had been written on the palearctic species (Lackschewitz, 1933; Tjeder, 1948; Mannheims, 1951), but no comparable treatment of the North American Prionocera were available. Most of the species descriptions were inadequate for identification. Because Prionocera is a northern genus, it was expected that several species might be circumboreal. Therefore I decided to include both the palearctic and nearctic species in this revision, to determine how many species are involved, their distributions, their affinities, and to describe and illustrate them, and finally to provide keys for their recognition.

METHODS

This study is based on approximately 2,200 specimens representing 20 species. Most of the specimens examined were pinned and dried; fewer than 100 were in alcohol.

Approximately 2,000 specimens were borrowed from institutions; about 1,600 of these were from the Canadian National Collection, Ottawa. The remainder were collected by the author at Churchill, Manitoba, 25 June-11 July 1977; 26 June-14 July 1978; at Nederland, Colorado, 22 June-12 July 1979 and at Schefferville, Quebec, 22 June-21 July 1981.

The species in this genus are difficult to separate without making dissections. Many specimens cited in the literature proved to be misidentified and several names had been misapplied. Therefore, only specimens seen by the author are included in this monograph.

Field Methods

The most effective collecting method proved to be capturing specimens individually. Species of Prionocera fly in open wet habitats in and among herbaceous vegetation. Trampling through their habitat dislodges them and makes them easier to see and thus to net. At the right time and place some species are quite abundant and several can be netted with a single sweep. However, mating pairs should be netted separately.

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In Schefferville I used a Malaise trap which I had constructed based on the design of Dufour (1980) and operated with and without a mercury vapour lamp. This trap failed to attract Tipulinae. Cold night temperatures just a few degrees above 0°C probably inhibited night flying insects. Only a few midges and some moths were attracted to the light.

Also in Schefferville, three emergence traps modified from floating aquatic traps (LeSage & Harrison, 1979) were used without success. This perhaps was due to the low population numbers encountered in 1981.

Preparation of specimens

Collected specimens were placed in cork-topped glass shell vials (10 x 2.5 cm) containing a 3 cm plug of facial tissue moistened each collecting day with 2 drops of ethylene dichloride. After 2-3 hours, adult flies were papered in the manner described by Byers¹⁹⁶¹ (1961). Unfortunately, the distribution of pleural hairs on these papered flies were obscured by the legs. Therefore later collections were pinned. Styrofoam sheets, 2.5 cm thick, covered with a smooth sheet of paper were found to be ideal for pinning long-legged crane flies. The pin

bearing an insect was pushed into the styrofoam leaving a space of a few millimeters below the body; the legs could then be suitably arranged and held in place by additional pins if necessary. After a day or two of drying, the pinned insects were removed and properly labelled.

Dissection

For more detailed study the genitalia and other sections to be studied were first gently wetted with water by a fine brush. The section was cut off with a pair of small scissors, cleared in warm NaOH, or KOH (2 pellets/12 ml H₂O) for 10-15 minutes, and then neutralized in warm lactic acid for 10 minutes and finally put into a drop of glycerine on a slide for study. For permanent storage, insect parts were removed with a drop of glycerine to genitalia vials. Each vial was pinned beneath the rest of its respective specimen.

Some specimens borrowed from European collections had the genitalia preserved in balsam on plastic mini-slides pinned beneath the rest of the specimen. Slides unsuitable for study were removed from the pin and gently warmed in xylol until the balsam and often the plastic slide itself, had dissolved. The still brittle insect fragments were then softened in warm NaOH for 10 minutes and handled as described above.

Illustrations

Drawings were made with the aid of a Wild dissecting

microscope and an ocular grid. As far as possible each specimen was drawn from a standard orientation.

Corresponding structures were drawn to the same size to emphasize morphological differences.

Measurements

The measurement "body length" refers to the shortest distance between the tip of the abdomen and the most anterior portion of the head (excluding antennae), regardless of the position in which the specimen is preserved. Because of the differences in contraction or deflection of parts, this measurement provides only a very rough estimate of general size.

"Wing length" is the distance between the wing's tip and its point of attachment.

The nasus is measured in profile from its tip (excluding projecting hairs) to its base.

The hypogynial valvulae are measured laterally from their tips to the membranous connection ventrally with sternite 8.

Colour

All colour designations with reference numbers are based on Kelly (1965), and the colour names are based on McKnight (1977). Where a colour range is given, such as "grayish blue to dark bluish gray (186,192)", this does not mean 186 to 192 all inclusive but that the hue varies

between no. 186 and no. 192.

I always noted colour under the same illumination, a 6 volt stereomicroscope lamp with a light blue daylight filter. Prionocera is not a colourful genus, but there are significant if subtle colour differences useful in distinguishing species. The use of a standardized colour chart encompassing the entire spectrum of colours seen by the human eye together with a simple dictionary of colour names greatly enhances communication. The centroid colour charts are obtainable from the U.S. Bureau of Standards, but even when one does not have the set at hand, the simple, albeit sometimes wordy, colour names make for easy recognition and comprehension especially for those relatively unfamiliar with the English language.

Immature Stages

Larvae were found in the submerged or wet vegetation in the general region where the adults were found flying. Third and fourth instar larvae, individually housed in petri dishes 9 cm in diameter along with some of their substrate (e.g., mosses or decaying vegetation) and wetted regularly could be kept until pupation.

The pupae were carefully placed in a tall jar on a wad of toilet tissue which was always kept damp. A few grass stalks or thin twigs were added to give the teneral adult a perch while hardening. More than one species of

Prionocera was usually found flying over the same terrain at the same time. The adults are very similar and the larvae are more so. Therefore, identification of larvae found in the field was not possible.

Gravid females were induced to lay eggs by cutting off their heads (Forer, 1982). Some females obligingly laid their eggs when put into a plastic shell vial. These eggs were later carefully flushed out with water and placed on toilet paper mulch (Forer, 1982). Newly hatched larvae did not survive on ground-up nettle leaves as do Nephrotoma and other Tipulinae (Forer, 1982), but I could raise some of them as far as third instars on bits of substrate (submerged sedges and mosses) from the female's habitat.

TAXONOMIC AND NOMENCLATURAL HISTORY

The genus Prionocera was erected by Loew (1844) to accommodate a single European species which he described and named Prionocera pubescens.

In 1863 Loew rejected the name Prionocera in favor of Stygeropis, and in that paper he described Stygeropis sordida from North America. Subsequently he described two more North American species: Stygeropis dimidiata and S. fuscipennis (Loew, 1866) (= Tipula illustris, see below).

Apparently Loew presumed that Prionocera was preoccupied by the coleopterous genus "Prionocera." The problem was created by Shuckard (1839) who had misspelled the name Priocera Dum. Subsequently Bergroth (1889), recognizing that Loew had made an illegitimate name change, resurrected the name Prionocera. This usage was followed by Mik (1890) and Kertész (1902).

Wallengren (1882) recognized that Tipula diana Meigen (1818) (a synonym of turcica Fabricius, 1787), Tipula serricornis Zetterstedt (1838), and Tipula subserricornis Zetterstedt (1851) belonged to Loew's genus Prionocera. However, he preferred to consider Prionocera as a subgenus of Tipula.

In his synopsis of the Swedish Tipulidae Wahlgren (1905) elevated Prionocera to generic rank and included salicetorum Siebke, serricornis Zetterstedt and turcica

Fabricius. He erroneously synonymized subsericornis with turcica. Lundström and Frey (1916) subsequently transferred tumidicornis to Prionocera.

The palearctic species of Prionocera were revised in a monograph by Lackschewitz (1933), who recognized the following six species: serricornis, subsericornis, turcica, and three new species: abscondita, anceps and proxima. As, however, Lackschewitz relied entirely upon species descriptions, having no recourse to the types, he misidentified both serricornis and subsericornis. He transferred tumidicornis Lundström and salicetorum Siebke to the genus Tipula, an interpretation followed here.

Tjeder (1948) redescribed and figured ten species of Prionocera in his monograph of the Swedish species. Of Lackschewitz's six species, he recognized only two: proxima and turcica. (I am placing proxima in synonymy with subsericornis.) Tjeder studied Zetterstedt's original material and established the identities of serricornis and subsericornis. He placed anceps Lackschewitz in synonymy with serricornis and suggested that serricornis sensu Lackschewitz was a new species, but lacking specimens he declined to name it. The species misidentified as subsericornis by Lackschewitz was misidentified again by Tjeder as "pubescens Loew". Tjeder described five species as new: anderi, lapponica, recta, ringdahl and setosa. (I am placing lapponica in

synonymy with recta.)

The genus Prionocera was revised again by Mannheims (1951). He recognized 13 species, of which the following eight corresponded with those of Tjeder: lapponica, proxima, recta, ringdahli, serricornis, setosa, subserricornis and turcica. Having seen Loew's type material, Mannheims placed anderi Tjeder in synonymy with pubescens Loew, and pubescens sensu Tjeder he named tjederi. The species which Tjeder (1948:90) had recognized as being misidentified as serricornis by Lackschewitz was renamed lackschewitzi by Mannheims. In addition, Mannheims mentioned, but did not describe parrii (Kirby) from Greenland and North America. (I am recognizing neither lackschewitzi nor parrii here.)

From North America, Williston (1893) described Stygeropsis bergrothi, here considered to be a nomen dubium. Alexander (1919) transferred Ctenophora parrii Kirby (1834) to Loew's genus and included a new species, Stygeropsis parrioides. The name parrii is considered here to be a nomen dubium and parrioides has been transferred to Tipula (see below). Alexander described Stygeropsis unimicra, (1915) and S. ominosa, (1920a); by the end of the year he had accepted the name Prionocera (Alexander, 1920b). He described 12 additional species and subspecies of Prionocera. Arranged chronologically they are: Prionocera electa, 1927; P. altivolans and P.

laetipennis, 1935; P. rostellata var. churchilliana and var. prominens, 1942; P. oregonica, 1943a; P. primoveris, 1943b; P. uinticola, 1948a; P. fulvicauda, 1948b; P. gracilistyla, 1956; and P. broweriana, 1961.

In 1942 Alexander moved fuscipennis Loew and parrioides Alexander to Tipula (Arctotipula). The name fuscipennis had to be dropped in favour of the junior synonym illustris Doane (1901) because fuscipennis was preoccupied by Tipula fuscipennis Curtis (1834). Savtschenko (1961) moved altivolans and laetipennis to his new subgenus Tipula (Angarotipula). Alexander (1962) recognized that illustris and parrioides also belonged to this new subgenus.

Dietz (1918) described Pachyrhina hybrida and P. oslari from Colorado. These species were subsequently transferred to Prionocera (Alexander, 1965). In this revision I synonymized hybrida Dietz with Tipula (Angarotipula) illustris and oslari Dietz with Prionocera dimidiata.

I recognize only four of Alexander's species of Prionocera: unimicra, ominosa, electa and oregonica. No varieties of P. rostellata (= dimidiata Loew) are recognized. I have placed Prionocera primoveris, P. uinticola and P. fulvicauda in synonymy with P. oregonica; P. gracilistyla is placed in synonymy with P. recta Tjeder and P. broweriana with P. unimicra. Five

new species are described making a total of 20 species included in the genus Prionocera (see Appendix A).

The oriental species of Prionocera are omitted from this study. They include Prionocera flaviceps Enderlein (1912) from Sumatra, P. indica Edwards (1926) from French Indo-China (Laos) and P. chosenicola and P. serenicola described by Alexander (1945) from northern Korea.

MORPHOLOGY AND TERMINOLOGY OF THE TIPULIDAE

There have been several important studies of the morphology of the Tipulidae, the earliest being that of Reaumur (1740). Westhoff (1882) described the male genitalia of the genus Tipula and Byers (1961) described the internal and external anatomy of both the male and female in the members of the genus Dolichopeza and, more recently, of those of the genus Chionea (1983). The earlier studies were summarized by Frommer (1963), who also provided a convenient table of equivalent terminologies used by these workers.

McAlpine (1981) developed a uniform terminology to apply to all Diptera. In order to facilitate phylogenetic comparisons of the Tipulidae with other families, McAlpine's terminology is followed here. Since Alexander and later workers based their crane fly terminology on the morphological work of Crampton (1942) and because McAlpine also based his work, in part, on the work of Crampton, only a few important changes of traditional crane fly terminology had to be made here, and these will be explained below.

Head: (fig. 1). The compound eye occupies a large proportion of the side of the head. No true ocelli are present in this family. However, in Prionocera and in several species in the large genus Tipula, a round to oval structure, the pseudo-ocellus, is found on either

side of a slightly raised frontal vitta just behind the antenna. This structure may be light sensitive. The rostrum, bearing the mouthparts distally, is more elongated in the Tipulinae and is thought to be composed of the clypeus, gena (in part) and subgena (in part). In most Tipulinae the rostrum bears a small nasus distally. The gena is the region bordered by the rostrum, antenna, compound eye and ventral edge of the head. The postgena is the posteroventral area lateral to the occiput.

Thorax: (fig. 1). The true prescutum (presct) is greatly reduced in all Tipulidae and is marked posteriorly by the prescutal pits (Matsuda, 1976; McAlpine, 1981). These pits have been called humeral pits or pseudosutural foveae (Alexander, 1942a; Byers, 1961).

The scutum (sct) is divided into an anterior and a posterior section by the V-shaped transverse suture (trn sct) characteristic of the family Tipulidae. The entire region between the transverse suture and the pronotum has been referred to as the "prescutum" (Alexander, 1942a; Byers, 1961). Tangelder (1983) distinguished the anterior and posterior sections as "scutum 1" and "scutum 2," respectively. The transverse suture is apparently a secondarily developed internal-strengthening ridge having no muscle attachments. Three broad longitudinal stripes dominate the mesonotum in the Tipulinae. The median

stripe, extending from near the edge of the pronotum to the transverse suture, thus traversing both the prescutum and anterior scutum, may be further divided longitudinally by a narrow vitta. Because of this secondary division, the mesonotum in Prionocera, and in the Tipulinae in general, is alternately described as having four rather than three stripes. The lateral stripes are confined to the scutum, extending from the prescutal pits across the transverse suture to the posterior section of the scutum. These stripes tend to be less distinct posteriorly.

The postnotum consists of a mediotergite (mtg) (postscutellum, Byers, 1961) flanked by a laterotergite (pleurotergite, Alexander, 1942; Byers, 1961). The laterotergite is further divided into a dorsal anatergite (anatg) and ventral katatergite (ktg).

The strong pleural suture divides the mesopleuron into the anterior episternum and posterior epimeron (pteropleurite, Alexander, 1942a; mesepimeron, Byers, 1961). The episternum in turn is divided longitudinally by the anapleural suture into a dorsal anepisternum (anepst) and a ventral katepisternum (kepst) (sternopleurite, Alexander, 1942a; pre-episternum, Byers, 1961). The epimeron (pteropleurite, Alexander, 1942a; mesepimeron, Byers, 1961) is similarly divided into an anepimeron (anepm) and a katepimeron (kep_m) by the

transepimeral suture. This suture lies at the level of the posterior spiracle (p spr) and is therefore not contiguous with the anapleural suture but is more ventral to it; consequently the katepimeron is very small. The much longer anepimeron appears to be secondarily divided into a dorsal and ventral region by a shallow groove which is contiguous with anapleural suture of the episternum and can therefore be mistaken for the transepimeral suture.

Wing: (fig. 2). A few changes in the interpretation of the wing venation should be noted. These are based on McAlpine (1981). There is only one subcosta which either joins the costa, atrophies at the tip, or, as in Prionocera, is connected to R1 by a short transverse vein, sc-r. Previous authors (Alexander, 1927a, 1929, 1981; Byers, 1961) have considered this veinlet to be the first section of Sc2. A costal cross vein (c-r) (free tip of Sc2, Alexander, 1942a) may be present in the pterostigmal region. Anterior media (MA) occurs as a short, stout, transverse vein between posterior media and radius. This is the anterior arcus of Alexander (1927, 1929); it is atrophied in Prionocera. Three branches of posterior media reach the wing margin, there being no evidence of a fourth branch in the Mecopteroidea (McAlpine, 1981). There are two cubital veins, anterior cubitus with two branches: CuA1 and CuA2 and posterior cubitus, CuP, a fold just behind CuA1. CuA1 corresponds

to M4 of Alexander (1927, 1929) and later authors, and his "m-cu" is here interpreted as the basal section of CuA1. The true medial cubital cross vein is a very small element between CuA1 and the discal cell:

Male terminalia: (figs. 3, 4, 10). There are nine distinct segments in male Tipulidae. A tenth segment is apparently lacking or is confined to the anal region (Dahl, 1980).

The 9th tergite, especially in Prionocera, usually bears various processes and lobes. These processes appear to be secondary extensions of the 9th tergite, but it is possible that the more ventrally situated single median lobe and/or the paired apical process are remnants of a 10th tergite.

The proctiger or the anus-bearing region, lies beneath the distal edge of the 9th tergite. It is reinforced laterally by an irregularly sclerotized region that I refer to as the rectal sclerite. This may be the vestige of a paraproct, although true paraprocts have not been identified in the Diptera (Crampton, 1942; McAlpine, 1981). Dobrotworsky (1967a) illustrated Leptotarsus (Macromastix) with rectal sclerites ("lateral plates") and cerci ("anal styles"). This suggests that a vestige of an 11th segment may be present, at least in some Tipulinae.

My interpretation of the terminalia in the subfamily Tipulinae is that the ninth tergite and sternite are fused, but the sternal portion has been very much reduced. Only a very narrow anterior region remains to which are attached the enlarged gonocoxites. Each gonocoxite bears two gonostyli distally (see Part II). Dahl (1980) has shown that in Limonia (Tipulidae) and Trichocera (Trichoceridae) only the anterior portion of the ninth sternal region in the prepupa develops into the sternal region of the adult. The gonocoxites and gonostyli which she refers to collectively as the claspers, develop from the distal part of the ninth sternal region. In contrast, the gonocoxites in the Anisopodidae develop from the lateral region of the genital primordium (ibid.). Therefore, it would appear that the gonocoxites in the Tipulidae and the Trichoceridae are not homologous to the gonocoxites in the Anisopodidae, and by extension, in the rest of the Diptera. However, as Matsuda (1979) has pointed out, substitution and heterochrony can alter developmental pathways and obscure underlying homologies. I am retaining McAlpine's terminology here, and refer, therefore, to gonocoxites and gonostyli.

The gonocoxites have been variously referred to as "9th sternite" (Tjeder, 1948), "basistyles fused with the 9th sternite" (Alexander, 1942, 1967; Byers 1961; Matsuda, 1976; Oosterbroek, 1980) and "basimeres fused

with the 9th sternite" Frommer, 1963). The gonostyli have been termed "styles" (Tjeder, 1948), "dististyles" (Alexander, 1942a, 1967; Byers, 1961, Oosterbroek, 1980) and "telomeres" (Frommer, 1963).

The gonocoxites are fused ventrally in most of the Tipulinae, although a partially membranous connection usually remains. They lie beneath the 9th tergite, consequently most of their dorsal surface is internal and membranous. However there is a variable retention and development of dorsal fragments of the gonocoxites characteristic of the different taxa within the Tipulinae. In Prionocera (fig. 3) dorsal fragments (gon frag) ("ipr", Tjeder, 1948) extend towards the sperm pump, and are membranously joined to each other anteriorly, at their point of attachment to the posterior apodeme of the sperm pump. ~~These~~ internal remnants of the gonocoxites lie dorsal or lateral to the aedeagus, and posterior to the sperm pump, occupying the position of the parameres found in the other subfamilies of crane flies. The Tipulinae lack true parameres as defined by McAlpine (1981).

There is a lot of confusion surrounding the naming of parts of the male genitalia. Following McAlpine (1981), I am reserving the term aedeagus for the intromittent organ. In the Tipulinae the aedeagus arises from the sperm pump and extends through the aedeagal guide. The

aedeagus ranges from a short inflexible tube with limited exertion (e.g., in Prionocera) to a very long, thin, flexible tube capable of being exerted for most of its length and also of being completely retracted within the abdomen.

At the base of the aedeagus is the bulbous sperm sac enclosed by the sperm pump (vesica, Tjeder, 1948; Byers, 1961; aedeagus, Oosterbroek, 1980). There is a moveable ejaculatory apodeme (dorsal apodeme, Tjeder, 1948; moveable apodeme, Byers, 1961; compressor apodeme, Frommer, 1963; Oosterbroek, 1980) which is found at the point of invagination of the sperm sac wall. McAlpine (1981:53) describes an aedeagal apodeme which may be homologous to the ejaculatory apodeme in the Tipulidae. However, the term aedeagal apodeme seems inappropriate because, in the Tipulidae, the apodeme is clearly associated with the sperm pump and not with the aedeagus.

• The sperm pump in Prionocera has a single rigid transverse posterior apodeme and a pair of rigid lateral apodemes. Muscles originating on the anterior and posterior surfaces of the ejaculatory apodeme and inserting on the paired lateral and single posterior apodemes of the sperm pump, respectively, control the transmission of sperm.

The movement of the sperm pump in Prionocera is restricted by the attachments of the gonocoxal fragments

dorsally and the aedeagal guide ventrally. In most other genera of the Tipulinae (e.g., Tipula, Nephrotoma, Ctenophora, Dolichopeza) the sperm pump can rotate up to 180° in the sagittal plane (Byers, 1961; Phylogeny section). Such rotation is controlled by muscles from the abdominal wall to the walls and apodemes of the sperm pump (Byers, 1961; Frommer, 1963).

The aedeagal guide (adminiculum of authors) is always attached ventrally to the medial posterior margin of the gonocoxites. It encompasses the aedeagus for most of its length in Prionocera but only very narrowly in many other Tipulinae. In all Prionocera and most Tipulinae the aedeagal guide is not fused but the two halves of the guide may overlap dorsally. The aedeagal guide may extend towards or be attached to the sperm pump as in Prionocera (Tjeder, 1948) and Dolichopeza (adminicular rods, Byers, 1961). Lateral lobes of the aedeagal guide (gonapophyses, Byers, 1961) are not present in Prionocera.

Female terminalia: (figs. 8,9). The abdomen is generally considered to comprise 10 segments. It has been suggested that portions of the 11th may also be present or at least fused with the 10th (Crampton, 1942; Frommer, 1963; Matsuda, 1976; McAlpine, 1981). However, Dahl (1980) showed that in both the Tipulidae and the Trichoceridae the female has only nine segments.

Tergite 8 lies dorsal to but separate from sternite 8, except in the genus Dolichopeza (Byers, 1961), where these sclerites are narrowly joined anteriorly. Tergite 8 is generally shorter than tergite 7, whereas sternite 8 is at least as long as tergite 8 and 9 combined, and in addition bears the hypogynial valvulae distally. These valvulae vary from being heavily sclerotized (e.g., Ctenophora) to a very reduced bilobed flap (e.g., Tipula (Vestiplex)).

The hypogynial valvulae are paired, hollow, flattened blades which together form a V-shaped structure beneath the cerci. Tjeder (1958) considered the hypogynial valvulae in the tribe Limoniini to be composed of three separate valves. His terminology was applied to genera in the Tipulidae by Vane-Wright (1967). There is no basis for claiming that the hypogynial valves are composed of three separate valves. Each blade has a medial ("ventral valve", Tjeder, 1958) and a lateral ("lateral valve", Tjeder, 1958) surface. The surfaces of each blade are closely adpressed distally and ventrally but are separated proximally and dorsally by a triangular dorsal surface ("dorsal valve", Tjeder, 1958). In Dolichopeza this dorsal surface is broader medially, and extends roof-like over the pocket described by Byers (1961).

The hypogynial valves may be homologous to the

anterior gonopophyses of the Orthopteroids (Crampton, 1942; McAlpine, 1981). They function as an ovipositor. (Females of Prionocera, captive in a vial, were observed to raise their cerci out of the way, and expel their eggs individually by a rhythmic downward thrust of the hypogynial valves.)

The 9th segment lies with its anterior margin partially telescoped under the 8th. It consists of two parts: (1) sternite 9 is a variqusly shaped sclerotized complex ventral to, closely associated with, and sometimes fused with tergite 9 laterally, and (2) the genital fork (furca or vaginal apodeme), a much smaller, usually single sclerite lying with its stem dorsal to the oviduct and its posterior arms flanking the opening of the bursa copulatrix. Sternite 9 appears to be composed of paired elements, usually with a narrow membranous connection between. Crampton (1942) suggested that this complex, or at least parts of it may be homologous to the posterior valvulae of Orthopteroids. Byers (1961) had referred to this structure as "fused valvulae"; however, in a later paper (1979) and currently (personal communication), he refers to this structure simply as the 9th sternum. There is no evidence of anything homologous to the orthopteran valvulae in the Mecopteroidea.

Between sternites 8 & 9 there is a membranous genital chamber. The entrance to the bursa copulatrix, or common

spermathecal duct, opens on the dorsal wall of this chamber and the gonopore, opening of the common oviduct, is on the ventral wall, on the ridge formed by the proximal edges of the hypogynial valves.

Tergite 10 is strongly sclerotized and is sometimes fragmented distally. It has been suggested that these fragments may represent an 11th segment (Byers, 1961; Frommer, 1963; Matsuda, 1976). Dahl (1980) found that in the Tipulidae and the Trichoceridae the so-called 10th tergite develops from the distal portion of the 9th segment in the prepupa and that the cerci are formed from detached lateral elements of the 9th sternite.

Developmental pathways may be misleading. The apparent 9th segment, as observed by Dahl in the females mentioned above, could be a composite 9th and 10th segment. The 10th segment then is only expressed in the adult. I have retained the terminology of McAlpine (1981) and refer to separate 9th and 10th tergites.

There is no sclerotized sternite 10. The infra anal plate, a hairy membranous flap enclosing the anus ventrally at the base of the cerci may represent the 10th or the 11th sternite, or possibly a fusion of the two (Frommer, 1963; McAlpine, 1981). Or, if Dahl (1980) is correct, it must be part of the 9th segment.

The cerci (fig. 8) are a pair of elongate blade-like

lobes. Their tips are bluntly rounded and narrowed distally. In most Tipulinae they are separated proximally by a narrow posterior extension, referred to as the 10th or the 11th tergite. A small basomedial section of the cercus, the supraanal (Tjeder, 1958) is defined by an internal strengthening ridge, the supraanale apodeme, and a longitudinal ridge, (longitudinal list-like apodeme, Tjeder, 1958) extends from the cercal articulation and runs towards the narrowed tips.

True cerci develop between tergites 10 and 11 (McAlpine, 1981). If the so-called cerci in the Tipulidae and the Trichoceridae develop from lateral elements of the 9th sternum, as found by Dahl (1980), they cannot be homologous with the blade-like cerci of lower orders, and are therefore misnamed.

THE GENUS PRIONOCERA LOEW

• Prionocera Loew, 1844: 170. Type-species, pubescens
(monobasic).

Stygeropis Loew, 1863: 298 (unjustified new name for
Prionocera Loew). Type-species, Prionocera pubescens
Loew (automatically).

DIAGNOSIS

Flagellomeres without verticils, slightly to strongly distended ventrodistally giving antenna a serrate appearance; male with distal processes on the 9th tergite; female with hypogynial valves broadly rounded distally, extending to or beyond point of separation of long slender cerci.

DESCRIPTION

ADULT. General appearance: a moderately sized pruinose and hairy tipuline; male body length 7.7-13.9mm, wing length 10.2-16.6mm; female body length (6.7)* 9.6-17.6mm, wing length (8.5)10.4-18.0mm.

MALE: Head: compound eyes separated dorsally by almost twice eye width as seen from above; frons slightly

*Measurements in brackets are of the syntype of sordida Loew, a small and somewhat shrivelled specimen.

raised behind antennal bases (not a gibbous tubercle), flanked by oval, lens-like structure (pseudo-ocellus); pseudo-ocellus varying (sometimes within same species) from black to strong orange-yellow (267,68); vertex and occiput hairy, quality and quantity of hairs varying with species, vertex longitudinally divided by glabrous darker region; gena heavily pruinose with no or very few scattered short hairs; postgena broadly rounded, densely covered with long hairs; rostrum relatively short, half length of rest of head, with hairs; nasus, if present, small, not longer than broad; palpus short, 5th segment slightly shorter than preceding ones combined, no sensory area on 3rd segment.

Antenna: scape cylindrical, 3 times as long as wide, with scattered long hairs; pedicel small, globular, with scattered shorter hairs dorsally; flagellum 11 segmented, flagellomeres pubescent, without verticils but may have several hairs dorsally on lower segments; 1st flagellomere slightly to strongly distended distoventrally, succeeding flagellomeres progressively less distended; 10th, cylindrical, usually slightly longer than 9th; 11th cylindrical, abruptly smaller, thinner, attached subapically and dorsally on 10th.

Thorax: anterior pronotum darker medially, densely hairy, posterior pronotum concave, recessed beneath anterior edge of prescutum, shiny, glabrous; prescutal

pit ranging from dusky black to shiny deep-orange yellow (267,69), may form a prominent triangular area with apex at pit and base adjacent to paratergite; dorsum dominated by three longitudinal stripes, sometimes ill-defined, middle stripe extending from anterior edge of prescutum to scutal suture, usually longitudinally and narrowly divided by lighter glabrous line; lateral stripes extending from prescutal pit to posterior edge of scutum, becoming contiguous behind scutal suture, stripes defined by slightly lighter, hairy region; scutellum pruinose, hairy, flanked by glabrous light orange-yellow (70), tympanal fossa; pleuron pruinose light to dark gray (264,266), distinguished from that of most Tipulinae by presence of hairs: anepisternum, anepimeron and katepimeron with hairs or bare, katepisternum hairy at least on dorsal half, metepisternum divided into dorsal glabrous metanepisternum and ventral hairy metakatepisternum, metepimeron glabrous, mediotergite of postnotum hairy, anatergite densely hairy, katatergite bare, lighter on dorsal crest, darker ventrally.

Wing: without pattern, varying from almost hyaline to infumed with gray to brown, more strongly infumed in costal and subcostal cells, in base of wing and in pterostigmal region; very narrow hyaline area in costal cell extending from middle of Rs to c-r; obliterative streak; marking oblique to perpendicular wing fold characteristic of Tipulinae, a whitened area broadest and

most intense anteriorly beginning with abrupt narrowing of radius at its junction with Sc, sometimes including proximal half of stigma, extending posteriorly through distal tip of Rs and bases of R3 and R4+5 through the proximal and posterior edges of discal cell; wing membrane without macrotrichia; wing veins with macrotrichia restricted to R1 and base of 2A; subcosta ending in R1 just before pterostigmal region; c-r usually weakly present; Rs of moderate length, not short and oblique; three branches of radius reaching wing margin: R1+2, R3 and R4+5; R2 very short, closing distal end of cell R1; media apparently arising from cubitus; small brace vein MA obliterated; three branches of media reaching wing margin: M1, M2 and M3; discal cell always closed by medial cross vein, m-m; short element M1+2 making cell M1 petiolate; m-cu extremely short or absent, meeting discal cell distal to fork of M.

Halter: light yellow-brown to dark yellow-brown (76,78), knob usually darker with dorsal patch of hairs too variable within species for taxonomic use.

Legs: strong orange-yellow to dark yellow-brown (68,78), tips of femora and tibiae often darkened; legs of moderate length, basitarsi shorter than tibiae; tarsal claws toothed or simple, varying with species and even within specimen.

Abdomen: ranging from medium gray to gray-brown (265,61) with darker brown (61,65) dorsal longitudinal stripe, lateral and distal borders of tergites lighter; hairs on abdomen shorter than on head and thorax, anterior half of 2nd sternite bare; segments 1-7 unmodified, each with pair of spiracles in pleural membrane; 8th tergite shorter than 7th, 8th sternite longer than 7th, genitalia consequently tipped dorsally to about 30° above longitudinal axis.

Genitalia: 9th tergite (figs. 10-28) narrowly fused at base to narrow 9th sternite, membranously joined laterally to gonocoxites, bearing two or three pairs of distal processes and sometimes a single median lobe, processes usually contrastingly lighter distally: dorsal processes sublateral and most prominent, apical pincer-like processes on ventral edge of tergite usually beneath dorsal processes, lateral processes a distal prolongation of lateral edge of tergite, single median lobe (when present) a broad pale truncate plate between dorsal and ventral processes; rectal sclerite small, irregular sclerotization on either side of membranous base of anal segment at attachment to venter of 9th tergite (in some species these sclerites join dorsally, forming a narrow sclerotized yoke). Gonocoxites overlain by 9th tergite, membranous dorsally except for an irregular sclerotized fragment (fig. 3) extending from dorsal mediodistal edge of gonocoxite towards posterior apodeme of sperm pump,

attached to latter and narrowly to each other by membranous strands allowing for some movement of aedeagal complex in sagittal plane; ventrally gonocoxites attached anteriorly to very reduced 9th sternite, and connected membranously to each other but separated distally by small sclerotized ventral attachment (infolded flaps, 'H' of 8th sternite, Tjeder, 1948) of aedeagal guide. Outer and inner gonostyli (figs. 29-48) membranously attached to each other at base, possibly functioning like thumb and forefinger in spreading female genitalia during copulation. Gonostyli covered with long hairs on outer surfaces (i.e., lateral on outer gonostylus, medial on inner gonostylus) and with shorter hairs on inner surfaces; outer gonostylus a fleshy leaf-like lobe more or less concave on medial surface; inner gonostylus more heavily sclerotized, somewhat concave across base on lateral surface, differentiated into a dorsal crest, glabrous distal beak and smaller haired proximal beak; distal beak bearing several kinds of sensilla characteristic of, and apparently restricted to, this genus, observable by light microscope: beak tip with what appear to be circular pores covered with a very thin membrane, probably campaniform sensilla (Snodgrass, 1926, Baker, 1978), base of beak in several species bearing several pigmented flat-topped, peg-like sensilla, each on a circular base approximately 8.6μ in diameter. Aedeagus short, slender tube arising anteriorly on sperm pump,

curving closely around its ventral wall, extending posteriorly the length of 9th tergite; aedeagal sheath broadened laterally, extending from base of aedeagus to just below its tip, posterior edge of sheath sometimes marked by tooth-like thickening. Aedeagal guide (figs. 3-7) a paired structure narrowly attached to medial, ventrodistal edge of gonocoxite, halves membranously fused ventrally, cradling tip of aedeagus, curving around with major section (dorsal plate) lying dorsal to aedeagus, narrowing anteriorly, curving around and attaching to lateral wall of sperm pump. Sperm pump with several apodemes: ejaculatory apodeme, a moveable, trapezoidal to broadly fan-shaped sclerite with a posterior keel on its dorsal wall, shape varying within species; a single rigid posterior apodeme perpendicular to aedeagus, joined to rigid, paired lateral apodemes projecting anteriorly within abdominal cavity.

FEMALE. Similar to male except as follows: slightly larger than male; legs and antennae comparatively shorter; flagellomeres always less distended than in male, becoming progressively smaller and more cylindrical distally, 11th smallest or subequal to 9th and/or 10th, centered on tip of 10th; tarsal claws never toothed.

Genitalia: (figs. 8, 9, 49-82) 8th tergite and sternite entirely separate, never fused anteriorly as in Dolichopeza (Byers, 1961); 8th sternite with dorsolateral

edge variously lobed or sloping (figs. 49-65), providing useful taxonomic characters. Hypogynial valves borne distally on 8th sternite, separation from sternite marked ventrally by variously shaped membranous region (figs. 66-82); ratio of hypogynial valves to 8th sternite useful for species separation; valves extending posteriorly to or beyond point of separation of cerci, fused proximally, separated distally, inner (medial) surface with posteriorly directed bristles. Ninth sternite membranously joined to 9th tergite, broadly V-shaped, not heavily sclerotized, with narrowed tip projecting hood-like posteriorly beyond opening of common spermathecal duct; genital fork with paired short posterior arms flanking spermathecal duct, longer stem dorsal to oviduct. Tenth tergite narrowly extending between cercal bases, lateral edge of tergite straight to broadly curved posterolaterally, a small triangular sclerite more or less membranously separated, lying proximal to cercal base and medial extension of tergite. Cercus with external ridge ("list-like" apodeme, Tjeder, 1958; Vane-Wright, 1967) running length of cercus, marking middle of cercus proximally, becoming dorsolateral edge of blades distally; raised triangular supraanale (Tjeder, 1958) on cercal base, lateral to median extension of 10th tergite demarked by strong oblique internal supraanal apodeme. Infra anal plate trapezoidal, shallowly emarginate to almost bilobed distally.

DISCUSSION

The genus Prionocera was defined and named by Loew (1844) principally on the basis of the serrate antennae which lack verticils. This is still the best character for distinguishing Prionocera. In the subgenus Angarotipula of Tipula, the flagellomeres are also without verticils but the segments in the male are broadest medially rather than distally.

Prionocera is also distinguished from most other tipulines by having a hairy head and thorax. Several northern and high altitude crane flies are also quite hairy, for example, Tipula (Vestiplex) arctica, the subgenus Arctotipula and some high altitude Nephrotoma species (Byers, pers. comm.). This would seem to indicate that hairiness is a response to the environment and not necessarily an indication of relationship. Tipula (Angarotipula), which is not a hairy subgenus but does have northern species, shares with Prionocera the character of long dense hairs on the anatergite. The anatergite is bare in the other hairy species and subgenera mentioned above.

The compound eyes in Prionocera are comparatively small, allowing for a larger gena, postgena and vertex, and the pseudo-ocelli are very prominent. This is also characteristic of other northern and high altitude crane flies and of the subgenus Angarotipula.

6

The wings, similar to those of many tipulines, are not distinctly patterned but do have a darker pterostigmal region and a clearly defined paler area along the region of the distal wing fold. In Prionocera this fold seems to be a little more striking than in other tipulines because it tends to be broader and whiter. The wings are almost bare. The membranes have no macrotrichia, and on the veins macrotrichia are confined to R1 and the base of 2A. The same ~~holds true~~ for the subgenera Angarotipula and Arctotipula but most other tipulines also have hairs on branches of the radius, media and along the entire length of 2A.

The male genitalia provide the most striking features that set this genus apart. The sperm pump and the very short aedeagus, which is partially ensheathed by an aedeagal guide, form a compact complex which has limited movement in the sagittal plane. This is in contrast to the much longer thread-like flexible aedeagus and 180° or more rotation possible in most other tipuline genera. In Prionocera movement of the aedeagal complex is restrained by various attachments. The dorsal gonocoxal fragments are attached to the posterior apodeme of the sperm pump, and the anterior end of the aedeagal guides are attached to its lateral walls. These are membranous attachments which allow for some pivoting of the pump in the sagittal plane. In Dolichopeza, the aedeagus is longer and more flexible and the pump pivots against the paired lateral

attachments of the aedeagal guide (adminicular rods, Byers, 1961), but there is no dorsal gonocoxal connection. In most Tipula and Nephrotoma species the sperm pump is completely free and muscle attachments on its apodemes to the body wall allow for almost 180° rotation of the pump in the sagittal plane (Byers, 1961).

The presence of the aedeagal guide in Dolichopora and Prionocera is probably a plesiomorphic feature of the tipulines (see Phylogeny section). In Prionocera the medial membranous connection of the gonocoxal fragments to each other just posterior to the sperm pump is here thought to be a fore runner of the sclerotized horizontal connection of the gonocoxites as found in the subgenus Tipula (Angarotipula).

Females of Prionocera show no particular modifications of the basic ground plan of the Tipulinae.

"GEOGRAPHIC DISTRIBUTION (Map 1)

The genus Prionocera has a northern circumpolar distribution. In North America it extends from the Aleutian Islands to Newfoundland. Collections have been made from the low arctic (Victoria Island and the Boothia Peninsula) to as far south as the Sangre de Cristo Range in the southern Rocky Mountains of New Mexico. In the Palearctic region Prionocera has been extensively

collected in Fennoscandia and scattered collections have been made in the U.S.S.R., along a coastal strip of the Barents and Kara Seas in the west, and in Kamchatka in the east. The genus is also known from Greenland, England, and northern Europe, extending to the south along the Alps into Switzerland. Only two species have been recorded from both sides of the Bering Sea: P. ominosa, a nearctic species, and P. subserricornis, a circumpolar species. Lack of records from most of the U.S.S.R. cannot be interpreted as a lack of occurrence; no firm conclusions, therefore, can be drawn concerning the palearctic distribution of Prionocera.

The genus has also been recorded from North Korea (Alexander, 1945) and Laos (French Indo-China, Edwards, 1926). The Laotian specimen, judging from the description, is probably a species of Tipula (Anqarotipula).

Prionocera is primarily a boreal genus. It is a characteristic component of the wetlands (muskeg) in the taiga and forest-tundra regions of the boreal zone (Pruitt, 1978). These regions are roughly equivalent to the Canadian and Hudsonian zones respectively of Merriam (Munroe, 1968). Prionocera species occur in the more open bogs and fens of these regions. I found the larvae shallowly submerged among mosses and the previous years' decaying vegetation, mostly sedges and

other small herbaceous plants. The present distribution of this genus closely approximates the extent of the muskeg in the northern hemisphere with a long southern extension into the wetlands of high altitude oroboreal (Hämet-Ahti, 1981) forests in the Rocky Mountains, a small southern extension into the Great Lakes-St. Lawrence Forest region in eastern Canada and a larger southern extension into the northern temperate zone in Europe. The evolution and dispersal of the genus is therefore intimately linked with the history and development of the boreal zone.

The boreal flora acquired many of its modern characteristics in the Tertiary period. Eastern Siberia and Alaska are part of the same continental plate. Geological evidence suggests that some type of Asian-Alaskan land connection existed from the late Cretaceous until the Pliocene (Matthews, 1979). Lowland boreal forests first appeared in both North America and Asia during the middle to late Miocene. The Beaufort Formation (Miocene) exposed on the western edge of the Canadian Archipelago, is thought to include a representative of the early coniferous forests that may have been forerunners of the forests now found in the boreal zone (ibid.). It contains a unique and rich assemblage of species from which developed the relatively depauperate boreal biota of today. This formation includes a mixed hardwood-conifer flora in southern Banks

Island grading into a diverse assemblage of conifers in a forest-tundra zone in Meighen Island in the north.

Recent comparisons of conifer fossils with those from similar sites of Miocene age from Siberia show that this boreal region was of Holarctic extent. The tree species are similar to but not identical with modern species. Some of the mosses may be conspecific with extant species. Well-preserved beetle fragments are similar to their counterparts in modern holarctic species (ibid.).

There are as yet no identified Prionocera remains in the fossil record. The earliest fossil Tipulidae recorded from North America are from the White River and Green River beds dated Eocene (Cockerell, 1920; Wilson, 1978). In Europe the oldest fossils are from the Eocene-Oligocene transition (Alexander, 1931; Savchenko, 1966). In all these fossil beds the family is numerous and already clearly differentiated into subfamilies and genera (Savchenko, 1966; Brodo, 1967). Tipulids were recently identified from the Paleocene Paskapoo Formation, Alberta (Wighton, pers. comm.).

If Prionocera is indeed an old genus related to the genus Tipula (see Part II), then it must have been in existence at about the same time as the cylindrotomines in the early Tertiary. Furthermore, by analogy with the beetles mentioned above, it is quite likely that Prionocera was well-developed with a holarctic

distribution by the late Miocene or early Pliocene. It should be looked for in the Beaufort Formation and in other boreal sites of similar age.

Quaternary events are considered to be primarily responsible for the distributional patterns of extant insects. The frequency of climatic changes resulting in successive advances and retreats of the ice were generally faster than the rate of evolution of most northern insects (Matthews, 1979). The individual species of Prionocera, however, are very similar to one another, which suggests a relatively recent origin. Speciation during the Pleistocene cannot be ruled out.

Populations of Prionocera must have survived the drastic temperature fluctuations and encroachments of the ice in some or all of the various refugia postulated (Scudder, 1979). The fragmented wetlands inhabited by Prionocera expanded and merged together with the retreat of the ice. For a time, a Beringian corridor allowed for some cross-migration of species between Asia and North America. Evidence suggests that during the Pleistocene this land bridge was a rather dry tundra-steppe (Young, 1971). Yet there might have been scattered, shallow, wet depressions which could have harboured Prionocera. The present transcontinental extent of muskeg has made this "vegetation type" an avenue for transcontinental dispersion. This more recent history probably accounts

for the wide distributions of several Prionocera species (see Maps 4,7,9,10,14,15,16). Many other species from quite diverse groups have similar, broad distributions across the boreal zone (Scudder, 1979).

Insects often fail to inhabit all of the area open to them. Distributions of northern insects are still in a state of flux with species probably still recolonizing the areas glaciated in the most recent Pleistocene advance (Scudder, 1979). Some Prionocera species may not have dispersed far from their refugia. It is possible that P. woodorum (Map 18) for instance, survived in and is still more or less restricted to the unglaciated central Yukon valley. On the other hand, the major centres of botanical endemism identified by Argus (1977) are not so much related to glacial refugia as to later perturbations in the landscape.

The collection records of Prionocera are too incomplete for any realistic statement about the distribution of some of the rarer species. Species originally thought to have very restricted distributions (e.g., unimicra, oregonica, recta) are now shown to have much broader ranges. Further careful collecting could result in other range extensions. The very short flight season, the often local and not too abundant occurrence

of some species coupled with unfavourable collecting seasons often encountered in the north have undoubtedly distorted our records.

FLIGHT RECORDS: 9 May-15 August

Prionocera is rare to locally abundant and where it occurs it is usually one of the first species to appear in the spring.

KEY TO ADULTS OF PRIONOCERA

1. Crane flies with verticils on flagellomeresTipulidae (non Prionocera)
- Crane flies lacking verticils2
2. Flagellomeres broadest medially; male without posterior processes on tergite 9; female with hypogynial valvulae very short, broad and fleshyTipula (Angarotipula)
- Flagellomeres broadest distally (fig. 1); male with posterior processes on tergite 9 (figs. 10-28); female with hypogynial valvulae 1/4 or more the length of sternite 8, lightly sclerotized (figs. 49-65)Prionocera..3
3. Conspicuously hairy, hairs on vertex and thorax as long and dense as coxal hairs; nasus small or absent4
- Not conspicuously hairy, hairs on vertex and thorax shorter and less dense than coxal hairs; nasus distinct13
4. Nasus squarish, about as long as broad5

- Nasus absent or a minute bump9
5. Obliterative streak and stigma not contrasting with each other; females with cerci upcurved distally (figs. 60, 56); (female of cryptica unknown); males with no lateral processes on tergite 9 (figs. 12, 19); (male of sordida unknown)6
- Obliterative streak and stigma contrasting with each other (fig. 2); females with cerci downcurved distally (figs. 57, 58); males with lateral processes on tergite 9 (figs. 20, 21)8
6. Pleuron brownish pink to moderate reddish brown (33,43), female small (body length 6.7-11.4mm, wing length 8.8-10.9mm); hypogynial valvulae very short, 0.25 length of sternite 8, separated from it by small squarish membranous region, ventral edge narrowly more heavily sclerotized (figs. 60, 77). Male unknown. Known only from southern Manitobasordida (Loew)
- Pleuron bluish gray; other characters not as above7

7. Male with apical process on tergite 9 narrow, tooth-like, close to lateral edge (fig. 19); inner gonostylus obtusely curved between dorsal beak and proximal beak (fig. 40); a circular, raised, densely hairy area on lateral (inner) surface of gonostylus base (visible with 24 X magnification). Female with hypogynial valvulae 0.4 times length of sternite 8, separated from it by narrow fork-shaped region, ventral edge broadly more heavily sclerotized (figs. 56, 73). Boreal, holarctic.

.....pubescens Loew

Male with apical process on tergite 9 broad, abruptly toothed posteromesally, close to centre of tergite (fig. 12); inner gonostylus emarginate between dorsal and proximal beaks; a flattened, elliptical area on lateral (inner) surface of gonostylus base (difficult to see) (figs. 35, 36). Female unknown. Known only from southern Ontariocryptica, new species

8. Male with dorsal process of tergite 9 longer than broad, lateral process narrow (fig. 20); distal beak of inner gonostylus cylindrical with lightly pigmented sensilla (fig. 41); cerci of female short, broad and almost straight (fig. —

57); nearctic specimens ususally with dark brown hairs on head and thorax. Arctic and boreal, holarcticrecta Tjeder

Male with dorsal process squarish, no lateral process (fig. 21); distal beak on inner gonostylus broad and flat, without pigmented sensilla (fig. 42); cerci of female long, narrow, tip downcurved (fig. 58). All specimens with yellowish white (92) hairs on head and thorax. Arctic and boreal, palearcticringdahli Tjeder

9. No nasus, rostral hairs not projecting beyond tip; male with dorsal process of tergite 9 short, very broad (figs. 17, 22)10

Nasus minute bump-like or absent, rostral hairs projecting beyond tip of nasus; male with dorsal process squarish, about as long as broad (figs. 15, 16, 21)11

10. Male: 9th tergite without lateral process, dorsal process very broad, obscuring most of apical process, extending laterally to tergite edge, space between processes $2/3$ or less width of process; broad, membranous, triangular region

mesal and anterior to apical process (fig. 17).

Female: hypogynial valvulae $1/3$ length of 8th sternite (figs. 54, 71); 11th flagellomere smallest. Arctic and boreal, nearctic

.....ominosa (Alexander)

Male: tergite 9 with dorsal process not extending laterally to tergite edge, space between processes $2/3$ or more width of process; evenly sclerotized region anterior and mesal to apical process (fig. 22). Female: hypogynial valvulae very short, $1/4$ or less length of sternite 8 (figs. 59, 76). Arctic and boreal, palearctic

.....serricornis (Zetterstedt)

11. (9) Inner gonostylus (male) with distal beak broad and flat, two proximal beaks (figs. 35, 42); cerci (female) narrow, downcurved distally (figs. 53, 58)12

Inner gonostylus (male) with distal beak short, narrow, cylindrical, one proximal beak (fig. 37); female unknown. Known only from Quebec and Labradornaskapi, new species

12. Dorsal thoracic stripes dark brown to grayish brown (59, 61); wing membrane nearly hyaline,

contrasting with stigma; pseudo-ocellus dark grayish brown to black (62,267); 1st & 2nd flagellomeres (male) distended, succeeding more nearly cylindrical. Arctic and boreal, palearcticringdahli Tjeder

Dorsal thoracic stripes medium gray to black (265,266); wing membrane strongly tinged with light yellowish brown, stigma only slightly darker; pseudo-ocellus light orange-yellow to strong yellowish brown (70,74); flagellomeres in male strongly distended. Arctic and boreal, nearcticelliptica, new species

13. (3) Pleuron almost bare, no hairs on anepisternum .14

Pleuron hairy, anepisternum with hairs16

14. Entire anepimeron bare; flagellomeres in male strongly distended, distal width twice basal width, female flagellomeres slightly distended; inner gonostylus with a characteristic protruding rounded distal edge on broad base, distal beak short, without pigmented sensilla (fig. 45). Boreal, holarctictjederi Mannheims

Hairs on dorsal anepimeron, ventral anepimeron

bare; flagellomeres not strongly distended,
almost cylindrical in female; inner gonostylus
with small rounded base, long cylindrical,
slightly curved distal beak with several
pigmented sensilla (fig. 33)15

15. Apical process on tergite 9 with a single sharp
point (fig. 24); male with small tooth on
tarsal claws; gena yellowish white to light
yellow (92,86); female with cerci long, narrow
and slightly downcurved near tip (fig. 61).
Arctic and boreal, widespread, holarctic
.....subsericornis (Zetterstedt)

Apical process on 9th tergite with three small
rounded points (fig. 23); tarsal claws simple;
gena light gray to dark yellowish brown
(264,78); female unknown. Known only from
Abisko, Swedensetosa Tjeder

- 16.(13) Rostrum contrastingly coloured, dark dorsally,
lightened ventrolaterally17

Rostrum uniformly dark, or tip may be slightly
lighter20

17. Shiny black to dark brown on vertex and

anteriorly on thoracic stripes; flagellomeres strongly distended in male, slightly distended in female; tergite 9 with dorsal process bigger than lateral process, apical process tooth-like, ventral to dorsal process (fig. 14).

Boreal, nearcticelecta Alexander

Vertex and thoracic stripes gray or brownish gray to strong yellowish brown, pruinose, not shiny; flagellomeres only slightly distended in male, almost cylindrical in female; tergite 9 with dorsal and lateral processes subequal, elongate, apical process variable18

18. Male: tergite 9 with dorsal process long and rectangular, lateral process long and triangular, apical process tooth-like, ventral to dorsal process (fig. 28); aedeagal guide with dorsal plate flat (figs. 4, 6). Female: tergite 10 conspicuously hairy (fig. 8); hypogynial valvulae 0.4 length of sternite 8, triangular laterally (fig. 65). Known only from the Yukonwoodorum, new species

Male: tergite 9 with dorsal and lateral processes long, triangular; apical process on median projection between and not ventral to dorsal processes (figs. 18, 26); aedeagal guide with

dorsal plate not flat, variously shaped (figs. 5, 7). Female: tergite 10 with very fine hairs, not conspicuously hairy; hypogynial valvulae $1/2$ or more length of sternite 8, tips broad19

19. Obliterative streak and stigma contrasting with each other (fig. 2); male with dorsal plate of aedeagal guide with rounded dorsal expansion bearing 3 or 4 small teeth (fig. 7); dorsal process of tergite 9 slightly shorter and broader than lateral process (fig. 26); female with broad dorsolateral lobe on sternite 8, hypogynial valvulae $2/3$ length of sternite 8 (figs. 63, 80). Widespread in Holarcticturcica (Fabricius)

Obliterative streak and stigma not strongly contrasting; male with dorsal plate of aedeagal guide subapically expanded in a narrow dorsally curved flange (fig. 5); dorsal and lateral processes of tergite 9 subequal (fig. 18); female with rounded dorsolateral edge on sternite 8; hypogynial valvulae $1/2$ length of sternite 8 (figs. 55, 72). Boreal and oroboreal, nearcticoregonica Alexander

20.(16) Ventral anepimeron bare or almost so21

Ventral anepimeron distinctly hairy23

21. Proximal flagellomeres in male distinctly distended, 1st flagellomere (in both sexes) not elongated, only slightly longer than 2nd, 11th (male) less than 1/2 length of 10th; tergite 9 (male) with dorsal process squarish, about as long as broad, no lateral process, no medial lobe (fig. 27); inner gonostylus with relatively small base, long beak, no pigmented sensilla (fig. 48); aedeagus without distal teeth. Female with sloping dorsolateral edge on sternite 8; hypogynial valvulae 0.5 length of sternite 8, square-tipped (figs. 64, 81). Boreal and oroboreal, widespread in Nearcticunimicra (Alexander)

Flagellomeres only slightly distended, 1st flagellomere (in both sexes) elongate, 1.5 or more times length of 2nd; 11th (male) 1/2 or more length of 10th; tergite 9 (male) with dorsal process broader than long, lateral process small and narrow, medial lobe present (figs. 10, 13); inner gonostylus with broad base, distal beak narrow, cylindrical or sharply pointed (figs. 29, 32); aedeagus with

distal teeth (fig. 4); female with dorsolateral lobe on sternite 8, hypogynial valvulae 0.3 length of sternite 8, rounded distally22

22. Inner gonostylus (male) with distal beak sharply pointed, without sensilla (fig. 29); female with subdorsal longitudinal membranous region on hypogynial valvulae, without subapical hair (figs. 49, 66). Known only from eastern subarctic Russia.
.....abscondita Lackschewitz

Inner gonostylus with distal beak cylindrical, tip rounded, several pigmented sensilla along edge (figs. 32, 33); female with oblique narrow membranous region across tip of hypogynial valvulae (fig. 51), a single subapical dorsal hair (125 X mag.). Widespread nearctic, with one record from northern Europe
.....dimidiata (Loew)

- 23.(20) Thoracic stripes yellowish brown, median stripe traversed longitudinally with pruinose light blue line; hairs on thorax pale orange-yellow, very short; male with dorsal process on tergite 9 large, rectangular, lateral process short, truncate (fig. 11). Known only from Point

Barrow, Alaskabyersi, new species

Thoracic stripes uniformly dark grayish brown,
hairs whitish, long; male with dorsal process
on tergite 9 narrow, almost conical, no lateral
process (fig. 12). Female unknown. Known only
from southern Ontariocryptica, new species

DESCRIPTIONS OF SPECIES

Prionocera abscondita Lackschewitz

Prionocera abscondita Lackschewitz; 1933: 136-137, figs.

3a,b,c, (male terminalia, antennae); Mannheims, 1951:

63-64, fig. 31 (male terminalia).

DIAGNOSIS

Inner gonostylus with distal beak tapering abruptly to a sharp point, no pigmented sensilla, base broadly rounded; hypogynial valves with lateral lobe angular; not conspicuously hairy.

DESCRIPTION (figs. 10, 29, 49, 66)

ADULT. General appearance: gray to brownish gray with short yellowish white (92) hairs on thorax and abdomen, not conspicuously hairy; male wing length 11.5-12mm; female wing length 15mm.

MALE. Head: bluish gray to yellowish gray (191, 93), vertex dark grayish brown (62) with short moderate brown (58) hairs; gena pale yellow (89) with scattered very short pale yellow hairs; rostrum dark brown (59), light yellowish brown (76) ventrodistally, proclinate dark brown (59) hairs dorsally, projecting beyond moderate (.087-.10mm) nasus; pseudo-ocellus dark brown (59).

Antenna: moderate brown (58) with dark orange-yellow (72) on pedicel and base of 1st flagellomere; 1st flagellomere long, more than 1.5 length of 2nd; proximal flagellomeres slightly distended ventrodistally, distal width less than twice basal width; 11th flagellomere very narrow, half length of 10th.

Thorax: prescutal pit not forming apex of broad, yellowish triangular area; dorsal stripes brownish gray (64), glabrous; median stripe narrowly bisected by black line anteriorly, fading to light grayish yellowish brown (79) posteriorly, stripes bordered by light grayish yellowish brown (79) region; postsutural area, scutellum and mediotergite bluish gray to dark gray (191, 192), with fine pale hairs, not conspicuously hairy; pleuron bluish gray (191) with light grayish olive (109) patches; anepisternum, katepisternum and dorsal half of anepimeron with hairs, ventral half of anepimeron and katepimeron bare; anatergite grayish olive (110) katatergite broadly pale yellow (89) on crest, grayish olive (110) at base.

Wings: membrane tinged with light yellowish brown (76), veins moderate yellowish brown (77), stigma, costal and subcostal cells slightly darker than wing membrane; obliterative streak perpendicular to wing axis, weakly indicated, beginning as a pale area in R1 just proximal to stigma.

Legs: no teeth on tarsal claws.

Abdomen: olive gray (113) with dark brown (59) dorsal longitudinal stripe; segments broadly edged laterally, narrowly edged distally in pale yellow (89); hairs very short.

Genitalia: 9th tergite with hairs on posterior half only; dorsal process broad, rectangular, space between subequal to process width; lateral process short, angular; apical process curved medially, sharply pointed; medial lobe present; rectal sclerite small, irregular. Gonocoxites not separated ventrally by protruding membrane; gonocoxal fragment narrow. Outer gonostylus broad, most of medial surface concave, with clearly defined raised edge. Inner gonostylus with broad base, dorsal crest abruptly narrowing to a sharply pointed distal beak, without pigmented sensilla, proximal beak short, broad, angled towards outer gonostylus. Aedeagus almost straight distally, small dorsal tooth near tip, more proximal lateral tooth; aedeagal guide with dorsal plates flattened.

FEMALE. Similar to male, except as follows: flagellomeres not distended, 1st flagellomere long, more than 1.5 times 2nd, lightened to moderate orange-yellow (71) basally; 9th, 10th and 11th shortest, subequal.

Genitalia: sternite 8 with angular lateral lobe on

distal edge; hypogynial valves short, one-third length of sternite 8, separated from sternite by Y-shaped membranous region with broad stem bisecting sternite; valvulae with a subdorsal longitudinal narrow membranous region, tip broadly rounded, no subapical hairs; (tergite 9 distorted); sternite 9 with medial projection slightly longer than broad; 10th tergite with lateral edge almost straight bearing short, fine hairs; cerci moderately broad, straight, tip slightly downcurved.

TYPE SPECIMENS

Holotype (examined), male, Finland, Trifona, (now USSR: Petsamo Distr., Pechenga), No. 436, Hellén, spec. type No. 4820 (ZMH); paratypes (not seen), 1 male, 1 female, Siberia: Polar Ural Karische Tundra, Gouv. Tobolsk, 19 vii 1909, F. Saizew (Leningrad).

The type has the right wing nicked in the middle of the costal region, tarsal claws are missing on the left front leg, and the entire right hind leg is missing. The genitalia had been preserved in balsam on a plastic microslide pinned beneath the specimen. It was necessary to dissolve the balsam and remove the genitalia to glycerine in order to verify that the differences noted were real, and not because of the orientation of the specimen.

DISCUSSION

Prionocera abscondita is very similar to dimidiata, differing most conspicuously in the sharply pointed inner gonostylus of the male and the more angular lobe on sternite 8 of the female. It has a grayish brown presutural area which contrasts somewhat with the bluish gray postsutural region, whereas dimidiata is usually bluish gray in both regions. However, some older specimens of dimidiata also tend to have a brownish caste to the presutural area but this may be caused by fading. (Specimens which have been warmed in NaOH lose their dark bluish gray colour and become moderate brown or lighter.)

Mannheims (1951) noted that abscondita is smaller than the European specimens of dimidiata (= absentiva).

Prionocera dimidiata however, is quite variable in size in North America, as noted in the discussion of that species, and encompasses the size range of abscondita. No body lengths were given for abscondita because the genitalia had been removed before measurements were taken.

GEOGRAPHIC DISTRIBUTION (Map 2)

This species is only known from the tundra, above or at tree line, in contrast to its sister species dimidiata which, in the Palearctic region, has only been collected

near Berlin (Lackschewitz, 1933; Mannheims, 1951).

FLIGHT RECORDS: 5-19 July

SPECIMENS EXAMINED (2 males, 1 female)

PALEARCTIC: USSR: Murmansk Region, Petsamo Distr.,
Pechenga, 69°28'N 31°04'E, male (holotype), Hellén (ZMH);
Ponoj (=Ponoy), 67°02'N 41°03'E, 1 female, R. Frey (ZMH);
Dudinka, 69°27'N 86°13'E, 1 male, Wuorentaus (MAKB).

Prionocera byersi, NEW SPECIES

DIAGNOSIS

Thoracic dorsum predominantly strong yellow-brown
(74), longitudinally bisected by broad light bluish gray
(190), hairs pale, short; nasus present; male
flagellomeres not strongly distended; inner gonostylus
with distal beak long, broad and flattened.

DESCRIPTION (based on 2 males, 2 females), (figs. 11, 30,
50, 67)

ADULT. General appearance: head, thorax and abdomen

predominantly strong yellow-brown (74), not conspicuously hairy, hairs short, pale orange-yellow to strong yellowish brown (73,74); male wing length 12.2-12.8mm (holotype 12.2mm); female wing length 12.9-13.8mm (allotype 12.9mm).

MALE. Head: light yellowish brown (76), vertex with a light bluish gray (190) patch medially bisected by a dusky darker line, hairs light orange-yellow to deep yellowish brown (70,75) laterally, finer hairs on raised prominence between pseudo-ocelli; gena grayish yellow (90) to dusky black towards rostrum, with scattered hairs; rostrum dark grayish brown (62), lightened to dark orange-yellow (72) distolaterally near palpus, hairs short appressed, dark brown (59) dorsally; extending fringe-like beyond nasus, paler and longer laterally; nasus distinct but small (.075-.1mm); pseudo-ocellus moderate orange-yellow (71), flat to almost conical.

Antenna: dark brown (59), base of 1st flagellomere lightened to dark orange-yellow (72); 1st flagellomere not conspicuously elongated, subcylindrical, slightly distended ventrodistally, distal width less than 1.5 times medial width; succeeding flagellomeres progressively less distended, 7-10th cylindrical; 11th half or more length of 10th.

Thorax: prescutal pit forming apex of strong yellowish brown (74) triangular region; dorsal stripes

deep yellowish brown (75), median stripe broadly bisected by line of pruinose light bluish gray (190) extending to and broadening across scutellum; stripes bordered by moderately yellowish brown (77); scutellum and mediotergite bluish gray (191) with fine pale hairs; pleuron not conspicuously hairy, light bluish gray (190), short pale hairs on all segments except for small katepimeron; anatergite bluish gray to yellow gray (191,93); katatergite broadly light orange-yellow (70) on crest, dark gray (206) posteriorly.

Wings tinged with light yellowish brown (76), veins moderate orange-yellow (71); costal and subcostal cells and stigma slightly more infumed than membrane; oblitative streak perpendicular to wing axis, weakly indicated, beginning as a paler area proximal to stigma.

Legs: tarsal claws with or without teeth.

Abdomen: grayish yellowish brown to moderate yellow-brown (80,70), dorsal longitudinal stripe barely visible; tergites not contrastingly edged distally and laterally; hairs pale, very short, appressed.

Genitalia: 9th tergite with a patch of hairs between dorsal processes, another anterior to each dorsal process; dorsal process subrectangular, longer than broad, separated by slightly more than width of process; lateral process short, truncate, apical process

subrectangular with short sharp medially directed tooth; no medial lobe; rectal sclerite small, irregular. Gonocoxites not separated ventrally by protruding membrane; dorsal fragment of gonocoxite broadly triangular, narrowed tips almost meeting medially. Outer gonostylus with broad base, narrowed and angulated dorsally, medial surface concave except for poorly defined raised edge. Inner gonostylus with longitudinal groove on medial surface of base; no dorsal crest; distal beak long, broad and flattened; no pigmented sensilla; broad proximal beak. Aedeagus with straight tip, subapical narrow ring more prominent dorsally. Aedeagal guide with dorsal plate narrow, flat, rectangular, only slightly narrowed proximally.

FEMALE. Similar to the male except as follows: 1st flagellomere and base of 2nd with short dark hairs; 1st less than 1.5 times length of 2nd; flagellomeres 2-8 very slightly distended distally; last 3 flagellomeres subequal, slightly longer than 8th.

Genitalia: sternite 8 with broadly rounded to slightly lobed dorsolateral edge; hypogynial valves approximately .4 times the length of 8th sternite, separated from sternite by broadly U-shaped membranous area; valvulae with narrow, triangular, more sclerotized area ventrally, tips broad with very short subapical hair dorsally (125 X magnification) on paratype, none visible on allotype; 9th

tergite not rounded posterolaterally; 9th sternite with median projection relatively short and broad; 10th tergite broadly rounded laterally with short, fine hairs; cerci broad, slightly upturned preapically.

TYPE SPECIMENS

Holotype, male, Alaska, Point Barrow, 17 vii 1953, P.D. Hurd (USNM). Allotype, female, same data. Paratypes, 1 male, 1 female, same data as holotype (CNC, USNM). The holotype lacks most of the left fore leg and both middle legs. The allotype has the right wing nicked before the stigmal area. The genitalia of all four specimens have been removed, softened, placed in glycerine in microvials, and pinned beneath their respective specimens.

VARIATION

On the prescutum of the holotype the strong yellowish brown triangular region does not extend posteriorly as far as the prescutal pit. The holotype does not have a tooth on the tarsal claws, however, there is a distinct small tooth on the claws of the male paratype.

DISCUSSION

This species is probably closely related to P. recta and P. elliptica. The processes on the 9th tergite are very similar to the former but the inner gonostylus with its broad distal beak is more similar to the latter. Unlike either of these species it has a well-developed nasus, does not have strongly distended flagellomeres and is not conspicuously hairy.

GEOGRAPHIC DISTRIBUTION AND FLIGHT RECORD (Map 3)

Prionocera byersi is only known from Point Barrow, Alaska, where it was collected with P. recta on a single day, 17 July 1953.

ETYMOLOGY

This species is named in honour of George W. Byers, in recognition of his outstanding contributions to both crane fly and scorpion fly research.

Prionocera cryptica, NEW SPECIES

DIAGNOSIS

Inner gonostylus much broader than long, with very long dorsal crest abruptly narrowing to a short cylindrical distal beak; tip of rostrum and nasus with dark brown (59) stripe dorsally bearing dark brown hairs.

DESCRIPTION (based on holotype), (figs. 12, 31)

ADULT. General appearance: head, thorax and abdomen dark yellow-brown to light yellowish brown (78,76), hairs long, white to light orange-yellow (263,70); male wing length 10.5mm.

MALE. Head: light yellowish brown (76), vertex dark grayish brown (62), not bisected by a darker line, hairs light orange-yellow (70), long; gena yellowish gray (93) with short scattered hairs; rostrum dark grayish brown (62) with long pale hairs, dark brown (59) stripe dorsally bearing darker hairs and extending beyond moderate nasus (.075mm); pseudo-ocellus brownish black (65).

Antenna: dark grayish brown (62), base of 1st flagellomere somewhat lightened; 1st flagellomere not conspicuously elongated, less than 1.5 times 2nd, moderately distended, distal width 1.5 times medial

width, succeeding flagellomeres progressively smaller and less distended, (10th & 11th lost).

Thorax: prescutal pit forming apex of dark orange-yellow (72) triangular region; dorsal stripes glabrous dark grayish brown (62), median stripe bisected by, and stripes bordered by, light grayish yellowish brown (79) region; stripes indistinct on postsutural area, postsutural area and scutellum yellow-gray (93), divided by dark brown line; mediotergite light gray, scutellum and mediotergite with long pale hairs; pleuron light bluish gray (190), hairs long, on all segments except for small katapimerom; anatergite light gray (264), katatergite pale yellow (89) dorsally, medium gray (265) ventrally.

Wings: tinged with light yellowish brown (76), veins moderate yellowish brown (77); stigma, costal and subcostal cells scarcely darker than membrane; oblitative streak not strongly contrasting, beginning as weakening in R1 just proximal to stigma and continuing somewhat diagonally before wing tip.

Legs: tarsal claws without teeth.

Abdomen: dark orange-yellow (72), broadly bisected dorsally by dark yellow-brown (78) longitudinal stripe; tergites broadly edged laterally with yellowish white (92), no lighter edge distally; hairs yellowish white,

erect.

Genitalia: 9th tergite with long hairs anterior to dorsal process, dorsal process almost conical (holotype slightly distorted, right side of 9th tergite and right dorsal process slightly longer than left); without lateral process; apical processes short, broad, set close together with straight posterior edge produced in a medially directed, short, sharp tooth; without medial lobe; rectal sclerite long and thin. Gonocoxites not separated ventrally by protruding membrane; dorsal fragment of gonocoxite broadly triangular, heavily sclerotized at short proximal tip. Outer gonostylus with ventral edge broadly curved, dorsal edge straight, ventral surface concave except for narrowly raised, poorly defined edge, broader at tip. Inner gonostylus with broadly rounded base, elongate crest narrowing abruptly to short cylindrical beak, without pigmented sensilla on beak, without proximal beak; lateral surface with broad elliptical hairless area bearing row of short setae (row not as distinct on right inner gonostylus). Aedeagus slightly broadened and bent dorsally at tip, without subapical teeth; aedeagal guide narrow, collar-like distally, abruptly broader subapically, forming rounded "shoulders", dorsal plate broad, flat, narrower towards sperm pump.

FEMALE. unknown.

TYPE SPECIMEN

Holotype, male, Ontario, Bells Corners, 45°17'N, 75°48'W, 9 May 1971, Fanja Brodo (No. 18348 CNC). The type is glued to a point, all legs are broken off, both antennae have been broken but several flagellomeres and tarsomeres and claws from two legs are glued to the label.

DISCUSSION

This species may be closely related to P. ellipticum, sharing with that species the oval patch traversed by short stout setae on the lateral surface of the inner gonostylus. It is differentiated from ellipticum by having a nasus, flagellomeres which are only slightly distended, and by differences in the shape of the inner gonostylus.

GEOGRAPHIC DISTRIBUTION AND FLIGHT RECORD (Map 3)

The single specimen of P. cryptica represents one of the southernmost and the earliest seasonal record for this genus. The holotype was found among a collection of Tipula (Angarotipula) illustris Doane made in a Typha and Carex marsh under an electrical power line just west of the city limits of Ottawa. I had hoped to find more specimens, and even to rear this species during the

course of this study. However despite diligent searching every spring for 13 years, no more specimens were found.

ETYMOLOGY

The surprising find of a single specimen of Prionocera in the Ottawa region, which I could not identify, led to my doing a revision of this genus. The name cryptica refers to its cryptic and elusive occurrence.

Prionocera dimidiata (Loew)

Stygeropsis dimidiata Loew, 1866: 129; 1872: 3; Alexander, 1920:199 (includes suberricornis and 1 male intergrade dimidiata x suberricornis).

Prionocera dimidiata; Kertész, 1902: 278; Alexander, 1927b: 215 (includes P. turcica); 1942:219, fig. 25c (antenna); Alexander, 1965: 19.

Tipula rostellata Doane, 1901: 100.

Prionocera rostellata; Alexander, 1965: 19. (new synonymy)

Prionocera rostellata churchilliana Alexander, 1942b: 206; 1965: 19. (new synonymy)

Prionocera rostellata prominens Alexander, 1942b: 206-207; 1965: 19. (new synonymy)

Pachyrhina oslari Dietz, 1918: 112-113.

Prionocera oslari; Alexander, 1965: 19. (new synonymy)

Prionocera absentiva Mannheims, 1951:64, fig.32 (male terminalia). (new synonymy)

DIAGNOSIS

Male 9th tergite with dorsal process broadly rectangular, lateral process narrowly angular, median lobe present; 1st flagellomere in both sexes long, 1.5 length of 2nd.

DESCRIPTION (figs. 3, 4, 13, 32, 33, 51, 68)

ADULT. General appearance: bluish gray to brownish gray dorsally, bluish gray laterally, thorax and abdomen not conspicuously hairy, with yellowish white to dark brown (92,59) hairs; male body length 7.8-11.2mm, wing length 10.2-14.2mm; female body length 11.7-16.5mm, wing length 12.3-16.5mm.

MALE. Head: vertex dark olive brown to olive black (96,114), usually divided by capillary black line, hairs short, brownish black to light grayish brown (65,60); gena bluish white (189) with scattered short light hairs; rostrum bluish gray to dark brown (191,59), light yellowish brown (176) distolaterally with proclinate brownish black (65) hairs projecting beyond moderate (.075-.15mm) nasus; pseudo-ocellus dark brown to brownish

black (59,65).

Antenna: flagellum brownish black (65); 1st flagellomere long, more than 1.5 times 2nd; proximal flagellomeres slightly produced ventrodistally, distal width less than twice basal width; 11th flagellomere relatively long, more than half length of 10th.

Thorax: prescutal pit brown (191,55), not forming apex of yellowish triangular region; dorsal stripes glabrous, grayish blue to dark bluish gray (186,192), or with brownish gray (64) caste on stripes, median stripe bisected by light bluish gray (190) line and stripes bordered by light bluish gray (190) region bearing yellowish white to dark brown (92,59) hairs; postsutural area, scutellum and mediotergite grayish blue to brownish gray (186,64), with fine hairs, not conspicuously hairy; pleuron generally bluish gray (191), hairs yellowish white (92); ventral half of anepimeron and small katepimeron bare; anatergite light olive gray to olive gray (112,113); katatergite grayish yellow to pale yellow (90,89) dorsally, olive gray (113) ventrally.

Wings: infumed with light yellowish brown to grayish yellowish brown (76,80), veins dark orange-yellow to brownish black (72,65), darker distally; costal and subcostal cells and stigma dark orange-yellow to moderate yellowish brown (72,77) not contrasting with membrane; weakly developed oblitative streak extending from

distal tip of Rs through 1st section of M1+2 and 2nd section of M3.

Legs: tarsal claws with or without teeth, varying within individuals.

Abdomen: bluish gray (191) with dark brown (59) dorsal longitudinal stripe, hairs short, tergites usually edged distally and laterally in pale yellow to grayish yellow (89,90).

Genitalia: tergite 9 with hairs only on posterior one-third to one-half of tergite; dorsal process broadly rectangular, slightly convex in dorsal aspect, space between subequal to width of process; lateral process narrow, angular; apical process curved medially, sharply pointed; medial lobe broad, pale, shallowly emarginate distally; rectal sclerite small, irregular. Gonocoxites without protruding membrane ventrally; gonocoxal fragment narrow, gradually attenuated towards sperm pump. Outer gonostylus broad, most of medial surface concave with clearly defined narrow raised edge. Inner gonostylus with base broad, longer than distal beak; dorsal crest gradually narrowing to slender glabrous distal beak; beak rounded at tip, with several (6-12) small, pigmented, sensilla laterally near base; proximal beak small, tooth-like. Aedeagus with small dorsal tooth near tip and occasionally with small tooth on each side, proximal to dorsal tooth. Aedeagal guide with dorsal plate

flattened, relatively broad.

FEMALE. Similar to male, except as follows:
flagellomeres not produced; 1st flagellomere elongate,
twice length of 2nd, lightened to strong brown (55)
basally; 10th and 11th subequal or 11th slightly longer.

Genitalia: sternite 8 with rounded to somewhat pointed dorsolateral lobe; hypogynial valves short, 1/3 length of sternite 8, separated from sternite 8 by broad Y-shaped membranous region, extending narrowly and posteriorly between bases of hypogynial valves, and narrowly anteriorly on 8th sternite; valvulae with narrow oblique membranous area near tip, tip almost truncate, bearing single short subapical hair (visible with 125 X magnification); tergite 9 not rounded posterolaterally; sternite 9 with median projection twice as long as wide; 10th tergite with lateral edge almost straight, bearing short fine hairs; cerci moderately broad, straight or slightly upturned near mid-length.

TYPE SPECIMENS

The lectotype, here designated, is a female which best matches the original description and measurements. It bears the following labels: H.B.T/ 134/ dimidiata m/ TYPE 10319/ Stygeropis dimidiata. "H.B.T." refers to Hudson Bay Territory, which at the time of this collection

referred to a huge tract of land encompassing the Bay. The number "134" was probably given to the specimen by Osten Sacken who sent material to Loew for identification. The hand-written "dimidiata m", is in Loew's handwriting (Osten Sacken, 1903); and "m" is an abbreviation for "mihi" or "mine", indicating that this is indeed a specimen upon which the description was based.

The lectotype is damaged. The head, prothorax and all legs are missing and the tips of both wings are torn. The distinguishing characteristics of this specimen upon which the name dimidiata is based are the rounded dorsolateral lobes on the 8th sternite, the fine yellowish white hairs on the thorax, the lack of hairs on the ventral half of the anepimeron, the bluish gray thoracic stripes, the wing suffused with brown and with stigma and costa only slightly darker and a weak oblitative streak.

Loew (1866) described this species from a female collected by Kennicott in Hudson's Bay Territory. A range of measurements (in lines) is given, implying that more than one specimen was seen. There were nine specimens in the type collection at the Museum of Comparative Zoology, Cambridge, Massachusetts, comprising four different species. For convenience of discussion, I have numbered these specimens from 1-9 (see Appendix B).

The lectotype is No. 1.

Of the two other female specimens that I judge to be conspecific with dimidiata and that are part of this type collection, No. 2 has only the "O. Sacken" label and its measurements are too small to be a syntype; No. 3 bears the label "H.B.T." and its measurements are too large. Specimens 4 and 5 are a mating pair of P. turcica labelled "H.B.T./ O. Sacken", therefore quite obviously not the specimens seen by Loew. Specimens No. 6, 7, 8 (2 females and 1 male respectively) are P. subsericornis. No. 6 bears the labels: H.B.T./ 134/ "Stygeropsis sp dup" (sic). The number "134" and the old handwritten generic determination label suggest that this was the companion specimen to the specimen sent to Loew for determination. Its measurements are larger than those given for the type. No. 7 bears the label: "Type No. 10319", and measures slightly smaller than the type description. No. 8 is a male of P. subsericornis. No. 9 is a female of Tipula sp. labelled: Loew Coll./ Type 10319, and is also somewhat small.

Considering that the so-called type material included four different species, it is not surprising that Alexander also confused the identity of this taxon. In his earlier identifications, Alexander labelled this species dimidiata (Loew), occasionally confusing it with P. pubescens (Loew). However since 1942, both he and J.

Speed Rogers (determinations in UMMZ) called this species P. rostellata and reserved the name dimidiata for the species here recognized as turcica.

SYNONYMY

Tipula rostellata was described from 2 males and 2 females collected by Morrison in Colorado (no further data) and designated type no. 151, and deposited in the Washington Agricultural College & S. of S. (Doane, 1901). No specimens bearing that number were located. However, I have seen a female labelled "Colo./ Collection C.V. Riley/ Tipula rostellata Doane Paratype/ A.L. Melander Collection 1961" (USNM), and a male and a female labelled "Colo./ Collection C.V. Riley" (WSU). In the Alexander collection (USNM), slide No. 596, is a male labelled "ex Riley Coll., P. rostellata as Tipula, metatype". There are an additional two females labelled "Colo." (USNM). This Colorado label is identical to the label found on the other specimens mentioned above. I judge all these specimens to be conspecific with dimidiata.

Because I consider rostellata a synonym of dimidiata, I likewise do not recognize its subspecies. They were described from single male specimens collected at Churchill, Manitoba. The genitalia are slide-mounted. Prionocera r. churchilliana is clearly conspecific with dimidiata. The distinguishing feature of P. r.

prominens, a "ridge or carina" on the 9th tergite, is the ventral edge of this tergite seen through the semitransparent lateral processes.

Pachyrhina oslari Dietz (1918), male holotype, South Park, Colo., No. 6436, 6/20/16, E.J. Oslar (ANSP); female allotype, South Park, Colorado, No. 6436, published as 6/18/16, (label data: June 16, 1916), E.J. Oslar (ANSP); paratypes: 1 male South Park, Colo., No. 6436, E.J. Oslar (ANSP); 1 female, John Smith Ranger Sta., Cochetopa Nat. Forest, July 2, 1913, Colo., A.K. Fisher (ANSP); I have examined these specimens and judge them to be conspecific with dimidiata. An additional female paratype, Cochetopa, Colo., A.K. Fisher, is listed as being deposited in the collection of the United States Biological Survey (Dietz, 1918).

Prionocera absente Mannheims (1951), male holotype, Jungfernheide (Berlin), 1889, Peters (listed as being in the Berlin Museum, but not there, pers. comm., Schumann, 1983). Paratypes: 7 males, without locality labels, probably topotypic (Mannheims, 1951) and labelled by Mannheims "Jungfernheide, 1889, Peters." Five of these paratypes are in the Berlin Museum and three in Bonn. One on the specimens in Bonn must be the holotype.

I have examined two male paratypes, nos. 52 and 53 (MAKB). The genitalia indicate that absentiva is a synonym of dimidiata. The German specimens have

yellowish~~white~~ (92) hairs on the abdomen and pleuron, but the hairs on the head and thoracic dorsum are strong brown (55) and the abdominal tergites lack lighter lateral and distal borders. These variations are found in some North American populations.

VARIATION

Specimens from New Mexico and Colorado tend to be larger than those from Labrador and Northern Quebec. The darkest specimens are from New Mexico and are predominantly dark bluish gray (192) with abdominal segments having only a very narrow, or in some cases no yellow (90) distal and lateral border as opposed to the broader and lighter borders found in most other specimens. Also the wings are duskier and hairs on the gonostylus are brownish black (65) rather than the more common deep brown (56) or light orange yellow (70). Populations from the Yukon, Northwest Territories and Alaska tend to be lighter with a brownish caste on the thoracic stripes.

DISCUSSION

This species is very closely related to the much rarer palearctic P. abscondita Laakschewitz which has a more restricted northern distribution. See discussion under

that species.

GEOGRAPHIC DISTRIBUTION (Map 4)

Prionocera dimidiata is the most common and widespread species in this genus. It is found in the subarctic, boreal, and subalpine regions of North America ranging from Alaska to Labrador, south of the Arctic Circle except at the Mackenzie Delta, and ranging south along the Rocky Mountains as far as the Southern Sangre de Cristo Mountains in New Mexico.

In the Palearctic Region this species has only been collected from Jungfernheide (Berlin) (Mannheims, 1951).

FLIGHT RECORDS: 29 May-15 August.

This species is locally abundant from late June to the first three weeks of July. It was collected exceptionally early in Yellowknife (29 May) and late (15 August) from Echo Lake, Colorado.

SPECIMENS EXAMINED (536 males, 208 females)

NEARCTIC: CANADA: ALBERTA: Banff Nat'l Pk., ♂, 9 vii 55, G.E. Shewell (CNC); 6♂, 7 vii 55, J.R. McGillis (CNC); Bilby, 53°42'N 114°06'W, 2♂, 8-25 vi 24, O. Bryant (as dimidiata & sordida, pinned, BMNH;

slides No. 1441 & 3589, wing & antenna, USNM); Devon (SW Edmonton), 14♂, 4♀, 12 vi 80, D.M. Wood (CNC); Kananaskis Forest, Seebe Forest Exp. Sta., ♀, 26 vi 68, H.J. Teskey (CNC), wing, legs, antenna (slide No. 68-32-6, as sordida, Alexander Coll., USNM); Sunwapta Pass, Banff-Jasper Hwy., 6600', ♂, ♀, 5-9 vii 55, R. Coyles (CNC). BRITISH COLUMBIA: Atlin, 2200', 3♂, ♀, 14-23 vi 55, B.A. Gibbard; Riske Creek, Ballpark Pond, 52°N 122°5'W, ♂, 10 v 78, R.J. Cannings (SUBC). LABRADOR: Hebron, 2♂, 10-16 vii 54, J.F. McAlpine (CNC); Hopedale, ♀, 24 vii 22 (CNC); Greenbush, 37 km NW Schefferville, P.Q., 4♂, ♀, 7-11 vii 81, F. Brodo (CNC); Nutak, ♂, 23 vii 54, E.E. Sterns (CNC); ♂, ♀, 23 vii 54, J.F. McAlpine (CNC). MANITOBA: Churchill, ♂, ♀, 8-30 vii 52, J.G. Chillcott (CNC); ♀, 24 vi 48, ♂, 29 vi 49, L.A. Miller (CNC); ♂, ♀, 9-17 vii 49, J.B. Wallis (CNC); ♀, 25 vi 48, G.E. Shewell (CNC); 2♂, 1-3 vii 47, T.N. Freeman (CNC); 7♂, 2♀, 24 vi-10 vii 77, F. Brodo (CNC); 52♂, 6♀, 28 vi-14 vii 78, F. Brodo (CNC); same data ♂, ♀, (V.I.L.); ♂, ♀, 29 vi-6 vii 49, (CNC); Eastern Creek, nr. Churchill, ♂, ♀, 25 vi 52, J.G. Chillcott (CNC); Farnworth Lake., nr. Churchill, 10♂, 2♀, 12-26 vi 52, J.G. Chillcott (CNC); Fort Churchill, ♂, H.E. McClure (Holotype No. 17 CH 41, P. rostellata churchilliana, slide no. 7493, Alexander Coll. USNM); ♂, H.E. McClure (Holotype no. 3 CH 38, P. rostellata prominens Alexander, slide no. 7494, Alexander Coll. USNM); 30♂, 10♀, 3-28 vi 52, J.G. Chillcott (CNC);

2

MicroD

2♂, 23 vi-8 vii 52, C.D. Bird (CNC); 1♂, ♀, 20 vi 48; Fred Ide (SEM); 10♂, 2♀, 20 vi 48, Fred Ide (UMMZ); Mile 505, Hudson Bay Railroad, 2♂, 13 vi 52, J.G. Chillcott (CNC); 25 mi E Churchill, 13♂, 6♀, 29 vi-4 vii 77, F. Brodo (CNC); Warkworth Creek, nr. Churchill, 31♂, 4♀, J.G. Chillcott (CNC). NORTHWEST TERRITORIES: Keewatin Distr., Eskimo Point, 2♀, 1 vii 50, G.R. Roberts (CNC); Padley (?Padley, 62°N 96°50'W), ♀, 22 vii 50, R.A. Hennigar; Mackenzie Distr., Aklavik, 25♂, 3♀, 16-21 vi 53, C.D. Bird (CNC); ♀, 30 vi 56, R.E. Leech (CNC); Ford Lake, 63°11'N 107°19'W, ♂, 4 vii 66, G.E. Shewell (CNC); Salmita Mines, 64°05'N 111°15'W, ♂, 1 vii 53, J.G. Chillcott (CNC); Yellowknife, Kam Lake, ♂, 2♀, 20 vi 66, G.E. Shewell (CNC); Yellowknife, 7♂, 3-6 vi 53, J.G. Chillcott (CNC). ONTARIO: Cape Henrietta Maria, Hudson Bay, 11♂, 14♀, 3-6 vii 48 (UMMZ); 3♂, 9-22 vii 48, W.Y.W. (UMMZ); ♂, ♀, 3-6 vii 48 (SEM); Fort Albany, James Bay, 4♂, ♀, 10-25 vi 42, F.A. Urquart (UMMZ); Fort Severn, 55°59'N 87°38'W, ♀, 2 vii 40, C.E. Hope (ROM). QUEBEC: Bradore Bay, 51°28'N 57°14'W, 4♂, 2♀, 9-16 vii 30, W.J. Brown (CNC); Fort Chimo, 3♂, 22-28 vi 48, H.N. Smith (CNC); 3♀, 23 vi-5 vii 48, R.H. MacLeod (CNC); ♂, 6 vii 54, J.G. McAlpine (CNC); Rupert House, 51°30'N 78°24'W, ♀, 18 vi 49, E.J. LeRoux (CNC); Schefferville, ♂, 7 vii 81, F. Brodo (CNC); 37 km NW Schefferville, Annabel Bog, 67♂, ♀, 13-20 vii 81, F. Brodo (CNC); same data, ♂ (C.D.). YUKON: Kluane 61°02'N 138°23'W, pond SE of Slims

R. bridge, ♀, 16 vi 79 (ex pupa, emerged 18 vi 79), S.G. Cannings (SUBC); Otter Lake, 130°25'N 62°31'W, 4000', ♂, 16 vii 60, J.E.H. Martin (CNC); Swim Lakes, 133°N 62°13'W, 3200', 7♂, 2♀, 13-18 vi 60, J.E.H. Martin (CNC); Whitehorse, ♂, 20 vi 49, D.L. Watson (CNC); ♂, ♀, 1, 14 vii 49, L.C. Curtis (CNC); ♀, 30 vi 48, W.R. Mason (CNC); ♀, 27 vii 49, J.K. Horie (SUBC). "Hudson's Bay Territory", 2♀, Kennicott, one designated as lectotype of dimidiata (MCZ).

U.S.A.: ALASKA: Isabel Pass, Mile 206, Richardson Hwy., 2900', ♂, ♀, 13-17 vii 62, P.J. Skitsko (CNC); 2♂, 13 vii 62 R.E. Leech (CNC); Katmai, 4♂, 2♀, 10 vi 19, Jas. S. Hine (OSU); McKinley Nat'l Pk., No. 16, Horseshoe Lake, ♀, 26 vi 57, G.W. Byers (SEM); Igiak Bay, 61°43'N 166°08'W, 3♀, 23 vi-4 vii 52, P.S. Humphrey (UMMZ); Savonoski, Naknek Lake, ♂, vi 19, J.S. Hine (OSU); Unalakleet, ♀, 17 vi 61, R. Madge (CNC). COLORADO: Boulder Co., Corona Pass, 10,600', 2♂, 6 vii 61, J.G. Chillcott (CNC); Lefthand Bog, 40°04'N 105°34'W, 10,700', 18♂, 7♀, 11-17 vii 79, F. Brodo (CNC); same data, ♂ (SEM), ♂ (C.D.); North Boulder Creek, 40°02'N 105°34'W, 10,600', 19♂, 2♀, 5 vii 79, F. Brodo (CNC); Rainbow Lakes, 40°01'N 105°35'W, 10,100', 44♂, 14♀, 2-10 vii 79, F. Brodo (CNC); same data, ♂, 2♀ (SEM), 2♂ (V.I.L.); Mt. Research Station, Nederland, 20♂, 6♀, 25-29 vi 79, F. Brodo (CNC); Chaffee Co., Buena Vista, 7,800', ♀, 22-23 vi 61, J.R. Stainer (CNC); Clear Creek Co., Summit Lake,

Mt. Evans, 12,800', 6♂, 24 vii 61, J.R. Chillcott (CNC);
 ♂, 24 vii 61, W.R.M. Mason (CNC); Echo Lake, Mt. Evans,
 9,600', ♀, 26 vii 61, B.H. Poole (CNC); 10,600', 2♂,
 13-25 vii 61, C.H. Mann (CNC); 12,000', ♂, 15 viii 49,
 R.R. Dreisbach & R.R. Schwab (UMMZ); Floral Park,
 Berthoud Pass, No. 2, 2♂, 30 vi 74, George W. Byers
 (SEM); No. 3, 9♂, ♀, 9 vii 74, G.W. Byers & C.W. Young
 (SEM); Eagle Co., Tennessee Pass, 10,240', 2♂, ♀, 9-17
 vii 30, J.M. Aldrich (USNM); Grand Co., Middle Fork of
 Williams Fork River, 11,425', ♂, 19 vii 29, C.F. Clagg
 (as rostellata, slide no. 596, Alexander Coll. USNM)
 Saguache Co., Cochetopa, Nat. Forest, John Smith Ranger
 Station, ♀, 2 vii 13 (ANSP); Summit Co., Loveland Pass,
 12,000', ♂, 7 viii 61, J.R. Chillcott (CNC); Jackson Co.,
 10 mi N junction routes 14 & 40, ♀, 2 vii 62, R. & K.
 Dreisbach (MSU); Rocky Mountain Nat'l Pk., Cache La
 Poudre Lake, Continental Divide, ♂, 14 vii 40, Marian E.
 Smith (as oslari, slide no. 7090, Alexander Coll. USNM)
 Marshall Pass, 10,856', ♂, 28 vii 08, J.M. Aldrich
 (USNM); Brainerd Lake, 9,500', ♀, 27 vi 62, R. & K.
 Dreisbach (MSU); State Creek Ranger Station, ♂, 10 vii
 29, C.F. Clagg (as rostellata, slide no. 596, Alexander
 Coll. USNM) South Park, 2♂, ♀, 20 vi 16, E.J. Oslar (♂
 holotype, ♀ allotype, & ♂ paratype of oslari ANS);
 Colorado, no further data, ♀, 2 vii 62, Riley coll., A.L.
 Melander, paratype rostellata, (USNM); 2♀, (USNM); ♂,
 H.K. Morrison, ex Riley coll., (slide no. 596, "metatype"

rostellata, Alexander Coll. USNM); ♂, ♀, C.V. Riley coll. (WSU). MINNESOTA: Rochester, 3♂, 19 vi 22, H.G. Dyar (USNM). NEW MEXICO: Sante Fe Co., no. 5, Aspen Basin, 15 mi NE Sante Fe, 10,300', 21♂, 2♀, 16 vi 79, G.W. Byers (SEM); no. 9, Aspen Basin, 17 mi NE Sante Fe, 10,500', 2♂, ♀, 22 vi 81, G.W. Byers & S. Teale (SEM). WYOMING: Albany Co., Nash Fork campground, 11 km NW Centennial, 41°21'09"N 106°14'21"W, 3105m, ♂, 9 vii 81, Stephen Teale (SEM); Carbon Co., Silver Lake, 30 km Centennial, 2♂, ♀, 10-11 vii 81, S. Teale (SEM); Silver Lake campground, Medicine Bow Mts., 10450', ♂, 18 vii 81, G.W. Byers #2; Sheridan Co., no. 2, 4♂, ♀, 13 vii 50, G.W. Byers (UMMZ); Yellowstone Nat'l Pk., 3♀, 29 vii 30, J.S. Alexander (UMMZ); Yellowstone Canyon, ♂, 4 vii 22, H.G. Dyar (USNM); Yellowstone Lake, 5♂, 12-27 vii 22, H.G. Dyar (USNM).

PALEARCTIC: GERMANY (BRD): Berlin, Jungfernheide, 2♂, 1889, Peters (paratypes, absentiva Mannheims) (MAKB).

Prionocera electa Alexander

Prionocera electa Alexander, 1927b: 188-189; 1942: 219; 1965: 19.

DIAGNOSIS

Shiny black to shiny dark brown on vertex and anteriorly on thoracic stripes; white oblitative streak contrasting with dark stigma and dusky wing tip; nasus present.

DESCRIPTION (figs. 14, 34, 52, 69)

ADULT. General appearance: stripes dark, contrasting with lighter background; hairs short, sparse, pale yellow to yellowish white (89,92); male body length 10.0-11.4mm, wing length 12.1-13.9mm; female body length 12.1-13.6mm, wing length 11.8-15.1mm.

MALE. Head vertex shiny dark brown to black (59,267), hairs short, dark brown to light yellow-brown (78,76); gena pubescent yellowish white (92) to brilliant orange-yellow (67) adjacent to antennal bases and base of rostrum, sometimes bearing scattered short dark yellowish brown (78) hairs; rostrum shiny, strong yellowish brown to black (74,267) dorsally, contrastingly lightened to dark orange-yellow (72) laterally, hairs deep brown (56), proclinate, projecting beyond moderate (.1-.15mm) rather broad nasus; rostrum bare posterodorsally; pseudo-ocellus dark brown to black (59,267).

Antenna: flagellum brownish black (65), scape, pedicel and basal half of 1st flagellomere usually dark orange-yellow (72); 1st flagellomere not conspicuously

elongated; 1st-4th strongly distended distoventrally, distal width twice width of base, succeeding flagellomeres progressively less distended, 10th cylindrical, longer than 9th; 11th minute, less than 1/4 length of 10th.

Thorax: prescutal pit not forming apex of yellowish triangular region; dorsal stripes glabrous, deep brown to black (59,267), shiny anteriorly, becoming pruinose posteriorly, median stripe bisected by narrow line, stripes bordered with light grayish yellowish brown (79) region; postsutural area and scutellum concolourous with dorsal stripes; scutellum covered with short hairs; mediotergite pruinose with fine hairs; pleuron light bluish gray to bluish gray (190,191), anepisternum sparsely hairy medially, katepisternum hairy on dorsal half, anepimeron sparsely hairy on dorsal half just below wing, and anteriorly on lower section; katepimeron bare; anatergite light blue gray to grayish brown (190,61); katatergite light orange-yellow (70) dorsally, dusky, grayish brown (61) ventrally.

Wing: membrane yellowish gray (93); veins dark yellowish brown to brownish black (78,65), most veins seamed with moderate yellowish brown (77); costal and subcostal cells and wing base moderate to strong yellow (87,84); stigma contrasting with membrane, distal half of stigma and bases of cells R1+2+3 and R4 dark yellowish

brown (78), proximal half of stigma pale yellow (89); strongly developed oblitative streak extending from proximal half of stigma to posterior wing margin, perpendicular to costa.

Legs: tarsal claws toothed.

Abdomen: grayish yellowish brown to deep yellowish brown (80,75) divided longitudinally by dark yellowish brown (78) stripe; segments edged distally and laterally in pale orange-yellow (73); hairs dark brown (59) dorsally, yellowish white (92) ventrally.

Genitalia: 9th tergite more convex than in other species; hairs extending over two thirds of tergite, dorsal process deflected dorsally about 45° from longitudinal axis of body, with lateral edge of process longer than medial; dorsal processes separated at base by width of process; lateral process very small, triangular; apical process broad at base, tip sharply narrowed and curved medially; medial lobe not free, its distal edge contiguous with bases of apical processes; rectal sclerites joined by narrow dorsal extension. Gonocoxites with protruding membrane ventrally; gonocoxal fragment long narrow, attenuated towards sperm pump. Outer gonostylus with broad basal half concave on medial surface, distal half narrower. Inner gonostylus with no distinct dorsal crest; distal beak lacking peg-like pigmented sensilla, but armed with several basiconic

sensilla; proximal beak small, pointed and lying just proximal to small distinctive curved notch. Aedeagus with tip bent ventrally, small subapical dorsal tooth, no lateral tooth. Aedeagal guide extending distally as a sclerotized collar, dorsal sclerite long, narrow and flat.

FEMALE. Similar to male, except as follows: flagellomeres not distended, 1st flagellomere more extensively pale than in male, 1.3 or less length of 2nd; last 3 flagellomeres cylindrical, narrower, penultimate fractionally shorter than the other two..

Genitalia: sternite 8 with dorsolateral edge sloping, no lateral lobe; hypogynial valves half length of sternite 8, separated from sternite by narrow curved membranous region, extending broadly and anteriorly on sternite; valvulae broadly sclerotized ventrally, tip narrowly rounded, with single short subapical hair (visible with 125 X magnification); 9th tergite rounded posterolaterally; 9th sternite with medial projection longer than broad; 10th tergite straight-edged with only fine hairs distolaterally; cerci moderately broad, almost straight to tip.

TYPE SPECIMENS

Holotype (examined), male, Hopedale, Labrador, 1 vii

1923, W.W. Perrett (no collector on label) (CNC), left wing and right antenna (slide No. 3590, Alexander Coll. USNM).

This specimen lacks the left fore leg and both hind legs. The 2nd and 3rd flagellomeres of the left antenna are partially fused and distorted.

DISCUSSION.

A presumed mating pair of P. electa and P. turcica from the Churchill area, J. G. Chillcott collector, are in the CNC collection. Both these specimens have a strongly pigmented stigmal region preceded by a contrasting oblitative streak giving them a remarkably similar appearance. Whether this actually represents a genuine case of interspecific mating is open to question. Another mismatched pair also presumed to be a mating pair was described as the holotype and allotype of P. fulvicauda Alexander, (see discussion under P. oregonica). These are the only recorded incidences of possible attempted interspecific matings in either Prionocera or other crane flies (Byers, 1961, 1983).

GEOGRAPHIC DISTRIBUTION (Map 5)

Prionocera electa appears to be a rare species; it has been found sporadically from Labrador to Churchill,

Manitoba.

Larvae from Schefferville were found in saturated moss, and judging from gut contents and fecal pellets, were eating both moss and the rich algal flora clinging to the moss.

FLIGHT RECORDS: 16 June-27 July.

SPECIMENS EXAMINED (6 males, 12 females)

NEARCTIC: CANADA: LABRADOR: Cartwright, ♂, ♀, 2, 20 vii 55, E.E. Sterns (CNC). QUEBEC: Fort Chimo, ♀, 6 vii 48, R.H. MacLeod, (CNC); Great Whale River, 2♀, (1 ex pupa), 30 vi, 7 vii 49, J.R. Vockeroth (CNC); Schefferville, 5♀, 4-18 vii 81, F. Brodo, (CNC); same data, ♀ (SEM); 2♂, 16 vi, 22 vii 48, E.G. Munroe, (CNC); MANITOBA: Churchill, ♂, ♀, 1 vii 49; ♂, 26 vi 52, Chillcott, (CNC); Herchmer, ♂, ♀, 5, 6 vii 48, J.B. Wallis (CNC).

Prionocera elliptica, NEW SPECIES

DIAGNOSIS

Inner gonostylus with distal beak broad and flat; female with rounded to angular lobe on 8th sternite; oblitative streak and stigma not strongly contrasting with each other or with membrane.

DESCRIPTION (based on 50 males, 30 females), (figs. 6, 15, 35, 53, 70)

ADULT. General appearance: medium gray to dark gray (265, 266); hairs long, conspicuous, pale yellow (89); male body length 9.6-11.2mm (holotype 11.1mm), wing length 10.6-12.8mm (holotype 12.3mm); female body length 11.0-14.1mm (allotype 13.8mm), wing length 13.1-15.2mm (allotype 13.8mm).

MALE. Head: vertex grayish brown to medium brown (61, 58), usually divided by capillary black line, hairs long, erect, pale yellow (89); gena light gray to dark gray (264, 266) with scattered short hairs; rostrum dark brown to medium gray (59, 265), covered with long, fine, proclinate, pale yellow hairs (89), hairs projecting beyond rostrum; nasus minute bump or absent; pseudo-ocellus light orange-yellow to strong yellow-brown (70, 74) (moderate orange-yellow in the holotype).

Antenna: flagellum medium brown to dark brown (58,59), usually lightened to strong brown basally, 1st flagellomere slightly longer than 2nd, with cylindrical base and strong distoventral dilation; proximal flagellomeres strongly distended distoventrally, distal width twice basal width; 10th and 11th cylindrical, 11th half width and slightly more than half length of 10th.

Thorax: prescutal pit not forming apex of broad, yellowish triangular region; dorsal stripes glabrous, medium gray to dark gray (265,266), median stripe longitudinally bisected by black line, fading posteriorly; stripes bordered by light gray (264) region; postsutural area, scutellum and mediotergite medium gray to dark gray (265,266) bearing long hairs; pleuron light gray to medium gray (264, 265) with long hairs on all pleural segments except on small katapimeron; anatergite medium gray (265); katatergite medium to dark gray (265,266), broadly edged with light orange-yellow (70).

Wings: membrane tinged with light yellowish brown (76); subcostal cell slightly darker; veins and stigma strong yellowish brown (74); obliterative streak extending obliquely near wing tip, only slightly paler than stigma.

Legs: tarsal claws usually without teeth.

Abdomen: light olive gray to grayish yellowish brown

(112,80) with dark yellowish brown (78) dorsal longitudinal stripe; tergites narrowly edged with pale yellow to light orange-yellow (89,70) distally, more broadly edged laterally; hairs erect, pale yellow (89) ventrally and on 1st tergite, recumbent, shorter and darker medially on succeeding tergites.

Genitalia: tergite 9 with hairs confined to posterior half of tergite; dorsal process squarish, haired, space between subequal to process width; lateral process small, truncated; apical process relatively narrow, abruptly and sharply curved medially; median lobe broadly fused to base of apical process; rectal sclerite thin rectangular. Gonocoxites relatively small, without protruding membrane medially; gonocoxal fragment broadly triangular with expanded triangular tip at sperm pump. Outer gonostylus with broad squarish base, attenuated distally, medial surface convex except for narrow raised edge. Inner gonostylus with broad base separated by long oval notch from broad flat distal beak; base with slanted ventral edge and with oval less sclerotized area on lateral surface bearing one or more rows of short, stout hairs; distal beak without pigmented sensilla; two proximal beaks, a squarish medial beak abundantly haired and a conical lateral beak, somewhat distal to medial beak, with finer shorter hairs. Aedeagus with tip curved dorsally, bearing subapical lateral tooth. Aedeagal guide with collar-like membranous tip, dorsal plate broad

and flat.

FEMALE. Similar to male except as follows: entire antenna lighter than in male, especially basally; 1st flagellomere slightly constricted subapically, less than 1.5 times length of 2nd; basal flagellomeres slightly distended distoventrally giving a serrate appearance; last 3 flagellomeres smaller, cylindrical and subequal.

Genitalia: sternite 8 with distinct rounded to angular dorsolateral lobe; hypogynial valves moderately long, 0.40-.45 length of 8th sternite, narrow ventral edge of valvulae more heavily sclerotized, small squarish membranous region at base, distal edge straight, bearing slender, subapical hair; tergite 9 somewhat rounded posterolaterally; sternite 9 with median projection long and narrow; 10th tergite with prominently rounded posterolateral edge; cerci relatively long, tips narrower, and usually slightly downcurved.

TYPE SPECIMENS

Holotype, male, and female allotype, pinned together, Coral Harbour, Southampton Island, N.W.T., 2 vii 1948, G.E. Shewell (No. 18349 CNC). Paratypes, 46 males, 29 females as follows:

CANADA: NORTHWEST TERRITORIES: Franklin Distr., Boothia Peninsula, Lady Melville Lake, 69°25'N 93°15'W,

♂, 3 vii 51, J.G. Chillcott (CNC); Repulse Bay; ♂, 4 vii 50, J.E.H. Martin (CNC); Spence Bay, 3 ♂, ♀, 5-8 vii 51, J.G. Chillcott (CNC); Victoria I., Cambridge Bay, ♀, 26 vii 50, G.K. Sweatman (CNC); 71°17'N 114°W, ♂, 25-30 vi 75, G. & M. Wood (CNC). Keewatin Distr., Baker Lake, ♀, 14 vii 47, T.N. Freeman (CNC); Chesterfield, 2 ♂, ♀, 12-26 vii 50, J.G. Chillcott (CNC); same data, ♂ (V.I.L.); ♂, 29 vii 50, J.R. Vockeroth (V.I.L.); Southampton I., Coral Harbour, 6 ♂, 9 ♀, 30 vi-13 vii 48, G.E. Shewell (CNC); same data ♂, ♀ (USNM); same data 4 ♂, 25-27 vi 52, P.R. Ehrlich (CNC), ♂ (V.I.L.). Mackenzie Distr.; Nr. Beechey L., 65°14'N 106°50'W, ♂, 11 vii 66, G.E. Shewell (CNC); Coppermine, 2 ♀, 14 vii 51, S.D. Hicks (CNC); Ford L., 63°11'N 107°19'W, ♀, 2 vii 66, G.E. Shewell (CNC); Muskox L., 64°45'N 108°10'W, 5 ♂, ♀, 11-25 vii 53, J.G. Chillcott (CNC). QUEBEC: Payne Bay (=Bellin), ♀, 21 vii 58, E.E. MacDougal (CNC). YUKON: North Fork Crossing, Mi 42, Peel Plt. Rd., ♂, 25 vi 62, R.E. Leech (CNC).

U.S.A. ALASKA: Igiak Bay, 61°43'N 166°08'W, 7 ♂, 5 ♀, 2-19 vii 52, P.S. Humphrey (UMMZ); Isabel Pass Mi 206 Richardson Hwy., 2900', 63°20'N 145°30'W, 2 ♂, 13 vii 62, R.E. Leech (CNC); Mt. McKinley Nat'l Pk., 2600', ♂, 26 vi 57, G.W. Byers & party (SEM); No. 16, Horseshoe Lake, 1550', 4 ♂, 2 ♀, 26 vi 57, G.W. Byers; Nome, 2 ♂, 2 ♀, 2-9 vii 51, D.P. Whillans (CNC); Prince of Wales, 55°40'N 133°W, ♀, 21 vii 26, D. Jenness (CNC); Prudhoe Bay, 70°18'N 148°21'W, ♂, 2 vii 71, Cat. No. 239, Stephen F.

McLean (SEM); Umiat, 69°25'N 152°20'W, ♂, 13 vii 47, C.
Schultz (UMMZ); Unalakleet, 63°52'N 160°50'W, 2♂, 16 vi
61, B.S. Heming (CNC); shore of Arctic, 69°40'N 141°W, ♀,
27-30 vii 12, J.M. Jessup (USNM).

VARIATION

This species is predominantly gray with a more or less brownish caste dorsally on the head. There is no nasus, but in some specimens (including the holotype), there is a very small knob-like protrusion on the rostrum bearing a fringe of hairs. On the holotype, the 8th and 9th flagellomeres of the right antenna are distorted. Most tarsal claws in the male of this species are without teeth. However, occasionally a minute tooth occurs near the base of a claw. The presence of such a tooth is not correlated with the leg position (i.e. front, middle or hind leg) nor with the claw position (medial or lateral). No tooth was observed on the holotype.

DISCUSSION

Prionocera elliptica is a Nearctic species very similar to the Palearctic P. ringdahli Tjeder. They are separated by several relatively minor characteristics. Prionocera elliptica is generally a grayer fly. In ringdahli the dorsal stripes usually have a brownish

caste. The stigma stands out less in elliptica because the wing membrane is more infumed, the stigma is not much darker, and the oblitative streak is not very whitened. Prionocera ringdahli is almost clear-winged with a distinctly darker stigma and a more whitened oblitative streak. The pseudo-ocellus in elliptica is light orange-yellow to strong brown whereas it is grayish brown to black in ringdahli. The flagellomeres in the male of elliptica are strongly distended and the 11th is at least half the length of the 10th. However, in ringdahli only the first two flagellomeres are distinctly distended, the rest are increasingly more cylindrical, and the 11th is tiny, less than one-half the length of the 10th.

There are also minor differences in the male genitalia. In P. elliptica the dorsal processes on the 9th tergite are broader and somewhat closer together, the lateral processes, although also very small, are usually more evident than in ringdahli, and the apical processes have a broader, more triangular base than in ringdahli. On the lateral surface of the inner gonostylus in P. elliptica there is an elliptical weakly sclerotized area bearing one or more rows of short stout hairs. In ringdahli the base of the inner gonostylus is broader, not as tapered distally and the hairs on the lateral surface are scattered, not on a well-defined area.

The females of elliptica are distinguished by

distinctly rounded to somewhat pointed lobe on the dorsolateral edge of the 8th sternite, whereas in ringdahli this edge is rounded, not lobed. The 10th tergite in elliptica is broadly rounded and somewhat protruding posterolaterally, whereas in ringdahli the lateral edges are more nearly straight.

The sister species P. elliptica and P. ringdahli can be distinguished from the very similar holarctic species P. recta by the more distinctly developed nasus in the latter and the longer dorsal and lateral processes on the 9th tergite. The inner gonostylus in P. recta has a narrower, more cylindrical distal beak. The cerci in female P. recta are broader and more nearly straight rather than downcurved. In North America P. recta tends to have brown rather than pale yellowish white hairs on the head and thorax.

GEOGRAPHIC DISTRIBUTION (Map 6)

Prionocera elliptica has been collected from the west coast of Alaska to northern Quebec. It may extend across the Bering Sea but I have not seen any specimens of this species or of the sister species P. ringdahli from eastern Siberia. It is one of the more northerly distributed species, not extending south much beyond tree line.

FLIGHT RECORDS: 16 June-26 July.

Prionocera elliptica is apparently less common than either P. ominosa or P. recta, possibly because of a somewhat shorter flight period.

ETYMOLOGY

The name elliptica refers to the elliptical patch on the lateral surface of the inner gonostylus, the peculiarities of which are diagnostic for this species.

Prionocera naskapi, NEW SPECIES

DIAGNOSIS

Conspicuously hairy on head and thorax; dorsal process on 9th tergite broader than long, no lateral process, apical process narrow, hook-like, close to edge of tergite.

DESCRIPTION (based on 10 males), (figs. 16, 37)

ADULT. General appearance: head and thorax grayish brown to dark grayish brown (61,62), pleuron light bluish gray (190), hairs on head and thorax conspicuous, dark grayish yellowish brown to light yellowish brown (81,76),

varying with specimen; male body length 8.9-9.5mm, wing length 10.7-11.4mm (holotype 10.7mm).

MALE. Head: vertex dark grayish brown (62), bisected with longitudinal black line, hairs relatively long; gena light bluish gray (190), with short dark hairs; rostrum entirely dark grayish brown (62) with proclinate short stiff hairs on distal two thirds, hairs appressed distally, projecting beyond bump-like rostral tip, no nasus; pseudo-ocellus brownish black (65).

Antenna: flagellum dark grayish brown to brownish black (62,65) 1st flagellomere with subcylindrical base and distended distoventrally, succeeding flagellomeres distended, almost triangular in lateral outline, distal flagellomeres progressively smaller and less distended, 10th cylindrical, slightly longer than 9th; 11th small, approximately one-half length and width of 10th.

Thorax: prescutal pit not forming apex of broad, yellowish triangular region; dorsal stripes dark grayish brown (62), median stripe divided by narrow light yellowish brown (76) line, becoming duskier anteriorly, stripes bordered by light yellowish brown (76) region bearing long dense hairs, hairs dark grayish yellowish brown to light yellowish brown (81,76); postsutural area, scutellum and mediotergite dark grayish brown to light yellowish brown (62,76), with long hairs; pleuron light bluish gray (190), with long hairs on all but small

katepimeron; anatergite light olive gray (112);
katatergite dark yellow to light yellow (88,86) dorsally,
dark gray (266) ventrally.

Wings: tinged with light brownish gray to light
grayish yellowish brown (63,79); veins deep yellowish
brown (75); costal and subcostal cells light yellowish
brown (76); stigma with distal half slightly darker than
proximal half; oblitative streak weakly developed,
extending from proximal, paler half of stigma and
continuing almost perpendicular to costa near wing tip.

Legs: no teeth on tarsal claws.

Abdomen: light gray (264) with dark brown (59) dorsal
longitudinal stripe, tergites narrowly edged distally,
more broadly edged laterally in pale yellow (89);
tergites and sternites with dark yellowish brown to light
yellowish brown (78,76), appressed hairs dorsally, more
erect laterally, ventrally and dorsally on 1st tergite.

Genitalia: tergite 9 with hairs only on distal half,
dorsal process broader than long, slightly tapered
distally, separated by width of process or less; no
lateral process; medial lobe not distinct, fused to bases
of apical processes; apical process narrow, hook-like,
close to lateral edge of tergite; rectal sclerite long
and thin. Gonocoxites not separated ventrally by
protruding membrane; dorsal fragment of gonocoxite

narrow. Outer gonostylus triangular, dorsal edge broadly curved, ventral edge almost straight, medial surface concave except for raised tip. Inner gonostylus with distinct dorsal crest, narrow cylindrical distal beak, no pigmented sensilla on beak, broadly emarginate between distal beak and small rounded proximal beak, lateral (inner) surface of base with elliptical patch densely covered with short hairs, patch not or hardly raised. Aedeagus with tip straight, slightly elongated dorsal edge, no subapical teeth. Aedeagal guide with narrow, collar-like extension posterior to broadly rounded, almost lobe-like "shoulder"; dorsal plate flat, narrowing some distance before sperm pump.

FEMALE: unknown.

TYPE SPECIMENS

Holotype, male, Québec, Schefferville, 18 July, 1981, F. Brodo (No. 18350 CNC). Paratypes, 9 males as follows: QUÉBEC: Schefferville, 2♂, 18 vii 81, F. Brodo (CNC); same data, ♂ (SEM); Iron Arm bog, E of Schefferville, ♂, 18 vii 81, F. Brodo (CNC). LABRADOR: Goose Bay, 4♂, 11-12 vi 48, W.W. Judd (CNC); same data, ♂ (USNM).

The genitalia of the holotype and of four paratypes (one from Schefferville, three from Goose Bay) have been

removed, softened, placed in glycerine in microvials and pinned beneath their respective specimens. The holotype lacks the right fore leg.

VARIATION

The specimens from the Schefferville area, including the holotype, are the darkest. The hairs on the holotype are dark grayish yellowish brown (81); the wing membrane is tinged with light brownish gray (63); the 11th flagellomere is slightly longer than one-half the length of the 10th. The specimens from Goose Bay have a more golden brown aspect.

This is one the smaller species of Prionocera, and although the genitalia are somewhat telescoped within the abdomen, the dorsal processes are usually visible and serve to identify this species.

DISCUSSION

Prionocera naskapi is the sister species of P. pubescens. It differs from the latter in the following details: the dorsal process on the 9th tergite is distinctly broader in naskapi and extends closer to the centre of the tergite and obscures more of the apical process beneath. The nasus is absent except for a minute prominence at the tip of the rostrum. The flagellomeres

are less produced and the 11th tends to be slightly longer than in pubescens. The gonocoxal fragment is narrower and bent medially. The inner gonostylus has a distinctly developed crest and an elliptical rather than a rounded densely haired patch which is not raised as in pubescens. Prionocera naskapi and P. pubescens may be most closely related to P. tjederi, differing most conspicuously from the latter by their hairyness and the shape of the inner gonostylus.

GEOGRAPHIC DISTRIBUTION (Map 6)

In contrast to its sister species P. pubescens, P. naskapi has a very narrow range. It is known only from northeastern Canada: Goose Bay, Labrador and the Schefferville area, Quèbec.

FLIGHT RECORDS: 11-18 July.

The very short flight period and the narrow geographic range may be exaggerated by the paucity of collections made in northeastern Canada.

ETYMOLOGY

Following a practice established by C.P. Alexander, I am pleased to name this species after the Naskapi Indians

who extensively roamed and still live in Labrador and Northern Quebec where this species was collected.

Prionocera ominosa (Alexander)

published as Stygeropsis parrii; Alexander, 1919: 8-9, figs. 7, 12, 23, 24, 26 (wing, antenna, outer & inner gonostyli, tergite 9, based on a mixed collection of P. ominosa and P. recta, fig. 26, 9th tergite, applies to P. ominosa); 1965: 19.

Stygeropsis ominosa Alexander, 1920a: 199; 1965: 19.

DIAGNOSIS

Very hairy, dorsal stripes brown; no nasus; male with dorsal process of 9th tergite broad, short, extending almost to lateral edge of tergite, space between $2/3$ or less width of process; apical process separated by broad membranous V-shaped area; female with dorsolateral edges of 8th sternite sloping; hypogynial valvulae short, $1/3$ length of 8th sternite; cerci short, broad, almost straight to slightly upturned at tip.

DESCRIPTION (figs. 17, 38, 54, 71)

ADULT. General appearance: brown with long pale

yellow to pale orange-yellow (89,73) hairs on head and thorax; male body length 9.9-11.2mm, wing length 11.5-14.7mm; female body length 11.8-16.8mm, wing length 11.5-16.3mm.

MALE. Head: vertex light brownish gray (63) with longitudinal black (267) line; hairs on vertex longer than hairs on middle of pronotum; gena light gray to yellow-gray (264,93), with 3 or 4 very short hairs; rostrum grayish brown (61), not contrastingly lightened laterally, with fine proclinate hairs not projecting beyond tip; no nasus; pseudo-ocellus strong yellowish brown to dark yellowish brown (74,78).

Antenna: flagellomeres moderate brown to brownish black (58,65); 1st flagellomere not noticeably elongated, less than 1.5 length of 2nd, strongly distended distoventrally; flagellomeres 2-9 progressively less distended, triangular in lateral profile, distal width of proximal flagellomeres twice that of base; 10th cylindrical; 11th half length of 10th.

Thorax: broad triangular light yellowish brown to moderate orange-yellow (76,71) region anterior to prescutal pit; dorsal stripes glabrous, grayish yellowish brown to dark grayish yellowish brown (80,81), median stripe narrowly bisected by brownish black to light grayish yellowish brown (65,79) line, darker anteriorly, stripes bordered by a light grayish yellowish brown (79)

region bearing long hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes and borders or slightly grayer. Pleuron light bluish gray to medium gray (190, 265), all segments, except small katepimeron bearing long hairs; anatergite medium gray (265), katatergite light orange-yellow (70) dorsally, olive gray (113) ventrally.

Wings: membrane tinged with light grayish yellowish brown (79), costal and subcostal cells slightly darker, stigma light yellowish brown (76), weakly contrasting with membrane; veins strong yellowish brown (74);

- obliterative streak not strongly whitehed, very narrow at proximal end of stigma, perpendicular to wing axis.

Legs: tarsal claws without teeth. . .

Abdomen: light grayish brown to grayish yellowish brown (60, 80), dorsal longitudinal stripe dark grayish yellowish brown (81); tergites broadly edged laterally, narrowly edged posteriorly in pale orange-yellow to dark orange-yellow (73, 72); hairs slightly longer and more prominent ventrally.

Genitalia: tergite 9 with hairs on posterior half only; dorsal process short, broad, rectangular, extending to, or almost to lateral edge of tergite, space between less than width of process; no lateral process; apical process broad with sharply pointed apices, separated at

base by membranous V-shaped area; no medial lobe; rectal sclerite small, irregular, lightly sclerotized.

Gonocoxites without protruding membrane; gonocoxal fragment broadly triangular. Outer gonostylus broadly oval, medial surface convex, except for narrow, raised, edge, more prominent on dorsal side. Inner gonostylus with dorsal crest sloping towards short distal beak; distal beak with ridge on medial surface, slightly swollen at tip, no pigmented sensilla; proximal beak small, broadly triangular. Aedeagus narrowly S-shaped (viewed laterally), distal one-third bent ventrally, no subapical teeth. Aedeagal guide with membranous, collar-like, posterior extension; dorsal plate broad and flat.

FEMALE. Similar to male, except as follows: 1st flagellomere often lightened to dark orange yellow (72) basally, subcylindrical, less than 1.5 length of 2nd; proximal flagellomeres somewhat distended giving a serrate appearance; 11th smallest, cylindrical.

Genitalia: sternite 8 with rounded to sloping dorsolateral edge, no distinct lobe; sternite longitudinally divided ventrally by narrow membranous area, broadening anteriorly and flanked by heavily pigmented area; hypogynial valvulae short, broadly triangular, one-third length of 8th sternite (0.27-0.30, n=10), bearing 1 to 3 subapical hairs (visible with 125 X magnification) tergite 9 rounded posterolaterally;

sternite 9 with median projection short, about as long as broad; tergite 10 broadly rounded distolaterally, bearing fine hairs; cerci relatively broad, short, straight or gently upturned at tip.

TYPE SPECIMENS

Holotype (examined), female, Savonoski, Naknek Lake, Alaska, July 1919, James S. Hine, collector (OSU). This specimen has been severely damaged by dermestids. All that remains are part of the thorax, wings and right antenna (adhering to the thorax), and the right middle leg. A slide (no. 1463) of the left antenna and a leg of the holotype is in the C.P. Alexander slide collection, United States National Museum, Washington, D.C.

This is a very badly damaged specimen. The following characteristics, however, distinguish the species: the distinctly serrate antennae which includes the 10th flagellomere; the 11th flagellomere is the smallest; the strongly infumed wings not strongly contrasting with the stigma and oblitative streak; the general golden brown colour of the thorax, and the large triangular orange-yellow area anterior to the prescutal pit. The brief original description mentions a somewhat darker specimen than the one described above. This discrepancy could be caused by fading.

SYNONYMY

This species has been referred to as P. parrii. For a discussion concerning the legitimacy of that name see P. parrii, Doubtful and Excluded Species (p. 215).

DISCUSSION

Prionocera ominosa is the sister species of the palearctic P. serricornis. The differences, though minor, are consistent. In North America P. ominosa has been confused with P. recta and P. elliptica. All three of these species have long, relatively dense hairs on the head and thorax and strongly distended flagellomeres. Prionocera recta differs from P. ominosa in being bluish gray rather than brownish, having a small nasus, and in the male, a small but distinctly developed lateral process and a long subrectangular dorsal process. Males of P. elliptica are distinguished by having a much narrower dorsal process on the 9th tergite and longer hypogynial valvulae in the female.

GEOGRAPHIC DISTRIBUTION (Map 7)

This is a nearctic species found in northern boreal and subarctic subregions. It is a conspicuous component of the very early spring fauna in the wetlands of the north. Prionocera ominosa occurs together with, and has

been confused with, P. recta and the rarer P. elliptica. I have seen 372 pinned specimens collected from the west coast of Alaska to northeastern Quebec, and from as far north as the southern arctic islands, plus a single female from Kamchatka which I judge to belong to this species rather than to the very closely related sister species, serricornis.

FLIGHT RECORD: 28 May-31 July.

This is one of the earliest Prionocera. Most of the specimens were collected in June to mid July, which may explain why I failed to find this species in either Churchill, Manitoba or Schefferville, Quebec. I was probably in the field too late for this species. Prionocera ominosa is often locally very abundant, as evidenced by the large number of specimens collected from several localities in the Northwest Territories.

SPECIMENS EXAMINED (251 males, 106 females)

NEARCTIC. CANADA: MANITOBA: Churchill, 2♂, 16, 30 vi 47, T.N. Freeman (CNC); ♂, ♀ (with attached terminalia), 15 vi 47, (USNM); Fort Churchill, 3♂, 3-10 vi 52, J.G. Chillcott (CNC); 4♂, 3♀, 16-20 vi 48, Fred Ide (UMMZ); Farnworth L, nr. Churchill, ♂, ♀, 12 vi 52, J.G. Chillcott (CNC); Mile 505 Hudson Bay Railroad, ♂, 13

vi 52, J.G. Chillcott (CNC); Pikwitonei, ♀, 31 v 49, J.B. Wallis (CNC). NORTHWEST TERRITORIES: Franklin Distr.: Bathurst Inlet, 4♂, 13-28 vi 51, C.D. Bird & W.I. Campbell (CNC); Repulse Bay, ♂, 27 vi 50, P.F. Bruggemann (CNC); 3♂, 29 vi 50, J.E.H. Martin (CNC); Spence Bay, 11♂, 3♀, 30 vi 51, J.G. Chillcott (CNC); ♂, 27 vi 51, A.E.R. Dawne (CNC); Thelon River, ♀, 22 vii 49 (CNC); Victoria Island, Cambridge Bay, 25♂, 5♀, 7-11 vii 50, E.H.N. Smith (CNC); 14♂, 3♀, 11-18 vii 50, G.K. Sweatman (CNC); Holman, ♂, ♀, 17-18 vi 52, D.P. Gray (CNC); Victoria Island, 71°17'N 114°W, ♂, ♀, 1-5 vii 75, G. & M. Wood (CNC). Keewatin Distr.: Baker Lake, 2♂, 12-14 vii 47, T.N. Freeman (CNC); Chesterfield, 83♂, 28♀, 30 vi 24 vii 50, J.G. Chillcott (CNC); 27♂, 15♀, 7-31 vii 50, J.R. Vockeroth (CNC); Eskimo Point, 3♂, 11♀, 30 vi-5 vii 50, G.R. Roberts (CNC); 8♂, 6♀, 29 vi-3 vii 50, G.G. Dilabio (CNC); Mackenzie Distr.: Aklavik, 17♂, ♀, 16-20 vi 53, C.D. Bird (CNC); 3♂, ♀, 16-29 vi 56, R.E. Leech (CNC); 10♂, 3♀, 21 vi 53, J.S. Waterhouse (CNC); Coppermine, 5♂, ♀, 18-23 vi 51, S.D. Hicks (CNC); Fort Smith, ♀, 30 v 50, W.G. Helps (CNC); Muskox Lake, 64°45'N 108°10'W, 3♂, 9-11 vii 53, J.G. Chillcott (CNC); Salmita Mines, 64°05'N 115°15'W, 16♂, ♀, 16-30 vi 53, J.G. Chillcott (CNC); Yellowknife, ♂, ♀, 1-3 vi 53, J.G. Chillcott (CNC). QUEBEC: Payne Bay, ♂, 25 vi 58, E.E. MacDougall (CNC). YUKON: Hershel Island, ♂, 8 vii, 53, C.D. Bird (CNC); Ogilvie Mts., North Fork Pass, 4100', 2♀, 20 vi 62, P.J.

Skitso (CNC); 4300', 5♂, ♀, 19 vi 62, R.E. Leech (CNC); Rampart House, 67°25'N 140°59'W, ♂, 5 vi 51, C.C. Loon (CNC); Swim Lakes, 133°N 62°13'W, 3200', ♂, 8 vi 60, J.E.H. Martin (CNC); ♂, 18 vi 60, E.W. Rockburne (CNC); Whitehorse, ♀, 28 v 49, L.C. Curtis (CNC); Km. 141 Dempster Hwy., ♂, 24-28 vi 82, G. & M. Wood (CNC).

U.S.A. ALASKA: Alcan Hwy., Summit Pass, Richardson Hwy., ♂, 7 vii 49, E.K. Miller (UMMZ); Cape Thompson, Pond 6 Ogotoruk Cr., 55°15'N 159°31'W, ♀, 15 vi 60, W.C. Hanson (SEM); ♂, 21 vi 60, J.J. Davis (WSU); Igiak Bay (=Kokechik Bay), 8♂, 5♀ (including a mating pair), 23 vi-4 vii 52, P.S. Humphrey (UMMZ); W of Kongengevick, Camden Bay, ♂ (no. 438), ♀ (no. 434), 4 vii 14, Canadian Arctic Expedition, Frits Johansen (CNC); ♂, same data, 2 slides, No. 488 (USNM); Mt. McKinley Nat'l Pk., 2600', ♂, 25 vi 57, G.W. Byers & party (SEM); Prudhoe Bay, 70°18'N 148°21'W, ♂, 10 vii 71, S. MacLean (SEM); Savonoski, Naknek Lake, ♀, vii 19, J.S. Hine (ominosa holotype, pinned OSU, & slide No. 1463, Alexander Coll: USNM) Umiat, ♀, 13 vi 47, K.L. Knight (UMMZ); 5♂, 5♀, 13-23 vi 47, L.A. Jachowski (UMMZ); 5♂, (2♂ on slides, Nos. 4960, 4962), C. Schultz (UMMZ).

PALEARCTIC. U.S.S.R. Kamchatka, ♀, 18-19 vi 17, Y. Wuorentaus (ZMH).

Prionocera oregonica Alexander

Prionocera oregonica Alexander, 1943a: 13-14; 1965: 19.

Prionocera primoveris Alexander, 1943b: 723-725, figs. 1 & 2 (wing, tergite 9); 1945: 399; 1965: 19. (new synonymy)

Prionocera uinticola Alexander, 1948a: 15-17, fig. 2 (tergite 9); 1965: 19. (new synonymy)

Prionocera fulvicauda Alexander, 1948b: 121-123; 1965: 19. (new synonymy)

DIAGNOSIS

Male with dorsal plate of aedeagal guide expanded subapically and laterally into a narrow dorsomedially curved flange; female with broad dorsolateral lobe on 8th sternite; hypogynial valves half length of 8th sternite, square tipped, with a single subapical hair (visible with 60 X magnification); cerci very slightly downturned at tip.

DESCRIPTION (figs. 5, 18, 39, 55, 72)

ADULT. General appearance: grayish brown dorsally, bluish gray laterally, with fine short yellowish white (92) hairs, not conspicuously hairy; male body length 8.3-9.9mm, wing length 10.4-12.8mm; female body length 10.1mm, wing length 11.2-11.8mm.

MALE. Head: vertex dark yellowish brown to dark olive brown (78,96), usually divided by capillary black line, hairs very short posteriorly, becoming longer anteriorly; gena bluish gray to grayish yellow (191,90) with scattered hairs; rostrum brownish black (65), in some specimens lightened to deep yellowish brown (75) laterally, brownish black (65) proclinate hairs on rostrum and projecting beyond moderate (.075-.175mm) nasus; pseudo-ocellus brownish black (65):

Antenna: flagellum dark grayish brown to brownish black (62,65), flagellomeres only slightly distended ventrally, 11th relatively long, half length or more of 10th.

Thorax: prescutal pit not forming apex of broad yellowish triangular region; dorsal stripes glabrous, dark grayish brown (62), median stripe bisected by narrow line and bordered by light grayish yellowish brown to grayish yellowish brown (79,80) region, with fine hairs; postsutural area, scutellum and mediotergite dark grayish brown to brownish black (62,65), not conspicuously hairy; pleuron light bluish gray to bluish gray (190,191) with fine hairs on all segments but small katepimeron; anatergite brownish gray (64), katatergite pale yellow (89) dorsally, bluish gray (191) ventrally.

Wings: membrane tinged with light grayish yellowish brown to light yellowish brown (79,76), costal cell,

subcostal cell and stigma moderate yellowish brown (77); veins dark brown (59) distally; obliterative streak not strongly contrasting with stigma, beginning narrowly at proximal end of stigma and extending somewhat obliquely near wing tip.

Legs: small tooth usually present on tarsal claws. Tooth present on type.

Abdomen: medium gray (265) with broad dark brown (59) dorsal longitudinal stripe, segments edged in pale yellow to pale orange-yellow (89, 73), more broadly edged laterally; hairs short, yellowish white (92).

Genitalia: tergite 9 with hairs covering dorsal process and distal three-fourths of 9th tergite; dorsal and lateral processes subequal at base, long, tapering, and broadly separated; a tapering, ventrally directed, medium projection bearing small apical process; prominent squarish rectal sclerite. Gonocoxites separated ventrally near base by protruding membrane; gonocoxal fragment broadly triangular. Outer gonostylus subtriangular, without distinct emargination or oblique ridge on distal edge, medial surface concave except for narrowly raised edge and broader distal tip. Inner gonostylus with base broader than length of distal beak; small squarish proximal beak; dorsal crest joining distal beak almost perpendicularly; distal beak smoothly curved, obliquely ridged on lateral surface, without pigmented

peg-like sensilla along edge. Aedeagus long, usually visible between gonostyli in dried specimens, distal one-third straight, tip slightly expanded dorsally, no subapical teeth. Aedeagal guide with dorsal plate relatively narrow, subequal to width of aedeagus, plates widely separated throughout most of their length, subapically-expanded in a narrow, dorsomedially curved flange.

FEMALE. Similar to male, except as follows: flagellomeres not distended, 1st flagellomere not elongated, less than 1.5 length of 2nd, lightened to moderate yellow-brown (77) basally; 9th, 10th & 11th subequal, slightly narrower than preceeding.

Genitalia: sternite 8 with broadly rounded dorsolateral edge, not lobed; sternite separated from valvulae by narrow membranous region, membrane narrowly extending between hypogynial valvulae and more broadly, anteriorly on 8th sternite; hypogynial valvulae half the length of sternite 8, square tipped, bearing a strong single subapical hair (visible with 60 X magnification); tergite 9 rounded posterolaterally; sternite 9 with median projection long and thin; tergite 10 broadly rounded distally with fine inconspicuous hairs; cerci very slightly downturned at tip.

TYPE SPECIMENS

Prionocera oregonica was described from a single male collected in Oregon, Wallawa Mts., Aneroid Lake, 7,500', 25 vi 1929, H.A. Scullen. (The original description and holotype slide incorrectly state "Blue Mts." [Alexander, 1954]).

I examined the holotype slide, No. 7467, containing the male genitalia, an antenna, fore leg and left wing. It is not a very good specimen because the aedeagus and all its associated structures are missing as are the left inner and outer gonostyli. However, the identity of this species is established by, and distinguished from, the very closely related P. turcica by the narrower dorsal process and the shorter apical process of the 9th tergite, and the longer 11th flagellomere. The slide and the pinned specimen (the latter I have not seen) are in the Alexander Collection, United States National Museum, Washington, D.C..

SYNONYMY

Prionocera primoveris Alexander was based on a male holotype, Sylvan Lake, Yellowstone, Wyoming, 8,000', 21 vi 1941; a female allotype, 7 males, 1 female paratype, Twogwotee Pass, Grand Teton National Forest, Wyoming, 9,650', 9 vi 1942, male paratype, Sylvan Lake, Yellowstone, 8,000', 21 vi 1942. All specimens collected by C.P. Alexander and in the United States National

Museum, Washington, D.C.

The male holotype is glued to a point. I removed and softened the genitalia for study and placed them in a microvial pinned beneath the specimen. I have also seen the genitalia of the male paratype, Sylvan Lake (slide No. 7273, USNM) which was illustrated in the original description, and a male paratype, Twogwotee Pass, Grand Teton National Forest, 9 vii 1942 (also slide No. 7273, USNM). Alexander distinguished primoveris from oregonica on the basis of their "differing conspicuously in the structure of the male hypopygium." The 9th tergite of primoveris is squashed on the slide and its distal processes are distorted. I am confident, however, that these are the same species because of the similarity of the other structures, especially the unique aedeagal guide.

The publication date of P. oregonica Alexander is February 18, 1943. It therefore takes priority over P. primoveris Alexander which was published in November, 1943. It should be noted, however, that the manuscript for P. primoveris was probably finished first because in the publication of that species Alexander makes no mention of P. oregonica, but he does compare P. oregonica with P. primoveris in the earlier published original description of P. oregonica.

Prionocera uinticola Alexander was described from a single male collected in Utah, Uinta Mts., Tryol Lake, John C. Fechser & Vasco M. Tanner collectors. I have seen the holotype, slide no. 8463, containing male genitalia (well-mounted), antenna, and right wing. The slide and the pinned specimen (the latter not seen) are in the USNM. The differences in the relative lengths of Rs and m-cu (sensu Alexander), and noted by Alexander in the description of uinticola, I judge to fall within the variation observed in oregonica. And the differences in detail of the structures of the hypopygium are distortions caused by flattening of the specimen on the slide.

The description of Prionocerra fulvicauda Alexander is based on a mixed collection. The male holotype and female allotype are pinned together with the labels: "R.M.N.P. Col./10,000 ft./ July 18 '41/ C.P. Alexander." There are four male paratopotypes two of which have their genitalia preserved on microscope slides, both numbered 8422. All type material is in the USNM.

The holotype is conspecific with P. oregonica and therefore must be synonymized under that name. The allotype and the two male paratopotypes are P. suberricornis. Alexander's description of fulvicauda is based primarily on the slide-mounted specimens of P. suberricornis, and not on the type specimen. It is not

surprising, therefore, that Alexander compared this species with the European P. proxima (here synonymized with P. suberricornis) and that North American specimens of P. suberricornis have been consistently misidentified as fulvicauda.

VARIATION

Alexander alludes to differences in the details of the structures of the the male terminalia among the species synonymized above. The differences are largely due to distortion and to differential orientation of the slide-mounted specimens. No tooth was observed on the tarsal claws of the single slide-mounted leg of the type.

DISCUSSION

Prionocera oregonica is very closely related to the holarctic species P. turcica. The 9th tergite and the gonostyli are very similar in the male. Prionocera oregonica is distinguished from P. turcica by the narrower and longer dorsal lobes, and by differences in the aedeagal guide (see figs. 5 & 6). Prionocera oregonica is also smaller, duskier, without a conspicuously lightened rostrum and the stigma and obliterative streak are not as conspicuous as in P. turcica. The 11th flagellomere in the male of P.

oregonica is comparatively longer. Females can be separated by the relative length of the hypogynial valves to the 8th sternite and by the shape of the ventral membranous region. In P. oregonica the hypogynial valves are shorter and the membranous area is narrow and perpendicular to the body axis rather than "W-shaped".

Prionocera oregonica and P. turcica are strikingly different from all other Prionocera in the development of the processes of the 9th tergite, particularly the apical process which is in a more dorsal position on a prolongation between the dorsal processes. The aedeagal guide in both species is expanded dorsally and is thus quite distinct from the simple flattened dorsal plate found in the other species of this genus.

GEOGRAPHICAL DISTRIBUTION (Map 8)

Prionocera oregonica is apparently quite rare and local. It is found in the same ecological habitats as its sister species P. turcica. Prionocera oregonica appeared to be restricted to higher altitudes in the western United States. It was therefore a surprise to find two males of this species in my collection from the Schefferville region, Quebec, and a female from Churchill, Manitoba. In these two areas the sister species P. turcica and primoveris co-exist.

FLIGHT RECORDS: 21 June-9 August.

SPECIMENS EXAMINED (27 males, 3 females)

CANADA: ALBERTA: Waterton Nat'l Pk., Cameron Lake, 5450', ♂, 9 vii 49, J. Baker (as primoveris, slide No. 7273, Alexander Coll. USNM). BRITISH COLUMBIA: Tweedsmuir Prov. Pk., Heckman Pass, ♂, 19 vii 78, R.A. Cannings (SUBC). MANITOBA: Churchill, ♀, 10 vii 77, F. Brodo (CNC). QUEBEC: Schefferville, ♂, 28 vi 81, F. Brodo (CNC); 37 km NW Schefferville, Annabel L., ♂, 14 vii 81, F. Brodo (CNC).

U.S.A.: CALIFORNIA: Shasta Co., Mt. Lassen, Hat Lake, 6450', ♂, 9 viii 1958, C.P. Alexander (as oregonica, slide No. 7467, Alexander Coll. USNM). COLORADO: Boulder Co., Rainbow Lakes, 10,100', 10♂, ♀, 2-10 vii 1979, F. Brodo (CNC); ♂, 2 vii 79, F. Brodo (SEM); Lefthand Bog, 40°04'N 105°34'W, ♂, 11 vii 79, F. Brodo (CNC); Mt. Research Station, Nederland, 9500', ♂, 26 vi 79, F. Brodo (CNC); Rocky Mountain Nat'l. Pk., Dream Lake, 10,000', ♂, 18 vii 41, C.P. Alexander (fulvicauda holotype, USNM). OREGON: Wallowa Mts., Aneroid Lake, 7500', ♂, 23 vii 29, H.A. Scullen (oregonica holotype, slide No. 7467, Alexander Coll. USNM). UTAH: Uinta Mts., Tryol Lake, ♂, Vasco M. Tanner, (uinticola holotype, slide No. 8436, Alexander Coll. USNM). WYOMING: Carbon Co., Silver Lake, 30 km W Centennial, 41°18'45"N 106°21'30"W, 3♂, ♀, 10-11

vii 81, S. Teale (SEM); Grand Teton National Forest, Twogwotee Pass, 9650', ♂, 9 vii 42, C.P. Alexander (primoveris paratype, |slide No. 7273, Alexander Coll. USNM); Yellowstone Nat'l. Pk., Sylvan Lake, 8000', 2♂, 21 vi 41, bog near Moran, 6800', ♂, 5 vii 41, Alexander (as primoveris, slide No. 7273, Alexander Coll. USNM) C.P. Alexander (primoveris holotype (pinned), and paratype slide No. 7273; CPA Coll. USNM).

Prionocera pubescens Loew

Prionocera pubescens Loew, 1844: 170-171, figs. 30, 31 (male head).

Prionocera anderi Tjeder, 1948: 96-98, fig. 14 (male terminalia) (Synonymy by Mannheims, 1951).

DIAGNOSIS

Male with rounded prominence on lateral surface of inner gonostylus densely covered with short stiff hairs; female with narrowly rounded dorsolateral lobe on 8th sternite; 9th sternite with short, broad median projection; cerci short, broad, straight or slightly upcurved.

DESCRIPTION (figs. 19, 40, 56, 73)

ADULT. General appearance: grayish brown (61) dorsally, light gray (264) laterally, with long erect yellowish white (92) hairs on head and thorax, shorter hairs on abdomen; male body length 9.2-11.1mm, wing length 11.3-12.8mm; female body length 12.1-14.0, wing length 12.3-13.3mm.

MALE. Head: vertex grayish brown to brownish black (61,65) hairs long; gena yellowish white (92) laterally, dark grayish brown (62) medially, with scattered short hairs; rostrum entirely dark grayish brown (62) with proclinate hairs on distal two-thirds, hairs projecting beyond moderate (0.075mm) nasus; psuedo-ocellus brownish black (65).

Antenna: flagellum dark grayish brown (62), 1st flagellomere with subcylindrical base, strongly produced distoventrally, succeeding flagellomeres more triangular in lateral outline, progressively smaller and less produced; 10th cylindrical, slightly longer than 9th, 11th minute, less than one-half length and width of 10th.

Thorax: prescutal pit and region anterior to pit brownish black to deep brown (65,56); dorsal stripes dark grayish brown (62), median stripe narrowly divided by light yellowish brown (76), becoming black anteriorly, stripes bordered by light yellowish brown (76) region bearing long dense hairs; postsutural area, scutellum and mediotergite dark grayish brown to light yellowish brown

(62,76), bearing long hairs; pleuron bluish white to bluish gray (188,191), anepisternum, katepisternum, entire anepimeron covered with long yellowish white (92) hairs; anatergite grayish yellow (90); katatergite pale yellow (89) dorsally, dark gray (266) ventrally.

Wings: membrane tinged with light grayish yellowish brown (79), costal and subcostal cells and distal half of stigma light yellowish brown (76), stigma not contrasting with membrane; veins deep yellowish brown (75); obliterative streak weakly developed, beginning in paler proximal half of stigma, continuing diagonally near wing tip.

Legs: tarsal claws without teeth.

Abdomen: light bluish gray (190) with dark brown (59) dorsal longitudinal stripe, tergites narrowly edged distally, more broadly edged laterally in pale yellow (89); tergites and sternites with yellowish white hairs (92), hairs appressed dorsally except on 1st tergite, more erect laterally and ventrally.

Genitalia: tergite 9 with hairs laterally on posterior half; dorsal process short, about as long as broad, slightly tapered posteriorly, separated by more than width of process; width; no lateral process; medial lobe broadly fused to bases of narrow hook-like apical process; apical process close to lateral edge of tergite;

rectal sclerite small, inconspicuous. Gonocoxites without protruding membrane ventrally; dorsal fragment of gonocoxite broadly triangular. Outer gonostylus with broadly curved ventral edge, somewhat emarginate on dorsal edge, medial surface concave with narrow raised edge somewhat broader distally and ventrally. Inner gonostylus with slight dorsal crest merging gradually with cylindrical distal beak; no pigmented sensilla on beak; broadly emarginate between distal beak and small proximal beak; medial surface of basal area with rounded prominence densely covered with short hairs. Aedeagus with tip straight; no subapical teeth. Aedeagal guide with narrow, collar-like extension posterior to broad, flat, dorsal plate; dorsal plate narrowing some distance before sperm pump.

FEMALE. Similar to male, except as follows: base of antenna usually lightened; 1st flagellomere subcylindrical, less than 1.5 length of 2nd; 2nd to 8th slightly distended, giving a serrate appearance; 10th and 11th cylindrical, subequal and smallest.

Genitalia: sternite 8 with narrowly rounded dorsolateral lobe; hypogynial valvulae short, slightly more than one-third (0.38-0.42) length of 8th sternite, separated from sternite by narrow membranous three-forked region; valvulae with broad, triangular, more heavily sclerotized ventral edge, broad tip, no subapical hairs;

tergite 9 somewhat rounded posterolaterally; sternite 9 with short broad median projection; tergite 10 straight edged, not conspicuously hairy; cerci broad, straight to strongly upcurved.

TYPE SPECIMENS

Prionocera pubescens, the type species of this genus, was described by Loew (1844) from a single male collected in the "Posener Gegend". The type, which I borrowed from the Zoologisches Museum, Humboldt-Universität, Berlin, lacks wings, legs and 7 flagellomeres on the left antenna. The right antenna is intact. The abdomen is glued to a card pinned below the specimen and the genitalia are below that, in balsam, affixed to a mini-slide.

The specimen bears a faded brown ink, handwritten label "pubescens Lw", followed by the labels: "9147," and "Holotypus designatus Mannheims." The features characteristic of this species are visible in the type specimen. The 9th tergite has slightly damaged dorsal processes probably because of the shrinking of the balsam, but the shapes and broad space between these processes and between the apical processes are diagnostic. The characteristic shape of the inner gonostylus is clearly evident. Other features evident on the type, that distinguishes this species from closely

related species, are the developed nasus, produced flagellomeres and long dense pale hairs on the head and thorax.

SYNONYMY.

Prionocera anderi Tjeder was synonymized with P. pubescens Loew by Mannheims (1951) who compared the type of anderi with that of pubescens. Tjeder had mistakenly applied the epithet pubescens to the species subsequently named tjederi.

I examined the type of anderi (Tjeder Collection, ZMLS). It bears the labels: FALUN/ DJUPTJARN/ TJEDER, and a red holotype label. The genitalia have not been removed but are clearly recognizeable and diagnostic of this species. In addition, I saw three paratypes, two from Dlr. Leksand, collected by E. Klefbeck and one from Abisko, Sweden, collected by Ringdahl (ZMLS). The paratypes have had their genitalia removed and placed in vials alongside their respective pinned specimens. I concur with Mannheims that anderi is conspecific with pubescens.

VARIATION

This is one the smaller species of Prionocera. The male genitalia tend to be considerably telescoped within

the 8th segment making positive identification, without resorting to removing genitalia, difficult. The females are also difficult to recognize, especially when the lobes on the 8th sternite are obscured.

DISCUSSION

Prionocera pubescens and P. naskapi are probably sister species. See discussion under naskapi.

GEOGRAPHIC DISTRIBUTION (Map 9)

This species has a greater latitudinal range in the Palearctic, where it extends from northern Fennoscandia to Central Europe. In North America it is apparently confined to the subboreal region.

FLIGHT RECORDS: 10 May-25 July

The earliest seasonal records are from central Europe and the latest records are from northern Fennoscandia.

SPECIMENS EXAMINED (70 males, 18 females)

NEARCTIC: CANADA: ALBERTA: Fawcett, ♂, 10 vi 34, E.H. Strickland (as sordida, slide No. 3589, Alexander Coll. USNM). NORTHWEST TERRITORIES: Mackenzie Distr., Fort

McPherson, 2♂, ♀, 24 vi 57, S.D. Hicks (CNC); Fort Smith, ♀, 12 vi 50, J.B. Wallis (CNC); Muskox Lake, 64°45'N 108°10'W, 3♂, 2♀, 9-11 vii 53, J.G. Chillcott (CNC); Norman Wells, ♂, 22 vi 49, W.R.M. Mason (CNC); Salmita Mines, 64°05'N 111°15'W, 16♂, ♀, 30 vi-8 vii 53, J.G. Chillcott (CNC). MANITOBA: Eastern Cr. nr. Churchill, ♂, 25 vi 52, J.G. Chillcott (CNC); Churchill, 2♂, 9 vii 78, F. Brodo (CNC); same data, ♂ (SEM), ♂ (C.D.); Farnworth Lake nr. Churchill, 4♂, ♀, 12 vi 52, J.G. Chillcott (CNC); Fort Churchill, 3♂, 20-23 vi 52, C.D. Bird (CNC); ♂, 24-25 vi 52, J.G. Chillcott (CNC); Gillam, , 24 vi 49, J.B. Wallis (CNC); Herchmer, 2♂, ♀, 29 vi-5 vii 49, J.B. Wallis; Mile 505, Hudson Bay Railroad, ♂, 13 vi 52, J.G. Chillcott.

PALEARCTIC: BELGIUM: PROV. LUXEMBOURG, Vence, ♂, 29 v 55, Ed. De Laever (MAKB).

FINLAND (Heikinheimo et al, 1971, 1981): ETALA-HAME: Tammela, ♀, 28 v 64, Brander (MAKB); Kalvola, ♀, V.G. Borg (MAKB). KEMIN LAPPI: Ahvenjarvi (=Kussajoki, 67°38'N 25°15'E), ♀, E. Thunberg (ZMH); Vuosso (? = Vuotso), ♀, 19 vi 66, Mittendorf (MAKB). INARIN LAPPI: Utsjoki, 60 km S, ♂, ♀, 27 vi 58, Fendler (MAKB).

GERMANY (B.R.D.): Mosbruch, ♂, ♀, in copula, 2 vi 51, Mannheims (MAKB).

NORWAY: HORDALAND: Noer Haugen, Samnanger, ♂, 15 v

50, Ekskurjon (ZMUB); Adlandsvingene, Samnanger, 2♂, 15 v 50, Ekskursjon (ZMUB).

POLAND: Poznan ("Posener Gegund," holotype of pubescens), ♂, no further data (ZMHB).

SWEDEN: DALARNA: Falun, Djuptjärn, Stora Kopparberg, ♂, 12 vi 32, Tjeder (anderi holotype, ZMLS); Leksand, NW of Sägmära, 3♂, 2 vi 35, E. Klefbeck (anderi paratypes, ZMLS). NORBOTTEN: 67°58'N 23°38'E, ♀, 25 vii 51, J.R. Vockeroth (CNC). OSTERGÖTLAND: Vaxmoisen (N. Ljungsbro), ♂, 26 v 62, K. Ander (ZMLS). TORNE LAPPMARK: Abisko, 5♂, 20 vi 71, H. Lundberg (BMNH); 6♂, 25 vi-8 vii 51, J.R. Vockeroth (CNC); ♂, 15 vii 22, Ringdahl (anderi paratype, ZMLS). UPPLAND: Stockholm Region, ("Hlm", "Bhn"), ♀, no further data (NRS). VASTERBOTTEN: Degerfors, ♂, no further data (ZMLS).

SWITZERLAND: SCHWYZ: Rothenthurn, ♂, 25 v 80, C. Dufour (CNC).

U.K.: ENGLAND: NW Yorkshire, Austwick Moss, 3♂, 27 vi 38, C.A. Cheetham (BMNH).

U.S.S.R.: LATVIA: Curon, Bathen, ♂ (BMNH), ♀ (MAKB), 27 v 28, Dr. P. Lackschewitz; ?Kaluna, ♂, 17 v 32, Dr. P. Lackschewitz (ZMLS); ?Palt Moor, 2♂, 27-29 v 20, Dr. P. Lackschewitz (BONN & LUND); Lettland, Euxküll am Schwanensee, ♀, 10 v 36 (MAKB). MURMANSK POLUOSTROV KOL'SKIY: Kantalaks, ♂, R. Frey (ZMH); Kusomen, ♀, R.

Frey (ZMH).

Prionocera recta Tjeder

published as Stygeropis parrii; Alexander, 1919: 8-9, figs. 7, 12, 23, 24, 26. (Description based on a mixed collection of P. serricornis and P. recta. The figures apply to P. serricornis.)

published as Prionocera serricornis; Lackschewitz, 1933: 138-139, figs. 4a, b, c (male terminalia, antennae) (nec Zetterstedt, 1838).

Prionocera recta Tjeder, 1948: 92-93, fig. 4G (male head & antenna), fig. 11 (male terminalia); Mannheims, 1951: 65-66, fig. 35 (from Tjeder, 1948, fig. 11).

Prionocera lapponica Tjeder, 1948: 93-94, fig. 4H (male head & antenna), fig. 12 (male terminalia); Mannheims, 1951: 66, fig. 36 (from Tjeder, 1948, fig. 12). (new synonymy)

Prionocera lackschewitzii Mannheims, 1951: 71. (new synonymy)

Prionocera gracilistyla Alexander, 1956: 123-125; 1965: 19. (new synonymy)

DIAGNOSIS

A dark gray fly with long hairs on head and thorax,

hairs ranging from yellowish white to deep brown (92,56), (darker specimens from central Canadian arctic); flagellomeres distended in both sexes, but more evident in the male; nasus small or reduced to minute knob; 9th tergite with long subrectanular dorsal process, lateral process smaller and narrower; inner gonostylus with small base and long slender dorsal beak; cerci and hypogynial valvulae short and broad; 8th sternite with broadly rounded dorsolateral edge.

DESCRIPTION (figs. 2, 20, 41, 57, 74)

ADULT. General description: predominantly gray with long yellowish white to deep brown (92,56) hairs on head, thorax and abdomen; male body length 9.4-13.9mm, wing length 13.1-16.5mm; female body length 13.0-17.6mm, wing length 14.2-17.5mm.

MALE. Head: vertex light brownish gray to dark gray (63,266), with longitudinal brownish black to black (65,267) line, usually expanded medially; hairs long, as long as hairs on postgena; gena light gray to brownish gray (264,64) with several hairs near antennal sockets; rostrum dark grayish brown (62), not lightened laterally or ventally, covered with long stiff proclinate hairs, hairs projecting beyond nasus; nasus minute knob-like to small rectangular (up to .1mm); pseudo-ocellus moderate orange-yellow to dark yellowish brown (71,78), very

prominent in some specimens.

Antenna: flagellomeres dark brown to brownish black (59,65) 1st flagellomere slightly longer than 2nd with cylindrical base and strong distoventral dilation; proximal flagellomeres also strongly distended distoventrally, triangular in lateral profile, distal width twice width at base; distal flagellomeres progressively less distended; 10th cylindrical; 11th abruptly smaller, cylindrical, one-third to one-half length and width of 10th.

Thorax: prescutal pit not forming apex of a well-defined yellowish triangular area; dorsal stripes brownish gray to black (64,267), occasionally dark brown (59); median stripe often shiny black anteriorly, bisected by narrow line, lateral stripes bordered by medium gray (265) region bearing long hairs; midline of median stripe with scattered, shorter hairs; postsutural area and scutellum concolorous with dorsal stripes and borders or slightly grayer, with long hairs; pleuron light bluish gray to dark bluish gray (190,192), bearing long stiff hairs except on small katepimeron; anatergite dark gray (266), katatergite dark gray (266), narrowly edged with strong brown (55) to more broadly bordered with strong yellow (84).

Wings: membrane tinged with light grayish brown (60), bases of outer radial cells somewhat darker; veins deep

brown to dark brown (56,59); subcostal cell and stigma light yellowish brown (76), costal cell slightly paler; obliterative streak contrasting strongly with membrane, extending almost perpendicular to costa, near wing tip.

Legs: tarsal claws simple or with small tooth.

Abdomen: brownish gray to dark grayish brown (64,62), dorsal longitudinal stripe dark grayish yellowish brown (81); tergites very narrowly edged with light orange-yellow (70); hairs long (.25mm or longer), erect, often paler than on head and thorax.

Genitalia: tergite 9 with hairs on posterior half; dorsal process longer than broad, rounded and slightly widened distally, with abundant, relatively short curved hairs; space between dorsal processes subequal or broader than width of process; lateral process small, narrowly angular or truncate, shorter than dorsal process; apical process broad, medially curved distally, forming an acute tooth; medial lobe not free, fused to bases of apical processes; rectal sclerite large, rectangular, sometimes connected medially by narrow dorsal sclerotization. Gonocoxites without protruding membrane ventrally; gonocoxal fragment broadly triangular. Outer gonostylus broad at base, narrowing distally, medial surface concave except for poorly defined narrow raised edge. Inner gonostylus with small base, small squarish to triangular proximal beak, distal beak long, slender, bearing lightly

pigmented sensilla ventrolaterally, no distinct dorsal crest, lateral surface of base with small ridge just posterior to a lateral groove, ridge more pronounced in Palearctic specimens. Aedeagus with midsection straight, ventrally curved tip with pigmented and/or thickened subapical rim, no subapical teeth. Aedeagal guide membranous posteriorly, cradling tip of aedeagus, dorsal plate relatively broad, broadly attached to sperm pump.

FEMALE. Similar to male, except as follows: scape and 1st flagellomere often lightened to dark orange-yellow (72) basally, 1st flagellomere slightly constricted subapically, less than 1.5 length of 2nd; flagellomeres 2-8 somewhat distended distoventrally, giving a serrate appearance; last two flagellomeres narrower, cylindrical, and subequal.

Genitalia: sternite 8 with rounded dorsolateral edge, not lobed; sternite divided longitudinally by irregular weakly sclerotized area extending from base of hypogynial valvulae to two-thirds length of the sternite; hypogynial valvulae short, one-third length of sternite 8, ventral edge narrowly more heavily sclerotized, tip broad, straight, bearing two subapical hairs (visible at 60 X magnification); tergite 9 rounded posterolaterally; sternite 9 with median projection relatively short and broad; tergite 10 rounded posterolaterally, bearing short hairs; cerci short, broad, almost straight.

TYPE SPECIMENS

Holotype, male, Lappland, Torne Lpm., Jebrenjokk, 22 vii 26, O. Ringdahl, in Tjeder Collection, Zoological Museum, Lund, Sweden.

The type which I saw in 1983 lacked a collector's label. The genitalia had been removed to a genitalia vial placed beside the pinned specimen. Unfortunately the 9th tergite, the sperm pump and the aedeagal complex were badly damaged, however the gonostyli were intact and are very distinctive for this species. The pinned portion of the type is in good condition lacking only the tip of the left wing and tarsal segments of the left hind leg.

SYNONYMY

Prionocera lapponica was described from a single male collected in Swedish Lapland, Lule Lappmark, Sarek, Pate, 10 vii 1907 by B. Poppius. The type, which I borrowed from the Naturhistoriska Riksmuseet, Stockholm, had had the genitalia removed and preserved in balsam on a mini-slide pinned beneath the specimen. The aedeagus and associative structures, the right pair of gonostyli, and only half of the 9th tergite are preserved, the latter in lateral aspect with the processes obscured or broken. The left wing is glued to a card and only the middle and

hind legs of the right side are intact.

Tjeder differentiated recta from lapponica primarily by colour and by differences in the shape of the processes of the 9th tergite. The differences noted fall within the range of variation observed in this species.

Prionocera recta and P. lapponica were described consecutively in the same paper (Tjeder, 1948). I am designating recta rather than lapponica as the name for this species, because it has page priority and because the type of recta is in slightly better condition and the description and illustrations are more typical of this species.

Prionocera lackschewitzi Mannheims was a renaming, by Mannheims (1951), of a species which had been previously illustrated and described by Lackschewitz (1933), but had been misidentified by Lackschewitz as "serricornis". Tjeder (1948:90) had noted that this taxon was either a new species or conspecific with P. lapponica, but not having seen any of Lackschewitz's material, Tjeder declined to deal with it. Mannheims (1951:71) noted that according to the description and figures given by Lackschewitz (1933:138-39, figs. 4a,b,c) this species differed from lapponica Tjeder in the shape of the dorsal process of the 9th tergite. In P. lapponica, the dorsal process is described as being somewhat conical whereas in lackschewitzi it is slightly broadened medially.

Mannheims did not compare lackschewitzi to recta, the illustrations and descriptions of which appear to resemble more closely those of lackschewitzi. The rather minor differences mentioned in the shape of the dorsal process falls well within the general variation of P. recta.

Mannheims designated as a "lectotype" for lackschewitzi the first specimen listed by Lackschewitz (1933:139) under "serricornis", i.e. Fennia: Kuusamo, (R. Frey, M.H.). I borrowed a specimen from Helsinki bearing the following labels: Kuusamo/ R.Frey/ 897/ Prionocera serricornis Ztt. det. Laksch./ Mus. Hel. N:o 1547/ Prionocera serricornis, 2(?) Zett./ Mus. Zool. Helsinki Loan No.D 5463/ Prionocera lackschewitzi Mannh. (J.M (???), det. Bo Tjeder. Only one specimen of "serricornis" from Kuusamo, collected by Frey and deposited in Helsinki was listed by Lackschewitz (1933). Therefore, the specimen which I saw must be the one designated as lectotype by Mannheims. It was damaged, but enough of the genitalia was intact to show unequivocally (after being softened in KOH and lactic acid) that it does not correspond to the description and figures given by Lackschewitz for "serricornis" but, ironically, does correspond to his "P. anceps," now recognized as being P. serricornis Zetterstedt.

This was an unfortunate designation. Mannheims was

actually selecting a holotype and not a lectotype, this being the first formal recognition of the existence and naming of a new species. Secondly, the specimen in question was apparently never seen by Mannheims.

Prionocera gracilistyla was described from a male holotype, Point Barrow, Alaska, June-August, 1950, N.A. Webber, Collector's No. 2644, female allotype, 27 vii 1949, Weber, No. 2514 and 8 males and 1 female paratopotypes, July 10-23, 1952, P.D. Hurd. All specimens are in the United States National Museum, Washington, D.C.

The type, which I examined, was in good condition except that only the right hind leg is complete. The genitalia have not been removed but the distinctive dorsal and lateral processes on the 9th tergite were clearly visible. The specimen bears whitish hairs on the head and thorax, and the nasus is reduced to a small bump. I am confident that this specimen is conspecific with P. recta.

VARIATION

The most striking variation in this species is in hair colour. The Scandinavian and Russian specimens, including the type, have long yellowish white (92) hairs on the head and thorax with shorter hairs of the same colour on

the abdomen. Most North American specimens have darker hairs ranging from light brown to deep brown (57,56), with abdominal hairs shorter and several shades lighter. The darker hairs look coarser and give these specimens a much more bristly appearance. The Alaskan specimens, including those described as gracilistyla, have hairs ranging from yellowish white to light orange-yellow (92,70). Some specimens with pale hairs were found among collections of the darker haired specimens from several localities across the Canadian Arctic.

Prionocera is also distinguished by its glabrous venation, therefore, it was surprising to find several palearctic specimens (2 from Finland, the Norbotten specimen from Sweden and the Russian specimen from Tobolsk) with scattered hairs on R3 and R4+5. The tarsal claws are simple on all nearctic specimens. On most of the Russian specimens there is a small tooth, but only on one of each pair of claws on a leg.

As in all species of Prionocera, there are differences in the shapes and angles of the processes of the 9th tergite in males. These differences may be exaggerated by differential orientation and drying of the specimen.

The inner gonostylus has a small rounded ridge near the distoventral corner of the base on the lateral surface. This ridge is more pronounced in the Palearctic and Alaskan specimens.

DISCUSSION

Prionocera recta has been confused with P. serricornis and P. ringdahli from Europe and P. ominosa and P. elliptica from North America. Their similarity indicates a close relationship. All these species have long hairs on the head and thorax, distended flagellomeres and a reduced or entirely absent nasus. Males of P. recta are easily distinguished by the long dorsal lobes on the 9th tergite and the characteristic inner gonostylus with its small base and longer cylindrical distal beak. Females have a rounded, not lobed, dorsolateral edge on the 8th sternite and moderately long hypogynial valvulae.

GEOGRAPHIC DISTRIBUTION (Map 10)

This is one of the more northern, and also one of the more widespread species. It has been collected across boreal and subarctic North America from the west coast of Alaska to southern Baffin Island and in northern Fennoscandia and along the Siberian coastline. Its distribution is apparently restricted to north of the 60th parallel. It was taken in the gray willow (Salix cinerea) region in Lappland (Tjeder, 1948:94).

FLIGHT RECORDS: 2 June-11 August

Most flies were collected from the middle of June to the end of July.

SPECIMENS EXAMINED (273 males, 131 females)

NEARCTIC: CANADA: NORTHWEST TERRITORIES: Franklin Distr., Baffin I., coast, Camp Kungovik, 65°35'N, 5♂, 8♀, 13-16 vii 29, J.D. Soper (CNC); Frobisher Bay, 2♂, 2♀, 24 vi-2 vii 48, T.N. Freeman (CNC); ♂, 2♀, 2 vi 48, F.G. Dilabio (CNC); ♂, 10-11 viii 59, E.G. Munroe (CNC); Nettiling L., ♂, ♀, 23 vi 25, J.D. Soper (CNC); Boothia Peninsula, Lady Melville L., 69°25'N 93°15'W, 2♂, ♀, 3 vii 51, J.G. Chillcott (CNC); Spence Bay, 29♂, 10♀, 25 vi-6 vii 51, J.G. Chillcott (CNC); 26♂, 5♀, 27 vi-21 vii 51, A.E.R. Downe (CNC); Victoria I., Bernard Harbour, 68°46'N 114°42'W, 2♂, Nos. 822, 828, vii-viii 15, ♂, No. 423, 1-14 vii 16, Canadian Arctic Expedition, Frits Johansen (CNC); Cambridge Bay, 17♂, 7♀, 8-18 vii 50, E.H.N. Smith (CNC); 15♂, 4♀, 11 vii 50, B.A. Gibbard & G.K. Sweatman (CNC); Holman, 12♂, 17-18 vi 52, D.P. Gray (CNC); 71°17'N 114°W, 9♂, 5♀, 25-30 vi 75, G. & M. Wood (CNC). Keewatin Distr.: Baker Lake, ♂, ♀, 14, 26 vii 47, T.N. Freeman (CNC); Chesterfield, 6♂, 3-22 vii 50, J.R. Vockeroth (CNC); 14♂, 5♀, 4-15 vii 50, J.G. Chillcott (CNC); Padley (?Padlei, 61°55'N 96°40'W), ♂, 2♀, 2 vii 50, R.A. Hennigar (CNC); Southampton I., Coral Harbour, 59♂, 36♀, 18 vi-1 vii 52, P.R. Ehrlich (CNC); same data,

♂, ♀ (SEM), ♂ (V.I.L.); 7♂, 11♀, 1-5 vii 48, G.E. Shewell (CNC); Seahorse Point, ♂, 17 vi 38, British Canadian Expedition 36-39, T.H. Manning (BMNH); 64°15'N 89°30'W, ♂, 22 vii 50, J.G. Chillcott (CNC); Melville Peninsula, Repulse Bay, 18♂, 4♀, 25 vi-24 vii 50, J.E.H. Martin (CNC); same data, ♂ (V.I.L.); 8♂, 3♀, 26-30 vi 50, P.F. Bruggemann (CNC). Mackenzie Distr.: Aklavik, ♀, 16 vi 56, E.F. Cashman (CNC); ♀, 16 vi 56, R.E. Leech (CNC); Coppermine, 3♂, 3♀, 18 vi-14 vii 51, S.D. Hicks (CNC); ♂, 4 viii 48, H.T. Sacklette (CNC); Salmita Mines, 64°05'N 111°15'W, ♂, ♀, 18 vi 53, J.G. Chillcott (CNC). QUEBEC: Sugluck, 2♀, 28 vi 54 H. Huckel (CNC). YUKON TERRITORY: Dickson L., Mt. Mye, 133°08'N 62°21'W, 5,000', ♀, 14 vi 60, E.W. Rockburne (CNC); 60-75 mi N Rampart House, 67°25'N 140°59'W, ♂, 24-26 vi 12, J.M. Jessup, (J.M. Aldrich coll., USNM); km 155 Demster Hwy., 3♂, 22-24 vi 82, G. & M. Wood (CNC).

U.S.A.: ALASKA: Alcan Hwy., Summit Pass, Richardson Hwy., No. 17, S of Isabel Pass before Denali Hwy., ♂, 7 vi 49, E.K. Miller (SEM); Anchorage, ♀, 2 vi 51, R.S. Bigelow (CNC); Collinson Pt., 69°59'N 144°54'W, No.1195, ♂, 22-23 vi 14, Canadian Arctic Expedition, Frits Johansen (CNC); Igiak Bay (=Kokechik Bay), 2♂, 15 vi, 17 vii 52, P.S. Humphrey (UMMZ); Umiat, 69°22'N 152°08'W, ♂, 5 vi 47, Knight (UMMZ); Ogotoruk Cr., Cape Thompson, CH 123 Pond 6, No.1137, 68°05'N 165°45'W., ♀, 15 vi 60, W.C. Hanson (WSU); Point Barrow, ♂, 5♀, 10-23 vii 52, P.D.

Hurd (gracilistyla paratypes, USNM) 3♂, 6♀, 17-23 vii 53, P.D. Hurd (USNM); ♂, 27 vii 49, N.A. Weber (gracilistyla paratype, slide No. 9592, Alexander Coll. USNM) ♂, ♀, Nos. 2649, 2652, vi-viii 50, N.A. Weber, (BMNH); ♂(No.4, no date) ♀, 18 vii 1882, John Murdock (USNM).

BALEARCTIC: FINLAND: ENONTEKION LAPPI: Le Saana, ♂, 30 vi 62, Björn Federley (ZMH), INARIN LAPPI: Inari See, ♀, 19 vi 66, Mittendorf (MAKB).

SWEDEN: LULE LAPPMARK: Sarek, Pärte, ♂, 10 vii 07, B. Poppius (lapponica holotype, NRS). NORBOTTEN: 67°58'N 23°38'E, ♂, 25 vii 51, J.R. Vockeroth (CNC). TORNE LAPPMARK: Abisko, Mt. Lullenhatjamo Snowfield, ♀, 3 vii 71, H. Lundberg (BMNH); Jebrenjokk, ♂, 22 vii 26, O. Ringdahl (recta holotype, ZMLS).

U.S.S.R.: Polar Ural, Gouv. Tobolsk, ♂, 9 vi 09, F. Saizew (MAKB); Taimyr, near Dikson, 7♂, 12 vii-9 viii 79, V.I. Lantsov, (CNC).

Prionocera ringdahli Tjeder

Prionocera ringdahli Tjeder, 1948: 90-91, fig. 10 (male terminalia).

DIAGNOSIS

Stigma contrasting with obliterative streak; male with broad flat distal beak on inner gonostylus; female with rounded dorsolateral edge on 8th sternite.

DESCRIPTION (figs. 21, 42, 58, 75)

ADULT. General description: a gray fly, usually with brownish caste on thorax, hairs long, pale yellow (89); male body length 9.1-10.9mm, wing length 11.3-14.3mm; female body length 10.4-12.5mm, wing length 14.2-14.4mm.

MALE. Head: vertex grayish brown to medium brown (61,58), divided by capillary black line, hairs long, erect, proclinate distally; gena light gray to dark gray (264,265) with scattered short hairs; rostrum dark brown to brownish black (59,65), not lightened laterally, with long fine proclinate hairs, hairs projecting beyond small nasus (.05-.06mm); pseudo-ocellus dark grayish brown to black (62,267).

Antenna: flagellum dark grayish brown to dark brown (62,59), usually lightened to medium brown (58) basally; 1st flagellomere slightly longer than 2nd, cylindrical with strong distoventral dilation; 2nd distoventrally distended, distal width twice width at base; succeeding flagellomeres scarcely distended; 10th & 11th flagellomeres cylindrical, 11th tiny, half the width and less than one-half length of 10th.

Thorax: without a triangular yellowish area anterior to prescutal pit dorsal stripes glabrous, medium brown to grayish brown (59,61), median stripe bisected by black to light brownish gray (267,63) line; stripes bordered by light brownish gray to grayish brown (63,61) region, bearing long hairs, hairs shorter and reclinate anteriorly around median stripe, longer and erect posteriorly; postsutural area, scutellum and mediotergite medium gray to brownish gray (265,64) with long hairs; pleuron light gray to dark gray (264,266) with long hairs on all pleural segments except on small katepimeron; anatergite medium gray to olive gray (265,113); katatergite dark grayish olive (111) broadly edged dorsally with pale yellow (89).

Wings: membrane almost hyaline, slightly tinged with light grayish yellowish brown (79), costal and subcostal cells somewhat darker; veins dark grayish brown (62); stigma contrasting with membrane, deep yellowish brown (75) distally, colourless proximally; obliterate streak broad anteriorly, including proximal half of stigma, running obliquely near wing tip, inconspicuous posteriorly because of almost hyaline membrane.

Legs: tarsal claws without teeth.

Abdomen: light olive gray to grayish yellowish brown (112,80) with dark yellowish brown (78) dorsal longitudinal stripe; tergites narrowly edged distally,

more broadly edged laterally with pale yellow to light orange-yellow (89,70); hairs erect ventrally, recumbent and shorter medially on all tergites.

Genitalia: tergite 9 with hairs confined to posterior half; dorsal process slightly longer than broad, with 2 or 3 strong hairs, space between broader than width of process; lateral process very small, truncated or absent; apical process relatively narrow, abruptly and sharply curved medially; median lobe broadly fused to bases of apical processes; rectal sclerite long, thin, rectangular. Gonoxocites with protruding membrane ventrally; gonocoxal fragment broadly rectangular medially. Outer gonostylus with broad squarish base, narrowing distally, medial surface concave except for narrow raised edge. Inner gonostylus with broad squarish base separated by oval notch from long broad flat distal beak; distal beak without pigmented sensilla; no dorsal crest; two proximal beaks, squarish medial beak abundantly haired, conical lateral beak somewhat distal to the medial beak, with finer, shorter hairs. Aedeagus with tip curved dorsally, bearing subapical lateral tooth. Aedeagal guide with parallel-sided narrow membranous tip, dorsal plate flat, abruptly broadened.

FEMALE. Similar to male except as follows: pedicel and 1st flagellomere lighter; 1st flagellomere less than 1.5 length of 2nd, slightly constricted subapically;

succeeding flagellomeres slightly distended distoventrally giving a serrate appearance; last three flagellomeres smaller, cylindrical and subequal.

Genitalia: sternite 8 with rounded dorsolateral edge, not lobed; hypogynial valvulae relatively long, 0.4 to 0.45 length of 8th sternite, broadly rounded distally, bearing slender subapical hair, ventral edge of valvulae with narrow rectangular sclerotization; tergite 9 not rounded posterolaterally; sternite 9 with medium projection relatively broad; 10th tergite with sides almost straight, bearing fine hairs; cerci relatively long, narrow and slightly downcurved.

TYPE SPECIMENS

Holotype, male; Abisko, labelled 4 vii 1917, (published as 1919, Tjeder, 1948), O. Ringdahl, Tjeder Collection, Zoological Museum, Lund, Sweden.

The type, which I borrowed in 1983, does not bear a collectors label. The genitalia had been removed to a genitalia vial on a separate pin. The left gonosyli are missing. The pinned part of the specimen has lost the right flagellum beyond the first segment, the middle left leg and the right hind leg beyond the first tarsomere.

VARIATION

The thoracic stripes vary from medium brown to grayish brown. There are slight differences in the shapes and spacing of the processes of the 9th tergite, the lateral processes are very small to apparently absent in some specimens.

DISCUSSION

Prionocera ringdahli and P. elliptica are sister species. See discussion under elliptica.

GEOGRAPHIC DISTRIBUTION (Map 11)

The range of this species seems to be quite limited, restricted to northern Fennoscandia and Russia. It has not been abundantly collected.

FLIGHT RECORDS: 17 June-2 July.

The flight season is probably longer than the few collection records suggest.

SPECIMENS EXAMINED (11 males, 7 females)

PALEARCTIC. FINLAND: ENONTEKION LAPPI: Le Pikko Malla, ♀, 3 vii 62, Björn Federly (ZMH). INARIN LAPPI: Utsjoki, ♂, 12, R. Frey (MAKB). KEMIN LAPPI: Kittilä, ♂, R. Frey

(ZMH); n Vuossa (?Vuotsa), ♀, 19 vi 66, Mittendorf (MAKB).

SWEDEN: NORBOTTEN: w Haparanda, 2♂, ♀, 17 vi 66, Mittendorf (MAKB). TORNE LAPPMARK: Abisko, 4♂, 4♀, 27 vi-1 vii 51, J.R. Vockeröth (CNC). ? LAPLAND: Halmäjäni, ♂, 2 vii 55, Birger Jensen (MAKB); Stoedalen, ♂, 2 vii 55, Birger Jensen (MAKB).

U.S.S.R.: MURMANSK: Ponoj (=Ponoy, 67°02'N 41°03'E), no. 4459, ♂, (ZMH).

Prionocera serricornis (Zetterstedt)

Tipula serricornis Zetterstedt, 1838: 843; 1851: 3969-3970; Wallengren, 1882: 17.

Prionocera serricornis; Tjeder, 1948: 88-90, fig. 1 (male terminalia), fig. 4 (male head), fig. 9 (male terminalia; Mannheims, 1951: 64-65, fig. 33 (from Tjeder, 1948, fig. 9).

Prionocera anceps Lackschewitz, 1933: 141, fig. 6 (male terminalia, antennae). (Synonymy by Tjeder, 1948: 88).

DIAGNOSIS

Very hairy, dorsal stripes brown, no nasus; male with

dorsal process of 9th tergite short, broad, extending almost to edge of tergite, space between two thirds or more width of process; apical process separated by evenly sclerotized area; female with dorsolateral edge of 8th sternite sloping, not lobed; hypogynial valvulae very short, broadly triangular, less than a quarter the length of 8th sternite; cerci short, broad, slightly upturned.

DESCRIPTION (figs. 22, 43, 59, 76)

ADULT. General description: distinctly brownish with hairs on head and thorax long, pale yellow to pale orange-yellow (89,73); male body length 9.9-11.4mm, wing length 11.6-14.4mm; female body length 10.8-14.6mm, wing length 12.3-15.4mm.

MALE. Head: vertex medium gray to light brownish gray (265,63), usually traversed by darker capillary line broadened medially, hairs long, subequal to postgenal hairs; gena light gray to medium gray (264,265), with two or three very short scattered hairs; rostrum grayish brown to dark grayish brown (61,62), light orange-yellow to deep yellowish brown (70,75) distally, not lightened ventrolaterally, with finer proclinate hairs, not projecting beyond tip; no nasus; pseudo-ocellus deep yellow-brown to brownish black (75,65).

Antenna: flagellomeres moderate brown to brownish

black (58,65), 1st only slightly longer than 2nd, subcylindrical base, strongly distended distoventrally; flagellomeres 2-9 distended, triangular in lateral profile, distal width of lower flagellomeres twice the width at base; 10th cylindrical; 11th tiny, cylindrical, less than one third the length of 10th.

Thorax: broad triangular region anterior to prescutal pit light yellowish brown to moderate orange-yellow (76,71); dorsal stripes glabrous, dark grayish yellowish brown to brownish black (81,65), median stripe narrowly bisected with brownish black to black (65,267), darker anteriorly, stripes bordered by light grayish yellowish brown to moderate yellowish brown (79,77) region bearing long pale hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes and borders or slightly grayer with long hairs; pleuron light bluish gray to medium gray (190,265), all segments, except for small katepimeron bearing long hairs; anatergite medium gray (265), katatergite light orange-yellow (70) on crest, olive gray (113) posteriorly.

Wings: membrane tinged with light grayish yellowish brown (79), costal and subcostal cells slightly darker; veins strong yellowish brown (74); stigma moderate orange-yellow (71), moderately contrasting with membrane; obliterative streak not strongly developed, broadly whitened at proximal end of stigma, narrower and less

conspicuous posteriorly, running almost perpendicularly through wing tip.

Legs: tarsal claws without teeth.

Abdomen: light grayish brown to grayish yellowish brown (60,80), dorsal longitudinal stripe dark grayish yellowish brown (81), tergites broadly edged laterally, narrowly edged posteriorly, in pale orange to dark orange-yellow (73,72); hairs slightly longer and more prominent ventrally.

Genitalia: tergite 9 with hairs confined to posterior third of tergite; dorsal process short, broad, extending laterally almost to edge of tergite, space between two thirds or more width of process; no lateral process; apical process broadly triangular, sharply pointed apex facing medially, not obscured by dorsal process, fused basally to evenly sclerotized area; rectal sclerite small, irregular, lightly sclerotized. Gonocoxites without protruding membrane ventrally; gonocoxal fragment broadly triangular. Outer gonostylus broadly oval, medial surface concave except for a narrow, poorly defined raised edge which becomes more prominent distally. Inner gonostylus with base broad, longer than distal beak; dorsal crest sloping towards short distal beak; distal beak more nearly parallel-sided, not ridged on medial surface, no pigmented sensilla; proximal beak small, broadly triangular. Aedeagus narrowly S-shaped

(viewed laterally), distal third bent ventrally, no subapical teeth. Aedeagal guide with short membranous, collar distally, dorsal plate flat, broader than aedeagus plus sheath.

FEMALE. Similar to male, except as follows: pedicel and base of 1st flagellomere usually lightened to dark orange-yellow (72), 1st flagellomere subcylindrical, 1.5 or less the length of 2nd; succeeding flagellomeres slightly distended, giving a serrate appearance; 10th & 11th subequal, smallest and cylindrical.

Genitalia: sternite 8 with rounded to sloping dorsolateral edge, not lobed; sternite longitudinally divided by narrow membranous area, broadening anteriorly and flanked by heavily pigmented area; hypogynial valvulae short, less than one-quarter (0.15-0.23, n=5) length of 8th sternite, broadly triangular, narrow at tip, bearing 1 or 2 subapical hairs (visible at 125 X magnification); tergite 9 somewhat rounded posterolaterally; sternite 9 with median projection short, about as long as broad; 10th tergite rounded distolaterally, without conspicuous hairs; cerci relatively broad, short, distal one-half slightly upturned.

TYPE SPECIMENS

The original description was apparently based on three males: 1, Sweden, Lapponia Tornensi, Juckasjervi, 25 June; 1, Karungi, in Salix flowers, 27 May; and 1, Finland, Alten, western alpine, 6 August. The specimen illustrated and designated as the lectotype by Tjeder (1948:88) was "the single (male) specimen of Tipula serricornis" which remained in the Zetterstedt collection, Museum of Zoology and Entomology, Lund University, Sweden. Tjeder noted that this specimen had no collection data and had been badly damaged by "mites", and that it agrees perfectly with Zetterstedt's description as far as can be judged from the specimen."

I examined the lectotype in 1983. Only part of the thorax and wings remain on the pin. The genitalia were in balsam, on a plastic mini-slide, pinned beneath the specimen. I removed them to glycerine in a genitalia vial because the specimen had been mounted laterally and important features were obscured. Zetterstedt described this fly as having four erect light coloured lobes distally on the anal segment. This is puzzling because this specimen has only two dorsal and no lateral processes. It must be assumed that Zetterstedt counted the apical processes which lie beneath the dorsal processes and are usually overlooked.

A headless specimen labelled "T. serricornis Zetterstedt, Alten," also in the Zetterstedt collection

and which may be the male from Finland referred to above, was determined as Tipula subnodicornis Zetterstedt by Tjeder (1948:90). I concur that this is not a Prionocera.

SYNONYMY

Lackschewitz (1933) described anceps as a new species having misapplied the name serricornis to the taxon here recognized as P. recta. Tjeder (1948) recognized anceps as a synonym of serricornis, and I concur.

I have seen the first two specimens listed by Lackschewitz as anceps. They are in the Zoological Museum Helsinki, and bear the following labels: (1) Lapponia/ J. Sahlbg./ 168/ Prionocera turcica / PRIONOCERA ANCEPS NOV. SP., LACKSCH./ Syntype and (2), Lapponia/ J. Sahlbg./ 124/ Prionocera serricornis / PRIONOCERA ANCEPS NOV. SP., LACKSCH./ syntype. The genitalia of specimen no. 124 are mounted on a plastic mini-slide pinned beneath the rest of the specimen.

DISCUSSION

Prionocera serricornis is the sister species of the nearctic P. ominosa. They differ most noticeably in the configuration of the 9th tergite. See discussion under ominosa.

In the palearctic region Prionocera serricornis is likely to be confused with P. recta and P. ringdahli which also have long dense hairs and distended flagellomeres. It differs from recta in being brownish rather than bluish gray, having a broader, shorter dorsal process and lacking a lateral process on the 9th tergite, and lacking a nasus. Prionocera serricornis differs from P. ringdahli also in having a broader dorsal process and by its shorter subcylindrical distal beak. The distal beak is broader and flattend in ringdahli. The hypogynial valvulae of the female are relatively longer in ringdahli.

GEOGRAPHIC DISTRIBUTION (Map 12)

This species is restricted to the palearctic and has been collected from northern Fennoscandia to Dudinka, U.S.S.R. (A female from Kamchatka, having the last two flagellomeres subequal, and relatively longer hypogynial valvulae, is here considered to be P. ominosa.)

Prionocera serricornis has been collected in the lower gray willow (Salix cinerea) and birch region (Tjeder, 1948).

FLIGHT RECORDS: 5 May-10 June.

SPECIMENS EXAMINED (13 males, 13 females)

PALEARCTIC: FINLAND: ENONTEKION LAPPI: Le Iso Mallo, 2♂, 28 vi-5 vii 62, Meinander (BONN, HEL). INARIN LAPPI: Ivalo Li, ♂, E. Thuneberg (ZMH). KEMIN LAPPI: Montell Muonia, 68°N 23°30'E, ♀, 5 v 25 (MAKB). KOILLISMAA: Kuusamo, ♂, R. Frey (lectotype of lackschewitzii, ZMH); Kuusamo Lehto, 2♂, 3♀, 18 vi 58, Fendler (MAKB).

SWEDEN: TORNE LAPPMARK: Abisko, 2♂, ♀, 30 vi-2 vii 55, Birger Jensen (MAKB); ♀, 10 vii 51, J.R. Vockeroth (CNC); Masugnsbyn, 2♂, 31 v 11, B. Poppius (ZMH); Lapland, 2♀, A. Roman (NRS). UPPLAND: Upl. PWg., ♀, no further data (NRS); 2♂, J. Sahlberg (syntypes of P. anceps ZMH); ♀, no further data (NRS).

U.S.S.R. ARCHANGELS: Archangelsk, 2♀, R. Frey (ZMH); Kusomen, ♂, R. Frey (ZMH). KRASNOYARSKIY: Dudinka, ♀, Wuorentaus (ZMH).

Prionocera setosa Tjeder

Prionocera setosa Tjeder, 1948: 86-88, fig. 8 (male terminalia); Mannheims, 1951: 63, fig. 30 (from Tjeder, 1948, fig. 8).

DIAGNOSIS

Sparsely hairy, more than half the pleuron bare; 9th tergite with narrow triangular dorsal process, tiny sublateral lateral process, apical process with three small rounded points on broadened tip.

DESCRIPTION (figs. 23, 44) (fig. 23 from Tjeder, 1948)

ADULT. General appearance: brownish gray, sparsely hairy, hairs on head and thorax short yellowish white (92); male wing length 12.32mm.

MALE. Head: vertex dark yellowish brown (78), divided by capillary black (267) line, hairs short, stiff, brownish black (65); gena light gray laterally to dark yellow brown (264, 78) medially, with inconspicuous short hairs; rostrum dark grayish brown (62), lightened to deep brown (56) laterally, brownish black (65) proclinate hairs dorsally projecting fringe-like beyond moderate (0.1mm) nasus, lateral hairs paler, longer; pseudo-ocellus dark brown (59).

Antenna: flagellum brownish black (65), flagellomeres slightly distended ventro-distally, distal width less than twice basal width, 1st flagellomere 1.5 length of 2nd; 11th relatively long, 0.7 length of 10th.

Thorax: no distinct yellowish triangular area anterior to prescutal pit; dorsal stripes glabrous, middle dorsal stripe dark yellowish brown (78), lateral stripes dark

grayish yellowish brown (81), middle stripe bisected by narrow line, stripes bordered by grayish yellowish brown (80) region bearing short yellowish white (92) hairs; postsutural area, scutellum and mediotergite light to dark gray (264, 266), with short hairs; pleuron light gray (264), almost bare, no hairs on anepisternum, lower half of anepimeron, and katepimeron; anatergite grayish yellow (90); katatergite pale yellow (89) dorsally, bluish gray (191) ventrally.

Wings: membrane tinged with light yellowish brown (76), costal and subcostal cells slightly darker; stigma deep yellowish brown (75); obliterative streak not strongly developed, beginning narrowly in Rs and running somewhat diagonally near wing tip.

Legs: no teeth on tarsal claws.

Abdomen: light grayish yellowish brown (79) with deep brown (56) dorsal longitudinal stripe; segments very narrowly edged in pale orange-yellow (73) distally, more broadly edged laterally; hairs short, yellowish white (92).

Genitalia: (based on description and figures of Tjeder, 1948: 86-87). 9th tergite with dorsal process narrow, triangular, somewhat medially bent, lateral process small, tooth-like, set in from tergite edge, apical process curved medially, with three small rounded

points on broadened tip; medial lobe broad, small, lying between dorsal and ventral process. Outer gonostylus somewhat slender with rounded apex. Inner gonostylus with broadly rounded base subequal in length to distal beak; dorsal crest broadly rounded; long narrow cylindrical and curved distal beak with several small pigmented sensilla along proximal edge; proximal beak a small thin lobe (see fig. 44). Aedeagus with small dorsal constriction distally, subapical dorsal tooth, no lateral tooth. Aedeagal guide with distal tip narrowly membranous; dorsal plate flat, short and narrow, subtended by small sclerotized attachment to sperm pump.

FEMALE. unknown.

TYPE SPECIMEN

Holotype, male, Abisko, 4 vii 1917, O. Ringdahl, Tjeder Collection, Zoological Museum, Lund Sweden.

The type, which I saw in 1983, had no collector's label. The genitalia had been removed, and placed in a genitalia vial on a separate pin. (Unfortunately this vial could not be located, Dr. Roy Danielsson, pers. comm.). Only the left hind leg remains on the pinned specimen. Small patches of minute silvery scale-like highly reflective material is stuck to the pleural segments of the abdomen.

DISCUSSION

Prionocera setosa is most closely related to P. subsericornis as pointed out by Tjeder (1948). Both species have a distinctive and very similar inner gonostylus and a similar medial lobe on the 9th tergite. They are both sparsely hairy, with the pleuron more than half bare, they have a moderate nasus, and the flagellomeres in the male are not strongly distended, and less so in the female.

They are distinguished by differences in the dorsal and lateral lobes of the 9th tergite. In setosa these lobes are not subequal but the dorsal lobe is longer and the lateral shorter than in subsericornis.

Tjeder described this specimen as being "hairy (on the) thorax sides, (and) the coxae have a long and denser hairity. Analagous hairity occurs also in (proxima) but hardly so dense as in this species." The specimen which I saw had almost a bare pleuron similar to subsericornis, except for hairs on the katepisternum and a few straggly hairs below the wing base on the anepimeron. The coxae, contrary to the original description, are no more hairy than in subsericornis.

MATERIAL EXAMINED (Map 13)

SWEDEN: TORNE LAPPMARK: Abisko, male (holotype), 4 vii 17, O. Ringdahl (ZMLS).

Prionocera sordida (Loew)

Stygeropis sordida Loew, 1863: 298; 1864: 182; Alexander, 1919: 9.

Prionocera sordida; Alexander, 1936: 274 (possibly misidentified); 1942: 220; 1965: 19.

DIAGNOSIS

A very small brown hairy fly known only from the female. Dorsolateral edge of 8th sternite rounded, not lobed; hypogynial valvulae short, triangular with a narrow sclerotization ventrally; cerci slightly to strongly upturned distally.

DESCRIPTION (figs. 60, 77)

ADULT. General appearance: deep yellowish brown with abundant long pale yellow (89) hairs; small, body length 6.7-11.4mm, wing length 8.8-10.9mm.

FEMALE. Head: vertex light grayish brown to light brown (60,57), divided by moderate brown (58) line, hairy, posterior hairs longer; gena yellowish gray (93),

pubescent, lacking hairs; rostrum moderate brown (58) to light yellowish brown (76) distally, not contrastingly lightened laterally, with proclinate hairs, hairs projecting beyond moderate (0.075mm) nasus; pseudo-ocellus strong brown (55).

Antenna: flagellum moderate brown (58); scape, pedicel, 1st and 2nd flagellomeres with several longer darker hairs dorsally; 1st less than 1.5 length of 2nd, somewhat constricted medially; 2nd and 3rd slightly distended ventrodistally, succeeding segments progressively smaller and more nearly cylindrical; 10th & 11th smallest, subequal.

Thorax: prescutal pit not forming apex of triangular yellowish region; dorsal stripes glabrous, deep yellowish brown (75), median stripe bisected by a paler line, stripes bordered by light yellowish brown (76) bearing pale hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes, bearing long pale hairs; pleuron brownish pink (33) to moderate reddish brown (43) on katepisternum; all segments except small katepimeron with long pale hairs; anatergite dusky moderate reddish brown (43); katatergite broadly pale orange-yellow (73) dorsally, dusky moderate reddish brown (43) ventrally.

Wings: membrane tinged with light grayish yellowish brown (79), veins brownish orange (54); stigma paler, moderate orange (53), costal and subcostal cells very

slightly darker; obliterative streak not strongly contrasting with membrane, beginning in proximal half of stigma, crossing wing obliquely near tip.

Abdomen: light brown to moderate brown (57,58), segments bordered with yellowish white (92) distally and laterally; darker dorsal stripe not apparent.

Genitalia: sternite 8 with dorsolateral edge broadly rounded, not lobed; hypogynial valvulae short, one quarter the length of sternite 8, separated from it by small squarish membranous region; valvulae triangular in lateral profile, tip narrow, ventral edge narrowly sclerotized, no subapical hairs; tergite 9 rounded posterolaterally; sternite 9 with short broad medial projection; tergite 10 not rounded laterally, inconspicuously hairy; cerci moderately broad, slightly to strongly upturned.

TYPE SPECIMENS

Loew (1863) described sordida from a female sent to him by Osten Sacken. Two females, each labelled "Type no. 10320", and bearing green labels "Winnip/Kennic" (collected by Kennicott in Winnipeg), (are in the collection at the Museum of Comparative Zoology, Cambridge, Massachusetts. The smaller specimen also bears a handwritten label "sordida/ m", probably written

by Loew (see ~~Osten Sacken~~, 1903). However, according to the measurements given in the type description (see Appendix B), the larger specimen fits the description more closely and has accordingly been selected as the lectotype.

The lectotype has no legs, and only the scape and pedicel remain on the left antenna; but the right antenna is intact. The paralectotype lacks fore legs, the mid right leg has a femur, tibia, and part of the 1st tarsomere, and the entire hind leg remains. The right antenna is present but only the scape and pedicel remain on the left; the tip of the ovipositor was broken off. Both specimens have had genitalia removed, softened, placed in glycerine in microvials, and pinned beneath their respective specimens.

DISCUSSION

Prionocera sordida is the smallest and palest species in this genus. Since females are generally the larger sex, it is to be expected, that the male when found, might be even smaller. Loew, in naming this species, described a dark fly, hence the name "sordida". This discrepancy may be due to fading.

Females in this genus are difficult to identify. The syntypes of sordida are very similar to several other

species, therefore it was necessary to dissect the genitalia for a more detailed study. This species, by virtue of its long hairs, nasus, weakly developed obliterate streak, short hypogynial valvulae, upturned cerci and small size is very similar to P. pubescens. However it differs from the latter in having a small squarish membranous region proximal to a much narrower sclerotization on the hypogynial valvulae.

The females of P. naskapi (the sister species of P. pubescens) and of P. cryptica are still not known. It is possible that P. sordida may be found to be conspecific with either one of these species.

SPECIMENS EXAMINED (Map 13)

CANADA: MANITOBA: Winnipeg, Kennicott, 2 females (MCZ).

Prionocera subsericornis (Zetterstedt)

Tipula subsericornis Zetterstedt, 1851: 3970-3971;

Wallengren, 1882: 18.

Prionocera subsericornis; Tjeder, 1948: 83-85, fig. 6

(male terminalia); 1955: 242-243; Mannheims, 1951:

61-62, fig. 28 (from Tjeder, 1948, fig. 6); Kloet &

Hincks, 1976: 1.

Prionocera turcica; Bergroth (nec Fabricius, 1781), 1889: 120; Mik, 1890: 154; Kertész, 1902: 279.

Prionocera proxima Lackschewitz, 1933: 135-136, fig. 2 (male terminalia, antennae); Tjeder, 1948: 85-86, fig. 7 (male terminalia); 1955: 242-243; Mannheims, 1951: 62-63, fig. 29 (from Tjeder, fig. 7). (new synonymy)

DIAGNOSIS

Male 9th tergite with very short triangular dorsal and lateral processes, medial lobe present; female with rounded dorsolateral lobe on 8th sternite, cerci narrow, downturned distally; hairs of head, thorax and abdomen short, yellowish white, not dense; pleuron almost bare.

DESCRIPTION (figs. 24, 44, 61, 78)

ADULT. General appearance: bluish gray to brownish gray with short, sparse yellowish white (92) hairs; male body length 9.7-12.3mm, wing length 10.5-13.5mm; female body length 11.3-15.5mm, wing length 11.6-17.6mm.

MALE. Head: vertex dark yellowish brown to olive brown (78,96), usually divided by capillary black (267) line, hairs short, stiff brownish black (65); gena yellowish white to light yellow (92,86) with inconspicuous short hairs; rostrum dark grayish brown to brownish black (62,65), lightened to moderate orange-

yellow (71) laterally on most specimens; base of rostrum bare dorsally, with short, stiff brownish black hairs (65) on distal two thirds, longer hairs projecting beyond moderate (0.125-0.175mm) nasus, lateral hairs paler and longer; pseudo-ocellus dark yellowish brown to brownish black (78,65).

Antenna: flagellum brownish black (65), flagellomeres slightly distended ventrodistally, distal width less than twice basal width; 1st flagellomere 1.5 or less the length of 2nd; 11th very narrow, one-half length and width of 10th.

Thorax: prescutal pit not forming apex of a broad yellowish triangular area; dorsal stripes glabrous, dark bluish gray to dark yellow brown (192,78), median stripe bisected by narrow line, stripes bordered by bluish gray (191) or yellowish gray (93), borders of stripes with short hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes, bearing long hairs; pleuron light bluish gray to bluish gray (190,191); almost bare, no hairs on katepimeron and on lower half of anepimeron; anatergite dark grayish yellow to pale yellow (91,89); katatergite pale yellow (89) dorsally, light bluish gray (190) ventrally.

Wings: membrane tinged with light yellowish brown (76), including costal and subcostal cells; veins and stigma deep yellowish brown to dark orange yellow.

(75,72); oblitative streak weakly developed in most North American specimens, beginning narrowly in R1 and running obliquely near wing tip, in European specimens proximal half of stigma yellowish white (92) included in a broader oblitative streak, bases of radial cells more strongly infumed, emphasizing streak.

Legs: tarsal claws with small tooth near base.

Abdomen: bluish gray (191) with deep brown (56) dorsal longitudinal stripe; segments edged in pale orange-yellow to grayish yellow (73,90); hairs short.

Genitalia: tergite 9 fine hairs on distal half; dorsal and lateral processes subequal, small, triangular, dorsal process somewhat medially bent; apical process narrow, sharply, curved medially; medial lobe short, broad, lying between dorsal and apical processes; rectal sclerite long, narrow, weakly sclerotized. Gonocoxites with small protruding membrane ventrally and proximally; gonocoxal fragment narrowly triangular. Outer gonostylus broadly triangular to broadly emarginate dorsally, almost "L-shaped"; medial surface with basal two thirds concave, with a raised edge, broader distally. Inner gonostylus with broadly rounded base subequal in length to distal beak; long, narrow, cylindrical, slightly curved, distal beak, with several (7-12) small pigmented sensilla along proximal edge; dorsal crest broadly rounded; proximal beak small, flattened lobe on lateral surface. Aedeagus

almost straight distally, with small dorsal tooth near tip, sometimes with smaller lateral tooth proximal to dorsal tooth. Aedeagal guide narrowly membranous at tip, dorsal plate flat, broader than aedeagus plus sheath.

FEMALE. Similar to male, except as follows: flagellomeres cylindrical, not distended; pedicel distally and base of 1st flagellomere lightened to strong brown (55); 1st flagellomere less than 1.5 length of 2nd; 10th and 11th slightly narrower than preceding, subequal in length and width.

Genitalia: Sternite 8 with rounded dorsolateral lobe, separated from hypogynial valvulae by narrow "W-shaped" membranous region; hypogynial valves one-half length of sternite 8, evenly sclerotized ventrally, tip broad, square-edged, single subapical dorsal hair extending beyond hypogynial valves (visible with 60 X magnification); tergite 9 not rounded posterolaterally; sternite 9 with medial projection longer than broad; tergite 10 with lateral edges almost straight, not hairy; cerci relatively long, narrow, downcurved distally.

TYPE SPECIMENS

Tipula suberricornis Zetterstedt was described from a male and a female from boreal Scandinavia. Only the male, labelled: "INTER SUUL et KONCSTUE/ Ing. Alp. Norv./

16-7 40" was found, and selected by Tjeder (1948: 83) as the lectotype.

When I studied this specimen in 1983 it had signs of insect damage (dermestid larval hairs clinging to the specimen and frass stuck to the pin). The genitalia were embedded in balsam on a mini-slide pinned beneath the rest of the specimen. Both antennae were broken; no flagellomeres remained on the right antenna and only the 1st remained on the left. All legs but the left front leg were missing, and only the right wing remained showing a stigma moderately contrasting with the oblitative streak.

SYNONYMY

Lackschewitz (1933) described P. proxima as new, having misapplied the name "subsericornis Zetterstedt" to another species. (The latter species was subsequently named tjederi by Mannheims (1951)). No holotype was designated. The description of proxima was based on many specimens collected in Germany, Austria, Finland and U.S.S.R. The lectotype, selected by Mannheims (1951), which I have not seen, is a male from Germany, Insel Usedom, Ahlbeck, 14-22 viii 23, Zerny. It is in the Naturhistorisches Museum Wien (Vienna, Austria).

However, I have seen five males from northern Finland and one male from Trifona, U.S.S.R., with Lackschewitz's

label, including a dissected specimen from Enari, Finland, bearing a red (type?) label.

VARIATION.

I had the advantage of studying a broad ranging series of specimens collected across North American and from the west coast of Alaska to the east coast of Labrador, and from England, Sweden, Finland, Germany, and Russia. My conclusion is that only one species is involved here. Prionocera subsericornis was differentiated from P. proxima by Tjeder (1948) on the basis of an angulated outer gonostylus, both a single dorsal and a pair of lateral subapical teeth on the aedeagus, and a larger moveable apodeme on the sperm pump. Some, but not all, of the northern Fennoscandian specimens have a distinctly angulated outer gonostylus, as in the type of subsericornis. But several specimens from Abisko are not angulated and are of the "proxima" type and others seem to be intermediates between the two. Two specimens from Finland (Hailuoto and Kittilä) among Lackschewitz's proxima material have a distinctly angulated outer gonostylus suggesting that Lackschewitz, also, considered this to be a variation within a single species.

Most specimens examined from both the Palearctic and Nearctic have a very slight lateral thickening on the aedeagus just proximal to the more pronounced dorsal

tooth. This thickening marks the distal end of a membranous aedeagal sheath. In some specimens it is more pronounced, hence more tooth-like. However, this is not correlated with the angulated outer gonostylus as suggested by Tjeder.

The blade of the moveable apodeme is also somewhat variable in shape from broadly rectangular to more fan-shaped.

The palearctic specimens tend to have clearer wings and a more contrasting oblitative streak and stigma, with a broader section of R1 included in the oblitative streak. In most nearctic specimens the oblitative streak starts just posterior to R1 and the wing membrane is more infumed. Several European specimens (Sweden, U.S.S.R.) have a more infumed wing and a weaker oblitative streak, similar to most North American specimens.

There are many minor variations in the width, length, and angle of of the dorsal and lateral processes of the 9th tergite. As in all species of this genus, differential drying tends to exaggerate these differences.

The rostrum is contrastingly lightened laterally in most nearctic specimens and more or less concolorous in most palearctic specimens. Examples of both types can be

found on each side of the Atlantic. And in several Swedish and Alaskan specimens the dorsal rostral hairs are longer and paler, similar to, rather than contrasting with the lateral and ventral rostral hairs.

DISCUSSION

Prionocera subsericornis is probably closely related to P. setosa, judging from Tjeder's illustrations (1948:87). It differs most strikingly from the latter in the shape of the processes on the 9th tergite. The apical process has three points in setosa, but only a single sharp point in subsericornis. The dorsal process is somewhat larger and the lateral process shorter than in subsericornis.

Prionocera subsericornis and P. setosa share the following characteristics with P. dimidiata and P. abscondita. (1) Shorter and not so dense hairs on the head and thorax. (2) Flagellomeres not strongly distended. (3) Well-developed median lobe. The median lobe may be an apomorphic character indicative of close relationships. The other two characters would seem to be plesiomorphic.

The dorsal and lateral processes of P. subsericornis may be homologous to the mediodistal and laterodistal corners respectively of the dorsal process of such

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species as dimidiata, ominosa, serricornis and unimicra. If this is the case, there are no true lateral processes in this species.

GEOGRAPHIC DISTRIBUTION (Map 14)

This is one of the more widely dispersed species. In North America it extends south of tree-line, from western Alaska to Labrador, and as far south as the Rocky Mountains in Colorado. In Europe it extends as far south as southern England, Germany and Poland. A single specimen was collected from Kamchatka.

It is found in marshy ground near water (Tjeder, 1948)

FLIGHT RECORDS: 8 June-2 August (September)

Most specimens were collected from the middle of June to the end of July. There is an unusually late record of a specimen from Rheinland, Germany, labelled "vii-xi, 1946".

SPECIMENS EXAMINED (131 males, 65 females)

NEARCTIC. CANADA: ALBERTA: Bilby ♂, 22 vi 24, O. Bryant (UMMZ) Nordegg, ♀, 5 vii 21, J. McDonnough (CNC). LABRADOR: Nutak, ♀, 23 vii 54, E.E. Sterns (CNC); ♂, 23 vii 54, J.F. McAlpine (CNC). MANITOBA: Churchill, 5♂, ♀,

12-13 vii 78, F. Brodo (CNC); 6♂, 2♀, 25 vi-9 vii 77, F. Brodo (CNC); 6♂, 2♀, 12-29 vii 52, J.G. Chillcott (CNC); 2♂, ♀, 13 vii 50, J.A. Shemenchuk (CNC); 3♂, 8 vi 49, J.B. Wallis (CNC); ♂, 4♀, 19-29 vii 50, H.J. Teskey (CNC); ♂, 22 vi 49 (no further data) (CNC); ♂, 14 vii 51 (no further data) (CNC); 25 mi E Churchill, 15♂, 6♀, 1-4 vii 77, F. Brodo (CNC); Fort Churchill, 2♂, 23 vi 52, C.D. Bird (CNC); 14♂, 5♀, 20 vi-10 vii 52, J.G. Chillcott (CNC); Warkworth Creek, nr. Churchill, 19♂, 7♀, 21 vi-7 vii 52, J.G. Chillcott (CNC). NORTHWEST TERRITORIES: Mackenzie Distr.: Aklavik, 2♂, ♀, 29 vi-23 vii 56, R.E. Leech (CNC); 4♂, ♀, 17-21 vi 53, C.D. Bird (CNC); Yellowknife, ♀, 29 vi 49, R.R. Hall (CNC); ♀, 16 vii 49, Fr. Ebner (CNC); ♂, 20 vi 66, G.E. Shewell (CNC); nr. Wholdaia Lake, 61°01'N 103°40'W, ♀, 6 vii 66, J.G. Chillcott (CNC). ONTARIO: James Bay, Fort Albany, 7♂, 2♀, 10 vi-2 vii 42, F.A. Urquart (UMMZ). QUEBEC: Poste de la Baleine, Ile de la passe, 3♂, 8 vii 71, (in alcohol) (MPUL); Rupert House, 51°30'N 78°45'W, ♀, 30 vii 49, E.J. LeRoux (CNC). YUKON: Gravel Lake, km 626 Klondike Hwy, 63°49'N 137°54'W, 2♂, 2 vii 79, S.G. Cannings (SUBC); Swim Lakes, 133°N 62°13'W, 3200', ♂, 18 vi 60, E.W. Rockburne (CNC). "Hudson Bay Territory", 2♂, ♀, Osten Sacken (MCZ).

U.S.A.: ALASKA: Katmai, ♀, 10 vi 19, J. Hine (OSU); King Salmon, Naknek R., 6♂, 3♀, 20-23 vii 52, W.R. Mason (CNC); ♀, 19 vii 52, J.B. Hartley (CNC); Kotzebue, 4♂, 27

vi 56, P.R. Ehrlich (SEM); McKinley Nat'l. Pk., 10♂,
20-26 vi 57, G.W. Byers (SEM); Savonoski, Naknek L., 2♂,
♀, vi 19, J. Hine (OSU). COLORADO: Chaffee Co., No. 4,
Cottonwood Lake, 9600', 10 mi. W Buena Vista, ♀, 17 viii
65, G.W. Byers (SEM); Rocky Mt. Nat'l. Pk., Dream L.,
10,000', 2♂, ♀, 18 vii 41, C.P. Alexander (allotype and
paratypes of fulvicauda Alexander, paratypes on two
slides, No. 6462, Alexander Coll. USNM).

PALEARCTIC: GERMANY (B.R.D): Hamburg, ♂, ♀, 7 v, 8 vi
46, O. Kröber (MAKB); (Hamburg?) Stadtpark, ♀, 10 v 46
(MAKB); Rheinland, ♀, viii-xi 46, E. Schmidt (MAKB).

FINLAND: ENONTEKION LAPPI: Le Iso Mallo, ♂, ♀, 28 vi
62, M. Meinander (ZMH); Kilpisjarvi, 60 km SO, 3♂, 2 ♀, 3
vii 58, Fendler (MAKB); Le Markkina, ♀, 2 vii 62, M.
Meinander (ZMH); Le Palojoensuu, 3♂, 2 vii 62, M.
Meinander (ZMH). INARIN LAPPI: Utsjoki, ♂, R. Frey
(MAKB). KEMIN LAPPI: Enare (=Inari), ♂, Hellén (ZMH);
Kittilä, ♂, A. Nyman (ZMH). POHJOIS-POHJANMAA: Hailuoto,
♂, Wuorentaus (ZMH); Tervola, ♀, L. Johnsson (ZMH).
VARSINAIS-SUOMI: Ab Korpo Jurmo, ♂, 9 viii 60, K.M.
Meinander (ZMH); Kuustö, ♂, Lundström (ZMH).

NORWAY: HORDALAND: Hardangervidda, Vivelí-Veigdalen,
Eidfjord, lak. nr. D VI, 1000 m, ♂ (alcohol), 22 vii 67,
K. Bjorklund (ZMUB); ♀ (alcohol) same data, lak. nr. 60,
280m, 17 vii 67, J. Wieken (ZMUB).

POLAND: Rothenberg a. Oser (=Czerwiensk), ♀, 10 v 46 (MAKB).

SWEDEN: NORBOTTEN: Granvik, ♂, ♀, 26 vii 51, Vockeroth (CNC) Haparanda, 3♂, 2♀, 17 vi 66, Mittendorf (MAKB); Lovikka, 5♀, 23 vii 51, Vockeroth (CNC); 67°58'N 23°38'E, ♀, 25 vii 51, Vockeroth (CNC). TORNE LAPPMARK: Abisko, 4♂, 2♀, 23 vi-8 vii 51, J.R. Vockeroth (CNC); Karesuando, 2♀, 25 vii 51, Vockeroth (CNC). UPPLAND: Hlm (=Stockholm Region), ♂ (NRS). VASTERGOTLAND: Göteborg, 2♂, 7 vii 66, Mittendorf (MAKB). Lapland, no further data, ♂, (NRS).

U.K.: ENGLAND: Catfield, ♂, 9 viii 20, J.J.F. -X. King (BMNH).

U.S.S.R.: KAMTSCHATKA: Bolscherjetsk, ♂, 2♀, 27 vi-7 viii 17, Y. Wuorentaus (ZMH). LATVIA: Curon, Paplakia (=Kurland, Paplaka), ♂, 25 v 27, Lackschewitz (MAKB). MURMANSK: Trifona (=Pechanga), 2♂, Hellen (ZMH).

Prionocera tjederi Mannheims

as Prionocera subsericornis; Lackschewitz, 1933:

139-141, fig. 5 (male genitalia, antennae), (nec Zetterstedt, 1851):

as Prionocera pubescens; Tjeder, 1948: 95-96, fig. 13 (male terminalia), (nec Loew, 1844).

Prionocera tjederi Mannheims, 1951: 70-71, fig. 38 (from

Tjeder, 1948, fig. 13).

DIAGNOSIS

An almost clear-winged fly with stigma and obliterative contrasting with membrane; streak; pleuron almost bare, no hairs on anepisternum, anepimeron and katepimeron; flagellomeres distended; inner gonostylus of male with a protruding almost circular ventrodiscal edge.

DESCRIPTION (figs. 25, 45, 62, 79)

ADULT. General appearance: dark gray to dark brown with short yellowish white (92) hairs, not conspicuously hairy; male body length 8.3-12.5mm, wing length 11.3-16.3mm; female body length 13.7-17.5mm, wing length 14.7-17.6mm.

MALE. Head: vertex dark yellow brown (78), sometimes divided by darker capillary line, hairs short, shorter than postgenal hairs; gena light bluish gray (190) with scattered short hairs; rostrum dark grayish yellowish brown to brownish black (81,193) sometimes lightened to deep yellow brown (75) laterally, with long proclinate hairs dorsally and projecting beyond moderate (0.175-.225mm) nasus; pseudo-ocellus medium yellow brown to dark grayish yellowish brown (77,81).

Antenna: flagellum dark yellowish brown to brownish black (78,65), 1st flagellomere less than 1.5 length of 2nd, lightened basally, abruptly distended ventrodistally, dark hairs on dorsal edge; proximal flagellomeres strongly produced ventrodistally; 10th cylindrical, longer than 9th; 11th tiny, one-fourth length of 10th.

Thorax: contrasting light orange-yellow to strong brown (70,55) triangular region anterior to prescutal pit; dorsal stripes dark yellowish brown to dark gray to blackish blue (78,266,188), median stripe narrowly bisected by lighter capillary line, stripes bordered by dark gray to light gray (266,264) region bearing short hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes, with short hairs, not conspicuously hairy; pleuron light bluish gray to dark grayish blue (190,187), almost bare, katepisternum with hairs, no hairs on anepisternum, anepimeron and katepimeron; anatergite light grayish brown to dark grayish brown (60,62); katatergite pale yellow (89) dorsally, bluish gray (191) ventrally.

Wings: membrane tinged with yellow-gray (93), costal and subcostal cells grayish yellow (90); veins dark yellowish brown (78); stigma deep yellowish brown (75) distally, paler proximally; oblitative streak including proximal part of stigma, contrasting with membrane,

almost perpendicular to wing axis.

Legs: tarsal claws with sharp basal tooth.

Abdomen: light brownish gray to bluish gray (63,191) with dark brown (59) dorsal longitudinal stripe; segments edged in pale yellow to grayish yellow (89,90); hairs short, appressed.

Genitalia: tergite 9 (obscured by 8th segment in dried specimens, usually only tips of dorsal process visible); hairs extending to middle of tergite laterally, restricted to base of processes medially; dorsal process laterally directed, slightly longer than broad; no lateral process; apical process broad at base, sharply narrowed and medially curved distally; medial lobe broadly fused to bases of apical processes; rectal sclerite triangular. Gonocoxites without protruding membrane ventrally; gonocoxal fragment broad, subtended by small squarish sclerite. Outer gonostylus broadly triangular, concave medially except for slightly raised distal tip. Inner gonostylus with basal region longer than broad, lateral surface with prominent ridge distal to longitudinal depression; a protruding, almost circular ventrodiscal edge; dorsal crest gently curved; distal beak short, narrow, without pigmented sensilla; proximal beak rectangular. Aedeagus curved ventrally at tip (viewed laterally), without subapical teeth. Aedeagal guide projecting collar-like posteriorly, usually visible

beyond distal edge of gonocoxites, dorsal plate flat, broad.

FEMALE. Similar to male, except as follows: 1st flagellomere shorter than scape, often narrowed proximal to expanded tip; succeeding flagellomeres slightly distended ventrodistally, giving a serrate appearance; 10th & 11th narrower, cylindrical and subequal.

Genitalia: sternite 8 with dorsolateral edge broadly rounded, not lobed; hypogynial valvulae short, one-third length of sternite 8, separated from sternite by small narrow w-shaped membranous region; ventral edge of valvulae narrowly sclerotized, bearing single short subapical hair dorsally on rounded tip (visible with 125 X magnification); tergite 9 not rounded posterolaterally; sternite 9 with medial projection short and broad; tergite 10 rounded laterally, not conspicuously hairy; cerci relatively short, broad and slightly upturned at tip.

TYPE SPECIMENS

Holotype, male, Dalarna, Orsa, O. Rådsjön, 14 vi 1967, Bo Tjeder, in Tjeder Collection, Zoological Museum, Lund, Sweden.

This species had been misidentified, redescribed and illustrated as P. pubescens by Tjeder (1948), based on two males collected in the province of Dalarna, Sweden. Mannheims (1951) recognized this as a new species and selected the male from Orsa as "lectotype". The specimens so selected should have been designated the holotype because Mannheims was the original author of a new species.

Of the specimens sent to me from Lund in 1983, courtesy of Dr. Bo Tjeder and Dr. Roy Daniellson, I saw the male genitalia of the specimen designated as lectotype by Tjeder, in a vial labelled "Prionocera tjederi, Lectotype, Orsa O. Rådsjön." There was an accompanying pinned male specimen from which the genitalia had been removed, bearing the labels: "Dlr. LIMA, TANDALEN, E. DAHL/ Prionocera pubescens det Bo Tjeder/ (red label) Lectotypus , Prionocera Tjederi Mnhs., design. 1952, Mannheims." This latter specimen is not the one specifically selected as "lectotype" by Mannheims (1951:71). I have therefore seen only the genitalia of the type of tjederi and not the rest of that specimen.

SYNONYMY

Lackschewitz (1933) misidentified this species as subsericornis Zetterstedt, and suggested that it is

conspecific with Prionocera pubescens Loew. Tjeder (1948), having had the benefit of studying Zetterstedt's types, correctly identified P. subserricornis and distinguished it from this taxon which he presumed to be P. pubescens (Loew). It was unfortunate that he was unable to study Loew's type material.

VARIATION

The European specimens tend to be darker gray and with less of a brownish tinge on the thorax. Tjeder attributes the darker colouration of his specimen from Lima to its being "somewhat immature". In my experience with crane flies in general, and this genus in particular, teneral specimens are paler, usually light to medium brown.

DISCUSSION

Prionocera tjederi is probably closely related to P. pubescens and has often been confused with the latter, as noted above. The male genitalia of these two species are very similar. The inner gonostylus in tjederi has a distinctive rounded and somewhat protruding ventrodistal edge and a strong ridge on its lateral surface. In pubescens these features are lacking, but on the lateral surface of its inner gonostylus there is a characteristic

densely haired circular patch not present in tjederi. Prionocera tjederi is almost bare and has a distinct nasus, whereas pubescens is conspicuously hairy and its the nasus is very small and knob-like.

GEOGRAPHIC DISTRIBUTION (Map 15)

Prionocera tjederi does not seem to be as abundant or as widespread as some of the other holarctic Prionocera. In north America it has not been collected east of Hudson Bay, and never in great numbers. I have only seen Palearctic material from Sweden and Finland. Lackschewitz cited speciens (as subsericornis) from Germany, Austria, East Baltic and Estland (Estonia) and U.S.S.R. However he did not know P. pubescens, a species which extends further south and is easily confused with tjederi (see above), hence his citations are suspect.

The Swedish specimens were collected in Sphagnum bogs along with Carex and Eriophorum (Tjeder, 1948).

FLIGHT RECORDS: 5 June-31 July.

SPECIMENS EXAMINED (21 males, 12 females)

NEARCTIC. CANADA: NORTHWEST TERRITORIES: Mackenzie Distr.: near Beechey Lake, 65°14'N 106°50'W, ♂, 11 vii

66, G.E. Shewell (CNC); Fort McPherson, 3♂, 3♀, 24-26 vi
57, R. Hurley (CNC); 2♂, 24 vi 57, S.D. Hicks (CNC);
Muskox Lake, 64°45'N 108°10'W, 2♂, ♀, 12, 31 vii 53, J.G.
Chillcott (CNC); same data, ♂ (SEM); Salmita Mines,
64°05'N 111°15'W, 2♂, ♀, 24 vi -4 vii 53, J.G. Chillcott
(CNC).

U.S.A.: ALASKA: Umiat, ♀, 5 vi 47, Knight, Schultz
(UMMZ).

PALEARCTIC. FINLAND: ENONTEKION LAPPI: 60 km S
Kilpisjärvi (=Enontekiö), ♂, 3 vii 58, Fendler (MAKB).
ETELA-HAME: Koijarvi, ♀, 16 vi 64 (MAKB); Somero, ♂, 21
vii 64, J. Kuusinen (MAKB). INARIN LAPPI: Enari (=Enare-
Inari), ♂, 4 vii 56, Nylander (ZMH). KEMIN LAPPI:
Muonio, ♂, Palmén (MAKB); Pallastunturit, ♀, 26 vii 51,
J. Kaisila (ZMH).

SWEDEN. DALARNA: Lima, Tandålen, ♂, 30 vi 31 (no date
with specimen, lacking genitalia, as pubescens, Tjeder,
1948:95), E. Dahl (ZMLS); Orsa, O. Rådsjön, ♂, 14 vi 37
(no date nor collector with specimen, genitalia only, in
vial), Bo Tjeder (ZMLS). LYCKSELE LAPPMARK: 50 km N
Storuman, 2♂, ♀, 15 vi 66, Mittendorf (MAKB). TORNE
LAPPMARK: Abisko, ♂, 22 vi 51, J.R. Vockeroth (CNC).
NORBOTTEN: 67°58'N 23°31'E, 2♂, 2♀, 25 vii 51, J.R.
Vockeroth (CNC); Pajola Rutijarvi, ♀, 22 vii 51, J.R.
Vockeroth (CNC).

Prionocera turcica (Fabricius)

Tipula turcica Fabricius, 1781: 237; 1787: 322; 1794:
237; 1805: 27.

Prionocera turcica; Mik, 1890: 76; Kertész, 1902: 279;
Lackschewitz, 1933: 133-135, figs. 1a,b,c (male
terminalia, antennae); Tjeder, 1948: 81-82, fig. 5
(male terminalia); 1955: 242-243; Mannheims, 1951:
60-61, fig. 27 (from Tjeder, 1948, fig. 5); 1963: 39;
Kloet & Hincks, 1976: 1.

Tipula diana Meigen, 1818: 189, Tab. VI, fig. 8 (female);
1851: 149-150; Schummel, 1833: 85, Tab. I, figs.
9,12,13 (male antenna, genitalia); Zetterstedt, 1851:
3966-3967; Wallengren, 1889: 17.

Stygeropsis diana; Schiner, 1864: 521; Mik, 1889: 101-103.

DIAGNOSIS

Male 9th tergite broadly emarginate between long,
tapering dorsal and lateral processes, dorsal process
slightly broader at base than lateral process; dorsal
plate of aedeagus expanded dorsally bearing 3 or 4 small
irregular teeth; female with broad dorsolateral lobe on
8th sternite; hypogynial valvulae two-thirds length of
8th sternite, square-tipped, bearing one or more
subapical hairs.

DESCRIPTION (figs. 26, 46, 63, 80)

ADULT. General appearance: predominantly gray to grayish brown with short pale yellowish white (92) hairs, not conspicuously hairy; male body length 7.6-13.6mm, wing length 10.5-16.7mm; female body length 12.3-16.0mm, wing length 14.2-17.3mm.

MALE. Head: vertex dark yellowish brown (78), usually divided by capillary black line, hairs yellowish white to grayish yellow (92,90), shorter than on postgena; gena pale yellow, pale orange-yellow or light gray (89,73,264), with very short scattered hairs; rostrum dark grayish brown to dark brown (62,59) dorsally, contrastingly lightened to dark orange-yellow (72) laterally, hairs brownish black (65) projecting beyond comparatively large (0.10-0.15mm) nasus; pseudo-ocellus black to dark grayish brown (267,62).

Antenna: dark grayish brown to brownish black (62,65), flagellomeres only slightly distended; 1st less than 1.5 length of 2nd; 11th one-third length of 10th.

Thorax: prescutal pit not forming apex of a broad yellowish triangular region; dorsal stripes glabrous, dark gray to dark grayish brown (266,62), median stripe usually brownish, narrowly bisected with light grayish yellowish brown to light gray (79,264) line, stripes bordered by light bluish gray to light grayish yellowish

brown (190,79) region bearing hairs; postsutural area, scutellum and mediotergite concolorous with lateral stripes, not conspicuously hairy; pleuron light bluish gray (190), epimeron and parts of episternum sometimes pale orange-yellow (73), hairs on all pleural segments except katepimeron; anatergite grayish brown to light yellowish brown (61,76), katatergite pale yellow (89) dorsally, bluish gray (191) ventrally.

Wings: membrane tinged with light grayish yellowish brown to light yellowish brown (79,76); costal and subcostal cells, wing tip and seams of veins slightly darker, stigma strong yellowish brown to moderate yellowish brown (74,77); contrasting with membrane; obliterative streak conspicuous, broadly whitened posterior to R1, contrasting with membrane, extending obliquely near infumed wing tip.

Legs: tooth on tarsal claws.

Abdomen: medium gray (265) with dark brown (59) dorsal longitudinal stripe, segments edged in pale yellow to moderate yellow (89,87), more broadly edged laterally, hairs short, yellowish white (92).

Genitalia: tergite 9 with hairs on dorsal process and laterally on posterior three-fourths of tergite, bare medially; dorsal and lateral processes long, tapering, broadly separated at base, dorsal process slightly

shorter and broader than lateral process; apical process small, tooth-like, borne on median projection between dorsal processes; no median lobe; 3 rectal sclerites: long, thin, lateral sclerite on each side, broader single dorsal sclerite. Gonocoxites with conspicuous protruding membrane ventrally; gonocoxal fragment long, narrow, gradually attenuated towards sperm pump. Outer gonostylus elongate, shallowly emarginate on ventral edge, usually with short oblique lateral ridge proximal to broad tip; medial surface concave except for narrow raised edge, broader at tip. Inner gonostylus with base broader than length of distal beak; small squarish proximal beak; dorsal crest sloping towards distal beak; distal beak smoothly curved, obliquely ridged on lateral surface, without pigmented sensilla. Aedeagus long, usually visible between gonostyli in dried specimens; tip straight, slightly expanded dorsally, no subapical teeth. Aedeagal guide with membranous distoventral tip; dorsal plate expanded dorsally, armed with 3 or 4 small irregular teeth.

FEMALE. Similar to male except as follows: flagellomeres not distended, 1st flagellomere less than 1.5 length of 2nd, lightened to strong brown (55) basally; 10th, 11th, and sometimes 9th subequal, smallest.

Genitalia: with broad dorsolateral lobe on sternite 8;

hypogynial valvulae long, two-thirds or more length of sternite 8, separated from it by broad W-shaped, membranous region; tip of valvulae broad, with 1 or 2 subapical dorsal hairs, distal hair visible (60 X magnification) beyond tip; tergite 9 rounded posterolaterally; sternite 9 with median projection long, thin, often angulated toward cerci; tergite 10 rounded posterolaterally, not conspicuously hairy; cerci slightly downturned at tip.

TYPE SPECIMENS

Tipula turcica was apparently described from a single specimen from "Kiliae Dom Daldorf" (=Kiel, Germany) (Fabricius, 1787). According to Zimsen (1964) only the pin and the original label remains in the Fabricius collection in Kiel.

The identity of this species is well established (Lackschewitz, 1933; Tjeder, 1948; Mannheims, 1951) and, therefore, according to the International Code of Zoological Nomenclature, Revised ed., (Art. 75a), designation of a neotype is not necessary.

SYNONYMY

The specific name Diana was suggested by Hoffmansegg and published by Meigen (1818) as a replacement name

because the epithet turcica was deemed to be unsuitable, because it implied a distribution restricted to Turkey. That this name change is not valid has been recognized for some time (see above).

• DISCUSSION

Prionocera turcica is very easily confused with the far less common Prionocera primoveris. See the discussion under that species. The two species apparently only have overlapping distributions in eastern North America.

This species has been frequently misidentified in North American collections as P. dimidiata. It has been noted that a male and female of turcica, pinned together, were mistakenly included with the type series of P. dimidiata.

GEOGRAPHIC DISTRIBUTION (Map 16)

Prionocera turcica is widespread, occurring from the northern edge of the northern boreal region south through the hemiboreal region. It apparently does not extend into the arctic region but it does extend south into the northern temperate region in Germany and Switzerland.

FLIGHT RECORDS: 23 May-15 August.

SPECIMENS EXAMINED (127 males, 85 females)

NEARCTIC: CANADA: ALBERTA: Banff Nat'l Pk., ♂, 7 vii 55, J.R. McGillis (CNC); Bilby, 53°42'N 114°06' W, ♂, 25 vi 24, O. Bryant (UMMZ); ♂, 5 viii 24, O. Bryant (as dimidiata, slide No. 1441, Alexander Coll. USNM); Kananaskis Environmental Science Centre, 2♂, 6 vi-20 vii 70, G. Pritchard (UC); Kananaskis Valley, ♀, 15 vi 68, H. Teskey (CNC & slide No. 1441, Alexander Coll. USNM); Nordegg, ♀, 12 vi 21, J. McDunnough (CNC); Wabamun, ♂, 10 vii 31, E.H. Strickland (as dimidiata, slide No. 1441, Alexander Coll. USNM); BRITISH COLUMBIA: Atlin, 2200', ♂, 3♀, 23-25 vi 55, H. Huckel (CNC); Quesnel, ♀, 16 vi 49, G.J. Spence (SUBC). MANITOBA: Churchill, 2♂, 26 vi-10 vii 77, F. Brodo (CNC); 6♂, 2♀, 5-16 vii 78, F. Brodo (CNC); same data, ♂, ♀ (C.D.), 2♂ (V.I.L.); ♀, 7 vii 49, J.A. Shemanchuk (CNC); 2♂, 28 vi-4 vii 47, T.N. Freeman (CNC); 2♂, ♀, 31 vi-23 vii 50, H.J. Teskey (CNC); ♂, 4 vii 47, B. Hocking (CNC); ♂, 29 vi 49, L.A. Miller (as dimidiata, slide No. 1441, Alexander Coll. USNM); ♀, 9 vii 33, A.T. Harper (CNC); ♀, "emergence area D", no further data (CNC); ♂, ♀, 4 vii 49 (CNC); 25 mi E Churchill, ♂, 10 vii 77, F. Brodo (CNC); Farnworth Lake nr. Churchill, ♂, 26 vi 52, J.G. Chillcott (CNC); ♀ (pinned with ♂ P. electa), 26 vi 52, J.G. Chillcott

(CNC); Fort Churchill, ♂, 12 vi 52, J.G. Chilcott (CNC); ♀, 8 vii 52, C.D. Bird (CNC); ♂, C.E. McClure (as dimidiata, slide No. 1441, Alexander Coll. USNM); Herchmer, 2♂, 29 vi-5 vii 49, J.B. Wallis (CNC). NEWFOUNDLAND: St. Anthony, 2♂, 3♀, 20 vi-2 vii 51, J.B. Wallis (CNC). NORTHWEST TERRITORIES: Mackenzie Distr.: Fort Smith, ♀, 8 vi 50, W.G. Helps (CNC); Norman Wells, 2♂, 22 vi 49, W.R.M. Mason (CNC); ♂, 12 vi 49, S.D. Hicks (CNC); Yellowknife, ♀, 8 vii 49, Fr. Ebner (CNC). ONTARIO: Ft. Severn, 56°N, ♂, ♀, 15 vii 40, C.E. Hope (♂ UMMZ, ♀ ROM); James Bay, Ft. Albany, 10♂, 3♀, 10-29 vi 42, F.A. Urquart (UMMZ, slides Nos. 4949, 4950). QUEBEC: Poste de la Baleine (Great Whale River), ♀, 7 vii 49, J.R. Vockeroth (CNC); 2♂, 1 vii 68 (MPUL); Saguenay, Rivière au Tonnerre (Thunder R.), ♂, 16 vi 30, W.J. Brown (CNC); Schefferville, 8♂, 4♀, 3-10 vii 81, F. Brodo (CNC); same data, ♂ (SEM); 11 km E. Schefferville, 2♀, 15 vii 81, F. Brodo (CNC); 26 km SE Schefferville, Astray L., 4♂, 2♀, 1-5 vii 81, F. Brodo (CNC); 37 km NW Schefferville, Annabel L., 2♂, 3♀, 25 vi-13 vii 81, F. Brodo (CNC). SASKATCHEWAN: Prince Albert, 2♂, 26 vi-1 vii 54, W.J. Turnock (CNC). YUKON: Swim Lakes, 133°N 62°13'W, 3200', 3♂, 9-15 vi 60, J.E.H. Martin (CNC); Watson Lake, ♀, 17 vi 48, Mason & Hughes (CNC). "Hudson Bay Territory," ♂, ♀, (mating pair), Osten Sacken (MCZ).

U.S.A.: ALASKA: Fairbanks, 2♀, 26 vi-1 vii 78, B. Wright (NSMH); King Salmon, Naknek R., ♀, 16 vii 52, W.R.

Mason (CNC).

PALEARCTIC: FAEROE ISLANDS: Thorshavn, Oven Aagen, ♂, ♀, 27 vi 26, Krugger (MAKB).

GERMANY (B.R.D.): Mosbruch, 2♂, 2 vi 51, Mannheims (MAKB); Mosbruch, Eifel, ♀, 23 vi 53 (MAKB).

FINLAND: ETALA-HAME: Tammela, ♀, 15 viii 65, Mannheims (MAKB); Urjala, ♂, ♀, 5, 23 vi 64, T. Brander (MAKB).

KEMIN LAPPI: Muonio, ♀, R. Frey (ZMH). VARSINAIS-SUOMI: Karislojo, ♂, R. Frey (ZMH); ♂, J. Sahlb (ZMH); ♀, Forsius (ZMH); ♂, Hellén (ZMH).

ICELAND: Husavik, Klinkow, 2♂, vii (NRS).

NORWAY: HORDALAND: Hardangervidda, Viveli-Veigdalen, Eidfjord, lak. nr. DIII, 1000m, 9♂, 2♀ (alcohol), 21 vii 67, F. Røhøde (ZMUB); same data, lak. nr. D V & D VI, 1000m, 2♀, 22 vii 67, K. Bjöklund (ZMUB); same data, lak. nr. D III, 1000m, 6♂, 21 vii 67, T. Nielson (ZMUB).
NORDLAND: Fauske, ♂, 26, vi 66, Mittendorf (MAKB).

SWEDEN: LYKSELE LAPPMARK: 50 km N Störuman, ♀, 15 vi 66, Mittendorf (MAKB). NORBOTTEN: Gränvik, 2♂, ♀, 26 vii 51, J.R. Vockeroth (CNC); W Haparanda, ♂, 17 vi 66, Mittendorf (MAKB); Lovikka, 3♂, 7♀, 23 vii 51, J.R. Vockeroth (CNC); Pajala Anttis, ♀, 23 vii 51, J.R. Vockeroth (CNC); Pajala Rutijarvi, ♂, 22 vii 51, J.R. Vockeroth (CNC); Muodoslompola, 2♂, 2♀, 26 vii 51, J.R.

Vockeroth (CNC). OSTERGOTLAND, ♂ (NRS).. SKANE: ♀, no further data (NRS). TORNE LAPPMARK: Abisko, 14♂, 5♀, 22 vi-10 vii 51, J.R. Vockeroth (CNC); Karesuando, ♂, 11♀, 25 vii 51, J.R. Vockeroth (CNC).*

SWITZERLAND: Neuchâtel, Cachot La Brévine, 1000m, (alcohol), ♂, 15 vii 87, C. Dufour (CNC).

U.K.: ENGLAND: Hampshire, New Forest, Brockenhurst, ♀, 23 v 69, R. Lane (BMNH); Norfolk, Catfield, ♂, 7 viii 20, J.J.F. -X. King (USNM); Surrey, Black Pond, Oxshott, ♂, 31 vii 22, F.W. Champion (USNM); Yorkshire, Austwick Mobb, ♂, 27 vi 38, C.A. Cheetham (BMNH). SCOTLAND: Monach Isles, 2♂, 2♀, 24-26 vii 70, G. Collis (BMNH).

Prionocera unimicra (Alexander)

Stygeropis unimicra Alexander, 1915: 128-129.

Prionocera unimicra; Alexander, 1965: 19.

Prionocera broweriana Alexander, 1961: 79-81. (new synonymy)

DIAGNOSIS

Dorsal stripes brown; ventral half of anepimeron bare or almost so; wing with stigma and obliterative streak contrasting with each other; male with flagellomeres.

moderately distended, 1st not elongated, 11th less than one-half 10th; female with broadly sloping dorsolateral edge on 8th sternite.

DESCRIPTION (figs. 27, 48, 64, 81)

ADULT. General appearance: more brownish than gray dorsally; hairs light orange-yellow to yellowish white (70,92), not conspicuously hairy; male body length 7.8-9.4mm, wing length 11.2-11.7mm; female body length 9.6-11.7mm, wing length 10.4-12.7mm.

MALE. Head: vertex moderate yellowish brown (75) usually divided by capillary black line, hairs almost as long as hairs on postgena; gena light orange-yellow (70), bare; rostrum dark grayish brown (62) dorsally to moderate brown (58) laterally, hairs dark brown to light orange-yellow (59,70), projecting beyond moderate nasus (.075-.15mm); pseudo-ocellus dark orange-yellow (72).

Antenna: flagellum deep brown (56), lightened to brownish orange (54) basally, proximal 2 or 3 flagellomeres distended, succeeding flagellomeres almost cylindrical; 1st less than 1.5 times length of 2nd; 11th less than one-half length of 10th.

Thorax: prescutal pit forming the apex of a deep yellowish brown to dark yellow brown (75,78) triangular region; dorsal stripes dark yellowish brown (78),

glabrous; median stripe bisected by narrow line, stripes bordered by light grayish yellowish brown to light yellowish brown (79,76) region, with moderately long hairs; postsutural area, scutellum and mediotergite concolorous with dorsal stripes, bearing moderately long hairs; pleuron bluish gray (191), anepistenum, katepisternum and dorsal half of enepimeron hairy, ventral half of anepimeron and katepimeron bare; anatergite light olive gray to olive gray (112,113); katatergite pale yellow (89) dorsally, broadly pruinose dark gray (266) ventrally.

Wing: membrane tinged with light yellowish brown (76), costal and subcostal cells and wing base slightly darker; veins and distal half of stigma deep yellowish brown to dark yellowish brown (75,78); obliterative streak well developed, including pale proximal half of stigma, running obliquely near wing tip.

Legs: no teeth on tarsal claws.

Abdomen: with segments deep yellowish brown (75) medially, often fading to moderate orange-yellow (71) distally, bordered laterally with yellowish white (92); hairs short, light orange yellow (70).

Genitalia: 9th tergite with hairs confined to distal half; dorsal process squarish or slightly broader at base, space between subequal to width of process; lateral

process very small or lacking; apical process curved medially, sharply pointed; median lobe lacking; rectal sclerite small, irregular. Gonocoxites without protruding membrane; gonocoxal fragment broadly triangular. Outer gonostylus triangular, tip usually bent in dried specimens; medial surface entirely concave, without distinct raised edge. Inner gonostylus with base shorter than length of distal beak, a small bump on lateral surface of base; no dorsal crest; distal beak moderately broad without pigmented sensilla; proximal beak very short and broad. Aedeagus with tip straight (viewed laterally), no subapical teeth. Aedeagal guide with semi-transparent narrow membranous tip; dorsal plate flat, narrowing midway towards sperm pump.

FEMALE. Similar to male except as follows: flagellomeres not distended; 1st flagellomere less than 1.5 times 2nd; 10th and 11th (and sometimes 9th) subequal, narrower than preceeding.

Genitalia: sternite 8 with dorsolateral edge sloping, not lobed; hypogynial valvulae one-half length of sternite 8, separated from it by broad Y-shaped region with very narrow membranous extension between bases of valvulae; ventral edge broadly and more heavily sclerotized, tips square-edged, no subapical dorsal hairs; sternite 9 rounded posterolaterally; sternite 9 with median projection subequal in length and width;

tergite 10 rounded laterally, not conspicuously hairy; cerci almost straight.

TYPE SPECIMENS

Holotype, male, Colorado, C.V. Riley collection, and slide 1-21-42 D, Type, Cat. No. 19979, United States National Museum, Washington, D.C. The pinned portion of the type lacks left legs, the tarsal claws of the right hind leg are missing, and the right wing is torn in the stigmal region. The slide mounted genitalia show the features of the 9th tergite beautifully, but the dorsolateral orientation obscures some of the features of the gonostyli.

SYNONYMY

Prionocera broweriana was described from a single male collected in Maine, Penobscot Co., Passadumkeag bog, 26 vi 1944, A.E. Brower (Alexander slide collection, USNM). The genitalia, left wing and all left legs are on one slide and the right wing, an antenna and right fore leg are on a second slide. I have not seen the pinned portion of this specimen.

The genitalia are somewhat squashed. Only the dorsal processes of the 9th tergite are clearly recognizable. The lateral and apical processes are obscured. The

aedeagus and aedeagal guide show the distinctive characteristics of this species, therefore I am confident that this species is conspecific with unimicra. The contrasting oblitative streak and stigma in the wings are clearly evident, as are the moderately distended lower flagellomeres.

In this specimen the petiole of cell M is longer than m, as noted by Alexander; however, the reverse is the case in several other specimens of this species.

DISCUSSION

The specimens from Labrador and northern Quebec have wing veins which are darker than those of the western specimens, giving the wing a duskier appearance.

GEOGRAPHIC DISTRIBUTION (Map 17)

Prionocera unimicra described from a unique male collected in Colorado, is now known to have a widespread distribution in the boreal zone. It extends from the Yukon to mainland Labrador and southwards along the Rocky Mountains at least as far as Boulder County, Colorado. The range of this species is similar to that of the much more commonly collected dimidiata. In fact these two species have been collected together in the same fens in both Colorado and Schefferville, Quebec. It apparently

does not extend into the arctic and it is restricted to North America.

FLIGHT RECORDS: 24 May-17 July.

SPECIMENS EXAMINED (100 males, 17 females)

NEARCTIC. CANADA. ALBERTA: Banff Nat'l Pk., Sunwapta Pass, 6700', 2♂, 9 vi 55, Shewell (CNC); Sunwapta Pass, Jasper Hwy., 6600', ♂, 5 vii 55, R. Coyles (CNC); Seebe, Kananaskis Env. Sci. Centre, 7♂, 4-16 vi 70, G. Pritchard (CAL). LABRADOR: Cartwright, 2♂, 26 vi 55, E.F. Cashman (CNC); Goose Bay, 7♂, 3♀, 5 vi 48, W.W. Judd (CNC), ♂, 9 vi 48, H.C. Friesen (CNC). MANITOBA: Churchill, 2♂, 17, 23 vi 48, G. Shewell (CNC); ♀, 4 vii 49, L.A. Miller (CNC); 10♂, ♀, 3 vi-12 vii 52, J.G. Chillcott (CNC); ♀, 21 vi 47, T.M. Freeman (CNC); 3♂, 4♀, 1-12 vii 78, F. Brodo (CNC); Herchmer, ♂, 29 vi 49, J.B. Wallis (CNC); Ninette, ♀, 7 v 48, J.F. McAlpine. NEW BRUNSWICK: Kouchibouguac Nat'l Pk., 2♂, 24 v 77, B. Cooper (CNC). NORTHWEST TERRITORIES: Mackenzie Distr.: Salmita Mines, 64°05'N 111°15'W, 2♂, 30 vi, 1 vii 53, J.G. Chillcott (CNC). NOVA SCOTIA: Halifax Co., Hubbards Bog, 5♂, 24 v 79, B. Wright (NSMH). ONTARIO: Moose Factory, ♀, 9 vi 49, D.P. Williams (CNC). QUEBEC: Fort Chimo, 2♂, 21 vi 48, H.N. Smith (CNC); 3♂, 21 vi 48, R.H. Macleod; Pt. Harrington (Harrington Harbour ?, 50°29'N 59°28'W), ♂,

30 vi 49, D.P. Williams (CNC); 37 km NW Schefferville,
18♂, 3♀, 25 vi-13 vii 81, F. Brodo (CNC); same data, ♀,
(SEM), ♂ (C.D.). YUKON: Koidern, km. 1874, 61°58'N,
140°25'W, ♂ (alcohol), 29 w 80, R. Cannings, (SUBC).

U.S.A.: COLORADO: Boulder Co., 40°04'N 105°34'W, 25♂,
2♀, 27 vi-11 vii 79, F. Brodo (CNC); same data, 2♂
(V.I.L.); ♂, C.V. Riley coll. (no further data) (holotype
of unimicra, USNM). MAINE: Penobscot Co., Passadumkeag
bog, ♂, 26 vi 44, A.E. Brower (holotype of broweriana,
No. 11,114, on two slides, Alexander Coll., USNM).

Prionocera woodorum, NEW SPECIES

DIAGNOSIS

Wings dusky, stigma and obliterative streak prominent;
male with outer gonostylus broadly L-shaped, covered with
dark hairs; female with long pale hairs laterally on 10th
tergite.

DESCRIPTION (based on 4 males, 6 females), (figs 8, 9,
28, 47, 65, 82)

ADULT. General appearance: head and thorax brownish
gray to dark grayish brown (64,62) dorsally, hairs short,
yellowish white (92), not conspicuously hairy; wings

dusky, stigma and obliterative streak strongly contrasting with each other; male body length 9.6-11.1mm, wing length 13.6-16mm (holotype 14.6mm); female body length 13.4-14.1mm, wing length 14.8-18.0mm (allotype 17.1mm).

MALE. Head: vertex light gray to light grayish brown (264,60), broadly bisected by brownish black (65) line, dorsal hairs short, proclinate; gena predominantly light gray (264) with short inconspicuous pale hairs; rostrum dark grayish brown (62) dorsally, lightened to dark orange-yellow (72) ventrolaterally, hairs shorter, darker and proclinate dorsally, projecting fringe-like beyond moderate (0.125-0.15mm) nasus, hairs longer and paler laterally; pseudo-ocellus black (267).

Antenna: relatively long, brownish black to black (65,267); pedicel and base of 1st flagellomere lightened to brownish orange (54); scape and dorsally on 1st flagellomere hairs short, dark; 1st flagellomere only slightly longer than 2nd; proximal flagellomeres distended, distal width twice width at base; 11th a third or less the length of 10th.

Thorax: prescutal pit not forming apex of yellowish triangular region; dorsal stripes anterior to transverse suture dark grayish brown (62), median stripe narrowly divided by narrow light line becoming blackish anteriorly, stripes bordered by light gray to light

grayish yellowish brown (264,79) region, not conspicuously hairy; short pale hairs bordering stripes; postsutural area, scutellum and mediotergite gray, lacking a brownish caste, bearing short hairs; pleuron light bluish gray to dark bluish gray (190,192) with pale hairs on each segment, except small katepimeron; anatergite light olive gray (112); katatergite broadly light yellow (86) dorsally, dark gray (266) ventrally.

Wings: membrane tinged with medium gray (264), veins at least distally, brownish black (65); costal and subcostal cells infumed with moderate orange-yellow (71); distal half of stigma brownish black (65), dark colour bleeding into wing tip; oblitative streak broad, contrastingly whitened, including proximal half of stigma and part of Radius, almost perpendicular to wing axis.

Legs: ~~tarsal~~ claws with long narrow tooth close to base.

Abdomen: medium gray to grayish yellowish brown (265,80), dorsal longitudinal stripe brownish black (65), tergites narrowly edged distally, more broadly edged laterally in pale yellow (89); hairs short, pale yellow proximally, brownish black (65) on 8th & 9th tergites.

Genitalia: 9th tergite with hairs on distal two thirds; dorsal process long, slender, truncated distally; lateral process slender, triangular; broadly emarginate

between dorsal and lateral processes; apical process narrow, tooth-like, sharply curved medially; medial lobe shallowly emarginate; rectal sclerite relatively broad. Gonocoxites conspicuously hairy, separated medioventrally by small membranous lobe; gonocoxal fragment broadly triangular. Outer gonostylus broadly L-shaped, extending posteriorly beyond inner gonostylus, with long hairs, medial surface concave except for clearly defined raised edge becoming more prominent distally. Inner gonostylus with broad base, no dorsal crest, long slender distal beak without pigmented sensilla; proximal beak small, pointed. Aedeagus with tip curved dorsally, bearing single medial subapical tooth and a smaller, more proximal sublateral tooth. Aedeagal guide with membranous ventral tip; dorsal plate narrow, parallel-sided, abruptly curving and narrowing close to sperm pump.

FEMALE. Similar to male except as follows: pedicel and most of 1st flagellomere lightened to moderate orange-yellow (71), scape covered with moderately long hairs, pedicel with shorter hairs, flagellomeres 1-3 with scattered short hairs dorsally, flagellomeres subcylindrical, 9th, 10th & 11th narrower, subequal.

Genitalia: sternite 8 with dorsolateral lobe; hypogynial valvulae moderately long, 0.4 length of sternite 8, separated from it by narrow membranous

region, broadened medially on 8th sternite; valvulae subtriangular, ventral edges broadly sclerotized, with a single strong subapical hair dorsally (visible with 60 x magnification); tergite 9 rounded posterolaterally, with dark hairs; sternite 9 with median projection long and narrow; tergite 10 gently rounded laterally, bearing long conspicuous pale hairs; cerci relatively narrow, slightly downcurved distally.

TYPE SPECIMENS

Holotype, male, Yukon, Barlow Lake, km 612, Klondike Hwy., 20 vi 82, G. & M. Wood (No. 18351 CNC). Allotype, female, Yukon, km 141, Dempster Hwy., 24-28 vi 82, G. & M. Wood (CNC). Paratypes, 3 males, 2 females, as follows: NORTHWEST TERRITORIES: Mackenzie Distr.: Aklavik, ♂, 16 vi 53, J.S. Waterhouse (CNC); ♀, 25 vi 56, R.E. Leech (CNC). YUKON: Barlow Lake, km 612, Klondike Hwy., ♂, 20 vi 82, G. & M. Wood (CNC); km 141, Dempster Hwy., ♂, ♀, 24-28 vi 82, G. & M. Wood (CNC).

The genitalia of the holotype, allotype, and a male paratype from Aklavik have been removed, softened, placed in glycerine in microvials and pinned beneath their respective specimens. The 11th flagellomere on the holotype is very short, one-fourth the length of the 10th. Only the dorsal stripe has a brownish caste; the lateral stripe is grayish and flanked by a large dark

bluish gray spot. The holotype lacks the left fore leg, and the allotype the left hind leg.

DISCUSSION

A female from Abisko, Torne Lappmark, Sweden, 8 vii 51, J.R. Vockeroth, (CNC), appears to belong to this species. However, because of its single occurrence in the Palearctic, and because of the following differences, I am not designating it as a paratype. 1) Several of the distal veins are deformed. 2) Only the last two flagellomeres are narrower and subequal. 3) The subapical hair on the hypogynial valvulae is lacking.

VARIATION

The male from Aklavik is teneral and so is a little lighter and the flagellomeres are shrivelled.

DISCUSSION

This species is most closely related to dimidiata and suberricornis, sharing with these species a distinct medial lobe and a rather sharply pointed proximal tooth on the inner gonostylus. Some specimens of suberricornis from northern Fennoscandia also have an L-shaped outer gonostylus.

GEOGRAPHIC DISTRIBUTION. (Map 18)

This fly has only been collected in the Yukon and in Aklavik, Northwest Territories, with a questionable record from Lapland, Sweden. Prionocera woodi may represent an endemic species isolated in the Yukon refugium.

FLIGHT RECORDS: 16-28 June (8 July, Sweden)

This seems to be an extremely early spring species which may explain its absence in other collections.

ETYMOLOGY

This species is named for its collectors, Grace and Monty Wood, in recognition not only of their team work in the field but also their respective contributions to Diptera research, particularly to their outstanding contributions to the Manual of Nearctic Diptera, Volumes I and II.

DOUBTFUL AND EXCLUDED SPECIES

Prionocera bergrothi (Williston) nomen dubium

Stygeropis bergrothi Williston, 1893: 64.

Prionocera bergrothi; Alexander, 1965: 19.

Williston based his description on a single male collected in Alaska and listed as being deposited in the University of Kansas. Unfortunately this specimen is not there, (Byers, et al., 1962; Byers, pers. comm.), and furthermore, has been lost for many years (Alexander, 1919: 9c).

The description of bergrothi is very general and could pertain to at least six of the eight species known to occur in Alaska. Therefore I consider bergrothi a nomen dubium.

Prionocera parrii (Kirby) nomen dubium

Ctenophora parrii Kirby, 1824: 218; Ross, 1826: 112;

Curtis, 1835: plate 493.

Stygeropis parrii; Osten Sacken, 1878: 40; Alexander,

1919: 8c-9c, figs. 7, 12, 23, 24, 26 (wing, antennae, male genitalia); Pierre, 1924: 20.

Tipula parrii; Lundbeck, 1898: 265; Kertész, 1902: 278;

Aldrich, 1905: 103.

Prionocera parrii; de Meijere, 1929: 46; Mannheims, 1951: 71; Alexander, 1965: 19.

The original description by Kirby was based on a single female probably collected near Winter Harbour, Melville Island, Northwest Territories (Henry, 1970). I have not seen any Prionocera which have been collected that far north in the gearctic, but this is undoubtedly due to the vagaries of collectors. At least three species can be expected to occur there: P. recta, P. ominosa and P. elliptica (see figs.).

Kirby described parrii as having serrate antennae. He presumed that the male would have bipectinate antennae, hence he placed his new species in Ctenophora. However, the wood-boring Ctenophora is not an arctic genus. Serrated antennae however, are a distinctive feature of the decidedly northern genus Prionocera. In those species in which the male has very strongly serrate antennae, the female antenna is moderately serrate also and this is true of the three Prionocera species mentioned above.

The wings of parrii were described as being "brownish towards their apex, at the exterior margin is a white spot crowned by a black one." This sentence could pertain to P. recta but probably not to P. ominosa or P. elliptica in which the oblitative streak and stigma are barely evident.

Alexander (1919: 8c-9c) redescribed and illustrated what he understood to be Stygeropis parrii (Kirby) from 10 specimens collected by the Canadian Arctic Expedition, 1913-1918. Six of these specimens are in the Canadian National Collection, Ottawa and an additional male is slide-mounted and part of the Alexander collection given by Dr. Alexander to the United States National Museum in 1982. This is a mixed collection of P. recta and P. ominosa. The diagrams, probably based on the slide-mounted specimen from Kongenevik, Camden Bay, pertain to P. ominosa (Alexander) but the written description seems to be a composite of both species. The description of the thorax and abdomen is that of P. recta but the description of the wing is that of P. ominosa. Subsequent workers, it should be noted, have used the name parrii for the species here recognized as ominosa, basing their identifications on the genitalia diagrams of Alexander.

Alexander never had the opportunity to study the type of parrii (Alexander, 1956: 124). When I visited the British Museum in 1979, a search was made by Dr. Tony Hudson, and the type could not be located.

In view of the fact that the type has been lost for over half a century, no specimens of Prionocera have been seen from the type locality, and the original description of parrii could pertain to several species but probably

not to the one provisionally designated as parrii by Alexander, I consider parrii a nomen dubium.

Tipula (Angarotipula) illustris Doane, 1901

Stygeropis fuscipennis Loew, 1865: 129; Alexander, 1919: 817, 933; 1920: 199.

Prionocera fuscipennis (Loew); Alexander, 1920b: 978, 996; 1927: 215; 1942: 220; Procter, 1946: 330.

Tipula illustris Doane, 1901: 97-98.

Prionocera fuscipennis (Loew); Alexander, 1942a: 220.

Tipula illustris Doane; Alexander, 1948: 23 (preoccupied by T. fuscipennis Curtis, 1834); 1961: 81; 1962: 10; 1965a: 19; 1965b: 337; 1967: 21.

Pachyrhina hybrida Dietz, 1918: 113.

Prionocera hybrida (Dietz); Alexander, 1965a: 19 (New Synonymy).

I borrowed the type of Pachyrhina hybrida Dietz in 1981 from the Academy of Natural Sciences, Philadelphia. It is conspecific with Tipula (Angarotipula) illustris Doane and therefore I am hereby synonymizing hybrida with illustris.

PART I

THE PHYLOGENY OF THE FAMILY TIPULIDAE

INTRODUCTION

The Tipulidae are a very ancient and species-rich family with a world-wide distribution. They number approximately 13,000 species, with flies ranging from a wing spread of 4mm to as much as 100mm. Crane flies are superficially very much alike and there is, in my opinion, little question that they form a monophyletic group. What is questioned is their relationship to the other Diptera and the phylogenetic arrangement within the family.

Many Europeans recognize the families Tipulidae, Cyndrotomidae and Limoniidae comprising the superfamily Tipuloidea (Mannheims, 1951; Savtshenko, 1961, 1979; Oosterbroek & Theowald, 1980). North American workers, on the other hand, consider the superfamily Tipuloidea to contain the single family Tipulidae which is divided into three subfamilies: Tipulinae, Cyndrotominae and Limoniinae (e.g., Alexander & Byers, 1981). This classification is adopted here.

Savtshenko (1979) considered the Tipuloidea to consist of the Tipulidae, Cyndrotomidae, Limoniidae, Trichoceridae, Tanyderidae and Ptychopteridae. He suggested, following Rohdendorf (1964), that the Tanyderidae, Trichoceridae and the Ptychopteridae are the more primitive families and that they are morphologically isolated from the Tipulidae s.l.

Other workers consider either the Tanyderidae or the Trichoceridae to be more closely related to the Tipulidae s.l., depending upon the relative importance given to larval versus adult characters. The characters of the larval mouthparts indicate a closer relationship to the Tanyderidae (Wood, pers. comm.). In McAlpine et al. (1981), these two families comprise the Tipulomorpha, and the Trichoceridae are placed in the Psychodomorpha. This is contrary to the prevailing view that the Tipulidae are more closely related to the Trichoceridae (Alexander, 1920; Crampton, 1942; Edwards, 1938; Rohdendorf, 1964; Hennig, 1981; Oosterbroek, 1980). The latter relationship is based primarily on wing venation.

The work of Dahl (1980) suggests two additional strong synapomorphies of the Tipulidae and Trichoceridae. In the male, in both of these families, the gonocoxites develop from the posterior portion of the 9th sternum. By contrast, in the Anisopodidae, and presumably in other Diptera, the gonocoxites develop from the lateral half of the genital primordium. Secondly, female Tipulidae and Trichoceridae are characterized by sclerotized spear-shaped cerci borne dorsodistally on the abdomen. These cerci, Dahl (1980) has shown, develop from 9th sternal elements which migrate to a dorsal position in the adult. Similar cerci are not found in other Nematocera.

Hennig (1968, 1981) suggested that there is probably a

sister-group relationship between the Polyneura (= Tipulidae s.l., plus Trichoceridae) and the Oligoneura (= the rest of the Diptera). That is, the Tipulidae and Trichoceridae represent an early offshoot from the main branch of nematoceran development. I believe that to be true of the Tipulidae but I am uncertain of their relationship to other families.

The subfamilies of the Tipulidae are relatively easy to distinguish. The bulk of the specimens are classified in the two largest subfamilies - the Tipulinae and Limoniinae, with fewer than 50 placed in the Cylindrotominae (Brodo, 1967). The phylogenetic relationship of these three subfamilies has never been satisfactorily worked out. The Cylindrotominae have had an anomalous position between the Tipulinae and Limoniinae (Peus, 1952; Brodo 1967). Edwards (1938) considered the Cylindrotominae to be more closely related to the Limoniinae because of similarities of the male genitalia and Lameere (1906) suggested that the Limoniinae are the more primitive of the two because of features of the wing venation. Savtshenko (1979) recognized that the similarities between the Tipulinae and Limoniinae are plesiomorphies and therefore not indications of a recent common ancestry.

The Limoniinae are the largest and most variable subfamily and are further divided into five tribes:

Limoniini, Pediciini, Hexatomini, Eriopterini and Lechriini. The Lechriini are restricted to the Ethiopian, Oriental and Madagascan Regions (Oosterbroek & Theowald, 1980a & 1980b). Based on descriptions in the literature, this tribe appears to me to be closely related to the Eriopterini and is not dealt with here.

Attempts have been made to classify the Tipulinae into tribes, or subfamilies, depending upon the rank assigned to this taxon. Kertész (1902) recognized three divisions, here referred to as tribes: Dolichopezini, Ctenophorini and Tipulini. These divisions are accepted by Saytshenko (1979) as reflecting the phylogeny of the Tipulinae. They have been rejected by others, however, because several genera, including Prionocera, do not fit readily into this classification and because a closer relationship is perceived between certain subgenera of Tipula and genera assigned to other tribes (Theowald, 1957; Frommer, 1963; Oosterbroek, 1980).

Within the Tipulidae there is a vast amount of variation, and the problem still is, as Hennig (1981) conceded, that there is no well-founded phylogenetic classification of the Tipulidae. He was referring principally to wing venation when he wrote "no one has clearly worked out which characters....can be reliably used for recognition of the various monophyletic groups."

The genus Prionocera belongs to the subfamily Tipulinae. Species now recognized as belonging to the subgenus Angarotipula Savtshenko of Tipula, have in the past been confused with Prionocera (see Part 1). The larvae of these two taxa are very difficult to separate (Byers, 1981; Gelhaus, in press). Tjeder (1948) suggested that although Prionocera seems to be related to Tipula, it may also be closely related to the subfamily Limoniinae, based on internal characters of the male genitalia.

I therefore undertook a cladistic analysis to determine the basic ground plan of both the genus Prionocera and the family Tipulidae, to work out the monophyletic groups within each, to show the major evolutionary trends, and to suggest the phylogenetic relationship of the genus Prionocera to the rest of the Tipulinae.

METHODS

In order to construct a phylogeny of the Tipulidae and place Prionocera within this scheme, the plesiomorphic or basic ground plan of this family had to be determined.

The general principles followed here are as set out by Oosterbroek (1980); and references therein. The Tipulidae were, therefore, compared with their presumed outgroups in the Nematocera - Tanyderidae, Anisopodidae, Trichoceridae, Ptychopteridae, Bibionidae and to the Mecoptera, the sister order of the Diptera (Hennig, 1981). Character states occurring both in the Tipulidae and within the outgroups may be either plesiomorphic (primitive) or may represent parallel development or convergence. Character states unique to, and thought to have evolved in the Tipulidae are considered to be apomorphic (derived) with respect to other Nematocera but may be plesiomorphic within this family. For instance, the more solidly built, retractable larval head capsule in the Tipulinae, is interpreted as a plesiomorphic feature within the family. The elongate rod-like sclerites, of the larval head in many Limoniinae, are considered to be a derived feature. Synapomorphies, therefore, are supposedly derived features which are present in at least the primitive members of the groups in question.

Characters usually occur in several states. A

transformation series of the states for each character under consideration, was arranged to indicate the presumed primitive condition and the hypothesized direction(s) of evolution. These character states were then correlated with their relevant taxa.

There must be concordance among the character transformation series. When discrepancies occurred hypotheses were re-evaluated and often restructured. Sometimes parallel or convergent lines of evolution were thus illuminated. Often hypotheses had to be re-evaluated by a re-assessment of the specimens, which usually included study of additional material. The most plesiomorphic state of a character is often not apparent even though one can recognize several obviously derived states.

Both the retention of a primitive character and the loss of an inherited character may occur independently in several different evolutionary lines. Such characters, therefore, are of limited use. For example, a trifold aedeagus has apparently been retained in both the *Cylindrotominae* and in some *Hexatomini*. However, the analysis of other characters, as discussed below, indicates that these two groups are not the most closely related. The tribes *Eriopterini* and *Limoniini* are characterized by the loss of tibial spurs but these spurs have apparently also been lost independently in some

Pediciini.

A clearly derived character, on the other hand, shared by two taxa is usually a good indication of common origin and therefore of close relationship. The bifurcate main branches of the pseudotracheae, and the reduction of the ninth sternite and concomitant enlargement of the gonocoxites appear to be two examples of such characters and are considered here to be synapomorphies of the Cylindrotominae and the Tipulinae.

Comparatively few species were selected for study and these came primarily from my own collecting in the Ottawa region (see Appendix C). The origin and major evolutionary centres of the crane flies are quite likely to be elsewhere, possibly in the tropics. It is also likely that some of the species which I selected are neither representative of their genus nor of their tribe. This, therefore, must be considered to be a tentative study which should be augmented with the study of more species and genera, especially from other continents, and the addition of many more characters.

Insect parts which were prepared for detailed microscopic study were handled in the manner described in Part I, Methods, Dissection. It was necessary to have all dissections readily available for comparison and re-evaluation throughout this study. Specimens were kept in a drop of glycerine on an individually numbered slide.

The number corresponded to the number on the pinned remains of that specimen.

ANALYSIS OF CHARACTERS

Forty-one characters (five larval, one pupal and thirty five adult) were studied and each was arranged in transformation series. The presumed plesiomorphic condition is represented by "(p)" and "1A, 2A etc." refer to the postulated apomorphic states with arrows between indicating the hypothesized path(s) of evolution. (Based on a scheme developed by Smith, 1976). Several important characters listed by Savtshenko (1979) were not included here because of insufficient data.

* Indicates a genus which I have removed from the tribe Limoniini to the tribe Hexatomini.

LARVAL CHARACTERS

(Based primarily on the literature: Alexander, 1920b; Brindle, 1960, 1961, 1963, 1967; Brindle & Bryce, 1960; Brodo, 1967; Bryce, 1957a, 1957b; Byers, 1961, 1981, 1983; Peus, 1952; Theowald, 1957.

1. Sclerotization of head capsule. An extensively sclerotized head capsule is found throughout the more primitive Nematocera and is common in the lower Holometabola. In the crane flies the head capsule has been at least partially retracted into the first thoracic segment and there is a tendency for progressive fragmentation of these head sclerites.

- (p) The head capsule is extensively sclerotized dorsally and laterally, with only shallow posterior incisions.

Hexatomini: Atarba, Austrolimnophila, Epiphragma,

*Helius, Hesperoconopa

Eriopterini: Arctoconopa, Chionea, Cladura, Gonomyia,

Gnophomyia, Ormosia

Pediciini: Dicranota, Pedicia, Ula

Limoniini: Antocha, Limonia

Cylindrotominae: all

Tipulinae: all

- 1A The head capsule is divided by deep, posterior incisions into six, elongate, slender, rod-like, spatulate sclerites.

Eriopterini: Molophilus

- 2A The head capsule is divided as above, but into four elongate sclerites: a dorsal pair, a lateral pair, but no ventral pair.

Hexatomini: Elephantomyia, Hexatoma, Limnophila,

- 3A As above, but there are only three elongate sclerites, a single dorsal sclerite and a lateral pair.

Hexatomini: Pilaria, Ulomorpha

Elongate paired dorsal sclerites, when present, are widely separated suggesting that the single dorsal sclerite is not the result of fusion. Fragmentation of the head sclerites probably occurred independently at least three times in the Limoniinae.

2. Fleshy lobes on thorax and abdomen. Various kinds of lobes are found on the thorax and abdomen of larvae in scattered families throughout the order. Lobes similar to those occurring in the Tipulidae are found in the Bibionidae but are here considered to be a parallel development. The absence of lobes is widespread in the Diptera, therefore, I consider this attribute to be a plesiomorphy.

(p) No fleshy lobes.

Limoniinae: all

Tipulinae: all

1A Dorsal and lateral longitudinal rows of fleshy lobes on the thorax and abdomen.

Cylindrotominae: all

Hypothesis 2: p $\longrightarrow$ 1A

I consider fleshy lobes to be an apomorphy of the Cylindrotominae.

3. Number of lobes on spiracular disc of mature larva.

Brindle (1967) suggested that the "generalized type" lacks lobes on the spiracular disc as in some Limonia. Most crane fly larvae have from two to six lobes surrounding the metapneustic spiracles. Five lobes are characteristic of the Anisopodidae (Peterson, 1981), the Axymyiidae (Wood, 1981) and Tanyderidae (Alexander, 1920). Four are found in the Trichoceridae (Alexander, 1981) and six in the Bibionidae (Savtshenko, 1979). First instar larvae of Dolichopeza (Byers, 1961) and Prionocera (Brodo, unpublished) have eight lobes, a distinct lateral and ventral pair and two smaller dorsal pairs. The mature larva of the Australian genus Clytocosmus (Dobrotworsky, 1967b) has ten lobes. Chionea first instar larvae have ten small thorn-like projections (Byers, 1983) in place of and probably homologous to these lobes. In both Chionea and Clytocosmus one can distinguish a lateral and ventral pair and three dorsal pairs. Possession of lobes is clearly a plesiomorphic feature in the Tipulidae.

(p) 6 lobes: one pair each on dorsal, lateral and ventral surfaces.

Cylindrotominae: all

Tipulinae: most

1A 10 lobes: 3 pairs of dorsal lobes, a lateral and a ventral pair.

Tipulinae: Clytocosmus

- 2A 10 lobes: lateral and ventral pairs secondarily divided

Tipulinae: Tipula (Nippotipula) abdominalis

- 3A 5 lobes: a single dorsal lobe, a lateral and a ventral pair.

Hexatomini: Atarba, Austrolimnophila, Epiphragma,

*Helius, Hexatoma (trace of 5th), Limnophila (Limnophila), Pilaria (trace of 5th)

Eriopterini: Arctoconopa, Cheilotrichia, Erioptera, Gonomyia, Gnophomyia, Molophilus, Ormosia

Pediciini: Ula

Limoniini: Limonia (in part)

- 4A 4 lobes: dorsal lobe(s) lost.

Hexatomini: Dactylolabis, Elephantomyia, Limnophila

(Eloeophila), L. (Lasiomastix), L. (Phylidorea), Pilaria, Polymera, Pseudolimnophila, Ulomorpha

Eriopterini: Gonomyia, Lipsothrix

Limoniini: Elliptera

- 5A 3 lobes: 1 dorsal lobe, a ventral pair (lateral pair lost).

Limoniini: Limonia (in part)

Eriopterini: Rhabdomastix

- 6A 2 lobes: the ventral pair only.

Eriopterini: Teucholabis

Pediciini: Dicranota, Pedicia

Limoniini: Antocha

7A 7 lobes: 3 dorsal lobes, a ventral and a lateral pair.

Eriopterini: Gonomyodes

8A No discernible lobes.

Hexatomini: Pilaria (filiata group)

Eriopterini: Chionea, Cladura, Hesperoconopa

Limoniini: Limonia (in part)

Hypothesis 3:

I am tentatively suggesting that six is plesiomorphic and characteristic of the Tipulinae and Cylindrotominae. In the latter, there is a reduction in the size of either the dorsal or the lateral pair. Five lobes (3A) on the spiracular disc is a synapomorphy of the subfamily Limoniinae and reduction of the number of lobes has occurred frequently. There is a sporadic tendency for an increase in the number of lobes in both the Tipulinae (1A, 2A) and Limoniinae (7A).

4. Marginal hairs on spiracular disc. A fringe of marginal hairs on the spiracular lobes is common in the Tipulidae and the Trichoceridae. These hairs help to maintain the respiratory openings above the water surface. When the lobes are contracted the hairs trap an air bubble and allow the larva to penetrate anaerobic regions. Savtshenko (1979) suggested that the earliest Diptera larvae were probably detritivores living in oxygen-poor conditions. If this were so then they may have had several lobes on the spiracular disc and these lobes were probably fringed with long hairs. First instar larvae of Dolichopeza and Chionea, unlike their respective later instars, have relatively long hairs on the lobes of the spiracular disc (Byers, 1961, 1983). This may be a plesiomorphic feature which is only expressed in the first instars.

(p) Lobes fringed with long hairs:

Hexatomini: Hexatoma, Limnophila (Dicranophragma), L.

(Lasiomastix), Pilaria, Pseudolimnophila, Ulomorpha

Eriopterini: Ormosia

Limoniini: Elliptera, Limonia (Rhipidia)

Tipulinae: Clytocosmus, Holorusia, Megistocera,

Prionocera, Tipula (Ankarotipula)

1A A fringe of short hairs.

Hexatomini: Dactylolabis, Epiphragma

Eriopterini: Erioptera, Gnophomyia, Gonomyia,

MolophilusPedicini: UlaLimoniini: Limonia (Limonia)

Tipulinae: Tipula (Nobilotipula) collaris, T.
 (Savtshenkia) ignobilis, T. (Trichotipula)
 oropezoides, T. (Yamatotipula) dejecta

2A No hairs on lobes of spiracular disc.

Hexatomini: Elephantomyia, *HeliusEriopterini: ChioneaPedicini: Dicranota, PediciaLimoniini: Limonia (Metalimnobia)

Cylindrotominae: all

Tipulinae: Ctenophora, Dolichopeza, Nephrotoma,
 Tipula (Lunatipula), T. (Vestiplex)

Hypothesis 4: p → 1A → 2A

Reduction and the loss of hairs on the lobes has occurred in unrelated genera. However, I consider hairless lobes to be an apomorphy of the Cylindrotominae.

5. Metapneustic spiracles. Most Tipulidae have a single pair of posterior spiracles and this is considered to be part of the ground plan of the family. Loss of spiracles is a derived condition.

(p) Presence of terminal spiracles.

Tipulidae: most

1A Loss of spiracles.

Hexatomini: Hesperoconopa

Limoniini: Antocha,

Hypothesis 5: p → 1A

The apneustic condition is related to an aquatic habitat. An unrelated loss of spiracles has occurred in the Hexatomini and the Limoniini. Non-functional spiracles have been demonstrated in the aquatic species Tipula abdominalis and T. sacra, indicating that these species also are secondarily aquatic (Pritchard & Stewart, 1981).

PUPAL CHARACTERS

(Alexander, 1920b; Byers, 1961, 1981, 1983; Brodo, 1967; Brindle, 1960, 1961, 1967; Peus, 1952)

6. Respiratory horns. The most common condition, widespread throughout the Tipulidae and other Nematocera, is the presence of a pair of long slender respiratory horns projecting anterodorsally just behind the head (Brindle, 1960, 1967). These horns are connected to the mesothoracic spiracles of the pharate adult (Byers, 1961; Pritchard & Stewart, 1982). The true pupal stage has rarely been recognized as it is entirely pharate within the last larval skin.

(p) Slender horns projecting beyond the head.

Hexatomini: Oxydiscus, Pilaria, Pseudolimnophila,
Ulomorpha

Eriopterini: Erioptera, Molophilus, Ormosia (in part)

Pediciini: Ula

Limoniini: Thaumastoptera

Cylindrotominae: Phalacrocer

Tipulinae: Brachypremna, Dolichopeza, Holorusia,
Leptotarsus, Nephrotoma, Prionocera, Tipula (in part)

1A Long slender horns strongly recurved.

Hexatomini: Austrolimnophila, Dactylolabis,
Epiphragma

Tipulinae: Dictenidia, Tipula flavolineata

2A Short slender horns, not or scarcely projecting beyond the head.

Hexatomini: Hexatoma

Eriopterini: Cheilotrichia, Ormosia (in part)

Cylindrotominae: Cylindrotoma, Lioqma

Tipulinae: Ctenophora, Tipula (in part)

3A Horns short and broad.

Hexatomini: Elephantomyia, Eloeophila, Limnophila,
Phylidorea

Eriopterini: Gnophomyia, Gonomyia, Lipsothrix,
Teucholabis

Pediciini: Dicranota, Pedicia

Limoniini: Limonia (Dicranomyia), L. (Metalimnobia)

4A Horns replaced by small, narrow, curved pits.

Eriopterini: Chionea, Cladura

5A Horns long, broad and leaf-like.

Limoniini: Elliptera, Limonia (in part)

6A Horns broad with filiform branches.

Limoniini: Antocha,

Hypothesis 6:

The shape of the horns is quite plastic and is related to the larval habitat. The more highly derived respiratory horns occur in the Limoniinae, especially in the tribe Limoniini.

ADULT CHARACTERS

(Based primarily on dissections and Edwards, 1938, Dobrotworsky, 1967a, 1967b and Alexander, 1981)

HEAD

7. Number of flagellomeres. Flagellomeres vary in the Tipulidae from 2 to 37 (Alexander, 1981). In most groups, however, they number from 11-14 and are constant

and characteristic within a group. Fourteen segments are characteristic of most Nematocera and are probably part of the ground plan in the Tipulidae. Both a reduction and an increase in the number of segments may be derived characters.

(p) 14 flagellomeres.

Hexatomini: most

Eriopterini: most

Pediciini: most

Limoniini: Antocha, Elliptera, Orimarga,

Thaumastoptera

Cylindrotominae: all

1A 13 flagellomeres.

Limoniini: Limonia (Limonia), L. (Metalimnobia)

Tipulinae: Nephrotoma (in part), Ptilogyna (in part)

2A 12 flagellomeres.

Limoniini: Limonia (most)

Tipulinae: Acracantha (females), Clytocosmus
(females, in part), Ptilogyna (in part)

3A 11 flagellomeres.

Pediciini: Dicranota (in part)

Tipulinae: Clytocosmus (both sexes, in part),
Ctenophora (females), Dolichopeza (in part),
Holorusia (in part), Leptotarsus (in part),
Nephrotoma (most), Platyphasia, Prionocera,

Ptilogyna (in part), Tipula

4A 10 or fewer flagellomeres.

Hexatomini: Hexatoma (4-10)

Eriopterini: Chionea (2-10)

Tipulinae: Acracantha (males, 10), Brachypremna (9),
Clytocosmus (males, in part, 10), Ctenophora
(males, 10), Dolichopeza (in part, 10), Holorusia
(in part, 10), Ischnotoma (10), Leptotarsus (in
part, 6-10), Megistocera (8-9)

Hypothesis 7:

A reduction or increase in the number of flagellomeres has occurred several times in the Tipulidae. Eleven flagellomeres is widespread in the Tipulinae. Therefore, I suggest that this number is an apomorphy of this subfamily. Some members of the Pediciini also have eleven flagellomeres, but I suggest that this is a convergence.

8. Shape of flagellomeres. Most crane flies have cylindrically shaped flagellomeres, as is the typical shape in other Nematocera. I think that branched and otherwise distended flagellomeres are derived features.

(p) Cylindrical flagellomeres.

Hexatomini: all

Eriopterini: most

Pediciini: all

Cylindrotominae: most

Tipulinae: Brachypremna, Dolichopeza, Leptotarsus,
Megistocera, Prionocera (in part), Tipula (in part)

1A Flagellomeres expanded ventrally giving a serrate appearance.

Cylindrotominae: Lioqma

Tipulinae: Acracantha, Holorusia, Ischnotoma,
Prionocera (in part)

2A Flagellomeres branched.

Hexatomini: GynoplistiaLimoniini: Limonia (Rhipidia) (males)

Tipulinae: Clytocosmus, Ctenophora (males),
Platyphasia, Ptilogyna

3A Flagellomeres narrower distally.

Cylindrotominae: Phalacrocer occidentalisTipulinae: Nephrotoma, Tipula (in part)

Flagellomere shape is too plastic to indicate
 phylogenetic relationship.

9. Verticils. A whorl of long hairs on the flagellar segments is common in the Tipulidae, and loss of these verticils I consider to be derived.

(p) Most flagellomeres with verticils.

Limoniinae: all

Cylindrotominae: all

Tipulidae: Ctenophora, Dolichopeza, Holorusia (in part), Ischnotoma, Leptotarsus, Nephrotoma, Platyphasia, Ptilogyna, Tipula (most)

1A Verticils restricted to the terminal segments.

Tipulidae: Acracantha, Clytocosmus

2A Verticils lost.

Tipulidae: Brachypremna, Megistocera, Holorusia (in part), Prionocera, Tipula (Angarotipula)

Hypothesis 9: p —————> 1A —————> 2A

Whereas character state 1A may be a synapomorphy of Acracantha and Clytocosmus, 2A has occurred independently several times.

10. Nasus. A small nose-like extension on the rostrum is characteristic of most Tipulinae and is not found in either of the other two subfamilies, nor in the other Nematocera. I consider the development of a nasus to be

an apomorphy of the Tipulinae.

(p) No nasus.

Limoniinae: all

Cylindrotominae: all

1A A distinct nasus present.

Tipulinae: Acracantha, Brachypremna, Ctenophora,
Holorusia, Ischnotoma, Leptotarsus, Megistocera,
Nephrotoma, Platyphasia, Tipula

2A Nasus vestigial or lacking.

Tipulinae: Clytocosmus, Dolichopeza, Prionocera,
Ptilogyna

Hypothesis 10: p —→ 1A —→ 2A

I think that the reduction or the loss of a nasus has occurred independently several times.

11. Hairs between ommatidia. Most Nematocera, including most Tipulidae, have hairless compound eyes and this is considered to be plesiomorphic (McAlpine, 1981).

However, hairs between the ommatidia are characteristic of the Anisopodidae, Blephariceridae, Trichoceridae and the tribe Pediciini.

(p) No hairs.

Tipulidae: most

1A Hairs between ommatidia.

Pediciini: all

Hypothesis 11: p —————> 1A

The presence of hairs between the ommatidia I consider to be an apomorphy of the Pediciini.

12. *Tentorium. The presence of a tentorium is widespread in the Insecta and common in the Nematocera. Crane fly larvae have lost the tentorium, but this structure, or vestiges of it, remain in the adults of several genera.

(p) The tentorium includes sclerotized arms between the anterior and posterior pits and part of a tentorial bridge which extends to, but not across the occipital foramen.

Hexatomini: Austrolimnophila, Dactylolabis,
 *Dicranoptycha, Epiphragma, Limnophila
 (Lasiomastix)

Eriopterini: Gnophomyia, Gonomyia

Pediciini: Ula

1A Only the tentorial arms between the anterior and posterior pits are present.

Hexatomini: *Helius, Hexatoma, Limnophila
 (Dicranophragma), L. (Eloeophila)

Eriopterini: Cheilotrichia, Cladura, Cryptolabis,
Erioptera, Molophilus, Ormosia
 Limoniini: Limonia (Limonia)

2A Only the anterior parts of the lateral arms are present.

Hexatomini: Prolimnophila
 Limoniini: Limonia (Metalimnobia), L. (Rhipidia)

3A The tentorium is reduced to the anterior stubs.

Hexatomini: Limnophila (Prionolabis), Pilaria
 Pediciini: Nasiternella
 Limoniini: Elliptera
 Cylindrotominae: Liogma, Phalacrocer replicata

4A No tentorium.

Hexatomini: Pseudolimnophila, Limnophila (Phylidorea)
 Erioptera: Chionea, Neocladura
 Pediciini: Dicranota, Ornithodes, Pedicia
 Limoniini: Antocha, Limonia (Dicranomyia)
 Cylindrotominae: Phalacrocer tipulina
 Tipulinae: all

Hypothesis 12: ♂ —→ 1A —→ 2A —→ 3A —→ 4A

The anterior tentorial arms are more persistent. Loss of all, or part of the tentorium has occurred several times and probably not in the straight-line relationship suggested above. The complete loss of a tentorium, f

believe to be an apomorphy of the Tipulinae. Distinct anterior stubs are evident in members of the sister group, the Cylindrotominae.

13. Pseudotracheae. These are small, sclerotized, trachea-like grooves on the inner surface of the two-segmented labella. They originate at the terminus of the food canal. Pseudotracheae are found in some crane flies, in Bittacomorpha and Ptychoptera (Ptychopteridae), and in several families of the higher Diptera. I suggest that the presence of pseudotrachea is plesiomorphic in the Tipulidae with subsequent loss representing apomorphic states.

(p) Pseudotracheae originate at the terminus of the food canal and extend along the ventral surface of the labellae; numerous parallel, thinner, side branches arise perpendicularly from this main branch.

Hexatomi: Limnophila (Eloeophila), L.

(Lasiomastix), L. (Phylidorea)

1A Pseudotracheae are bifurcate at the terminus of the food canal; one branch recurves posteriorly and the other extends distally. Numerous parallel side branches arise from each of the main branches.

Tipulinae: most

2A The perpendicular side branches are lost; the main

branches are bifurcate.

Cylindrotominae: most

Tipulidae: Brachypremna

3A Loss of pseudotrachea:

Hexatomini: Austrolimnophila, Dactylolabis,

Elephantomyia, Epiphragma, Hexatoma, Limnophila

(Dicranophragma), L. (Prionolabis), Pilaria,

Prolimnophila, Shannonomyia

Eriopterini: all

Pediciini: all

Limoniini: all

Cylindrotominae: Phalacrocer replicata

Hypothesis 13:

Pseudotracheae, in most Diptera, are in the form of a single broad main branch on each labella from which extend numerous parallel and narrower side branches. Therefore, I consider the bifurcate pseudotrachea to be a synapomorphy of the Cylindrotominae and Tipulinae. Loss of the pseudotrachea has occurred several times. I suggest that the side branches of the pseudotrachea have been lost independently in both Brachypremna and in the Cylindrotominae.

14. Lacinia. A lacinia is present in the lower Holometabola. I found a lacinia in the Anisopodidae, Blephariceridae, Dixidae, Tanyderidae and Trichoceridae. Presence of a lacinia must be part of the ground plan of the Tipulidae and a reduction or loss are then derived states.

(p) The lacinia is a long and slender hairy lobe.

Hexatomini: Austrolimnophila, Dactylolabis,
Epiphragma, Phyllolabis

Limoniini: Antocha, Elliptera, Limonia (Discobola),
L. (Geranomyia), L. (Limonia), L. (Metalimnobia)

1A The lacinia is reduced to a short, stubby lobe.

Hexatomini: Pseudolimnophila

Eriopterini: Cryptolabis, Erioptera

Pediciini: all

Cylindrotominae: Phalacrocer tipulina

2A No lacinia.

Hexatomini: Elephantomyia, Hexatoma, Limnophila,
Pilaria, Shannonomyia

Limoniini: Limonia (Dicranomyia)

Cylindrotominae: most

Tipulinae: all

Hypothesis 14: p —→ 1A —→ 2A

The reduction and the loss of a lacinia has occurred

several times. It is suggested that the complete lack of a lacinia is an apomorphy of the Tipulinae. The presence of a lacinia in some members of the Cylindrotominae indicates that this structure has been lost independently in this subfamily.

15. Length of last palpal segment. In most Nematocera, the last (5th) segment of the maxillary palpus is subequal to the 4th. An elongate 5th segment is presumed to be derived.

(p) 5th segment of the maxillary palpus subequal to the 4th.

Hexatomini: most

Eriopterini: all

Pediciini: Dicranota, Nasiternella, Uia

Limoniini: all

1A 5th segment longer than the 4th but less than twice its length.

Cylindrotominae: all

2A 5th segment elongate, twice or more the length of the 4th.

Hexatomini: Hexatoma

Pediciini: Ornithodes, Pedicia

Tipulinae: all

Hypothesis 15: p → 1A → 2A

I consider a somewhat elongated 5th palpomere (1A) to be an apomorphy of the Cylindrotominae and the considerably more elongate 5th palpomere (2A) to be an apomorphy of the Tipulinae. The latter character state also occurs in scattered genera of the Hexatomini and Pediciini, and I suggest that these represent two additional, parallel evolutionary events.

WINGS

16. Subcosta. As part of the ground plan in the Diptera, hence also in the Tipulidae, subcosta is a long vein ending in the costa and connected distally to R₁ by a short element, sc-r. It is presumed that the loss of the tip of Sc is a derived feature.

(p) Subcosta ending in costa; sc-r present.

Hexatomini: all

Eriopterini: all

Pediciini: all

Limoniini: all

Tipulinae: Leptotarsus

1A Tip of subcosta weakly attaining costa; sc-r present.

Tipulinae: Brachypremna, Holopusia, Nephrotoma

2A Subcosta not attaining costa but joined to R₁ by sc-r.

Cylindrotominae: all

Tipulinae: most

Hypothesis 16: p → 1A → 2A

The loss of the tip of subcosta I consider to be an apomorphy of the Cylindrotominae. A similar loss has occurred independently within the Tipulinae.

17. Position of cross vein sc-r. In the Tipulidae, the most common position of sc-r is as described in (p); therefore, I consider this state to be the most primitive.

(p) sc-r distal to fork of Rs.

Hexatomini: all

Eriopterini: (in part)

Limoniini: Limonia (Dicranomyia) in part, L.

(Discobola); L. (Geranomyia); L. (Limonia); L.

(Metalimnobia), L. (Rhipidia)

Cylindrotomini: all

Tipulinae: all

1A Cross vein sc-r basal to fork of Rs.

Eriopterini: Cryptolabis, Erioptera, Molophilus,

Ormosia, Trimicra

Pediciini: all

Limoniini: Elliptera, Limonia (Dicranomyia) in part,
Thaumastoptera

2A Cross vein sc-r lost.

Limoniini: Antocha

Hypothesis 17:

The basal position of sc-r has evolved several times in the Limoniinae, but significantly, not in the tribe Hexatomini. I consider this character state to be an apomorphy of the tribe Pediciini.

18. Presence of a secondary veinlet, c-r. Veinlet c-r occurs in the Tipulinae and has been known as second section of Sc2. As a general rule, evolution of wing venation has proceeded in the direction of loss of, or simplification of venation. The presence of veinlet c-r, therefore, is probably plesiomorphic in the crane flies. (The vein labelled Sc2 in Limonia (Alexander & Byers, 1981:160) I interpret as R1.)

(p) Cross vein c-r present.

Cylindrotominae: all

Tipulinae: all.

1A No cross vein c-r.

Hexatomini: all

Eriopterini: all

Pediciini: all

Limoniini: all

Hypothesis 18: p → 1A

The loss of c-r is here considered to be an apomorphy of the subfamily Limoniinae.

19. Presence of distal tip of R1+2. Part of the ground plan of the Tipulidae is R1+2 attaining the wing margin. This character state is also found in the Trichoceridae (McAlpine, 1981). (See also Hypothesis 20.)

(p) R1+2 reaches wing margin.

Hexatomini: all

Eriopterini: all

Limoniini: all

Pediciini: all

Tipulinae: most

Cylindrotominae: P. replicata

1A Tip of R1+2 atrophied.

Cylindrotominae: most

Tipulinae: Dolichopeza

Hypothesis 19: p → 1A

The tip of R1+2 has been lost independently at least twice.

20. Presence of a separate R2. This is a very short vein between R1+2 and R3, and its presence is generally considered to be plesiomorphic.

(p) R2 distinctly present.

Hexatomini: Austrolimnophila, *Dicranoptycha,
Hexatoma, Limnophila, Polymera, Prolimnophila,
Pseudolimnophila

Eriopterini: Cryptolabis, Empedomorpha, Erioptera,
Gnophomyia, Hesperoconopa, Lipsothrix, Ormosia,
Teucholabis

Limoniini: Antocha, Elliptera, Limonia
 (Alexandriaria), L. (Limonia), L. (Metalimnobia),
Orimaga, Thaumastoptera

Pediciini: all

Cylindrotominae: Phalacrocer replicata

Tipulinae: Leptotarsus, Nephrotoma, Prionocera,
Tipula (Yamatotipula), T. (Lunatipula)

1A Loss of R2 by the proximity of R1+2 and R3.

Pediciini: Pedicia, Dicranota

Cylindrotominae: most

Tipulinae: Brachypremna, Dolichocheza, Holorusia,

Megistocera

- 2A Loss of R2, no connecting veinlet between R1+2 and R3.

Hexatomini: Atarba, Elephantomyia, *Helius,
Phyllolabis

Eriopterini: Gonomyia, Rhabdomastix, Toxorhina

Limoniini: Elliptera illini

Hypothesis 20: p $\begin{array}{l} \longrightarrow 2A \\ \searrow \\ \longrightarrow 1A \end{array}$

The loss of R2 has occurred several times.

21. Radial veins. Veins R4 and R5 reaching the wing margin separately is part of the ground plan for the Nematocera and therefore also for the Tipulidae.

(p) R4 and R5 separate to margin.

Hexatomini: most

Eriopterini: most

Pediciini: all

1A R4+5 reaching wing margin.

Hexatomini: Atarba, *Dicranoptycha, Elephantomyia,
*Helius

Eriopterini: Teucholabis, Toxorhina

Limoniini: all

Cylindrotominae: all

Tipulinae: all

Hypothesis 21: p —→ 1A

The fusion vein R4+5 has occurred independently several times. I consider this to be a synapomorphy of the subfamilies Tipulinae and Cylindrotominae and an independent apomorphy of the Limoniini with unrelated occurrences of this fusion found in other tribes of the Limoniinae.

22. Presence of M1. Three branches of media reaching the wing margin is plesiomorphic in the Diptera, hence also in the Tipulidae. The vein previously interpreted as being M4 is considered to be CuA1, see fig. 2 (McAlpine, 1981).

(p) Cell M1 present, M1 and M2 reaching wing margin separately.

Hexatomini: Austrolimnophila, Epiphragma,

Dactylolabis, Hexatoma (in part) Limnophila (in part), Oxydiscus (in part), Pilaria (in part),

Polymera, Prolimnophila, Pseudolimnophila (in part)

Eriopterini: Cladura, Neocladura

Pediciini: Dicranota, Nasiternella, Pedicia

Cylindrotominae: Cylindrotoma, Phalacropera tipulina

Tipulinae: all

1A Cell M1 lacking, M1+2 reaching wing margin.

Hexatomini: Atarba, *Dicranoptycha, Elephantomyia,
*Helius, Hexatoma (in part), Limnophila (in part),
Oxydiscus (in part), Phyllolabis, Pilaria (in
 part), Pseudolimnophila (in part), Shannonomyia,
Ulomorpha

Eriopterini: most

Pediciini: Ula

Limoniini: all

Cylindrotominae: Lioqma, Phalacrocer replicata,
Triogma

Hypothesis 22: p —————> 1A

The loss of M1 has occurred several times. I consider this character state to be an apomorphy of the Limoniini.

23. Presence of MA. The anterior branch of media (MA) is a very short element between media and radius at the level of the humeral vein. Its presence is a plesiomorphic feature in the Diptera and therefore also in the Tipulidae.

(p) MA present.

Hexatomini: Limnophila, Pilaria, Pseudolimnophila,
Shannonomyia

Eriopterini: Cladura, Erioptera, Neocladura, Ormosia,

ToxorhinaPediciini: Ula

Tipulinae: most

Cylindrotominae: all

1A ~~MA~~ absent.Hexatomini: Elephantomyia, Epiphragma, Dactylolabis,
ProlimnophilaEriopterini: Gonomyia, MolophilusTipulinae: Prionocera

Hypothesis 23: p → 1A

I suggest that the loss of the short element MA is an apomorphy of Prionocera and that this loss has also occurred independently, several times, in the subfamily Limoniinae.

24. Presence of a distal wing fold. There is a characteristic wing fold in many crane flies just proximal to the stigma. This fold includes R1, Rs, base of M1+2 and 2nd section of M3. There is no comparable wing fold in other Nematocera nor in the Limoniinae.

(p) No wing fold.

Hexatomini: all

Eriopterini: all

Pediciini: all

Limoniini: all

Cylindrotominae: most

Tipulinae: Megistocera

1A A weak fold through the discal cell, parallel to media.

Cylindrotominae: Phalacrocerâ replicata

Tipulinae: Brachypremna, Leptotarsus

2A Distal oblique fold very well developed and including 2nd section of M3 (ventral side of the discal cell).

Tipulinae: Ctenophora, Dolichopeza, Holorusia,
Nephrotoma, Prionocera, Tipula

Hypothesis 24: p —→ 1A

→ 2A

I consider an oblique distal wing fold to be an apomorphy of the Tipula group. The weaker fold, which parallels media, has probably evolved independently in the taxa listed in 1A above.

LEGS

25. Tibial spurs. A pair of tibial spurs is present on each leg in the Mecoptera. Tibial spurs are commonly found in the Nematocera. Because of the widespread occurrence in the Tipulidae of a single spur on the

medial surface of the fore legs, and a pair of spurs on the middle and hind legs, I concur with Oosterbroek (1980) that this is part of the ground plan of the Tipulidae. The lateral spur on the fore legs has been lost.

(p) Tibial spur formula 1,2,2

Hexatomini: most

Pediciini: all

Cylindrotominae: all

Tipulinae: most

1A Tibial spur formula 1,1,2

Tipulinae: Ischnotoma, Leptotarsus, Tipula
(Yamatotipula)

2A Loss of spurs.

Hexatomini: *Dicranoptycha, Elephantomyia, *Helius

Eriopterini: all

Limoniini: all

Hypothesis 25: p —→ 1A —→ 2A

Loss of spurs has occurred several times. I suggest that the complete loss of spurs is a synapomorphy of the Eriopterini and Limoniini. The tibial spurs are barely visible in Dolichopeza. Oosterbroek (1980) found the tibial spur formula to be much more variable in the Tipulinae than outlined above. This is not a useful

character to show relationships in the Tipulinae.

MALE TERMINALIA

26. Configuration of 9th segment. The presumed plesiomorphic state in the Nematocera is tergite and sternite 9 fused to form a genital ring with the gonocoxites articulating separately and posteriorly on this ring (McAlpine, 1981). I think that this is also part of the ground plan in the Tipulidae.

- (p) Tergite and sternite 9 are fused, forming a genital ring.

Hexatomini: all

Eriopterini: Chionea, Cladura, Erioptera (Symplecta),

Gonomyia, Molophilus, Neocladura

Pediciini: Dicranota, Pedicia, Ula

- 1A There is a partial, secondary split separating a tergal and a sternal region but leaving a narrow proximal connection.

Eriopterini: Ormosia (Ormosia)

- 2A The genital ring is intact but the sternal portion has become membranous medially.

Hexatomini: *Dicranoptycha

Pediciini: Nasiternella

- 3A The gonocoxites articulate posterolaterally between a

separated tergal and sternal region.

Limoniini: Antocha, Elliptera, Limonia (Metalimnobia)

- 4A Sternite 9 is reduced to a small sclerite adhering to the aedeagus. The gonocoxites articulate laterally on tergite 9.

Limoniini: Limonia (Dicranomyia), L. (Geranomyia), L. (Limonia), L. (Rhipidia)

- 5A Sternite 9 is entirely lacking. The gonocoxites articulate laterally on tergite 9.

Limoniini: Limonia (Discobola)

- 6A Tergite and sternite 9 are fused forming a genital ring. The sternal portion is reduced to a narrow anterior section to which the elongated, separated gonocoxites are attached. The tergal portion of the genital ring partially covers the anterior bases of the gonocoxites.

Tipulinae: Brachypremna, Megistovera

- 7A As in 6A but the gonocoxites are membranously joined to each other at their bases.

Tipulinae: Leptotarsus

- 8A The genital ring is reduced ventrally as described above. The gonocoxites are attached distally to this ring with their dorsal surfaces membranously attached to, and almost completely covered by, the tergal portion of this ring. The gonocoxites are

membranously joined together ventrally. Thus a secondary genital ring is formed.

Cylindrotominae: all

Tipulinae: Holorusia, Nephrotoma, Prionocera, Tipula (Angarotipula), T. (Arctotipula), T. (Lindnerina), T. (Lunatipula), T. (Nobilotipula), T. (Trichotipula), T. (Vestiplex)

9A As in 8A but tergite 9 and the gonocoxites are partially fused.

Tipulinae: Dolichocheza (in part), Tipula (Arctotipula, T. (Pterelachisus), T. (Savtshenkia), T. (Yamatotipula)

10A Tergite 9 and gonocoxites solidly fused.

Tipulinae: Ctenophora, Dolichocheza (in part), Tipula (Beringotipula), T. (Platytipula), T. (Tipula), T. (Trichotipula)

Hypothesis 26:

I think that the plesiomorphic state is restricted to the subfamily Limoniinae. An apomorphy of the tribe Limoniini is the secondary split of the genital ring; the

gonocoxites articulate anterolaterally, rather than distally, on the 9th tergite (3A). A similar but unrelated split of the genital ring occurs in the Eriopterini.

A synapomorphy of the Cylindrotominae and Tipulinae is the abruptly reduced ventral section of the genital ring. My interpretation of this attribute is that there is a complete primary genital ring, but the ventral section of this ring is much reduced, leaving only a very narrow, anterior band. The gonocoxites are attached to this band, and are more or less overlain by the tergal section. I concur with Oosterbroek (1980) that the plesiomorphic state in the Tipulidae is as described in 6A. The fused and more globular gonocoxites, characteristic of the Cylindrotominae and most of the Tipulidae, is derived. An apomorphic feature of some species (e.g., Ctenophora, Tipula (Yamatotipula)) is the complete fusion of the 9th tergite to the gonocoxites making a secondary genital ring with only the gonostyli articulating distally. In several Nephrotoma and Tipula species there are, what I believe to be, secondary weakenings of this genital ring. These are interpreted as incomplete fusion lines between the gonocoxites and the sternites (Oosterbroek, 1980; Tangelder, 1983).

27. Anterior apodeme on gonocoxites. A small dorsal

anterior apodeme on the gonocoxite, articulating with the parameres, is thought to be plesiomorphic in the Nematocera (McAlpine, 1981).

- (p) Gonocoxal apodeme anteriorly directed, articulating with parameres.

Hexatomini: Atarba, Dactylolabis,

Pediciini: Dicranota, Ula

- 1A Gonocoxal apodeme reduced to a knob.

Hexatomini: Epiphragma, Limnophila (Lasiomastix),
Paradelphomyia, Pilaria, Polymera, Prolimnophila,
Shannonomyia, Ulomorpha

- 2A No gonocoxal apodeme, anterior medial edge of gonocoxite not heavily sclerotized.

Hexatomini: *Helius

Eriopterini: Cryptolabis

Limoniini: all

Cylindrotominae: all

Tipulinae: all

- 3A Anteromedial edge of gonocoxite heavily sclerotized, no gonocoxal apodeme.

Hexatomini: Limnophila (Eloeophila), L. (Phylidorea),
L. (Prionolabis)

- 4A Gonocoxal apodeme medially directed, not fused with parameres.

Hexatomini: *Dicranoptycha (in part), Elephantomyia,

Limnophila (Dicranophragma), L. (Idioptera),

• Pseudolimnophila

Eriopterini: Cheilotrichia, Cladura, Chionea,

Erioptera, Gonomyia, Neocladura, Neolimnophila

Pediciini: Ornithodes

5A Gonocoxal apodemes fused with parameres.

Hexatomini: *Dicranoptycha (in part), Hexatoma

6A Gonocoxal apodemes fused to each other and separate from the aedeagal complex lying below.

Eriopterini: Molophilus, Ormosia

Hypothesis 27:

The gonocoxal apodeme has been lost several times (2A).

I consider this loss to be a synapomorphy of the Cylindrotominae and Tipulinae, and an apomorphy of the Limoniini. This apodeme has been lost independently in two other tribes. The shape of the gonocoxal apodeme should prove useful in determining homologies within the subfamily Limoniinae.

28. Dorsal gonocoxal fragments. I think that the plesiomorphic state is separated gonocoxites which are separate from, and posterior to, the 9th tergite. (See hypothesis 26.) The dorsal surface of the gonocoxites

are sclerotized, but they may be membranous medially. (See hypothesis 27). In some groups, the gonocoxites have come to lie, at least partially, ventral to the 9th tergite. Consequently they are mostly membranous dorsally. In this case, I suggest that a fragment from each side of the dorsal surface of these gonocoxites has become more heavily sclerotized. This is correlated with the loss of the parameres. I suggest that the differential retention and subsequent loss of these dorsal gonocoxal fragments can be traced as outlined below. The "genital bridge" of some eriopterines is also formed from dorsal gonocoxal elements (see hypothesis 27), but is considered here to be the result of convergence.

- (p) The gonocoxites are separate from the 9th segment and completely sclerotized dorsally, but may be membranous medially.

Limoniinae: all

- 1A The gonocoxites are at least partially overlain by the 9th tergite, and are membranous dorsally but are without dorsal sclerotized fragments. The parameres are lateral to the aedeagus. (See hypothesis 30.)

Cylindrotominae: Cylindrotoma, Phalacrocer
occidentalis

- 2A A dorsal fragment from the medioposterior edge of each gonocoxite articulates with the parameres. The

parameres are fused and lie dorsal to aedeagus.

Cylindrotominae: Lioqma, Phalacrocer tipulina,

Trioqma

- 3A A dorsal fragment from the medioposterior edge of each gonocoxite articulates with the sperm pump (parameres are lost).

Cylindrominae: Phalacrocer replicata

Tipulinae: Prionocera, Tipula (Nippotipula)

- 4A Dorsal gonocoxal fragments (and parameres) are lost.

Tipulinae: Brachypremna, Megistocera

- 5A A broadly curved "genital bridge" is formed by the medial fusion of the gonocoxal fragments.

Tipulinae: Leptotarsus

- 6A A deep V-shaped "genital bridge" is formed by the medial fusion of elongate gonocoxal fragments from the posteromedial edge on each gonocoxite.

Tipulinae: Dolichopeza americana, Holorusia, Tipula (Arctotipula), T. (Lindnerina), T. (Lunatipula) (in part), T. (Pterelachisus) (in part), T. (Vestiplex), T. (Yamatotipula) (in part)

- 7A There is a disassociated medial V-shaped fragment that I consider to be a remnant of a "genital bridge."

Tipulinae: Tipula (Beringotipula), T. (Lunatipula) (in part), T. (Platytipula), T. (Schummelia), T.

(Tipula)

8A The gonocoxal fragments are reduced to a sclerotized plate anterior to the attachment of the gonostyli.

Tipulinae: Ctenophora, Dolichopeza (Oropeza),

Nephrotoma, Tipula (Labiotipula), T.

(Nobilotipula), T. (Pterelachisus) (in part), T.

(Savtshenkia), T. (Trichotipula), T. (Yamatotipula)

(in part)

9A Gonocoxal fragments fused anteriorly, forming a horizontal "genital bridge".

Tipulidae: Tipula (Angarotipula)

Hypothesis 28:

A synapomorphy of the Tipulinae and Cylindrotominae is the largely membranous nature of the dorsal surface of the gonocoxites, caused by their being at least partially overlain by the 9th tergite. A parallel development of the gonocoxal fragments has occurred in both these subfamilies. Parallel losses and/or further fragmentation of the gonocoxal fragments can be traced in both Dolichopeza (Byers, 1961) and Tipula.

Oosterbroek (1980: 321) suggested that the genital bridge is plesiomorphic in the Tipulidae and not associated with a more robust hypopygium as Vane-Wright

(1967) had postulated. My analysis indicates that the formation of a genital bridge represents an intermediate evolutionary step between fragments extending to the sperm pump and the subsequent loss of the bridge.

29. Gonostyli. Commonly in the Nematocera there is a single gonostylus articulating distally on each gonocoxite. In both the Tanyderidae and Blephariceridae this gonostylus is clearly bilobate. In the Tipulidae the most common condition is a pair of gonostyli, referred to as the outer and inner (or dorsal and ventral) lobes of the gonostylus. This pair is usually united, at least membranously, at the base. Frommer (1963) has shown that in the genus Tipula the two lobes of the gonostylus are moved by separate muscle groups. Sometimes one of these lobes seems to be clearly an outgrowth of the other (e.g., Brachypremna, Megistocera). I suggest that the plesiomorphic condition in the Tipulidae is a bilobate gonostylus on each gonocoxite. Differentiation of these lobes, or of their loss, I consider to be apomorphic features.

(p) The two gonostyli are more or less similar, long, narrow and at least moderately sclerotized.

Hexatomini: all

Eriopterini: Erioptera, Gnophomyia, Molophilus,
Neocladura, Neolimnophila, Ormosia (in part)

Trimicra

Limoniini: Antocha, Elliptera

- 1A There is a single gonostylus present, the other is presumed to be lost.

Eriopterini: Chionea, Cladura, Cryptolabis, Ormosia
(in part)

Pediciini: Dicranota, Ula

Limoniini: Limonia (Limonia)

Cylindrotominae: all

- 2A No gonostyli, but there is a compensatory development of processes on the gonocoxites.

Pediciini: Nasiternella, Pedicia

- 3A The gonostylus bears three or more lobes; one or more of these lobes is presumed to be secondarily divided.

Eriopterini: Cheilotrichia, Gonomyia

Limoniini: Elliptera, Limonia (Metalimnobia)

- 4A The gonostylus bears two lobes; the outer lobe is broad, simple and fleshy; the inner lobe is ornate and more heavily sclerotized.

Tipulinae: Ctenophora, Holorusia, Leptotarsus,

Prionocera, Tipula (Angarotipula), T.

(Arctotipula), T. (Pterelachisus) (in part), T.

(Yamatotipula) (in part)

- 5A The outer lobe of the gonostylus is reduced and spindle-shaped.

Tipulinae: Nephrotoma, Tipula (Trichotipula)

- 6A The outer lobe of the gonostylus is short, cylindrical and fleshy; the inner lobe is longer and more heavily sclerotized.

Pediciini: Ornithodes

Tipulinae: Dolichopeza, Tipula (Savtshenkia), T. (Vestiplex), T. (Yamatotipula) (in part)

- 7A The outer lobe of the gonostylus is short, fleshy, and arises some distance from the base of the more heavily sclerotized inner lobe.

Tipulinae: Brachypremna, Megistocera

- 8A The inner (ventral) lobe is almost circular and fleshy; the outer (dorsal) lobe is a long, narrow sclerotized hook.

Limoniini: Limonia (Dicranomyia), L. (Discobola), L. (Geranomyia), L. (Rhipidia)

Hypothesis 29:

This is a very variable character, however, I consider the loss of a gonostylus (1A) to be an apomorphy of the Cylindrotominae and for this to have occurred independently elsewhere. A synapomorphy of Brachypremna

and Megistocera is state 7A.

30. Parameres. Plesiomorphically in the Diptera, parameres are a pair of unsegmented processes situated between the posterolateral base of the aedeagus and the dorsomedial base of the gonocoxites (McAlpine, 1981). This is also part of the ground plan of the Tipulidae. There is a dual tendency in the crane flies for the parameres to be fused medially or to be lost.

(p) Parameres separate and articulating between the gonocoxites and the aedeagus.

Hexatomini: *Dicranoptycha, Elephantomyia,
Epiphragma, *Helius, Hexatoma, Limnophila
(Dicranophragma), L. (Idioptera), L. (Lasiomastix),
L. (Prionolabis), Pilaria, Polymera, Prolimnophila,
Shannonomyia

Eriopterini: Gonomyia, Neolimnophila

Pediciini: Nasiternella, Ula

Limoniini: all

Cylindrotominae: Cylindrotoma, Rhalacrocera
occidentalis

1A Parameres fused medially, lying dorsal to the aedeagus and articulating laterally with the gonocoxites.

Hexatomini: Atarba, Dactylolabis, Limnophila
(Eloeophila), L. (Phylidorea), Pseudolimnophila,

Ulomorpha

Eriopterini: Cheilotrichia, Chionea, Cladura,
Cryptolabis, Erioptera, Gnophomyia, Molophilus,
Neocladura, Ormosia, Trimicra

Cylindrotominae: Diogma, Liogma, Phalacroceratipulina, Triogma

2A Parameres lost, apparently fused with gonocoxites or aedeagal complex.

Pediciini: Dicranota, Ornithodes, Pedicia

3A Parameres lost, correlated with development of gonocoxal fragment.

Cylindrotominae: Phalacroceratipulina

Tipulinae: all

Hypothesis 30:

I think that the loss of the parameres is an apomorphy of the Tipulinae, and that the parameres have been lost independently in the Cylindrotominae. Within the Pediciini, the parameres have either become fused with the gonocoxites or have been lost.

31. Branches of the aedeagus. A three-branched aedeagus is found in the Blephariceridae, the Tanyderidae and in some Tipulidae. This feature correlates with the

presence of three spermathecal openings in the corresponding females, a presumed plesiomorphy in the Nematocera. A three-branched aedeagus is considered to be part of the ground plan in the Tipulidae and the loss of branches is, therefore, a derived feature.

(p) The aedeagus is tripartite.

Hexatomini: Limnophila (Phylidorea)

Eriopterini: Ormosia (O.) pseudosimilis, Phantolabis?

Cylindrotiminae: Cylindrotoma, Lioqma, Phalacroceras,
Triogma

1A The aedeagus is bipartite, the side branches have been retained, but the central branch is apparently lost.

Hexatomini: Phyllolabis

Eriopterini: Erioptera (Symplecta), Ormosia
(Rhypholophus)

Limoniini: Limonia (Rhipidia)

Cylindrotiminae: Diogma

2A The aedeagus is bifurcate at the tip.

Limoniini: Limonia (Limonia) parietina

3A There is a single aedeagus; the middle branch has been retained and the side branches are lost.

Hexatomini: most, (Limnophila (Lasiomastix) with
vestigial side branches)

Eriopterini: most

4

MicroD

Limoniini: most

Pediciini: all

Tipulinae: all (Nephrotoma ferruginea with vestigial side branches)

Hypothesis 31: p. —→ 1A —→ 2A
 ↘
 → 3A

Both the single and the bipartite aedeagus has evolved several times.

32. Aedeagal length. A short aedeagus rigidly attached to the sperm pump I consider to be plesiomorphic in the Tipulidae. A longer and more flexible aedeagus is derived.

(p) The aedeagus is short, rigid, and approximately the length of tergite 9, and arises distally on the sperm pump.

Hexatomini: all

Eriopterini: most

Pediciini: all

Limoniini: all

Cylindrotominae: all

1A The aedeagus arises anteriorly on, and curves dorsally around the sperm pump.

Eriopterini: Chionea (in part)

2A The aedeagus arises anteriorly on, and curves ventrally around the sperm pump. The sperm pump has some movement in the sagittal plane.

Tipulinae: Dolichopeza, Holorusia, Leptotarsus, Prionocera, Tipula (Arctotipula), T. (Nobilotipula)

3A The aedeagus is secondarily reduced to a very short, thin duct that arises distally on the spherical sperm pump.

Tipulinae: Brachypremna, Megistocera, Tipula (Nippotipula)

4A The aedeagus is elongate and can be considerably extended or withdrawn into the abdomen. A rotation of 180° or more of the sperm pump is possible.

Tipulinae: Ctenophora, Nephrotoma, Tipula (Anagarotipula), T. (Beringotipula), T. (Lindnerina), T. (Lunatipula), T. (Platytipula), T. (Pterelachisus), T. (Savtshenkia), T. (Schummellia), T. (Tipula), T. (Trichotipula), T. (Vestiplex), T. (Yamatotipula).

Hypothesis 32:

An aedeagus arising anteriorly on, and curving ventrally around, the sperm pump (2A), I consider to be an apomorphy of the Tipulinae. A secondarily reduced

aedeagus (3A) I suggest is a synapomorphy of Brachypremna and Megistocera and that a similar reduction has occurred independently in the subgenus Nippotipula of the genus Tipula. In several species of the genus Chionea (Eriopterini), the aedeagus arises anteriorly rather than posteriorly on the sperm pump, reminiscent of the Tipulinae. Such variation within this genus, suggests that there may be hidden variability within other genera, and that conclusions based on few species may be erroneous.

33. Lateral appendages of the aedeagal guide. The tripartite aedeagus is generally heavily sclerotized enclosing much narrower sperm ducts (endophallus, Frommer, 1963). In the subfamily Limoniinae the single aedeagus is commonly heavily sclerotized and often bears several apodemes. In the Tipulinae, on the other hand, the aedeagus is generally very long, narrow and flexible, and its pathway during copulation is controlled by the aedeagal guide (adminiculum, Byers, 1961; Frommer, 1963; Oosterbroek, 1980). This guide is attached to the inner ventral wall of the gonocoxites. It is free anteriorly or it extends to the sperm pump. It varies from having a shallow longitudinal groove to being fused dorsally, forming a cone through which the aedeagus glides during copulation.

My hypothesis is that the aedeagal guide is derived from the outer heavily sclerotized layer enclosing the sperm ducts of a tripartite aedeagus. It has become separated from the sperm pump, and the central section seems to have split dorsally and freed the narrow aedeagus within. This has allowed for the lengthening and coiling of the intromittent organ typical of the subfamily Tipulinae. In some groups the aedeagal guide maintains a membranous connection with the sperm pump (e.g., Dolichopeza, Megistocera, Prionocera). Commonly there are a pair of structures distoventrally which flank the aedeagal guide, or, in some species, appear to be more closely associated with the gonocoxites (i.e. gonapophyses, Byers, 1961); I suggest that these are derived from the vestigial lateral aedeagal branches.

Oosterbroek (1980) drew attention to the free remnants of an originally longer aedeagal guide that he considered to be the only good synapomorphy of Nephrotoma. He suggested that the "adminiculum" (aedeagal guide) consists of two sclerotized modifications derived from the middorsal margin of "sternite 9" (gonocoxites). He also concluded that in the Limoniinae the aedeagal guide and sperm pump are fused and that the Tipulinae are distinguished by the separation of these structures (ibid, p. 319). The implication is that the aedeagal complex in the subfamily Limoniinae has been derived from that of the Tipulinae and that it includes sternal

elements. I suggest that evolution happened the other way around. The separation of the aedeagal guide from the aedeagus is an apomorphy of the Tipulinae and secondarily the guide becomes fused to the gonocoxites. The presence of midventral plates in the membrane between the gonocoxites, I suggest, are fragments of an originally more extensive aedeagal guide.

- (p) Heavily sclerotized tripartite aedeagus, no separate aedeagal guide.

Cylindrotominae: most

- 1A Aedeagal guide with lateral branches.

Tipulinae: Brachypremna, Dolichocheza, Megistocera,

Nephrotoma, Tipula (Angarotipula), T.

(Beringotipula), T. (Labiotipula), T. (Lindnerina),

T. (Lunatipula), T. (Nippotipula), T.

(Nobilotipula), T. (Platytipula), T. (Savtshenkia),

T. (Schummelia), T. (Tipula), T. (Yamatotipula)

- 2A Aedeagal guide with lateral branches lost.

Tipulinae: Ctenophora, Holorusia, Leptotarsus,

Priocera, Tipula (Arctotipula), T.

(Pterelachisus), T. (Trichotipula), T. (Vestiplex)

Hypothesis: 33: p → 1A → 2A

The Tipulinae are characterized by a simple aedeagus and a separate aedeagal guide. I think that an aedeagal

guide, with a central section flanked by a pair of lateral branches, is an apomorphy of the Tipulinae. A parallel loss of these lateral branches has occurred separately in several genera, and repeatedly within the genus Tipula.

34. Relationship of aedeagal guide to sperm pump.

Presuming that the aedeagal guide is derived from external sclerotizations of the narrow endophallus, then plesiomorphically it would extend to the sperm pump.

(p) Aedeagal guide extending to sperm pump.

Tipulinae: Brachypremna, Dolichopeza, Megistocera,
Prionocera, Tipula (Nippotipula)

1A Aedeagal guide reduced.

Tipulinae: Ctenophora, Holorusia, Leptotarsus,
Nephrotoma, Tipula (Angarotipula), T.
(Arctotipula), T. (Beringotipula), T.
(Labiotipula), T. (Lindnerina), T. (Lunatipula), T.
(Platytipula), T. (Pterelachisus), T.
(Savtshenkia), T. (Tipula), T. (Trichotipula), T.
(Vestiplex)

Hypothesis 34: p $\longrightarrow$ 1A

The presumed attachment of the guide to the sperm pump has been severed independently several times. According

to Oosterbroek (1980: 320), there are no "adnuncular rods" in Megistocera. This may be a variable character in this genus.

35. Sperm pump. In its simplest form the sperm pump is a broadening of the basiphallus subtended by an ejaculatory sclerite, common to many Diptera (McAlpine, 1981). Such a sperm pump is found in the tribe Limoniini and in some Hexatomini (e.g., Epiphragma, Pilaria). However, because of many derived features also found in the groups with the simplest sperm pump, it appears that the basiphallus without projecting apodemes is a result of reduction. The sperm pump as described in (p), is the most widespread in the family, and is correlated with other plesiomorphies, suggesting that this is the most primitive configuration in the Tipulidae.

(p) The sperm pump bears immoveable apodemes in addition to the moveable ejaculatory sclerite, and the aedeagus arises posteriorly.

Hexatomini: most

Eriopterini: most

Pediciini: all

Limoniini: Elliptera, Antocha

Cylindrotominae: most

1A The sperm pump is a simple broadening of the basiphallus and is subtended by a small moveable

sclerite. The aedeagus arises posteriorly.

Hexatomini: Epiphragma, Pseudolimnophila,

Prolimnophila, Pilaria

Eriopterini: Cryptolabis

Limoniini: Limonia

Cylindrotominae: Phalacroceras occidentalis

- 2A The sperm pump bears immovable apodemes and is bent dorsally and posteriorly over the aedeagus, so that its morphological anterior end is now pointing in a posterior direction. The abruptly narrower aedeagus arises anteriorly.

Tipulinae: most

- 3A The spherical sperm pump is reversed to its plesiomorphic position, so that the abruptly short, slender aedeagus arises anteriorly.

Tipulinae: Brachypremna, Megistocera

Hypothesis 35:

A robust sperm pump with immovable apodemes and a broad ejaculatory sclerite is a synapomorphy of the Cylindrotominae and Tipulinae. The rotated sperm pump as described in 2A, I consider to be an apomorphy of the Tipulinae. I suggest that the sperm pump has become simplified in both Brachypremna and Megistocera. In the

former, the immoveable apodemes are also lost.

Simplification of the sperm pump (1A) has also occurred independently at least three times in the subfamily Limoniinae.

36. Ejaculatory sclerite. This sclerite is extremely variable in crane flies. Plesiomorphically, it seems to function like a plunger with the proximal cup-shaped end fitting just inside the rim of the enlarged basiphallus. The distal stem section (for muscle attachments) varies from being dorsoventrally to laterally flattened, and is broadly bifurcate to narrowly cylindrical.

(p) The ejaculatory sclerite is shaped like a plunger or a wine glass. The sperm duct enters the pump through a dorsal hole in this sclerite or through a medial notch on its posterodorsal rim.

Hexatomini: Atarba, *Dicranoptycha, Epiphragma,

*Helius, Hexatoma, Limnophila (in part),

Phyllolabis, Pilaria, Polymera, Pseudolimnophila,

Shannonomyia

Eriopterini: Cheilotrichia, Cladura, Cryptolabis,

Erioptera, Gnophomyia, Gonomyia, Ormösia

Pediciini: Ula

Limoniini: Elliptera

1A The ejaculatory sclerite varies from a cone-shaped to a disc-shape and covers the anteroventral

invagination of the sperm pump. The sperm duct appears to enter through the centre of this sclerite.

Limoniini: Limonia

- 2A The ejaculatory sclerite is flat and appears to be fused with the ventral surface of the aedeagal complex. The pumping action is apparently effected by another sclerite lying dorsal to the aedeagus. This sclerite is armed with two short closely spaced longitudinal ridges on its ventral surface which make contact with the membranous aedeagus beneath. The sperm duct enters the aedeagal complex anterior to and some distance from this pumping sclerite. This sclerite is probably derived from the parameres and/or parts of the aedeagal complex and is probably homologous to a dorsal sclerite found in some Hexatomini (e.g., Helius, Hexatoma).

Pediciini: Dicranota, Nasiternella, Ornithodes,
Pedicia

- 3A The ejaculatory sclerite lies dorsal to the sperm pump. The "cup-shaped" section is flat, broad, hinged anteriorly to the rim of the sperm pump, and covers an invaginated area of this pump. The sperm duct enters the sperm pump just posterior to the posterodorsal edge of the ejaculatory sclerite.

Hexatomini: Dactylolabis, Limnophila (Prionolabis),
Elephantomyia

- 4A The ejaculatory sclerite lies ventrally on the sperm pump. The proximal section is flat and thin in some species (e.g., Chionea) to quite broadly rounded in the others. The sperm duct enters the pump just posterior to the stem of the ejaculatory sclerite, at the region of a narrow flange.

Eriopterini: Chionea, Molophilus

Cylindrotominae: all

- 5A The ejaculatory sclerite is broad and flat proximally where it covers a large invaginated area on the sperm pump. The distal part of this sclerite is dorsoventrally flattened and bifurcate. The sperm pump is reversed (see hypothesis 32). Its morphologically ventral surface is in a dorsal position, consequently the ejaculatory sclerite has moved from a ventral to a dorsal position. The sperm duct enters posterior to, but morphologically anterior to, the ejaculatory sclerite.

Tipulinae: Leptotarsus

- 6A The orientation of the sperm pump is as in 5A above. The ejaculatory sclerite has a reduced, small, piston-like proximal part covering a smaller invaginated area of the sperm pump. The distal part of this sclerite is broadly fan-shaped to bifurcate.

Tipulinae: Ctenophora, Dolichopeza, Holorusia,
Nephrotoma, Prionocera, Tipula

7A The ejaculatory sclerite is small, cylindrical and partially invaginated posteriorly on the broadly spherical sperm pump.

Tipulinae: Brachypremna, Megistocera

Hypothesis 36:

I suggest that the plesiomorphic hollow, cup-shaped portion of the ejaculatory sclerite has become flattened, and moved from its posterior position covering the invagination on the sperm pump to either a ventral or a dorsal position. At the same time, the anterior section of the sclerite has become relatively smaller, while its posterior end has become broader. The dorsal position of the ejaculatory sclerite, in the Tipulinae, is a direct result of the reversal of the sperm pump and seems to have evolved from the configuration seen in the, Cylindrotominae and described in 4A. The reduced and posterior orientation of the ejaculatory sclerite in Brachypremna and Megistocera, I suggest, is a synapomorphy of these genera, and a result of reduction.

37. torsion of the male terminalia. In scattered groups within the Diptera, the male terminalia are permanently rotated 180° or more, to the right or to the left of the

horizontal axis. The unrotated state of the male terminalia is much more common and is considered to be plesiomorphic.

(p) Terminalia not rotated.

Hexatomini: all

Eriopterini: Chionea, Cladura, Cryptolabis,

Gnophomyia, Gonomyia, Neocladura, Neolimnophila

Pediciini: all

Limoniinae: all

Cylindrotominae: all

Tipulinae: most

1A Male terminalia permanently rotated 180°.

Erioperini: Cheilotrichia, Erioptera, Molophilus,
Ormosia

Tipulinae: Brachypremna, Megistocera

Hypothesis 37: p —————> 1A

Permanent torsion has probably evolved twice in this family. It is probably a synapomorphy of the eriopterine genera listed above and an independent synapomorphy of the two tipuline genera.

FEMALE TERMINALIA

38. Number of spermathecae. Three spermathecae are

common in the Diptera and presumed to be plesiomorphic in the Tipulidae.

(p) Three spermathecae.

Hexatomini: Hexatoma, Limnophila (Dicranophragma), L.
(Lasiomastix), L., (Phylidorea), Shannonomyia,
Ulomorpha

Eriopterini: Chionea (in part)

Pediciini: Pedicia, Ula

Cylindrotominae: all

Tipulinae: all

1A Two spermathecae.

Hexatomini: Atarba, Austrolimnophila, Epiphragma,
*Helius

Eriopterini: Cheilotrichia, Chionea (in part)
Cladura, Erioptera

Limoniini: Elliptera, Limonia (Dicranomyia), L.
(Metalimnobia)

Pediciini: Dicranota

Hypothesis 38: p —————> 1A

Reduction from three to two spermathecae has occurred several times. It has occurred independently within the genus Chionea, indicating that there may also be more variability in other genera than has heretofore been suspected.

39. Spermathecal character. Spermathecae are commonly heavily sclerotized, spherical structures and therefore easy to see in cleared specimens. However, in the Limoniinae there is a tendency for the spermathecae to become membranous and consequently difficult to see. Membranous spermathecae are turgid when full of sperm and an amorphous flattened sac when empty (Byers, 1983).

(p) Spherical, sclerotized spermathecae.

Hexatomini: Atarba, Epiphragma, Hexatoma, Limnophila
(Dicranophragma), L. (Lasiomastix), L.
(Phylidorea), Pseudolimnophila, Shannonomyia

Pediciini: Pedicia.

Cylindrotominae: all

Tipulinae: all

1A Spermathecae membranous, sac-like.

Hexatomini: Austrolimnophila, *Helius

Eriopterini: Cheilotrichia, Chionea, Cladura,
Gnophomyia, Molophilus, Ormosia

Pediciini: Ornithodes

Limoniini: all

Hypothesis 39: p ———→ 1A

There is a tendency for the spermathecae to become membranous in several genera of all four tribes of the Limoniinae. Membranous spermathecae are a characteristic

of the Limoniini and Eriopterini, therefore, it is suggested that this character state is a synapomorphy of these two tribes.

40. Spermathecal ducts. Three spermathecal ducts opening individually into the bursa, and corresponding to the tripartite aedeagus of the male, are thought to be part of the ground plan in the Diptera. Species in which the male has a simple aedeagus, the corresponding female has a single spermathecal opening in the bursa.

- (p) Three short spermathecal ducts open individually in the bursa,

Hexatomini: Limnophila (Phylidorea)

Cylindrotominae: Cylindrotoma, Liogma, Phalacrocer,
Triogma

- 1A Three short spermathecal ducts join together near the entrance of the bursa, forming a very short common duct.

Hexatomini: most

Eriopterini: most

Pediciini: all

Limoniini: all

- 2A Three long slender spermathecal ducts join a broader common duct some distance anterior to the bursa. A single, more posteriorly situated duct, joins the

common duct dorsally and a pair of ducts join laterally and more anteriorly. The anterior end of the common duct is unmodified.

Tipulinae: most

- 3A Similar to 2A but the three spermathecal ducts are subequal in width to the common duct. A pair of ducts branches off posterior to the single anterior duct.

Eriopterini: Chionea (in part)

- 4A Similar to 2A above but the anterior end of the common duct is broadened and variously modified.

Tipulinae: Dolichopeza

Hypothesis 40:

Evolution from three separate openings to one probably occurred separately in each subfamily. The variation noted within Chionea (Byers, 1983) suggests that parallel developments may be found in other genera. The distinctive arrangement found in the Tipulinae, I consider to be an apomorphy of that subfamily. The modification indicated in Dolichopeza, I suggest is an autapomorphy of that genus.

41. Stiff hypogynial setae. In most Nematocera the

hypogynial valves are unadorned and I suggest that that is the primitive state.

(p) Hypogynial valves unadorned or with scattered, fine hairs.

Cylindrotominae: all

Tipulinae: all

1A A fringe of long stiff setae on the mediodorsal edge of the hypogynial valves.

Hexatomini: all

Eriopterini: all

Pediciini: all

Limoniini: all

Hypothesis 41: p. $\longrightarrow$ 1A

The presence of stiff setae on the hypogynial valves, in all the tribes of the Limoniinae, is here considered to be an apomorphy of the subfamily.

PHYLOGENY OF THE FAMILY TIPULIDAE

Forty-one characters were analyzed and a proposed phylogeny of the tribes and subfamilies is presented in a cladogram (fig. 83). The numbers in the cladogram and in the discussion below refer to the hypothesis numbers of the previous section.

On the basis of the characters analyzed above, I suggest that the ground plan of the crane flies includes the following character states. In the larva: (1) head capsule extensively sclerotized dorsally and laterally, but membranous posteriorly; (2) no tentorium; (3) 6 lobes on the spiracular disc; (4) lobes fringed with long hairs; (5) a pair of terminal spiracles. In the pupa: (6) long slender respiratory horns. In the adult: (7) tentorial arms between anterior and posterior pits and at least the vestiges of a hypostomal bridge; (8) pseudotrachea with a single main branch and numerous parallel side branches; (9) lacinia long, slender and hairy; (10) subcosta ending in costa and sc-r near the distal tip of subcosta; (11) four branches of radius attaining the wing margin: R1+2, R3, R4 and R5; (12) cell M1 present; (13) MA present; (14) wing without a distal fold; (15) tibial spur formula 1,2,2; (16) 9th tergite and sternite fused to form a genital ring; (17) gonocoxites fully sclerotized, articulating separately and posteriorly on the genital ring; (18) aedeagus short,

rigid and tripartite; (19) parameres (paired), articulating laterally between the aedeagus and the base of the gonocoxites; (20) three spherical spermathecae on three short ducts, and each duct opening separately in the genital chamber.

The monophyly of the Tipulidae is based on the following synapomorphies. The larval head capsule is partially retracted within the thorax and is capable of limited extension and retraction during feeding and locomotion. This head capsule is incomplete posteriorly as a result of incisions. The larval tentorium is lost and the larvae are metapneustic. (Kristensen (1981) reported that all first instar larvae in Diptera are apneustic, but distinct spiracles were observed on all tipuline first instars which I have reared from eggs.) (See also Byers, 1961, 1983).

LIMONIINAE

The monophyly of this subfamily is based on two synapomorphies. The larval spiracular disc bears five lobes (3-1A), and there is a fringe of long stiff setae on the mediodorsal edge of the hypogynial valves (41-1A). Other characters common to these tribes are here considered to be plesiomorphies.

Tribe Hexatomini

No crane fly has been found with all 41 plesiomorphic character states described above. More of these states, however, are found in the tribe Hexatomini, suggesting that this tribe, as presently constituted, includes the more primitive crane flies. The Hexatomini are a very large and varied tribe, defined entirely by plesiomorphic features. The enormous variation, the highly derived aspect of some of the larvae (e.g., Limnophila, Pilaria) and the lack of any apparent synapomorphy suggest that this may be a polyphyletic group.

Tribe Eriopterini

This tribe is characterized by three branches of radius attaining the wing margin (a plesiomorphy) and the loss of tibial spurs (25-2A). I suggest that the latter is a synapomorphy which it shares with the Limoniini. Another suggested synapomorphy of the Eriopterini plus Limoniini is the relatively large membranous spermathecae (39-1A). Membranous spermathecae also occur in some Hexatomini and Pediciini. It is possible that this character is a synapomorphy of a section of the Hexatomini plus the tribes Eriopterini and Limoniini. Membranous spermathecae must have evolved separately in the Pediciini because the plesiomorphic state is present in Pedicia. Byers (1983), in characterizing the Eriopterini, included the lack of hairs interspersed among the ommatidia, simple rather than toothed tarsal claws and empodia well developed. These may be good

diagnostic characters, but they are also plesiomorphies, and, therefore, not adequate to show close relationship. My study suggests that the Eriopterini are Hexatomini which have membranous spermathecae and have lost their tibial spurs. These synapomorphies are shared with the Limoniini, suggesting that these are sister groups. Much more work should be done to clarify the phylogeny of the genera involved here and to study the apparently related genera of Lechriini.

Tribe Pediciini

The two derived characters which distinguish the tribe Pediciini are the hairs between the ommatidia (11-1A) and sc-r occurring near the middle rather than near the tip of the subcosta (17-1A). The latter character state also occurs in some eriopterines and limoniines but I think that this is an independent development because this seems to be restricted to the more highly evolved genera within each of the aforementioned tribes.

Other characteristics of the Pediciini are the larval head capsule which is only slightly excised dorsally; the tendency for the gonostyli to become reduced or lost, and the gonocoxites to become enlarged and to bear secondary projections. The aedeagal complex is relatively large and considerably derived. The ejaculatory apodeme, in all but the most primitive genus Ula, has moved to a ventral position and become fused with the aedeagal

complex. The pumping action is apparently effected by a horizontal sclerite lying dorsal to the membranous aedeagus. This sclerite may be derived from the parameres and/or the gonocoxal apodeme. It is present in Ula and is very similar to a sclerite lying dorsal to the aedeagus in some hexatomines (e.g., Dicranoptycha, Helius, Hexatoma). This may be a synapomorphy of the Pediciini and a section of the Hexatomini.

The placement of Ula in the tribe Pediciini has been questioned because of the presence of five lobes on the spiracular disc (Bryce, 1957b). All the other pediciine genera, as far as is known, (Byers, 1981) have only two ventral lobes. I suggest that the ground plan of this tribe includes five lobes on the spiracular disc and that the loss of the dorsal and lateral lobes is a feature of the more derived pediciine genera.

Tribe Limoniini

The Limoniini have been recognized by the fusion of R4+5 (21-1A). I think that this is an apomorphy of this tribe. The analysis of this character, however, shows that this fusion also occurred in the Cylindrotominae and Tipulinae, and that it has also occurred sporadically in the Hexatomini and Eriopterini. Furthermore, I suggest that by relying on this fusion, the genera Helius and Dicranoptycha have been incorrectly assigned to this tribe.

Snodgrass (1904) considered the Limoniini to be the most primitive tribe because of the separation of the 9th tergite and sternite from each other. I think that this character state is an apomorphy of the Limoniini and represents a secondary splitting of the genital ring (26-3A). The gonocoxites, in this tribe, articulate laterally rather than distally on the 9th tergite. One can trace within the genus Limonia a reduction of the 9th sternite and concomitant development of the ventral lobes on the gonocoxites. This splitting of the genital ring, I think, allows for greater flexibility during mating. And the gonocoxal lobes are a ventral protection of the otherwise exposed aedeagus. I suggest further, that within this tribe, there is also a reduction of the sperm pump to a simple broadening of the basiphallus subtended anteriorly by a conical to almost flattened circular ejaculatory sclerite.

The Limoniini exhibit several other derived features which, I think, add weight to my hypothesis that this is not one of the more primitive tribes. They are: tentorial arms present but no vestiges of a tentorial bridge (12-1A); lack of cell M1 (22-1A); loss of tibial spurs (25-2A); loss of the anterior apodeme on the gonocoxite (27-2A); two membranous spermathecae (38-1A, 39-1A). These are regarded as weak synapomorphies because they are losses or reductions of structures.

CYLINDROTOMINAE AND TIPULINAE

These two subfamilies share several synapomorphies suggesting a common ancestor. They are the bifurcate nature of the pseudotrachea (13-1A), the presence of the fusion vein R4+5 (21-1A), the configuration of the 9th segment (26-6A), the related internal and membranous character of the gonocoxites (28-1A), and the loss of the anterior gonocoxal apodeme (27-2A).

In several species of both subfamilies (e.g., Phalacrocer, Holorusia, Leptotarsus) the gonocoxites can be pulled off quite easily, revealing a genital ring intact. If the plesiomorphic state is, as I suggest, relatively elongated and separated gonocoxites (26-6A), then the subsequent fusion and reduction of these gonocoxites (26-8A) must have occurred

in each subfamily. There has also been a parallel development of gonocoxal fragments related the loss of the parameres. This development has progressed further in the Tipulinae, as outlined in the section below.

On the basis of the inferred synapomorphies discussed above, I conclude that the Cylindrotominae and Tipulinae are sister groups and together form the sister group of the Limoniinae.

CYLINDROTOMINAE

The monophyletic status of the Cylindrotominae is based on the longitudinal thoracic and abdominal rows of lobes on the larvae (2-1A) and possibly on their leaf-eating habit. (The latter character is not discussed above.) Additional apomorphies are the loss of marginal hairs on the spiracular disc (4-2A), the loss of the outer lobe of the gonostylus (29-1A) and the moderately long last segment of the maxillary palpus (15-1A). Characters such as the tripartite aedeagus (31) and the presence of anterior stubs of the tentorial arms (12) are regarded as plesiomorphies.

TIPULINAE

The monophyly of the Tipulinae is based on four strong apomorphies of the adult. They are: the presence of a nasus (10-1A); the presence of an aedeagal guide (33-1A); a reversed sperm pump (35-2A) and the posterior origin of the aedeagus (32-2A). Additional inferred apomorphies are the complete loss of a tentorium (12-4A) and the loss of a lacinia (14-2A); 13 flagellomeres (7-3A); an elongated 5th palpomere (15-2A); the loss of the parameres (30-3A); the shape of the ejaculatory sclerite (36-5A); and the configuration of the spermathecal ducts (40-2A).

PHYLOGENY OF THE SUBFAMILY TIPULINAE

The genera in the Tipulinae are very difficult to fit into a phylogenetic scheme. My study has been limited to specimens from nine North American genera and 13 of the more than 25 subgenera of Tipula. This has been supplemented with literature on Australian genera (Dobrotworsky, 1967a, 1967b). Several characters of phylogenetic importance are less important taxonomically and so were not discussed in those papers. Therefore my cladogram, fig. 84, only includes the North American genera.

the North American genera fall into two species groups. In the Brachypremna group, Brachypremna and Megistocera are recognized as sister groups on the basis of the following synapomorphies: the loss of verticils (9-2A), the arrangement of the gonostyli (29-7A), the torsion of the male terminalia (37-1A), and the simplified aedeagal complex. The last of these includes the loss of dorsal gonocoxal fragments (28-4A), a shortened aedeagus (32-3A) arising anteriorly on an unrotated sperm pump (35-3A), and a reduced ejaculatory sclerite (36-7A). I think that the aedeagal complex in these genera is derived from the robust aedeagal complex of the cylindrotomines and is a simplification of the more elaborate arrangement found in the other tipuline genera. This simplification may be related to the

permanent torsion of the male genitalia. Oosterbroek (1980) considers the shorter aedeagus in this subfamily to be the more primitive.

Leptotarsus is provisionally assigned to the Brachypremna group on the basis of shared plesiomorphies. These are the lack of a distal wing fold (24-p) and the enlarged gonocoxites, which, in Leptotarsus, are separate almost to their bases (26-7A). If this assessment is correct, then the formation of a genital bridge in Leptotarsus must have occurred independently of the genital bridge formed in the Tipula group. In Leptotarsus this bridge is formed between the anterior bases of the gonocoxites (28-5A), whereas in the Tipula group the bridge, when present, is formed from the gonocoxal fragments originating at the posterior ends of the gonocoxites.

The Tipula group is defined by three apomorphies. They are the distal wing fold (24-2A), the more complete formation of a secondary genital ring which includes the gonocoxites (26-8A), and the extension of a posteromedial gonocoxal fragment from each gonocoxite to the sperm pump (28-3A).

Character state 26-8A is also an attribute of the Cylindrotominae. The most parsimonious explanation seems to be that the inclusion of the gonocoxites into a secondary genital ring represents a parallel development

of these subfamilies. (A partial, but slightly different wing fold is present in Megistocera, Leptotarsus and Phalacrocer replicata and is thought to be ancestral to the Tipula-type of fold.)

The striking similarity of the V-shaped "genital bridge" as found in Dolichopeza americana, Holorusia and in several subgenera of Tipula, suggests a recent common ancestry. The anterior end of this bridge is membranously attached to the posterior apodemes of the sperm pump. A parallel reduction of this bridge can be traced in the subgenus Oropeza of Dolichopeza and in Tipula.

In Prionocera and the subgenus Nippotipula of Tipula, gonocoxal fragments are membranously connected to the sperm pump. In Prionocera the anterior ends of these gonocoxal fragments appear to be membranously attached to each other. This may be plesiomorphic in relation to the fused "V-shaped" genital bridge described above. In Ctenophora, Nephrotoma, several subgenera of Tipula, and the subgenus Oropeza of Dolichopeza, all that remains of an aedeagal guide is a broadened sclerite near the base of the gonostyli ("Sp2", Oosterbroek, 1980). A disassociated medial fragment ("Sp1", Oosterbroek, 1980) is all that remains of a genital bridge in several other subgenera of the genus Tipula.

One can trace a similar network of relationships based on the development of the aedeagal guide. The plesiomorphic condition in the Tipulinae, is I believe, an aedeagal guide which has an elongate midsection enveloping the aedeagus and is flanked by a pair of sclerotized appendages (e.g., Tipula (Lindnerina)). These appendages, as I have suggested above, are probably derived from the sclerotization around the lateral aedeagal ducts. One can trace, in both Dolichopeza and Tipula the reduction of the aedeagal guide and its tendency to become more closely associated with the ventral membranous region between the gonocoxites. Loss of the lateral appendages of the guide characterizes Prionocera and Tipula (Nippotipula).

Prionocera has been linked to the subgenus Angarotipula on the basis of elongate lobes on the spiracular disc which are fringed with long hairs, and the loss of verticils on the flagellomeres. Verticils have been lost in other unrelated groups (see hypothesis 9) and the shape of the flagellomeres in the subgenus Angarotipula and that of Prionocera is quite different. The larval similarity I suspect is plesiomorphic.

It appears from the above, that genera of the Tipula group show a close relationship to various subgenera of the genus Tipula. This conclusion was also reached by Oosterbroek, and by Frommer and Theowald before him

(Oosterbroek (1980)). Oosterbroek based his phylogenetic study on a slightly different group of genera. He pointed out the inadequacies of a phylogeny based on a limited representation of the subfamily. On the basis of the specimens which I have studied, I also conclude that the genera in the Tipulinae appear to be monophyletic except for the genus Tipula, which is clearly paraphyletic.

PHYLOGENY OF THE GENUS PRIONOCERA

The species of Prionocera are very similar to each other however, they can be assigned to four groups. The presumed phylogeny is presented in a cladogram (fig. 85). The synapomorphous characters are numbered 1-21 on the cladogram and are discussed below. For a more complete description of these characters and of the autapomorphous characters which distinguish each species, see Part I.

The monophyly of the turcica group is based on three strong characters. Both the dorsal and lateral processes of the 9th tergite are long and triangular (1). The paired apical process is reduced and is borne on a median dorsal extension of the 9th tergite which arises between, and not ventral to, the dorsal processes (2). The aedeagal guide is not a flat plate medially but is expanded either dorsally or laterally (3).

The dimidiata group is distinguished by two apomorphies. Pigmented sensilla are present on the lateral surface of the dorsal beak of the inner gonostylus (4) and a subapical tooth or sclerotization is present on the aedeagus (5). The sensilla (4) are presumed lost in abscondita and woodorum. In the former, because of synapomorphies which this species shares with dimidiata, this is a reasonable assumption. It is a questionable assumption for woodorum.

Prionocera recta is distinguished within the dimidiata group by its strongly distended flagellomeres (6). I am assuming that there is an inherited tendency for the flagellomeres to become distended and that this stronger distension occurs in three separate lines. Because of its postulated multiple occurrence, this is a weak apomorphy.

A subrectangular median lobe between the dorsal and apical processes distinguishes five species of the dimidiata group (7). Prionocera abscondita and P. dimidiata are sister species based on the dorsal process of the 9th tergite which is broader than long and the lateral process which is short and narrow (8). The synapomorphies of the sister species subsericornis and setosa are: (9) the inner gonostylus which has a long cylindrical dorsal beak and a small almost spherical base; and (10) the triangular, lateral and dorsal,

processes. In subsericornis the dorsal and lateral processes are very small and could be the remnants of a single dorsal process, in which case this species lacks a true lateral process.

The remaining species, woodorum and recta, are each distinguished by strongly distended flagellomeres (6).

The apomorphy which distinguishes the ringdahli group of eight species is the long hairs of the head and thorax (11). The species pair ominosa and serricornis are defined by two synapomorphies. The apical processes on the ninth tergite are relatively close together, sharply curved, and their inside edges form a hard-edged semicircle (12), and the nasus is lost (13). The six remaining species of the ringdahli group are distinguished by the presence of a dense hairy oval to roundish patch on the lateral surface of the base of the inner gonostylus (14). Prionocera naskapi and pubescens are related by the loss of the lateral lobes on the 9th tergite (15) and apical lobes of the ninth tergite being narrow and relatively far apart (16). Four species are related on the basis of the distal beak of inner gonostylus being relatively broad and flat (17). A questionable synapomorphy of electa and byersi is reduction of the length of the hairs on the head and thorax (18). The remaining species, ringdahli and elliptica, clearly form a sister group on the basis of a

very similar inner gonostylus (19) and a much reduced or absent nasus (20).

The monophyly of the tjederi group is uncertain. It is distinguished by having shorter hairs than in the ringdahli group, a probable plesiomorphy. A long, triangular furrow on the lateral surface of the base of the inner gonostylus (21) may be a synapomorphy of tjederi and unimicra. This feature is more pronounced in tjederi where it is set off by a ridge.

Prionocera sordida has been omitted from this discussion because only the female of this species is known and the more reliable apomorphies occur in the male.

The analysis above, suggests that the ground plan of Prionocera includes: (1) an aedeagal guide with flat dorsal plates; (2) a simple aedeagal guide without lateral processes or branches; (3) subrectangular dorsal processes on the ninth tergite; (4) lateral processes which are the distolateral extensions of the ninth tergite; (5) tooth-like apical processes which lie on the ventral edge of the ninth tergite; (6) male flagellomeres slightly distended distally; (7) short hairs on the head and thorax and several pleural segments bare; (8) inner gonostylus without pigmented sensilla.

Several features characterize most Prionocera. A

dorsally flattened aedeagal guide is found in 17 of the 19 species and a similar guide is found in species of Tipula and Dolichocheza. The more elaborate aedeagal guide found in two species of Prionocera is considered to be an apomorphy.

There are distal lobes or processes on the ninth tergite of other genera in the Tipulinae, however, the structures in Prionocera are unique and rather uniform.

Most crane flies have short sparse hairs on the head and thorax. Several Tipula species with northern distributions have long hairs on the head and thorax, similar to those found in Prionocera. Hair length may be a response to the environment.

The inner gonostyli of other tipulines are generally far more elaborate than that of Prionocera, but apparently do not have the pigmented sensilla which characterize the dimidiata group.

The tendency exists for distoventrally distended flagellomeres in other genera (e.g., Acracantha, Ctenophora, Ischnotoma). It is possible that the distended flagellomeres are derived from branched flagellomeres. The illustrations by Dobrotworsky (1967a) suggest that this may be the case. If so, then the strongly distended flagellomeres in Prionocera would have to be considered plesiomorphic, but this would not

substantially alter the proposed phylogeny.

CONCLUSIONS

The question in the back of my mind, while I was doing this study, was: "Which is the most primitive subfamily?" The primary split between the Limoniinae and the ancestor to the Cylindrotominae - Tipulinae must have occurred very soon after the origin of the Tipulidae. The Limoniinae tend to exhibit more derived characters in the immature stages (loss of spiracular lobes, loss of spiracles, reduced sclerites of the head capsule, derived pupal horns) whereas the salient derived feature of the Cylindrotominae - Tipulinae is a complex of characters associated with the external terminalia of the adult male. The Limoniinae tend to have the more primitive venation and to retain plesiomorphic features of the adult head (antennae, tentorium, lacinia).

The division resulting in the separate development of the Cylindrotominae and Tipulinae must have occurred soon after the primary division because each of these taxa also retains a host of plesiomorphies. The Cylindrotominae have the more plesiomorphic male and female genitalia and have partially retained the plesiomorphic features of the adult head capsule mentioned for the Limoniinae. The Tipulinae are

characterized by highly derived internal features of the male and female terminalia. Yet, the number and sclerotized nature of the spermathecae and the unadorned hypogynial valves are plesiomorphic. Therefore, I conclude that all three subfamilies have had a long evolutionary history. The Limoniinae, as a recognizable taxon, evolved only slightly earlier than the Cylindrotominae and Tipulidae.

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APPENDIX A

List of specific names applied to Prionocera, their current status and distributions; N = Nearctic, P = Palearctic. Oriental species listed below but not dealt with in this monograph.

P abscondita Lackschewitz

absentiva Mannheims = dimidiata (Loew)

altivolans Alexander = Tipula (Angarotip.)

anceps Lackschewitz = serricornis (Zett.)

anderi Tjeder = pubescens Loew

bergrothi (Williston) = nomen dubium

broweriana Alexander = unimicra (Alexander)

N byersi n. sp.

calvicornis Edwards = Zelandotipula

chosenicola Alexander (Oriental)

N cryptica n. sp.

diana (Meigen) = turcica (Fabricius)

N P dimidiata (Loew)N electa AlexanderN elliptica n. sp.

flaviceps Enderlein (Sumatra)

fulvicauda Alexander = oregonica Alexander

gracilistyla Alexander = recta Tjeder

hybrida (Dietz) = T. (Angaro.) illustris Doane

indica Edwards (Laos)

lackschewitzi Mannheims = recta Tjeder

laetipennis Alexander = Tipula (~~Angarotipula~~)

lapponica Tjeder = recta Tjeder

N naskapi n. sp.

N ominosa (Alexander)

N oregonica Alexander

oslari (Dietz) = dimidiata (Loew)

parrii (Kirby) = nomen dubium

primoveris Alexander = oregonica Alexander

proxima Lackschewitz = subsericornis (Zett.)

N P pubescens Loew

N P recta Tjeder

P ringdahli Tjeder

rostellata (Doane) = dimidiata (Loew)

r. churchilliana Alexander = dimidiata (Loew)

r. prominens Alexander = dimidiata (Loew)

salicetorum (Siebke) = Tipula (Arctotipula)

serenicola Alexander (North Korea)

N P sericornis (Zetterstedt)

P setosa Tjeder

N sordida (Loew)

N P subsericornis (Zetterstedt)

N P tjederi (Mannheims)

N P turcica (Fabricius)

N unimicra (Alexander)

N woodorum n. sp.

APPENDIX B

Measurements of the type of dimidiata compared with
 measurements of female specimens in the
 "dimidiata type collection," (MCZ) (See P.).

<u>Specimen</u>	<u>Body length</u>	<u>Wing length</u>
Type	6 - 6 1/2 lines 12.7 - 13.75 mm	6 1/12 - 6 1/2 lines 12.88 - 13.77 mm
No. 1	13.44 mm	12.08 mm
No. 2	12.16	11.68
No. 3	17.6	15.2
No. 6	17.6	18.4
No. 7	11.52	12.0
No. 9	13.12	9.92

APPENDIX C

List of species studied, Part I.

MECOPTERA

BITTACIDAE

Boreus brumalis Fitch

B. nivoriundus Fitch

MEROPEIDAE

Merope tuber Newman

PANORPIDAE

Panorpa sp.

DIPTERA

ANISOPODIDAE

Sylvicola fenestralis (Scopoli)

Sylvicola sp.

BIBIONIDAE

Penthetria heteroptera (Say)

BLEPHARICIDAE

Blepharicera sp.

DIXIDAE

Dixella sp.

MYCETOPHILIDAE

Sciophilinae

PTYCHOPTERIDAE

Bittacomorpha clavipes (Fabricius)

Ptychoptera quadrifasciata Say

Ptychoptera sp.

SCIARIDAE

Bradysia sp.

SIMULIIDAE

Simulium sp.

TANYDERIDAE

Protoplasia fitchii Osten Sacken

TRICHOCERIDAE

Trichocera hiemalis (De Geer)

T. regelationis (Linnaeus)

TIPULIDAE

Limoniinae

Hexatomini

Atarba sp.

Austrolimnophila harperi (Alexander)

Dactylolabis montana (Osten Sacken)

D. pemetica Alexander

D. supernumeraria Alexander

Dicranoptycha germana Osten Sacken

D. sobrina Osten Sacken

D. winnemana Alexander

Elephantomyia westwoodi O. S.

Epiphragma fasciapenne (Say)

Helius flavipes (Macquart)

Hexatoma brachycera (Osten Sacken)

Limnophila (Dicranophragma) fuscovaria O. S.

L. (Eleophila) solstitialis Alexander

L. (Idioptera) fasciolata Osten Sacken

L. (Lasiomastix) macrocera (Say)

L. (Lasiomastix) sp.

L. (Phylidorea) adusta Osten Sacken

L. (Phyl.) epimicta Alexander

L. (Phyl.) osceola Alexander

L. (Phyl.) sp.

L. (Prionolabis) rufibasis Osten Sacken

Paradelphomyia americana (Alexander)

P. pleuralis (Dietz)

Phyllolabis sp.

Pilaria quadrata (Osten Sacken)

P. recondita (Osten Sacken)

Polymera georgiae Alexander

Pseudolimnophila inornata (Osten Sacken)

P. luteipennis (Osten Sacken)

P. noveboracensis (Alexander)

Pseudolimnophila sp.

Shannonomyia lenta (Osten Sacken)

Ulomorpha pilosella (Osten Sacken)

Eriopterini

Cheilotrichia stigmatica (Osten Sacken)

Cheilotrichia sp.

Chionea valga Harris

C. lutescens Lunds

Cladura flavoferruginea Osten Sacken

Cladura sp.

Cryptolabis paradoxa Osten Sacken

Erioptera cana (Walker)

E. chlorophylla group

E. septemtrionis Osten Sacken

E. villosa Osten Sacken

E. (Trimicra) sp.

Gonomyia bidentata Alexander

G. flavibasis Alexander

Gnophomyia tristissima Osten Sacken

Molophilus forcipulus (Osten Sacken)

M. fultonensis Alexander

Neocladura delicatula (Alexander)

Neolimnophila ultima (Osten Sacken)

Ormosia arcuata (Doane)

O. dentifera Alexander

O. manicata (Doane)

O. romanovichiana Alexander

O. rubella (Osten Sacken)

Pediciini

Dicranota argentea Doane

D. cayuga (Alexander)

D. forceps (Alexander)

D. tenuipes (Osten Sacken)

Nasiternella hyperborea (Osten Sacken)

Ornithodes harrimani Coquillett

Pedicia (Pedicia) albivitta Walker

P. (Tricyphona) autumnalis (Alexander)

P. (T.) calcar (Osten Sacken)

P. (T.) johnsoni (Alexander)

Ula elegans Osten Sacken

Ula sp.

Limoniini

Antocha saxicola Osten Sacken

Elliptera

Limonia (Dicranomyia) liberta (Osten Sacken)

L. (Dicran.) longipennis (Schummel)

L. (Dicran.) rostrifera (Osten Sacken)

L. (Dicran.) simulans (Walker)

L. (Dicranomyia) sp.

L. (Discobola annulata (Linnaeus)

L. (Geranomyia) canadensis (Westwood)

L. (Limonia) parietina (Osten Sacken)

L. (Melanolimonia) morioides (Osten Sacken)

L. (Metalimnobia) annulus cinctipes (Say)

L. (Met.) solitaria (Osten Sacken)

L. (Met.) triocellata (Osten Sacken)

L. (Rhipidia) fidelis (Osten Sacken)

Cylindrotominae

Cylindrotoma distinctissima Meigen

Diogma glabrata Meigen

Liogma nodicornis (Osten Sacken)

Phalacropera replicata Linnaeus

P. tipulina Osten Sacken

Tipulinae

Brachypremna dispellens (Walker)

Ctenophora apicata Osten SackenC. (Tanyptera) sp.Dolichopeza (D.) americana NeedhamD. (Oropeza) dorsalis (Johnson)D. (O.) obscura (Johnson)D. (O.) sayi (Johnson)D. (O.) similis (Johnson)D. (O.) subalbipes (Johnson)D. (O.) tridenticulata AlexanderD. (O.) walleyi (Alexander)Holorusia grandis BergrothLeptotarsus testaceus LoewMegistocera longipennis (Macquart)Nephrotoma alterna (Walker)N. breviorcornis (Doane)N. eucera (Loew)N. ferruginea (Fabricius)N. gnata (Dietz)N. gracilicornis (Loew)N. lugens (Loew)N. tenuis (Loew)Prionocera (20 species)Tipula (Angarotipula) illustris DoaneT. (Ang.) parrioides (Alexander)T. (Arctotipula) besselsi Osten SackenT. (Arctotipula) sp.T. (Beringotipula) borealis Walker

- T. (B.) helderbergensis Alexander
T. (B.) resurgens Walker
T. (Labiotipula) leechi Alexander
T. (Lindnerina) senega Alexander
T. (Lind.) certa Loew
T. (Lunatipula) apicalis Loew
T. (Luna.) bicornis Forbes
T. (Luna.) disjuncta Walker
T. (Luna.) dorsimacula Walker
T. (Luna.) megaura Doane
T. (Luna.) monticola Alexander
T. (Luna.) triplex Walker
T. (Luna.) valida Loew
T. (Nippotipula) abdominalis (Say)
T. (Nobilotipula) nobilis (Loew)
T. (Platytipula) cunctans Say
T. (Plat.) pendulifera Alexander
T. (Plat.) ultima Alexander
T. (Pterelachisus) borealis Walker
T. (Ptere.) entomophthorae Alexander
T. (Ptere.) phoroctenia Alexander
T. (Ptere.) ternaria Loew
T. (Savtshenkia) fragilis Loew
T. (Sav.) nebulipennis Alexander
T. (Schummelia) hermannia Alexander
T. (Schummelia) sp.
T. (Tipula) paludosa Meigen

T. (Trichotipula) algonquin Alexander

T. (Trich.) oropezoides Johnson

T. (Trich.) umimaculata Loew

T. (Vestiplex) arctica Curtis

T. (V.) baloptera Loew

T. (V.) fultonensis Alexander

T. (Yamatotipula) caloptera Loew

T. (Y.) furca Walker

T. (Y.) kennicotti Alexander

T. (Y.) tephrocephala Loew

T. (Yamatotipula) sp.

Fig. 1. Morphology and terminology of head and thorax of Prionocera, lateral view.

<u>anatg</u> , anatergite	<u>nas</u> , nasus
<u>anepst</u> , anepisternum	<u>patg</u> , paratergite
<u>a spr</u> , anterior spiracle	<u>postgen</u> , postgena
<u>cx 1, 2, 3</u> , coxae	<u>presct</u> , prescutum
<u>dor anepm</u> , dorsal anepimeron	<u>presct pit</u> , prescutal pit
<u>fl 1</u> , 1st flagellomere	<u>presct sut</u> , prescutal suture
<u>gen</u> , gena	<u>ps oc</u> , pseudo-ocellus
<u>hit</u> , halter	<u>p spr</u> , posterior spiracle
<u>kepm</u> , katepimeron	<u>rst</u> , rostrum
<u>kepst</u> , katepisternum	<u>sct</u> , scutum
<u>ktg</u> , katergite	<u>sctl</u> , scutellum
<u>med sct</u> , median stripe of scutum	<u>trn sut</u> , transverse suture
<u>mr</u> , meron	<u>tym fo</u> , tympanal fossa
<u>mtanepst</u> , metanepisternum	<u>ven anep</u> , ventral anepimeron
<u>mtepm</u> , metepimeron	<u>ver</u> , vertex
<u>mtg</u> , mediotergite	<u>wg</u> , wing
<u>mtkepst</u> , metakatepisternum

Fig. 2. Wing of P. recta.1A, 2A, anal veinsc-r, costal crossveinCuA, anterior cubitusCuP, posterior cubitusM, mediaR, radiusRs, radial sectorSc, subcostasc-r, subcosta-radial cross
veinFigs. 3-7. Male terminalia. -3. P. dimidiata, dorsal

view, tergite 9 removed. -4-7. Aedeagal complex,

left lateral view. -4. P. dimidiata.-5. P. oregonica. -6. P. elliptica. -7. P. turcica.aed, aedeagusaed g, aedeagal guideaed sh, aedeagal sheathaed t, aedeagal toothd ap, dorsal apodeme of
sperm pumpl ap, lateral apodeme
of sperm pumpgon, gonocoxitegon frag, gonocoxal fragmenti gon, inner gonostyluso gon, outer gonostylusp ap, posterior apodeme of
sperm pumpsp, sperm pump

Figs. 8-9. P. woodorum, female terminalia. -8. Dorsal view. -9. Ventral view, hypogynial valvulae, 8th sternite removed.

cerci, cerci

cd, common spermathecal duct

co, copulatrix

gen fk, genital fork

infra, infraanal plate

l ap, longitudinal apodeme

m 10, median projection of tergite 10

med, median projection of sternite 9

s9, sternite 9

sth, spermatheca

su, supraanale

su ap, supraanal apodeme

t 10, tergite 10

Figs. 10-18. Male tergite 9, dorsal view.

- 10. P. abscondita.
- 11. P. byersi.
- 12. P. cryptica.
- 13. P. dimidiata.
- 14. P. electa.
- 15. P. elliptica.
- 16. P. naskapi.
- 17. P. ominosa.
- 18. P. oregonica.

ap, apical process

dp, dorsal process

lp, lateral process

ml, median lobe

Figs. 19-28. Male, tergite 9, dorsal view.

- 19. P. pubescens.
- 20. P. recta.
- 21. P. ringdahli.
- 22. P. serricornis.
- 23. P. setosa (redrawn from Tjeder, 1948, fig. 8B).
- 24. P. subserricornis.
- 25. P. tjederi.
- 26. P. turcica.
- 27. P. unimicra.
- 28. P. woodorum.

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Figs. 29-38. Outer and inner gonostyli, right medial view except where noted.

- 29. P. abscondita.
- 30. P. byersi.
- 31. P. cryptica.
- 32. P. dimidiata.
- 33. P. dimidiata, right inner gonostylus, lateral view.
- 34. P. electa.
- 35. P. elliptica.
- 36. P. elliptica, right inner gonostylus, lateral view.
- 37. P. naskapi.
- 38. P. ominosa.

0.25mm

Figs 39-48. Outer and inner gonostyli, right medial view.

- 39. P. oregonica.
- 40. P. pubescens.
- 41. P. recta.
- 42. P. ringdahli.
- 43. P. serricornis.
- 44. P. subserricornis.
- 45. P. tjederi.
- 46. P. turcica.
- 47. P. woodorum.
- 48. P. unimicra.

Figs. 49-56. Female terminalia, left lateral view.

- 49. P. abscondita.
- 50. P. byersi.
- 51. P. dimidiata.
- 52. P. electa.
- 53. P. elliptica.
- 54. P. ominosa.
- 55. P. oregonica.
- 56. P. pubescens.

d edge, dorsolateral edge of sternite 8

hy, hypogynial valvulae

s 8, sternite 8

t 10, tergite 10

49

50

51

52

53

54

55

1 mm

56

Figs. 57-65. Female terminalia, left lateral view.

- 57. P. recta.
- 58. P. ringdahli.
- 59. P. serricornis.
- 60. P. sordida.
- 61. P. subserricornis.
- 62. P. tjederi.
- 63. P. turcica.
- 64. P. unimicra.
- 65. P. woodorum.

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Figs. 66-73. Female sternite 8 and hypogynial valvulae,
ventral view.

- 66. P. abscondita.
- 67. P. byersi.
- 68. P. dimidiata.
- 69. P. electa.
- 70. P. elliptica.
- 71. P. ominosa.
- 72. P. oregonica.
- 73. P. pubescens.

hy, hypogynial valvulae

mem, membranous area

s 8, sternite 8

scl v, sclerotized ventral edge of valvulae

66

67

68

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Figs. 74-82. Female terminalia, ventral view.

- 74. P. recta.
- 75. P. ringdahli.
- 76. P. serricornis.
- 77. P. sordida.
- 78. P. subsericornis.
- 79. P. tjederi.
- 80. P. turcica.
- 81. P. unimicra.
- 82. P. woodorum.

74

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81

82

1 mm

Fig. 83. Cladogram of the family Tipulidae. The numbers refer to the hypothesis numbers in the text.

■ strong synapomorphy; ● weak synapomorphy

Fig. 84. Cladogram of the subfamily Tipulinae.

■ synapomorphy; □ plesiomorphy

Fig. 85. Cladogram of the genus *Prionocera*.

■ strong synapomorphy; ● weak synapomorphy

○ reversal

Map 1. Distribution records of *Prionocera Loew*.

Maps 2-4. -2. Distribution records of *P. abscondita* Lackschewitz. -3. Distribution records of *P. byersi* Brodo ○ ; and *P. cryptica* Brodo ● .
 -4. Distribution records of *P. dimidiata* (Loew).

Maps 5-6.

-5. Distribution records of *P. electa* Alexander.

-6. Distribution records of *P. elliptica* Brodo ●;
and *P. naskapi* Brodo ○.

Maps 8-9. -8. Distribution records of *P. pubescens* Loew
-9. Distribution records of *P. oregonica* Alexander.

Maps 10-11. -10. Distribution records of *P. recta* Tjeder.
 -11. Distribution records of *P. ringdahli* Tjeder

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13

Maps 12-13. -12. Distribution records of P. serricornis (Zetterstedt).

-13. Distribution records of P. sordida (Loew) ○; and P. setosa Tjeder ●.

Map 14. Distribution records of *P. subserricornis* (Zetterstedt).

5 of/de 5

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Map 15. Distribution records of *P. tjederi* Mannheims.

Map 16. Distribution records of *P. turcica* (Fabricius).

Maps 17-18. -17. Distribution records of *P. unimicra* (Alexander).

-18. Distribution records of *P. woodorum* Brodo.

END

29/06/89

FIN