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PHYLOGENETIC CLASSIFICATION OF THE CLINOCERINAE,
WITH A REVISION OF THE NEARCTIC SPECIES OF
TRICHOCLINOCERA COLLIN AND WIEDEMANNIA
ZETTERSTEDT (DIPTERA: EMPIDIDAE)

by

BRADLEY JAMES SINCLAIR

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

March 1993

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Phylogenetic classification of the Clinocerinae,
with a revision of the Nearctic species of
Trichoclinocera Collin and Wiedemannia
Zetterstedt (Diptera: Empididae)

submitted by

Bradley James Sinclair

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

Carleton University

ABSTRACT

Dance flies of the subfamily Clinocerinae are primarily aquatic, and confined to rocky streams, creeks, rivers, and seepage habitats. Genera are especially common and diverse in cool, mountainous regions. The Clinocerinae has traditionally been defined on the basis of weak, highly homoplastic characters. Consequently this has resulted in the inclusion of many odd and aberrant genera based on superficial resemblance. Prior to this study, 25 genera and 12 subgenera of Clinocerinae were recognized. In this study, 14 genera (including 5 new generic synonyms) are found to form a well defined monophyletic group. The following genera are recognized: Asymphyloptera Collin, Proclinopyga Melander, Rhyacodromia Saigusa, Trichoclinocera Collin, Clinocera Meigen, Oreothalia Melander, Roederiodes Coquillett, Clinocerella Engel, Hypenella Collin, Kowarzia Mik, Dolichocephala Macquart, Phaeobalia Mik, Bergenstammia Mik, and Wiedemannia Zetterstedt. Clinocerella, formerly a subgenus of Wiedemannia and Kowarzia, Phaeobalia, and Bergenstammia, formerly subgenera of Clinocera, are elevated to generic status. On the basis of male genitalic homologies, the genus Dryodromia Rondani is here removed from the Clinocerinae and placed in the Empidinae + Hemerodromiinae lineage. The genera Zanclotus Wilder and Dipsomyia Bezzi, are transferred to the subfamily Oreogetoninae. The genera Boreodromia Coquillett, Ceratempis Melander, Ephydrempis Saigusa, Niphogenia Melander, Sabroskyella Wilder, and Trichopeza Rondani are also removed from the Clinocerinae and placed in a redefined monophyletic empidoid subfamily, the Trichopezinae. The Trichopezinae includes six additional genera which were previously placed in three different

subfamilies. A cladistic analysis of the genera of the Clinocerinae, including a discussion of the relationships of this subfamily within the Empidoidea, is presented.

Six species of Wiedemannia (including four new species) are recognized in the Nearctic region. Fifteen Nearctic species of Trichoclinocera (including seven new species) are recognized. The habits and immature stages of this genus are also described for the first time. A cladistic analysis and zoogeographic analysis of Trichoclinocera is also presented.

New interpretations of homology in male and female genitalia and larval mouthparts of the Empidoidea are presented. The phylogenetic implications of these new interpretations upon the monophyly of the Empidoidea and Clinocerinae are discussed.

EXTENDED ABSTRACT

The subfamily Clinocerinae is distributed worldwide, and confined primarily to rocky streams, creeks, rivers and seepage habitats. The following fourteen genera are recognized: Asymphyloptera Collin, Proclinopyga Melander, Rhyacodromia Saigusa, Trichoclinocera Collin, Clinocera Meigen, Oreothalia Melander, Roederiodes Coquillett, Clinocerella Engel, Hypenella Collin, Kowarzia Mik, Dolichocephala Macquart, Phacobalia Mik, Bergenstammia Mik, and Wiedemannia Zetterstedt. Clinocerella, formerly a subgenus of Wiedemannia and Kowarzia, Phacobalia, and Bergenstammia, formerly subgenera of Clinocera, are elevated to generic status. The following new generic synonyms are proposed: Acanthoclinocera Saigusa and Seguyella Vaillant = Trichoclinocera; Lamposoma Becker, Eur Garrett Jones and Obstinocephala Garrett Jones = Dolichocephala. Proagomyia Collin is placed in Clinocerinae as incertae sedis. Dipsomyia Bezzi and Zanclotus Wilder, formerly in the Clinocerinae are transferred to the Oreogetoninae. Dryodromia Rondani, also formerly in Clinocerinae, is believed to be most closely related to Hesperempis Melander, which together are believed to belong to the Empidinae + Hemerodromiinae lineage.

The genera Boreodromia Coquillett, Ceratempis Melander, Ephydrempis Saigusa, Niphogenia Melander, Sabroskyella Wilder, and Trichopeza Rondani are also removed from the Clinocerinae. These genera, together with six additional genera that were previously placed in three different subfamilies, are classified in the redefined empidoid subfamily, Trichopezinae. This subfamily is described and the geographic distribution and relationships of the trichopezine genera are discussed.

Keys to genera are provided for the identification of adult specimens of Clinocerinae, all genera (including former clinocerines) are described and male and female terminalia of type species (wherever possible) are illustrated. Cladistic relationships of the Clinocerinae among the Empidoidea and relationships within the clinocerine genera are presented.

The following new species are described: Asymphyloptera chiricahua (type-locality East Turkey Creek, Arizona, USA), A. lutea (type-locality Santa Cruz de Turrialba, Costa Rica), and Proagomyia tridentata (type-locality Puerto Montt, Chile). The following new species of Trichoclinocera are described: T. agilis (type-locality Fall Creek Falls, Tennessee, USA), T. cascadiensis (type locality Starvation Creek, Oregon, USA), T. dasycoxa (type-locality Dromgold, Pennsylvania, USA), T. falcata (type locality Gatineau Park, Quebec, Canada), T. ozarkensis (type locality Haw Creek Falls, Arkansas, USA), T. pectinifemur (type locality Phoenixville, Pennsylvania, USA), and T. rupestris (type locality Newton Creek, Wyoming, USA). The following new species of Wiedemannia are described: W. apicalis (type-locality Taylor Canyon, Colorado, USA), W. uncinata (type-locality Starvation Creek, Oregon, USA), W. undulata (type-locality Shell Creek, Wyoming, USA), and W. vexillum (type-locality Martin River, Northwest Territories, Canada).

Kowarzia capicola (Smith), Dolichocephala cavaticum (Becker), D. fugitivus (Garrett Jones), and D. tali (Garrett Jones) are proposed as new combinations. Lectotypes are designated for Dolichocephala argus Melander, Clinocerella sorex (Engel), D. cavaticum, Ceratempis longicornis Melander, Boreodromia bicolor (Loew), and

Trichopeza albicincta Frey.

The genus Trichoclinocera is known from the Nearctic, Palearctic and Oriental regions and appears to be most closely related to Rhyacodromia. Twenty-two species are recognized worldwide, including eight new Nearctic species. Keys to species are provided for the identification of adult Nearctic specimens, all species are described, and their geographical distributions mapped. The first descriptions of the immature stages of species of this genus are also provided.

Four tentative species-groups of Trichoclinocera are recognized, with the following included species: (1) T. cyanescens group - T. cyanescens (Vaillant), T. lapponica (Ringdahl), T. rostrata (Vaillant), and T. tadjikistana (Vaillant); (2) T. longipes group - T. agilis sp.nov., T. ctenistes (Melander), T. dasycoxa sp.nov., T. falcata sp.nov., T. fumosa (Vaillant), T. hamifera (Melander), T. longipes (Walker), T. minor (Melander), T. ozarkensis sp.nov., and T. pectinifemur sp.nov.; (3) T. comata group - T. cascadiensis sp.nov., T. comata (Melander), and T. rupestris sp.nov.; (4) T. stackelbergi group - T. stackelbergi Collin. The following species are unplaced within species-groups of Trichoclinocera: T. dasyscutellum (Saigusa), T. dolicheretma (Melander), T. fuscipennis (Saigusa), and T. maewa Smith.

The following new synonyms are proposed: T. brunnipennis (Melander) = T. dolicheretma; and T. saltans (Vaillant) = T. hamifera. The following new combinations are proposed: T. comata, T. cyanescens, T. dasyscutellum, T. fumosa, T. lapponica, T. rostrata, and T. tadjikistana. Lectotypes are designated for T. comata, T. ctenistes, T. dolicheretma, T. brunnipennis, T. hamifera, T. lapponica, and T. stackelbergi. Cladistic

relationships among species-groups and species of Trichoclinocera are presented.

The genus Wiedemannia is known throughout the Palearctic and Afrotropical regions, western and arctic regions of North America and Nepal. There are six Nearctic species, of which 4 are new species. Keys to species are provided for the identification of adult Nearctic specimens, all species are described, and their geographical distributions mapped.

A lectotype is designated for W. simplex (Loew) and the following new synonym is proposed: W. impudica (Mik) = W. simplex. The Oriental species, W. glaucescens (Brunetti) is proposed as a new combination. Cladistic relationships among species-groups and species of Wiedemannia are presented.

The world species of Clinocera are surveyed and tentatively divided into seven species-groups. A key to species-groups is also presented. The following new combinations are proposed: C. gubernans (Melander) and C. velutina (Engel).

Because there were conflicting interpretations, the homologies of male and female terminalia and larval mouthparts of Empidoidea are re-evaluated. A four-component larval mandible (distal hook, two connecting sclerites and ventral sclerite) is proposed as a synapomorphy of the Empidoidea. A lever-like ejaculatory apodeme and loss of gonostyli are also considered synapomorphic for the Empidoidea. Acanthophorites are considered to be homologous with those of Asiloidea.

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1. INTRODUCTION

The superfamily Empidoidea was divided by Chvála (1983) into 5 families: Empididae (Oreogetoninae, Empidinae, Hemerodromiinae, Clinocerinae, Ceratomerinae, Brachystomatinae), Hybotidae (Ocydromiinae, Tachydromiinae, Hybotinae), Atelestidae, Microphoridae and Dolichopodidae. The monophyly of the Empidoidea is generally accepted, but the recognition of the additional families split off from the traditional Empididae remains debated. At present, I prefer to continue recognizing only two families: Empididae and Dolichopodidae, within the Empidoidea (see Sec. 5.1.1).

Clinocerine genera were originally included with hemerodromiine genera in the single subfamily Hemerodromiinae (Schiner 1862, Becker et al. 1903, Melander 1902) or Atalantinae (Kertész 1909, Engel 1918). Collin (1928) and Melander (1928) appear to be the first workers to isolate the clinocerines as a separate subfamily, Clinocerinae (also called Clinoceratinae¹).

Members of the subfamily Clinocerinae, along with the Oreogetoninae, Empidinae, and Hemerodromiinae are among the more basal empidoids. Despite recent

¹Clinocera Meigen is derived from the Greek words "klino" and "keras" meaning slant or bend horn. Keras has been transcribed into Latin using c- instead of k- and the ending has also been changed from -as to -a (Steyskal pers. comm.). The gender is feminine and the stem is Clinocer-. If the name had been formed as Clinoceras, the stem would have been Clinocerat-. Hence the correct spelling of the subfamily is Clinocerinae and not Clinoceratinae.

phylogenetic analyses, the inter-relationships of the above subfamilies and the relationships with the remaining Empidoidea remain uncertain (Chvála 1983, Cumming and Sinclair 1990, see Fig. 210).

Adults of Clinocerinae are bluish-grey, long-legged flies, generally found near water flowing rapidly over a rocky substrate. They are predators and scavengers, flying very close to the water in search of food. Resting on emergent rocks, adults appear to superficially resemble Dolichopodidae which are found in similar habitats.

Members of the Clinocerinae have traditionally been defined on the basis of characters such as pulvilliform empodium, narrow wings and pubescent eyes. I regard these as highly homoplastic and uninformative. This weak definition has resulted in the inclusion of many odd, aberrant genera that share these characters, but no others, and this has masked the relationships of the Clinocerinae to the remaining Empidoidea.

Prior to this study, 25 clinocerine genera were recognized. The most recent analysis placed them within the Hemerodromiinae on the basis of common aquatic habits, apneustic larval respiratory system and a six-component larval mandible (Vaillant 1981). The former two characters are very homoplastic and of little phylogenetic value. The homologies of the six-component mandible between these two subfamilies has been recently questioned (Sinclair 1992). Vaillant (1981) divided the Hemerodromiinae into the Hemerodromiini, Phyllodromiini, Trichopezini (1 genus) and Clinocerini (10 genera), with the clinocerines split between the two latter tribes. The Clinocerinae is recognized as a separate family in the Palearctic Catalogue, but not subdivided into tribes (Chvála and Wagner 1989).

Although the European species are well understood, the Nearctic species of Clinocerinae are in need of revision. The only keys available for identification are fifty years old (Melander 1928) and lack many recently recognized taxa. Farr (1953) attempted a revision of North American species of Clinocera Meigen. However, the study did not include all described species, nor all available specimens, nor were several of the types examined and the revision was never published. Wilder (1981a,b,c) revised the genera Roederiodes Coquillett, Niphogenia Melander, and Oreothalia Melander and erected two new monotypic genera, Sabroskyella and Zanclostus (Wilder 1982). Although large series of western species were collected, no further analysis was conducted and Dr. Wilder has since retired from entomology.

I suggest that the clinocerines and hemerodromiines do not form a monophyletic group and that the Trichopezini (concept expanded to include all remaining clinocerine genera that were omitted by Vaillant (1981)) is not closely related to Hemerodromiini, Phyllodromiini or Clinocerini. In order to test these hypotheses, the monophyly of the Clinocerinae (Clinocerini + Trichopezini) is examined and its relationships within the remainder of the Empidoidea are considered. This is the first major attempt at a phylogenetic analysis of the Clinocerinae and first detailed examination of the genera on a worldwide basis.

Since clinocerines, particularly Trichoclinocera, are commonly collected in stream surveys and emergence traps, species identification has been frustrating for many ecologists. Workable keys for the identification of the genera of Clinocerinae, Nearctic species of Trichoclinocera and Wiedemannia and species-groups of Clinocera are

provided, which should prove to be very helpful for stream survey studies. It is hoped that this revision will encourage more comprehensive revisionary studies, rather than single species descriptions and small regional analyses.

In order to present this new classification of the Clinocerinae, it was necessary to conduct a comparative morphological survey of larval mouthparts and male and female terminalia of the Brachycera. A survey of the cephalopharyngeal skeleton of larvae of the Empidoidea revealed that difficulties existed in the interpretation of the larval mouthhook sclerites. Sclerites that appeared distinctly mandibular are often labelled as maxillary structures. Due to this conflicting interpretation, the homologies of the larval mandible and associated mouthparts are re-examined. The phylogenetic implications of the new homologies of the larval mouthparts upon the monophyly of the Empidoidea and Clinocerinae are also analysed.

In addition, there are two conflicting hypotheses on the homologies of male terminalia of Eremoneura (Empidoidea and Cyclorrhapha). These hypotheses are evaluated and new interpretations of homology are presented, based on a broad survey of the orthorrhaphous Brachycera and the recently formulated ideas of Cumming and Sinclair (1990). This survey has resulted in a significant reinterpretation of the homologies of the male terminalia of the Clinocerinae.

The female terminalia, including spermathecae have largely been ignored by empidoid workers. The homologies of the female terminalia are evaluated, including a detailed survey of spermathecal shape in Empidoidea.

2. MATERIALS AND METHODS

2.1 MATERIALS

This study is based on the examination of approximately 20,000 adult specimens of Clinocerinae and other empidoids, borrowed from 40 institutions or individuals, as listed below. Acronyms given here follow Cumming (1989) and Cumming and Cooper (1992) and are used throughout the text to indicate deposition of specimens. All specimens collected by the author during the course of this study are housed in the CNC.

AMNH Department of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA (Dr. D.A. Grimaldi)

AMS 6-8 College St., Australian Museum, Entomology Division, Box A285, Sydney South, NSW 2000, Australia (Dr. D.J. Bickel)

ANSP Department of Entomology, Academy of Natural Sciences of Philadelphia, 19th & the Parkway, Logan Sq., Philadelphia, PA 19103, USA (Mr. D. Azuma)

BARC M. Bartak collection [private], Prague, Czechoslovakia

BMNH Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, England (Mr. J. Chainey)

BPBM Bernice P. Bishop Museum, P.O. Box 19000A, Honolulu, Hawaii 96817, USA (Dr. N.L. Evenhuis)

BYU Monte L. Bean Life Sciences Museum, 290 MLBM, Brigham Young University, Provo, Utah 84602, USA (Dr. R.W. Baumann)

CAES Department of Entomology, Connecticut Agricultural Experimental Station, 123

Huntington St., Box 1106, New Haven, CT 06504, USA (Dr. C.T. Maier)

CAS Department of Entomology, California Academy of Sciences, Golden State Park,
San Francisco, CA 94118, USA (Dr. P.H. Arnaud, Jr.)

CMNH Section of Invertebrate Zoology, The Carnegie Museum of Natural History,
4400 Forbes Ave., Pittsburgh, PA 15213-4080, USA (Dr. C.W. Young)

CNC Agriculture Canada, Biological Resources Division, Centre for Land and
Biological Resources Research, K.W. Neatby Bldg., C.E.F., Ottawa, Ont.
Canada K1A 0C6 (Dr. J.M. Cumming)

CUAC Department of Entomology, Long Hall, Clemson University, Clemson, SC
29634-0365, USA (Dr. P.H. Adler)

CU Department of Entomology, Cornell University, Comstock Hall, Ithaca, NY
14853, USA (Dr. J.K. Liebherr)

HSU Department of Biological Sciences, Humboldt State University, Arcata, CA
95521-4957, USA (Dr. R.L. Hurley)

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138,
USA (Dr. D.G. Furth)

MEM Mississippi Entomological Museum, Mississippi State University, Drawer DM,
Mississippi State, MS 39762, USA (Dr. R.L. Brown)

MSU Department of Entomology, Michigan State University, East Lansing, MI 48824,
USA (Dr. F.W. Stehr)

NM Natal Museum, Private Bag 9070, Pietermaritzburg, 3200 South Africa (Dr. D.A.
Barracough)

NYSM Biological Survey, New York State Museum, 3132 Cultural Educ. Cen., Albany,
NY 12230, USA (Dr. J.K. Barnes)

NZAC New Zealand Arthropod Collection, Landcare Research N.Z. Ltd., Private Bag
92170, Auckland, New Zealand (Dr. T.K. Crosby)

OSUC Department of Entomology, Oregon State University, Corvallis, OR 97331, USA
(Dr. N.H. Anderson)

PSU Frost Entomological Museum, Department of Entomology, The Pennsylvania
State University, University Park, PA 16802, USA (Dr. K.C. Kim)

PERC Purdue Entomological Research Collection, Purdue University, West Lafayette,
IN 47907, USA (Dr. J.A. MacDonald)

ROGC E.J. Rogers collection [private], Villa Grande, CA, USA

SMEK Department of Entomology, Snow Museum of Entomology, University of
Kansas, Lawrence, KS 66045, USA (Dr. R.W. Brooks)

UBC Spencer Entomological Museum, Department of Zoology, University of British
Columbia, Vancouver, B.C. Canada V6T 2A9 (Mr. S. Cannings)

UCB Essig Museum of Entomology, University of California, Berkley, CA 94720,
USA (Dr. J.A. Chemsak)

UCD R.M. Bohart Museum of Entomology, Department of Entomology, University of
California, Davis, CA 95616, USA (Dr. S. Heydon)

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UMSP Department of Entomology, University of Minnesota, 219 Hodson Hall, 1980

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USNM Systematic Entomology Laboratory, U.S. National Museum NHB 168,

Washington, D.C. 20560, USA (Dr. N.E. Woodley).

USU Department of Biology, Utah State University, Logan, UT 84322-5305, USA

(Dr. W.J. Hanson)

UZIL Zoologiska Institutionen, Lunds Universitet, Helgonavägen 3, S-223 62 Lund,

Sweden (Dr. R. Danielsson).

WOOC N.E. Woodley collection [private], Washington, D.C., USA

WSU James Entomological Collection, Department of Entomology, Washington State

University, Pullman, WA 99164-6432, USA (Dr. R.S. Zack and Dr. W.J.

Turner)

ZISP Zoological Institute, Academy of Sciences, St. Petersburg 199034, Russia (Dr.

V. Richter)

ZMH Zoological Museum, P. Rautatiekatu 13, SF-00100 Helsinki, Finland (Dr. P.

Vilkamaa)

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2.2 METHODS

2.2.1 SPECIMEN PREPARATION AND EXAMINATION

Abdomens, heads and larvae were macerated in crucibles of hot 85% lactic acid in order to examine genitalia, mouthparts and larval head capsules in greater detail. Maceration of large specimens was often assisted by extracting the internal oils, eggs, and muscle tissues with a fine probe. The specimen was then returned to lactic acid for further maceration if needed. Separation of the genital capsule from the remaining abdomen often enhanced more efficient clearing.

Details of macerated specimens were viewed under differential interference microscopy (Nomarski illumination). To make illustrations, specimens were mounted temporarily in glycerin on depression slides, using a small amount of shellac to anchor the specimen. From this set-up, figures were drawn using a drawing device attached to a Nikon Optophot microscope. Before inking on mylar, line drawings were checked for accuracy under a stereomicroscope. Specimens were later removed from the shellac and stored in plastic microvials pinned under the adult specimen. All specimens were examined with a Leitz Wetzlar stereoscopic microscope.

Details of certain structures were examined with the aid of a JSM-6400 Scanning electron microscope. Fore legs were mounted separately on paper points. Foreign particles were removed with a fine probe and then all specimens were sputter-coated with gold.

Larvae and pupae were collected from streams, creeks and rivers using the "kick sample" technique. This required disturbing and scraping the benthic substrate up into the current and catching the debris (including immature stages) into an aquatic net held downstream. Samples were immediately sorted in white enamel trays and immature stages removed and isolated in 50 X 9 mm seal-tight petri dishes. Small samples of filamentous algae were used to help maintain moisture and the entire set-up was placed in environmental chambers maintained at 12-15°C with a 16:8 L:D photoperiod.

2.2.2 TERMINOLOGY AND MORPHOLOGY

Terms used for adult and larval structures primarily follow those of the Manual of Nearctic Diptera (sensu McAlpine (1981) and Teskey (1981)), except as described below. The terminology of the cervical sclerites proposed by Marina (1979) and Ulrich (1971, 1984) is used. The cervical sclerites consist of thinly sclerotized, paired ventrocervical sclerites (= cornicula, Ulrich 1984), paired laterocervical sclerites and often an unpaired, thinly sclerotized, anterior ventrocervical sclerite. The antepnotum forms the pronotum (or "collar") and the term postnotum sensu Ulrich (1971) is used rather than laterotergite.

The term setae and setulae for fine, hair-like setae are used rather than bristle. The terms "stout", "slender", "weak" and "spine-like" setae are used in descriptions. Abbreviations of mesonotal chaetotaxy used in descriptions of genera and species are as follows:

dc - dorsocentral seta (Fig. 59)

npl	- notopleural seta (Fig. 63)
pal	- postalar seta
ppm	- postpronotal seta (Fig. 66)
presut spal	- presutural supralar seta (Fig. 62)
psut spal	- postsutural supralar seta
sctl	- scutellar seta

The interpretation of McAlpine (1981) for female terminalia has been followed with modification (see Sec. 3.2 for further details). Interpretation of male genitalic homologies follows "The Revised Epandrial Hypothesis" of Cumming and Sinclair (1990) (see Sec. 3.3 Male Terminalia).

Abbreviations used in the illustrations are listed in Appendix I.

2.2.3 SPECIES AND GENERIC CONCEPTS

In practice, differences in male genitalia and readily recognized secondary sexual characters (e.g. fore femur in Trichoclinocera) are primarily used to distinguish species. Elaborate male terminalia are particularly prevalent in the Empidoidea, especially when compared with female terminalia. The evolution of this great diversity of male terminalia is hypothesized to be due primarily to sexual selection through female choice (Eberhard 1985). Females are hypothesized to discriminate between mates on the basis of genitalia. The ability of males to stimulate females would be a display of male fitness. A consequence of sexual selection by means of female choice is the rapid and divergent

evolution of male terminalia (Eberhard 1985).

This practical definition of species appears to fit most closely the recognition species concept of Paterson (1985), in which species are defined as the most inclusive population of individual biparental organisms which share a common fertilization system. Specific mate recognition mechanisms, which ensure fertilization, maintain species cohesion. The subspecific category has not been used in this work.

A genus is recognized herein as a monophyletic group of species that does not render as paraphyletic any other described genera (Marshall 1987). Ideally a genus should also be characterized by readily recognized structures. Groups defined entirely on the basis of character losses or reductions (e.g. wing reduction) are not useful categories and attempts have been made to place these taxa into useful, easily diagnosed genera.

2.2.4 DESCRIPTIVE FORMAT

For each genus and previously described species, references to the original publication and each junior synonym are listed in order according to date of description. Label data for holotypes and allotypes of both new and described species are cited in full, following the style of O'Hara (1983). Under this system, labels are listed from the top downward, with data from each label enclosed in quotation marks. Labels are cited in full, in original spelling, punctuation and date, and lines are delimited by a slash mark(/). Additional information is included in [square] brackets. The depository of each type is given in parentheses.

Paratype and paralectotype data are listed alphabetically by province or state and

county, and are treated less rigorously than for other types. Counties (if given on label) are followed by locality, date of collection, given in order of day, month (in Roman numerals) and year, collector, number of males and/or females examined and habitat, if stated. Non-type specimens of described species have also been included, although data cited from labels is significantly reduced.

Genus and species descriptions are presented in a uniform format. Species descriptions do not repeat non-varying attributes of the genus. Diagnostic information additional to that presented in the keys, including comparison with similar taxa, is provided under the heading "Recognition". Variation is included in each description, while geographical variation and unusual variation (e.g. shape of clasping cercus), is additionally discussed under the heading "Comments".

Each generic description is followed by a catalogue of world species, extracted from regional catalogues by Melander (1965), Smith (1967, 1975, 1980, 1989), and Chvála and Wagner (1989) and updated to include all subsequent publications. These lists follow the format of O'Hara (1989), in which names of species are preceded by a letter indicating the region(s) of occurrence. Species in which specimens were examined during the course of this revision are indicated, with studied type material noted where appropriate (including depository). These species catalogues also include all new species described in this work, new synonyms, new status of subspecies, new combinations and lectotype designations. New combinations are discussed either under the heading "Notes about Synonymy" or "Included Taxa and Geographical Distribution". The following letters, following O'Hara (1989) are used to indicate region(s) of occurrence of each species:

A Afrotropical, sensu Crosskey and White (1977)

N Nearctic, sensu Griffiths (1980)

O Oriental, sensu Delfinado and Hardy (1973)

P Palearctic, sensu Soós and Papp (1984)

S Neotropical, sensu Griffiths (1980)

U Australasian, sensu Evenhuis (1989)

Undescribed species recognized from Museum collections during this study are listed following the species lists. Specimens are clearly labelled to help facilitate future revisionary studies.

Under the International Code of Zoological Nomenclature (1985), Chapter 3, Article 9 (11), a thesis does not constitute a publication. Hence all names given for new taxa must be considered manuscript names and are not available names. This also applies to changes of status, lectotypes designations and any other nomenclatural act (Article 7).

2.2.5 METHODS USED FOR PHYLOGENETIC RECONSTRUCTION

Phylogenetic relationships of the Empidoidea and Clinocerinae analysed in this study follow cladistic principles (sensu Hennig 1965, 1966). Character states are defined for each character and the polarity of each character state is diagnosed as ancestral (plesiomorphic) or derived (apomorphic) through outgroup comparison. Monophyletic groups recognized on the basis of shared derived characters (synapomorphies) are used to generate cladograms that minimized the need to infer homoplasy.

Outgroup comparison was based on examination of over 150 species from 25 families among the Asiloidea, Empidoidea and Cyclorrhapha (Table 3). Species from all biogeographic regions were examined.

Character states that tend to be extremely variable between taxa have been avoided because they are considered homoplastic. The subfamily Clinocerinae appears to have been a dumping ground for any odd looking genus which did not fit into any other subfamily. Inclusion was often based on the shared presence of certain character states such as hairy eyes, pulvilliiform empodium and reduced anal angle of the wing. In phylogenetic studies, I have put greater emphasis on male and female terminalia, which possess informative and useful distinguishing characters. In the Empidoidea, female terminalia often appear to be evolutionarily conservative and thus more useful in higher classification than male terminalia.

Cladograms were initially compiled without the aid of computer assistance. The parsimony algorithm program, PAUP (Swafford 1991), in conjunction with MacClade (Maddison and Maddison 1992), was later used to analyse the character matrix to see if other relations and tree topographies could be generated.

Homology is classically defined as the product of descent from a common ancestor (Wiley 1981). I have recognized homologous structures primarily by the use of distinctive landmarks and transformations traced through outgroups. Landmarks may include, for example; similarity of position or relationship of one part to another, points of articulation, or presence of apodemes. Potential homologous structures may be evaluated by using established phylogenies. For example, the apparent loss of the lacinia

and presence of an anterior ventrocervical sclerite in adults of both the Clinocerinae and Dolichopodidae are considered to be due to convergent evolution because of the convincing number of synapomorphies supporting the close relationship of the latter family to the Microphorinae. These similar modifications in relatively distantly related taxa are more convincingly explained as adaptations to similar habits and environments, rather than having evolved from a common ancestor (Ulrich 1984, Chvála 1988).

The term ground plan is used frequently throughout this work and is applied in the same manner as Hennig (1981) in his analysis of the phylogeny of insects. The ground plan of a taxon is the set of hypothesized character states that define the basal node or common ancestor of the members of the taxon (Kristensen 1984, Cranston *et al.* 1991). These character states are primarily plesiomorphies, but also include apomorphies.

3. COMPARATIVE MORPHOLOGY

Over the course of this revision of the Clinocerinae, several important character systems were studied in much greater detail and scope than normally used for phylogenetic analyses. The following three studies on the homologies of the larval mouthparts (Sinclair 1992) and female and male terminalia were commenced because of dissatisfaction with current interpretations and inadequate knowledge for accurate cladistic analysis. In each study, broad surveys of outgroups were conducted first, in order to appreciate fully the modifications and adaptations that have occurred in the Empidoidea and specifically in the Clinocerinae. The phylogenetic relationships of the Brachycera follow that of Woodley (1989) and Sinclair (1992).

3.1 LARVAL MOUTHPARTS

3.1.1 GROUND PLAN OF BRACHYCERA

Interpretation of the ground plan condition in Brachycera of the larval mandible and associated structures is established through comparison with the Nematocera outgroup, considered to be the Psychodomorpha. In addition, a broad survey of the Brachycera and also the work of Cook (1949) and Schremmer (1951) helped to establish the Brachycera ground plan. The typical ground plan mandible is found in the Xylophagidae, Rhagionidae, Vermileonidae and many Asiloidea (sensu Woodley 1989). The taxa examined in the following study are listed in Table 1.

In the Psychodomorpha, the larval mandible is subdivided, with the apical portion separated from the base by a narrow line of weakness. The abductor apodeme is inserted

on the posterodorsal margin of the basal component and the adductor apodeme is inserted on the ventral margin. The mandibular muscles originate on the posterodorsal margin of the head capsule (cranium) (Cook 1949).

From the weakly subdivided plesiomorphic condition, as seen in the Psychodomorpha, the ground plan mandible of the Brachycera has become separated into two freely articulated components: a sharp, heavily sclerotized distal hook and an inverted "U"-shaped basal sclerite. Using the apodemes as landmarks, the inverted "U"-shaped basal sclerite can be identified. The abductor apodeme is inserted on the posterodorsal margin of the basal sclerite as in the Psychodomorpha. The adductor apodeme has shifted anteriorly compared to that found in the Psychodomorpha and is inserted partially onto the ventral margin of the inner arm of the basal sclerite and also onto the base of the mandibular hook (Schremmer 1951). The abductor and adductor muscles originate partially on the dorsal plate (cranium) and partially on the tentorial arm (Roberts 1969). Thus, from the condition found in the Nematocera there is a trend toward a shift of the origin of the mandibular muscles to the tentorial arm, coincident with the reduction of the head capsule (Cook 1949).

From a near vertical plane as seen in the Psychodomorpha, the mandibles have shifted to the vertical plane and represent a synapomorphy of the Brachycera (Woodley 1989, character 1). The hypocondyle, at the posterolateral apex of the external arm of the basal sclerite, articulates with the cranium and the epicondyle, positioned midway on the inner, vertical arm of the basal sclerite, articulates with the tentorial phragma.

In the majority of taxa examined (e.g. Chrysopilus Macquart, Symphoromyia

Frauenfeld, Xylophagus Meigen, Coenomyia Latreille, Thereva Latreille, Promachus Loew, Mydas Fabricius) there is an external groove along the length of the adoral surface of the hook. This type of mandibular hook is termed the promuscis-type and is associated with a shift to the vertical plane, which enables both hooks to be juxtaposed to form a sucking tube or food canal (Schremmer 1951).

Additional ground plan mouthpart features of the Brachycera. - A "pore" near the epicondyle on the adoral surface of the basal sclerite of Rhagio Fabricius was illustrated by Roberts (1969, fig. 3), but not discussed. Exner & Craig (1976, fig. 17) identified a similar "pore" near the epicondyle on the mandible of tanyderid larvae as a campaniform sensillum. This is a mechanoreceptor that perceives strains in the exoskeleton and is described as a small cuticular cap, surrounded by a raised ring (McIver 1975).

A campaniform sensillum, which is homologous in position and structure to that in the Tanyderidae and Rhagionidae, is present throughout the Brachycera and in several other lineages of the Nematocera, including the Blephariceridae (Anthon and Lyneborg 1968), Psychodomorpha, Bibionidae and Tipulidae. In the Culicidae, a sensillum located near the epicondyle has been referred to in the literature as the mandibular puncture (= mandibular ring or mandibular pit organ) (Harbach and Knight 1980). The sensillum is described as a dome-shaped projection or conical papilla that projects beyond the surrounding ring (Harbach & Knight 1980). A sensillum in a similar position is also apparently present in the Nannochoristidae (Mecoptera).

Thus it can be concluded that a campaniform sensillum, located near the epicondyle, is probably part of the ground plan of the Diptera.

3.1.2 GROUND PLAN OF EREMONEURA

The Cyclorrhapha and Empidoidea form a well-supported monophyletic lineage known as the Eremoneura (Griffiths 1972, Cumming and Sinclair 1990).

In the plesiomorphic condition, as found in the Asiloidea, the maxilla is composed of well defined sclerites, articulated posteriorly with the basal mandibular sclerite. In the Eremoneura, the maxilla is an elongate, primarily membranous lobe, delimited at its base by the antenna (Teskey 1981a, figs 3.12-13). A primarily membranous maxilla is proposed as a possible synapomorphy of the Eremoneura. An elongate maxilla similarly placed with respect to the antenna, in Vermileonidae, is probably the result of convergence (Teskey 1981b, fig. 39.4).

The plesiomorphic condition of the labium, occurring in the Tabanomorpha and Asiloidea, is a large rectangular submental plate. The apomorphic state, a "V"-shaped labial hypopharyngeal sclerite, is present in the Empidoidea (Vaillant 1948, fig. 16) and basal taxa of the Cyclorrhapha (e.g. Melanderomyia, Megaselia).

Additional ground plan mouthpart structures of the Eremoneura. - Based on both outgroup and ingroup comparison, I consider that the larval ground plan condition of the Eremoneura is characterized by a two-component mandible, comprising a distal hook and an inverted "U"-shaped basal sclerite. There remain two articulation points, but the

epicondyle is expanded laterally and shifted to the ventral margin of the inner arm of the basal sclerite. The ancestral eremoneuran larva is hypothesized to have been predaceous (lacking a pharyngeal filter), similar to that observed in the Empidoidea. Specialized feeding methods and filtering structures characteristic of the Cyclorrhapha presumably developed later from the ground plan condition.

3.1.3 GROUND PLAN OF EMPIDOIDEA

During the present study, the larval mandibles were analysed in some examples of the following empidoid lineages: Oreogetoninae, Empidinae, Hemerodromiinae, Clinocerinae, Tachydromiinae, Ocydromiinae, and Dolichopodidae. Larvae of the five remaining subgroups (Atelestinae, Microphorinae, Ceratomerinae, Brachystomatinae, and Hybotinae) remain unknown.

Through a series of publications, Vaillant (1948, 1949, 1950b, 1951a, 1952a, 1952c, 1953a) presented the first detailed descriptions of the cephalopharyngeal skeleton of empidoid larvae. These studies included genera of the Clinocerinae, Hemerodromiinae and Dolichopodidae. Detailed descriptions of larvae of the Empidinae and additional genera of the Hemerodromiinae have also appeared (Trehen 1962, 1969).

In the present study, the larval mandibles of various genera within the above lineages were reanalysed. In addition, larval mandibles of first-instar Ocydromia Meigen (Ocydromiinae), and later instar Chersodromia Walker (Tachydromiinae) were examined, along with those of the apparently primitive genus Oreogeton Schiner (Oreogetoninae).

As discussed previously, the mandible of final instar larvae of the lower

Brachycera comprises two components, a distal hook and basal sclerite. In the ground plan of the **Empidoidea**, the larval mandible comprises four components, a distal mandibular hook (= dorsal hook of Vaillant 1951-1953 and Dyte 1967) and a subdivided basal mandibular sclerite. Using the apodemes as landmarks, it is apparent that the basal sclerite has become fragmented into two connecting sclerites and a ventral sclerite (= ventral hook of Vaillant 1951-1953 and Dyte 1967), a unique empidoid feature (Figs. 1,2). The abductor apodeme is inserted on the connecting sclerite bearing the external arm of the basal sclerite, the same region as in the **Brachycera** ground plan. However, the adductor apodeme has shifted anteriorly with the development of the ventral sclerite. The adductor apodeme is partially attached to both the ventral sclerite and to the base of the hook (Fig. 2; insertion points of the adductor apodeme similar to that described in the lower **Brachycera**). The hypocondyle articulates with the cranium, as observed in the **Brachycera** ground plan, and is not lost as suggested by Teskey (1981a). The epicondyle, having shifted ventrally as described in the **eremoneuran** ground plan, remains articulated to the tentorial phragma.

In the literature, the external arm of the basal mandibular sclerite (Fig. 3) has been referred to as the *cardo* (see discussion under **Asiloidea**); for example, de Meijere (1916, fig. 93) and Vaillant (1948, figs. 5,6). Using the apodemes as landmarks, this sclerite is clearly homologous to the basal mandibular sclerite of the **brachyceran** ground plan. Krivosheina (1960) correctly interpreted the external arm to be of mandibular origin.

The four-component mandible (distal hook, two connecting sclerites and ventral

sclerite) is tentatively proposed as a synapomorphy of the ground plan of the Empidoidea. The ground plan condition was first suggested by Dyte (1967) and is found in most Empidoidea lineages, including the Empidinae (Trehen 1962; Dyte 1967), Hemerodromiinae (Trehen 1969), Ocydromiinae, Tachydromiinae, and Dolichopodidae (Dyte 1967; Vaillant 1948).

In the genus Oreogeton, the mandible appears to be composed of a distal hook, a single connecting sclerite and a ventral sclerite (Figs. 4,5). The sclerites are closely articulated so that it is difficult to distinguish distinct boundaries. A mandible comprising three closely articulated sclerites could also represent the ground plan condition from which four- and then six-component mandibles have evolved. Although there appears to be a trend toward increased subdivision of the larval mandible, the ground plan condition is here hypothesized to include four components. This decision is based on the widespread occurrence of a four-component mandible throughout the superfamily and its presence in first instars, which tend to be evolutionarily conservative. However, examination of additional larvae from other primitive genera, for example Hormopeza Zetterstedt, would help resolve the ground plan condition.

Additional ground plan mouthpart structures and trends within the Empidoidea. - As observed throughout the lower Brachycera, a campaniform sensillum was observed in the genus Oreogeton (Fig. 5). It is positioned on the connecting sclerite, dorsal to the epicondyle. The presence of this sensillum helps to confirm the interpretation that these sclerites are derived from the basal mandibular sclerite.

The mandible of first instar larvae of Ocydromia is unmodified from that observed in mature larvae of Chersodromia (Figs. 6,7) and Dolichopodidae (Figs. 1,2). The mandible comprises a sharply pointed distal hook, two connecting sclerites (with a distinct external arm), and a large ventral sclerite.

From the ground plan, there has been a trend toward further subdivision and complexity in aquatic genera of Clinocerinae (Figs. 79,80) and Hemerodromiinae (Figs. 8,9). In several genera of Clinocerinae (Clinocera Meigen, Kowarzia Mik, Dolichocephala Macquart, Wiedemannia Zetterstedt, Trichoclinocera Collin) and Hemerodromiinae (Hemerodromia Meigen, Chelifera Macquart) the larval mandible is subdivided into six components (Vaillant 1951a, 1952a, 1952c, 1953a; Dyte 1967). A four-component mandible is known for the hemerodromine genus Phyllodromia Zetterstedt (Trehen 1969), but it is uncertain whether this represents the ground plan of the Hemerodromiinae or simply a reversal from the six-component condition. See "Reconstructed phylogeny of the genera of Clinocerinae" (Sec. 5.1.2, character 8) for discussion of six-component mandible.

3.2 FEMALE TERMINALIA

3.2.1 GROUND PLAN OF BRACHYCERA

The Rhagionidae is widely believed to represent one of the most basal lineages of the Brachycera. Thus the genera Rhagio and Symphoromyia are chosen to best represent the ground plan of Brachycera, based on their similarity with nematocerous taxa. The taxa examined in the following study are listed in Table 2.

Sclerites of the 3 terminal tergites (T) 8-10 are rectangular, with undivided posterior margins and sternite (S) 10 is equal in size to T10 (McAlpine 1981, fig. 2.94). The sclerites of the epiproct and hypoproct are absent in all Diptera (Griffiths 1981)¹. Females of the primitive lineages of the Brachycera have two-segmented cerci, except for a few genera of stratiomyids and rhagionids and all Athericidae and Tabanidae (Nagatomi and Iwata 1976, figs. 21, 25; Woodley 1989). The posterior margin of S8 is bilobed, often referred to as the hypogynial valves. From these lobes membranes extend anteriorly to the anterior margin of genital fork or S9. This membranous sheet forms the floor of the genital chamber. The genital fork is invaginated, forming the dorsal wall of the genital chamber (McAlpine 1981). The anterolateral margin of the genital fork is also attached by strips of sclerotized membrane (or sclerites) to T9. The anterior margin of the genital fork is generally complete, with the posterior margin often open. In the ground plan of Brachycera, there are three spherical spermathecae, with long spermathecal ducts. Near the genital fork the spermathecal ducts fuse into a single duct which passes over the anterior margin, through the ring of the genital fork, and into the genital chamber or vagina.

¹ An alternative interpretation is that segment 10 is absent in all Diptera and that these sclerites represent the epiproct and hypoproct. These sclerites, together with the cerci comprise the non-segmental telson (Jürgens 1987).

3.2.2 GROUND PLAN OF ASILOIDEA

In Asiloidea, T10 in the female is often divided into a pair of spine bearing sclerites, termed acanthophorites. Acanthophorites have been lost frequently in the Asiloidea; for example, Mythicomyiinae, Hilarimorpha Schiner and Scenopinidae. In these taxa, tergites 9 and 10 have either fused or T9 is lost. Despite the seemingly frequent absence, acanthophorites were regarded as being present in the ground plan of the Asiloidea, due to their widespread occurrence among the basal lineages of each asiloid family (Adisoemarto and Wood 1975).

Tergite 8 is often connected dorsomedially to the anterior margin of T9 by a narrow, sclerotized, strip. Tergite 9 is a narrow, transverse sclerite, undivided medially, with anterolateral sclerotized strips extending to S9, the genital fork. The genital fork is generally U-shaped, with the opening of the U directed posteriorly. Three spermathecal ducts extend over the genital fork and enter the genital chamber. In many Bombyliidae, the genital fork is reduced to several pairs of narrow rods, which are connected by membrane to the anterolateral filaments of T9 and S8 (Yeates 1989). The cercus is reduced to a broad, lightly sclerotized lobe, bearing setulae.

3.2.2.1 MODIFICATIONS TO THE GROUND PLAN SHOWN IN SEVERAL ASILOID TAXA

In Thereva, T9 retains the anterior, dorsomedial strip from T8, but the remaining sclerite is slender, thinly sclerotized and closely associated with the anterior margin of T10. Tergite 9 arches laterally to fuse with the genital fork (Irwin 1976, figs. 13,14,33).

The acanthophorites of Thereva are divided into 2 dorsal and 2 lateral lobes. The penial guide referred to by Irwin (1976) appears to be a sclerotized infolding of the posterior margin of S8, equivalent to hypogynial valves, which may also be observed in the bombyliid, Systropus Wiedemann.

In the asilid genera, Diogmites Loew and Proctacanthus Macquart, T9 is further reduced to a slender dorsal sclerite, with a remnant of the dorsomedial strip from T8. The anterolateral strips from T9 to the genital fork have developed into a pair of wide square sclerites, membranously connected to the genital fork (Adisoemarto and Wood 1975, fig. 6c).

3.2.3 GROUND PLAN OF EREMONEURA

In the primitive condition of the Eremoneura (Empidoidea + Cyclorrhapha), the pregenital segments are unmodified and telescopic, with segments more or less permanently exposed, for example in Rhamphomyia Meigen, Empis L., and Oreogeton (Steyskal and Knutson 1981, fig. 47.54). The first to seventh abdominal segments each bears a pair of spiracles.

Before I proceed to describe the ground plan, the homology of segment 9 of the female terminalia of Eremoneura requires further clarification. According to Griffiths (1983), the sclerites of the ninth segment of Cyclorrhapha are lacking in females, based on evidence of ontogenetic studies and structure of intersexes. Due to similarities in the terminal segment between Cyclorrhapha and primitive Empidoidea, Griffiths concluded that sclerites of the ninth segment were probably lost in the ground plan of Eremoneura.

McAlpine (1981) believed that T9 was indistinguishably fused to T10 and S9 was indistinguishable or absent in Cyclorrhapha. However, based on outgroup comparison with lower Brachycera and contrary to McAlpine (1981) and Griffiths (1983, 1984), remnants of S9 (genital fork) have been observed in many empidooids¹ [Figs. 20,25; Hilara Meigen and Empis (Lobanov 1979); Dolichopus Latreille (McAlpine 1981, fig. 2.102, 2.103); Stilpon Loew (Cumming and Cooper, 1992, fig. 6a)] and cyclorrhaphans [e.g. Microsania Zetterstedt (Platypezidae), Orthonevra Macquart (Syrphidae)].

In Empidoidea, sternite 9, the genital fork, generally appears as a small V-shaped sclerite forming the anterodorsal wall of the genital chamber (= copulatory pocket sensu Hippa (1986)). The spermathecal duct(s) pass over this sclerite and open into the genital chamber. In Syrphidae, the genital fork is often very well developed, as in more primitive brachycerans (see Hippa (1986) for variety of forms). Griffiths (1984) considered these internal sclerites in Syrphidae as secondarily derived; however, after a brief survey of several families of Cyclorrhapha, I consider the genital fork in higher flies to be homologous to more primitive Diptera. The homology of these internal sclerites has been largely overlooked by cyclorrhaphan specialists, preferring to give them special names that have limited meaning outside of their particular taxon of study

¹In addition, a pair of rectangular sclerites, membranously connected to the genital fork were found in Hormopeza copulifera Melander, yet not observed in other species of this genus. This pair of sclerites appear to be homologous to wide, square sclerites derived from T9 found in Asilidae. This will have to be investigated further.

(e.g. "spectacle-shaped sclerite" in Sphaeroceridae, Wheeler pers. comm.).

In Eremoneura, the genital fork often appears lacking or lightly sclerotized. Care must be taken in interpreting this sclerite, since the posterior margin of S8 is often invaginated, forming sclerotized lateral or ventral walls of the genital chamber (e.g. Rhyacodromia Saigusa (Fig. 29), Symballophthalmus Becker). In Syrphidae, there are often additional sclerites along the floor of the genital chamber (Hippa 1986, fig. 3D).

In the ground plan of Eremoneura, acanthophorites (T10) are present and appear to be homologous with those of Asiliodea. The cerci are elongate, setose lobes.

The number of spermathecae in Eremoneura varies from one to three. In the plesiomorphic state, there are three darkly sclerotized, spherical spermathecae, each at the end of a long, slender duct.

3.2.4 GROUND PLAN OF EMPIDOIDEA

Relative to studies of the male terminalia of Empidoidea, those of the female have largely been ignored. Chvála (1983) produced the first comparative survey of female terminalia of empidoids.

Acanthophorites are present in many primitive empidoid genera and thus I consider them to be part of the ground plan of this superfamily. In those lineages which retain acanthophorites, the apical segments are retracted partially within segment 7.

In Empidoidea there is only a single spermatheca, a synapomorphy of this lineage (Woodley 1989, character 35). Primitively, the spermatheca is a heavily sclerotized reservoir at the apex of a long spermathecal duct. This primitive form is found in the

Oreogetoninae, Empidinae (Empis, Rhamphomyia), Hemerodromiinae (Chelipoda Macquart, Metachela Coquillett), Trichopeza-group of genera (see Sec. 4.4.1), Atelestus Walker, Microphor Macquart and Schistostoma Becker.

3.2.4.1 MODIFICATIONS TO THE GROUND PLAN SHOWN IN SEVERAL EMPIDOID TAXA

Terminalia with acanthophorites. - In Empidoidea, unlike the terminalia in asiloids which possess acanthophorites, T8 is often desclerotized posterodorsally, with S8 reduced to a narrow strip, articulated or fused to the anteroventral margin of T8. The cercus is heavily sclerotized and bears stout setae. Terminalia which possess acanthophorites may be divided into at least three different types and all are believed to be derived from a common ancestor.

(1.) Trichopeza-type:

The Trichopeza-type of terminalia is distinguished by the presence of a large apodeme projecting medially from the anterior margin of T8, extending into segment 7. In addition, there is a row of long setae along the posterior margin of T7 and the cerci are projecting upright, bearing stout setae or spines similar to T10 (Figs. 164,167,170,175,176). This type of terminalia is found in the Trichopeza group of genera (see Sec. 4.4.1).

(2.) Ceratomerinae + Brachystomatinae-type:

In the subfamilies Ceratomerinae and Brachystomatinae, the terminalia are very similar to the Trichopeza-type but lack the large apodeme projecting from T8 (Fig. 10). In Ceratomerinae, the spermatheca is spherical and S8 is quite broad; however, the anterodorsal margin remains articulated to T8.

In Brachystomatinae, the spermatheca is a long, coiled tube and there is a narrow sclerite extending from S10 to the posterior margin of the genital fork (although the female of Homalocnemis Philippi was not available for study, the description of the female abdomen by Collin (1928), shows that the terminalia are fully exposed and not retracted within segment 7; see Sec. 5.1.1).

(3.) Microphorinae + Dolichopodidae-type:

The general structure of the abdomen of Microphorinae was described briefly by Chvála (1987). Segments 1-5 form the preabdomen into which the remaining segments are retracted (in Schistostoma and possibly also Amphithalassius Ulrich, the preabdomen includes segment 6). The sclerites of the apical segments (except Microphor) are only partially modified, with the posterior and/or anterior margin of each sclerite desclerotized, with large U-shaped notches. In Microphor, the sclerites are greatly reduced to slender rods, quite similar to the ovipositor of Dolichopodidae (Figs. 12,13). The retraction of the apical segments into segment 5 or 6 is possibly synapomorphic for Microphorinae + Dolichopodidae.

The acanthoporous (T10) setae are arranged in a horizontal row near the

posterior margin. There are 3 pairs of setae on T10 in Microphor (Fig. 12), Schistostoma (Fig. 10, Hennig 1976, fig. 55; Chvála 1987) and Amphithalassius (Ulrich 1991, fig. 40); 2 pairs of setae in Parathalassius Mik, Plesiothalassius Ulrich (Ulrich 1991, fig. 14) and apparently in Sciapodinae (Fig. 13, Irwin 1974, Meuffels and Grootaert 1990); Microphorella Becker has 4 pairs of setae (Chvála (1988, figs. 23,24) illustrates 3 long spines and a short lateral spine) [the description of Thalassophorus Saigusa did not facilitate comparison with other microphorines and specimens were not readily available for study]. The terminalia of the Microphorinae + Dolichopodidae are also characterized by slender, heavily sclerotized, apically pointed cerci, which are held horizontally.

In the literature, Microphor has been considered to have an unmodified 'telescopic abdomen', and is thus considered to be the most basal genus of the Microphorinae (Hennig 1971; Chvála 1983, 1988). However, I interpret the terminalia of Microphor to be very specialized, with reduced acanthoporous setae. The cerci of Microphor remain heavily sclerotized, bearing long apical setae (Fig. 12). The apical segments of Microphor are very similar to those of Sciapodinae (Fig. 13, Irwin 1974).

Acanthoporphorites do not occur in Plesiothalassius and Amphithalassius (Ulrich 1991) and may be secondarily lost. Although specimens were unavailable for study, figures and descriptions indicate that, although the setae on T10 are reduced, they are arranged similarly to those of other microphorines (Ulrich 1991, figs. 14,40). The sclerites of segment 8 are well developed and S8 does not articulate with T8 (Ulrich 1991, figs. 15,41). In Plesiothalassius, sternite 8 is expanded posteriorly, possibly replacing the need for acanthoporphorites during oviposition in sandy substrates.

The segmental homology of the terminalia of Trichopeza, Heleodromia, Brachystoma, and Schistostoma was misinterpreted by Chvála (1983, figs. 78-83, 85, 86; 1987, figs. 17-21, 43-45). Tergite 9 is actually T10, T10 is actually the cercus and what are labelled cerci are setose lobes encircling the anus. Hennig (1976, fig. 88) correctly interpreted the homology of the cercus of Schistostoma.

Terminalia lacking acanthophorites. - Acanthophorites appear to be lost at least once in the Empidoidea and lost in the ground plan of Cyclorrhapha. Female terminalia which lack acanthophorites are best illustrated by the Empidinae. The sclerites of segment 8 and 10 are rectangular (or T10 is split mid-dorsally) and the cercus is long, narrow, and densely covered by fine setae. I consider this type of terminalia as the derived condition compared to the presence of acanthophorites and this type is present in Oreogetoninae, Empidinae, Hemerodromiinae, Clinocerinae, Atelestinae, Ocydromiinae, Tachydromiinae, and Hybotinae.

Spermatheca. - Within the Empidoidea, the spermatheca has been frequently modified from that of the ground plan condition. Although Tuomikoski (1966) reported that there were no sclerotized spermathecae in Ocydromiinae, Hybotinae and Tachydromiinae, a faintly outlined, unpigmented, membranous spermatheca can be traced anteriorly from the genital chamber and genital fork after maceration in lactic acid. For example, the spermatheca of Platypalpus holosericus Melander is a wide tube, expanding into a large oval chamber anteriorly and in species of Chersodromia Walker and Stilpon Loew

(Cumming and Cooper 1992), the spermatheca is a narrow, membranous sac.

The spermathecae in Clinocerinae and Brachystomatinae are highly modified. In these two subfamilies, the darkly pigmented, apical spermathecal reservoir is reduced to a long, slender tube with glandular tissue at the apex of this slender reservoir (Fig. 87).

3.3 MALE GENITALIC HOMOLOGIES

3.3.1 GROUND PLAN OF BRACHYCERA

No single family or genus presents all the ground plan features of Brachycera, although most rhagionids and xylophagids, especially Rhagio and Arthropeas Loew come closest, and these two taxa are used to represent the ground plan. The ground plan conditions described below are based on outgroup comparison to nematocerous Diptera, particularly the putative sister group Psychodomorpha (Ovchinnikova 1989, Sinclair 1992). The taxa examined in the following study are listed in Table 3. The following colours in Rhagio scolopacea L. (Figs. 14-17) will be used to indicate homologous structures in Eremoneura: epandrium - brown; hypandrium and gonocoxite - orange; gonostylus - yellow; cercus and proctiger - dark green; ejaculatory apodeme and aedeagus - red; parameral sheath - purple.

Aedeagus and paramere. - Parameres as separate paired structures associated with the base of the aedeagus and the gonocoxal apodemes were postulated as the ground plan condition of Diptera (Wood 1991). Parameres fused to each other medially represent the derived condition and are found in a few derived clades in several nematocerous

infraorders (Wood 1991). In the ground plan of Brachycera, the parameres are also fused medially and form a sheath which encircles the apex of the aedeagus (Figs. 16,17).

A tubular aedeagus and sperm pump (housed in the expanded base of the tube), represented by an ejaculatory apodeme and paired lateral sclerites, are postulated to be part of the ground plan condition of Diptera (Wood 1991). In the brachyceran ground plan, the tube is reduced and the sperm chamber enlarged. Only the apex of the tubular aedeagus remains, firmly attached to the posteroventral margin of the parameral sheath. In the Nematocera, when the paramere is cone-shaped, the tip of the tubular aedeagus is also often firmly attached (e.g. Hesperinus Walker, Trichomyia Curtis).

The sperm chamber (= endophallus sensu Bonhag 1951) is positioned posterior to the ejaculatory apodeme within the parameral sheath (Fig. 16). Paired sperm ducts (vas deferens) from the testes enter the anterior region of the chamber near the ejaculatory apodeme. The anterodorsal wall of the chamber is formed by a pair of lateral sclerites, here termed lateral ejaculatory processes (Fig. 17) (= aedeagal dorso-anterior sclerite sensu Nagatomi (1984)). These processes are present in the ground plan of the Xylophagomorpha and Tabanomorpha, but secondarily lost in several more derived genera such as Xylophagus. Similar articulated, paired processes have been observed in a few nematoceran genera; for example, Hesperinus (Bibionomorpha) and Aspistes Meigen (Psychodomorpha: Scatopsidae). But in the latter genus, they do not appear to be associated with the anterior margin of the sperm chamber and hence are not considered homologous. Fused lateral processes arising from the base of the tubular aedeagus are found in the Tipulomorpha (e.g. Liogma O.S., Dolichopeza Curtis),

however they are not considered homologous to the articulated processes in the ground plan of the Brachycera.

In Rhagio, there are additional structures ventral to the lateral ejaculatory processes (Fig. 14) which may possibly represent "precursors" of the aedeagal tines observed in Athericidae and Tabanidae. However, detailed observations and distribution of this structure requires further analysis. Stuckenburg (1973, fig. 8) believed that the lateral ejaculatory processes in Rhagio were the "precursors" of the aedeagal tines.

Within the Brachycera, the sclerotized apex of the tubular aedeagal component becomes progressively encircled and incorporated into the parameral sheath. In the Stratiomyomorpha and Muscomorpha (sensu Woodley 1989), this aedeagal component is completely fused and indistinguishable from the paramere. Since the major component of the intromittent organ and functional gonopore is now parameral, this new structure is here termed the phallus.

The ejaculatory apodeme, a prominent feature of the sperm pump, is inserted into the base of the parameral sheath (Figs. 14, 17). In the Nematocera, the ejaculatory apodeme is either a flattened plate (e.g. Tipulidae, Hesperinus (Bibionomorpha), Paltostoma Schiner (Blephariceromorpha)), or simple lengthened rod-like structure (e.g. Bruchomyia Alexander, Trichomyia (Psychodidae)). In the primitive lineages of the Brachycera, this apodeme is often rod-shaped (Fig. 14). In several genera the apodeme is laterally expanded with a vertical keel (e.g. Xylophagus (Hennig 1976, fig. 45); Arthroceras Williston, Symphoromyia)).

The ejaculatory apodeme acts as a piston by the action of three sets of muscles

described in detail by Ovchinnikova (1989). The protractor, M_{11} (origin on ventral margin of ejaculatory apodeme and insertion on ventral, anterolateral margin of the parameral sheath) draws the piston forward into the sperm chamber and the retractor, M_{30} (origin on gonocoxal apodeme and insertion on posterior end of ejaculatory apodeme) pulls the piston back away from the chamber. The flexor, M_{12} (origin on dorsal margin of ejaculatory apodeme and insertion on lateral ejaculatory processes) assists in drawing the piston forward and contraction of sperm chamber. The action of the piston expels sperm through the narrow opening of the aedeagus or phallus.

Separate epandrium and hypandrium. - Separation between the epandrium and hypandrium is found in all Brachycera (Fig. 14) and appears to be a synapomorphy of the suborder. In the dipteran ground plan proposed by Wood (1991), the epandrium and hypandrium are fused to form a ring. Dissection of brachyceran genitalia, after removal of the terminalia from segment 8, is always easiest by separating the epandrium (including proctiger) from the hypandrium and gonocoxites (including parameres and aedeagus), allowing a ventral view of the former and a dorsal view of the latter. The epandrium may lie flat upon the gonocoxites, as in Rhagionidae and Stratiomyidae, or the anterolateral edge of the epandrium may articulate with the gonocoxites, as in other Brachycera. The latter type is similar to a pair of jaws and permits dorsoventral clasping.

Gonocoxites separate from hypandrium. - As in Nematocera, some Brachycera, including some Rhagionidae (Figs. 14,16), Bombyliidae, Therevidae, and Asilidae, still

retain a separate hypandrium. However, within many lineages the hypandrium is partially or completely fused with the gonocoxites. When fusion has left no trace of what is hypandrium and what are gonocoxites, it is convenient to refer to the whole compound structure as the hypandrium.

Gonostylus directed medially, moving in a horizontal plane. - Among Stratiomyomorpha (except Xylomyidae), Xylophagomorpha (except Rachicerus Walker), and Tabanomorpha (sensu Woodley 1989), gonostyli are unmistakably articulated, and move in opposition to each other much as they do in Nematocera (Fig. 15); this condition undoubtedly represents the plesiomorphic condition.

In contrast, the gonostyli of Xylomyidae move in a dorsoventral direction, parallel to each other, and the epandrium and cerci are so well developed and distinctly articulated that they appear to be capable of clasping. Dorsoventral or oblique clasping is also found in the ground plan of the Muscomorpha (sensu Woodley 1989).

There are two antagonistic sets of muscles associated with the gonostylus. The adductor muscle (M_{27}) is inserted on the inner edge of the gonostylus and originates along the anterior margin of the gonocoxite (Ovchinnikova 1989). The abductor muscle (M_{28}) is inserted on the outer edge of the gonostylus and originates on the lateral margin of the gonocoxite.

Epandrium undivided medially. - In the ground plan of the Brachycera, the epandrium is not divided mid-dorsally (Fig. 14). In the Asiloidea, the epandrium is often cleft mid-

dorsally and is sometimes completely split into two halves, where the halves may be capable of a clasping action of their own. Abduction of the apical margins of the epandrium may arise from the contraction of M_1 (Ovchinnikova 1989, figs. 166, 173, 183). In Apsilocephala Kröber large processes that are capable of clasping are present at each posteroapical corner of the epandrium. Eremoneura also have well developed articulated lobes along the posterior margin of the epandrium. The apical epandrial processes in Apsilocephala and Eremoneura are exceedingly similar and are termed surstyli (see discussion in Sec. 3.3.2).

Proctiger and subepandrial sclerite. - Following the ninth segment is the proctiger and anything posterior to it (Wood 1991). In the brachyceran ground plan, as in that of the Nematocera, it is small and tucked beneath the posterior margin of the epandrium (as in Pachyneuridae), and consists of small paired pad-like cerci, an oval or triangular midventral hypoproct (= sternite 10?) and a middorsal epiproct (= tergite 10?, see Sec. 3.2.1), which may be reduced and often absent.

A deep pouch separates the epandrium and proctiger from the gonopods and hypandrium. The roof of this space is usually membranous and is here termed the subepandrial membrane. The subepandrial membrane extends to the anterodorsal margin of the paramere (= dorsalbücke sensu Hennig 1976), and the dorsal surface of the parameral sheath represents the floor of this space. In some Asiloidea, especially Asilidae and Therevidae, a more extensive sclerite or pair of sclerites develop in the membrane, termed here the subepandrial sclerite (= ventral epandrial sclerite sensu Irwin and

Lyneborg 1981). When continuous with the hypoproct, the latter may be distinguished by the presence of setae.

In some Nematocera (e.g. Trichomyia) the subepandrial sclerite is also well developed. In lower Brachycera, the subepandrial membrane is rarely completely sclerotized from the anterior margin of the proctiger to the base of the parameral sheath. In the nemestrinid Neorhynchocephalus Lichtwardt, this sclerite is particularly well developed and ends distally in a ventrally projecting hook; the hypoproct is recognizable dorsal to this hook. Refer to Section 3.3.3 for a discussion of the origin and significance of a completely sclerotized subepandrial membrane.

3.3.2 EREMONEURA - GENITALIC HOMOLOGY CONTROVERSY

The homology of the structures comprising male terminalia in Eremoneura has been problematic. Much of the dispute over homologies has centred on the segmental origin of the clasping structures. In lower Brachycera, the clasping structures or gonostyli, arise ventrally and are articulated on the gonocoxites or hypandrium. The gonostyli are derived from sternite 9. In Eremoneura, the clasping structures arise dorsally and are articulated on the dorsal tergite. The segmental origin of the dorsal clasping structures has been disputed for 30 years.

There are two main theories concerning the origin of the claspers in Eremoneura:

(1.) Epandrial Hypothesis (sensu Hennig 1976):

In this hypothesis, the dorsal wall of the clasper or surstylus is believed to be

derived from tergite 10, arising from the apex of the epandrium (tergite 9). The ventral wall of the surstylus (= subepandrial sclerite) is considered to be derived from sternite 10. Additional lobes or grappling hooks on either side of the phallus were often labelled as telomeres (Hennig 1976) or parameres (McAlpine 1981, figs. 2.124, 2.128).

(2.) Periandrial Hypothesis (sensu Griffiths 1972):

Griffiths (1972) proposed a radical new interpretation of the homologies of male terminalia in Eremoneura, based on the interpretation of empidoid genitalic homologies presented by Bährmann (1960) and an unpublished thesis on the ontogenetic development of the terminalia in Eucalliphora (Black 1966).

In the empidoid subfamilies, Empidinae and Hemerodromiinae, Bährmann (1960) interpreted the lateral lamellae as 'basistyli', derived from sternite 9 (actually these structures are divided epandrial lobes, derived from tergite 9, see below). Griffiths (1972) considered this configuration as the plesiomorphic condition. In higher empidoids and Cyclorrhapha, the 'basistyli' are interpreted as having fused mid-dorsally, forming a new structure, termed the periandrium (derived from sternite 9). Griffiths considered one of the strengths of the periandrial hypothesis to be the preservation of the assumption of functional continuity, in which the clasping structures of Eremoneura could be interpreted as homologous with those of the lower Diptera and derived from sternite 9. Thus the hypopygium of Eremoneura according to the periandrial theory consists of a dorsal sclerite composed of the gonocoxites, with apical gonostyli (equivalent to surstyli of epandrial hypothesis). The ventral sclerite remains the hypandrium.

This theory has found favour because the segmental origin of the dorsal claspers in *Eremoneura*, as proposed under Hennig's epandrial hypothesis, do not agree with ontogenetic studies conducted on *Eucalliphora* (Black 1966) and *Drosophila* (Dobzhansky 1930). These studies have found that the claspers are articulated lobes differentiated from segment 9 (Griffiths 1981).

In a co-operative study, Wood, Cumming and Sinclair have been re-evaluating the homologies of the male terminalia in Diptera. This comprehensive study commenced with a survey of the male terminalia of the outgroup to Diptera. The first part of the survey of the male genitalic homologies in Diptera was recently published, where the ground plan of Diptera and genitalic homologies throughout the Nematocera was outlined (Wood 1991).

Preliminary results of the homologies of the male terminalia in *Eremoneura* were presented at the Second Dipterology Congress (Cumming and Sinclair 1990). After surveying the Brachycera, both the epandrial and periandrial hypotheses were rejected and a new interpretation of the male genitalic homologies of the *Eremoneura*, termed the "Revised Epandrial Hypothesis" was presented. A brief justification of this new interpretation is presented below.

Although the segmental origin of surstyli in Hennig's epandrial hypothesis is contradicted by ontogenetic studies, this does not necessitate the assumptions of the periandrial hypothesis. The dorsal clasping lobes could also be interpreted as being derived from the epandrium or tergite 9. This interpretation is supported by the

observation that remnants of gonocoxal apodemes are present in the basal lineages of the Empidoidea (e.g. Hormopeza, Fig. 18) and arise from the anterior margin of the ventral sclerite. The position of these apodemes clearly indicates that the ventral sclerite is the hypandrium + gonocoxite (sternite 9) and the primary dorsal sclerite of the hypopygium is not gonopodal in origin, but represents the epandrium or tergite 9.

As observed in the lower Brachycera, an apically cleft epandrium, often functioning as the primary clasping device, is a common feature in many asilids, therevids, apiocerids, and other asiloids. Additional processes have developed on the apices of the epandrium and have reached their greatest development in the articulated lobes of Apsilocephala. The gonostyli in these groups function as grappling hooks, pulling the female terminalia between the abducted lobes of the epandrium. Therefore the basic assumption of the periandrial hypothesis, that the preservation of clasping is performed by articulated gonopods in all Brachycera and does not involve other structures, is not supported.

Griffiths (1972, 1991) also believed that the periandrial hypothesis enabled the muscles involved in clasping to be homologized throughout the Diptera. However, only a single muscle is inserted at the base of what he refers to as the 'gonostylus'. A single muscle was observed in Lipara (Chloropidae) by Ovchinnikova (1989, fig. 225, M₄) and Calliphora by Salzer (1968, fig. 16, M₄₃). This muscle is either inserted directly onto the base of the lobe or onto the posterior half of the bacilliform sclerite. In contrast, the gonostyli of lower Brachycera have two sets of antagonistic muscles that are inserted directly to these structures (M₂₇, M₂₈, Ovchinnikova 1989).

Thus, based on outgroup analysis, it appears that the true gonostyli in *Eremoneura* have become reduced to small grappling hooks and the primary clasping structures have been taken over by the epandrium and newly evolved structures derived from tergite 9 (surstyli). Similar trends involving the epandrium were observed in many lineages of the Asiloidea.

3.3.3 GROUND PLAN OF EREMONEURA

The interpretation of the ground plan condition in the *Eremoneura* is established through outgroup comparison with the lower Brachycera, particularly the Asiloidea. No single family or genus presents all the ground plan features, although many oreogetonines (e.g. *Hormopeza*), empidines (e.g. *Empis* L.), and platypezids (e.g. *Microsania*) come closest. The homologies of the male terminalia, using the revised epandrial hypothesis (*sensu* Cumming and Sinclair 1990) are summarized below, as illustrated in *Hormopeza copulifera* Melander (Fig. 18). The colours in this figure indicate homologous structures shared by lower Brachycera (Figs. 14-17): epandrium - brown; hypandrium + gonocoxite - orange; cercus + proctiger - dark green; surstylus - reddish brown; subepandrial sclerite - light green; ejaculatory apodeme - red; phallus - purple.

Phallus. - As discussed above, the parameres fuse to enclose the aedeagus to form the phallus within the lower Brachycera and this structure is retained in *Eremoneura* (Fig. 18, purple). The ejaculatory apodeme is either rod-shaped or laterally compressed, projecting anteriorly beyond the hypandrium (Fig. 18, red).

Gonocoxites fused to hypandrium. - In the ground plan of the Brachycera, the gonocoxites are separate from the hypandrium. In the Eremoneura, the hypandrium and gonocoxites are completely fused. In more plesiomorphic Empidoidea, the gonocoxal component of the ventral sclerite of the hypopygium is still clearly identifiable due to the presence of short, paired gonocoxal apodemes (Figs. 18, 153, 187). As stated above, when complete fusion occurs, it is convenient to refer to the whole structure as the hypandrium.

Gonostylus. - In the Eremoneura, the gonostylus (= posterior paramere sensu Graham-Smith 1934; opisthoparamer sensu Salzer 1968; paraphysis sensu Griffiths 1972; telomere sensu Hennig 1976; paramere sensu McAlpine 1981) is a small, grapple-like hook that is closely associated with the base of the phallus and clasps dorso-ventrally (Michelsen 1988). In the lower Brachycera, there are two antagonistic sets of muscles inserted onto the base of the gonostylus. In Eremoneura, it appears that only the abductor muscle is inserted onto the gonostylus (muscle i, Graham-Smith 1934, fig. 7B; M_{iv} , Salzer 1968, fig. 18). The gonostylus moves anteriorly (adduction) as the phallus is swung into copulatory position (Griffiths, pers. comm.). The examination of the musculature of the gonostylus in basal lineages of the Cyclorrhapha is urgently required to discover whether only one set of muscles are present, as in higher cyclorrhaphans or if two sets of muscles are retained, as in lower Brachycera.

Griffiths (1981), citing Black (1966), considers the gonostyli of Eremoneura homologous to parameres of the Nematocera. Since the parameres are fused to form the

phallus in *Eremoneura*, these lobes must either represent gonostyli, or neomorphic structures. This controversy may be resolved with an investigation of the pupal development of the male genital disc in more primitive cyclorrhaphans, such as Syrphidae, of which many have well-developed articulated lobes.

Proctiger. - The proctiger (Fig. 18, dark green) (cerci and S10) is distal to the epandrium and usually tucked beneath its distal edge. The cerci are usually long, setose lobes and the hypoproct bears short setae.

Subepandrial sclerite and surstylus. - In the *Eremoneura*, the subepandrial membrane between the proctiger and base of the phallus, is completely sclerotized to form the subepandrial sclerite (Fig. 18, light green). This sclerite extends as a large plate at the base of the phallus (purple) to the proctiger, where it is often continuous with the hypoproct. Derived from the base of the subepandrial sclerite are two lateral rods, which extend to the tips of the epandrium or surstyli, if present. These rods are termed bacilliform sclerites or processus longi (light green).

Muscle 4 of Ulrich (1972), may possibly be homologous to muscle 183 of Bonhag (1951), M_{21} of Ovchinnikova (1989, figs. 135,183,225), and M_{42} of Salzer (1968, fig. 16). This muscle originates on the lateral wall of the epandrium and is inserted on the subepandrial sclerite and by manipulating the subepandrial sclerite appears to act indirectly upon the surstylus as an antagonist of the surstyler muscle (see below).

The surstyli develop independently in many subfamilies of Empidoidea (not

present for example in Hormopeza) and are present in the ground plan of the Cyclorrhapha. They are weakly articulated, apical lobes of the epandrium, of which the outer wall is derived from tergite 9 and the bacilliform sclerite forms the inner wall. The surstylus is manipulated by a single muscle (M_4 , Ovchinnikova 1989, fig. 158; M_{41} , Salzar 1968, fig. 16; muscle 7, Ulrich 1974, fig. 33; Ulrich 1976). On the basis of internal sclerites, I believe that Ulrich (1988, figs. 30,31) misidentified the surstylus in Microphor holosericeus (Meigen) and consequently, muscle 5 should be interpreted as the surstyler muscle and not muscle 7.

In summary, the ground plan of the Eremoneura includes fusion of the hypandrium with the gonocoxites, sclerotization of the subepandrial membrane forming the subepandrial sclerite with lateral bacilliform sclerites (processus longi), a deeply emarginate epandrium and reduced gonostyli. Surstyli develop independently in several subfamilies of Empidoidea and are present in the ground plan of the Cyclorrhapha.

3.3.4 GROUND PLAN OF EMPIDOIDEA

Based on a large diversity of empidid species, Bährmann (1960) provided the first comprehensive and detailed interpretation of the homologies of the structures comprising the male terminalia. Up to this point the various lobes were simply referred to as lamellae and there had been no attempts to search for homologous structures shared by orthorrhaphous Brachycera. Ulrich (1972) presented a different interpretation of the homologies of the male terminalia based on musculature. A more recent attempt at

interpreting the male terminalia of the Empidoidea was strongly influenced by the periandrial hypothesis (Chvála 1983). In this recent interpretation, the dorsal lamellae are considered the epandrium and the side lamellae the gonocoxites.

The ground plan of the Empidoidea is very similar to that of the Eremoneura and is again best illustrated by Hormopeza copulifera. The following section highlights modifications in the ground plan of the Empidoidea from that of Eremoneura.

Phallus. - From the base of the phallus projects a large plate (= hypandrium bridge sensu Ulrich 1975; = first ventral proctiger sclerite sensu Ulrich 1972), believed to be derived from the phallus, which hinges with the subepandrial sclerite. This hinge (termed "point y" sensu Hennig 1976) is an important landmark for distinguishing homologous structures throughout the Eremoneura. In the lower Brachycera, "point y" is where the subepandrial membrane is attached to the base of the phallus.

In the lower Brachycera there are three sets of muscles associated with the ejaculatory apodeme (Ovchinnikova 1989). In Empidoidea and Cyclorrhapha, the lateral ejaculatory processes and their flexor muscles (M_{32}) are absent, leaving only two pairs of muscles (Ulrich 1972, muscles 1,2). In addition, the ejaculatory apodeme no longer acts similar to a piston in the ground plan of the Empidoidea. The apodeme has become articulated with the base of the phallus and rocks dorsally to compress the sperm chamber (Figs. 18, 21, 26).

Gonostylus. - In Empidoidea, the gonostylus is fused to the gonocoxite, a synapomorphy

of this superfamily. The adductor and abductor muscles in the hypandrium appear absent in studies of the musculature of empidoid terminalia. Ulrich (1972, 1975) discusses one or two sets of muscles (4 and 5) that he believed could possibly be homologous to the muscles of the gonostylus, but these muscles are actually found within the epandrium which Ulrich called the 'gonocoxite'. See discussion under subepandrial sclerite (in ground plan of Eremoneura) concerning possible homology of muscle 4.

Separate epandrium and hypandrium. - In lateral view, the hypopygium of the Empidoidea is divided into three components. The dorsal component is the cercus (Fig. 18, dark green) (= upper lamellae sensu Collin 1961). The middle component, or epandrium (brown) (= side lamellae sensu Collin 1961) is deeply cleft and hinges on the ventral sclerite or hypandrium (orange) (= ventral lamellae sensu Collin 1961). Bährmann (1960) erroneously believed that the epandrium of the Empidinae and Hemerodromiinae was the basistylus (= gonocoxite) or derived from sternite 9.

Proctiger. - In the ground plan of the Empidoidea, the cerci are long, setose lobes (Figs. 172,187). In the Empidinae and Hemerodromiinae, the cerci, held dorsal to the epandrium, are heavily sclerotized and adapted for clasping. Bährmann (1960) believed that these cerci were the epandrium. Using the anus and subepandrial sclerite as landmarks, however, it is clear that they are cerci. Ulrich (1972) correctly interpreted the dorsal lobes in Empidinae as cerci.

In summary, in addition to features outlined in Sec. 3.3.3, the ground plan of the Empidoidea includes an ejaculatory apodeme that is articulated at the base of the phallus, and loss of gonostyli. In several subfamilies of the Empidoidea, surstyli have developed independently.

3.3.4.1 MODIFICATIONS TO THE GROUND PLAN SHOWN IN CLINOCERINAE

There have been several attempts to interpret the clinocerine male terminalia. Bährmann (1960) provided the first comprehensive analysis of the male terminalia of the Clinocerinae, based on comparison with a wide range of other empidoid species. Based on the musculature, Ulrich (1972) presented a drastically different interpretation; for example, he believed that the apical, articulated lobes were gonostyli. In contrast, Bährmann (1960) considered that these lobes were cerci. The interpretations of Ulrich (1972, 1975) have generally been accepted by current clinocerine researchers (e.g. Vaillant and Vinçon 1986, Wagner 1990) and are essentially similar to the periandrial hypothesis. In a landmark study of European Empidoidea, Chvála (1983) provided an interpretation that appears to be strongly influenced by the periandrial hypothesis of Griffiths (1972).

The hypopygium of most Clinocerinae is distinctively shaped and quite modified from the ground plan of Empidoidea (two exceptions are Asymphyloptera and Proagomyia; see generic descriptions for interpretation). The terminalia are arched dorsally over the abdominal tergites, such that the apical clasping structures are directed

anteriorly. Using the revised epandrial hypothesis (sensu Cumming and Sinclair 1990) and several distinctive landmarks, I present the following new interpretation of the homologies of the structural components of the Clinocerinae male terminalia. The same colour scheme as described under Sec. 3.3.3 is used below to assist in homologizing components and in the interpretation (Fig. 19).

Phallus. - The phallus is a narrow, tapering tube, arising apically from the hypandrium. A large plate or narrow sclerite extends from the base of the phallus to the base of the subepandrial sclerite (meeting at point y). In the ground plan of the Clinocerinae (as shown in Proclinopyga, Fig. 26), the ejaculatory apodeme is articulated with the base of the phallus. In some genera of Clinocerinae, the ejaculatory apodeme has become removed from the base of the phallus and now lies within the hypandrium (Figs. 19, 38, 46).

Epandrium and hypandrium. - The epandrium (= gonocoxite sensu Ulrich 1972) comprises a pair of round, bulbous sclerites, narrowly connected dorsobasally (= sclerite bridge sensu Ulrich 1972). The epandrium is articulated with a pair of short projections from the hypandrium.

The hypandrium (= pygidium sensu Mik) is cone-shaped, closed apically, and lacking gonocoxal apodemes. A sclerite (Fig. 19, purple) from the base of the phallus to the subepandrial plate lies on the mid-dorsal surface of the hypandrium.

Cercus. - The cercus (= terminal lamellae sensu Collin 1961; lamelles externes sensu Vaillant 1964; cercus sensu Bährmann 1960) has been the most misinterpreted component of clinocerine male terminalia, primarily because investigators have chosen species from highly derived genera. In basal clinocerines such as Proclinopyga (Fig. 26), the cercus is weakly divided into a ventral sclerite surrounding the anus, here termed the cercal plate (= anal lamellae sensu Collin 1961) and a dorsal clasping lobe, held erect beyond the epandrium, termed here the clasping cercus (= gonostylus sensu Ulrich 1972, gonopods sensu Chvála 1983). In more derived clinocerines, for example Clinocera and Wiedemannia, the cercal plate has become well separated from the clasping cercus. This transformation series clearly demonstrates that the cercal plate and clasping cercus are derived from the cercus.

Bährmann (1960, fig. 31 cf. figs. 21,39) generally interpreted the cercus correctly for clinocerines, but by choosing a species of Phaeobalia (a former subgenus of Clinocera) for detailed examination, he misinterpreted the clasping cercus as 'surstylus' and surstyli as 'secondary outgrowths'. Since the cercus in Phaeobalia is autapomorphic and unusually subdivided (Fig. 57), this configuration likely influenced Bährmann's interpretation.

There is a single muscle which is inserted onto the base of the clasping cercus and originates on the anterolateral margin of the epandrium (muscle 4, Ulrich 1972, M_{21} , Ovchinnikova 1989). The clasping cercus is abducted by this muscle and adducted indirectly by contraction of muscle 8, (= M_{29} sensu Ovchinnikova 1989) which, by pulling the subepandrial sclerite toward the anus, draws the lobes together.

Subepandrial sclerite and surstylus. - In primitive clinocerines the subepandrial sclerite (= ventral proctiger sclerite sensu Ulrich 1972) is fused directly to the base of the inner wall of the cercus. In Wiedemannia this sclerite is separated from the base of the cercus.

In Clinocerinae, the surstylus is not articulated. In basal genera of Clinocerinae, the surstylus is a long, narrow lobe (Figs. 21,22,26), while the surstylus is a short tooth-shaped lobe in many other genera (Figs. 38,53,57). In unmacerated specimens, these surstyli meet mid-dorsally, holding the phallus down between the epandrial lobes. In Clinocera and Oreothalia, the surstylus is a large, wide lobe, possibly functioning as a phallic guide or sheath (Figs. 19 (reddish-brown), 31,136).

4. DESCRIPTION OF TAXA

4.1 A KEY TO ADULTS OF THE MAJOR SUBDIVISIONS OF THE EMPIDOIDEA

(This key is modified from Steyskal and Knutson (1981) and Chvála (1983). This is a preliminary key, male characters distinguishing the Trichopezinae (couplets 5 and 6) are currently unknown.)

- 1 Rs originating at or near level of crossvein h; crossvein r-m in basal fourth of wing; male terminalia rotated forward beneath preceding segments 12
- 1' Rs originating well distal to level of crossvein h; crossvein r-m distal to basal fourth of wing; male terminalia not rotated forward beneath preceding segments 2
- 2 Cell dm absent, neither R_{4+5} nor M forked; all veins appearing to run without branching to wing margin; cell cup usually lacking, but when present shorter than cells bm and br, and A_1 weak and faint Tachydromiinae
- 2' Cell dm present or absent; when this cell absent, R_{4+5} or M or both forked, or R_{1+2} forked, or cell cup longer than cell bm, or foreleg raptorial 3
- 3 Foreleg raptorial, located near head, and distant from others; fore coxa greatly lengthened, at least twice as long as other coxae; fore femur more or less thickened Hemerodromiinae

- 3' Foreleg not raptorial; fore coxa short 4
- 4 Cell cup absent; first flagellomere very large with pedicel inserted thumb-like on inner side at base; proboscis arising from front of mouth-opening and slightly recurved Ceratomerinae
- 4' Cell cup present; first flagellomere normal in size, pedicel without a thumb-like extension on the inner side; mouthparts variable 5
- 5 Female abdomen truncate; sternite 8 slender, articulated with tergite 8; tergite 10 bearing stout setae (Fig. 167); if segments 8 and 10 unmodified, scape and pedicel yellow, flagellomere brown (Boreodromia) 6
- 5' Female abdomen pointed; if truncate, sclerites of segment 8 not modified and antenna not bicoloured 7
- 6 Cell cup less than a quarter length of wing, equal to or slightly shorter than cell bm; tergite 8 of female abdomen with large, anterior apodeme (Fig. 167)
..... Trichopezinae
- 6' Cell cup at least a third the length of wing, and slightly longer than cell bm; tergite 8 of female abdomen lacking large, anterior apodeme
..... Brachystomatinae

- 7 CuA₂ recurved with apex of cell cup (Fig. 86); in doubtful cases, R₄₊₅ forked, or setae present on postnotum, or palpus long and bearing numerous setae 8
- 7' CuA₂ forming distinct angle with basal part of A₁; setae absent on postnotum; palpus short, at most with a few setae near tip 10
- 8 Costa with short, stout, erect setae (Fig. 70); anal lobe of wing not developed, forming an obtuse angle (Fig. 68,69); labellum sucker-like (Fig. 65) (except Asymphyloptera and Roederiodes (Figs. 59,62)) Clinocerinae
- 8' Stout, erect costal setae lacking; anal lobe well developed, usually forming an acute angle; labellum not sucker-like 9
- 9 Prosternum isolated, not fused to proepisternum; if fused, labrum of female very stout, longer than head (Dipsomyia); cercus of male unmodified, fleshy and setose Oreogetoninae
- 9' Prosternum fused laterally to proepisternum forming precoxal bridge; labrum of female similar to male; cercus of male heavily sclerotized, modified for clasping Empidinae
- 10 Cell cup shorter than or about as long as cell dm, with its outer angle obtuse or right; proboscis short Ocydromiinae
- 10' Cell cup as long as bm, or longer, with its outer angle acute; proboscis variable 11

- 11 Wing with alula developed; Sc distinctly separate from R_1 ; eyes of male contiguous on frons, in female broadly separated Atelestinae
- 11' Wing with alula lacking; Sc very close to R_1 ; eyes usually contiguous above antennae in both sexes Hybotinae
- 12 Cell dm present; M forked, both branches reaching wing margin; C circumambient; body generally black Microphorinae
- 12' Cells dm and bm confluent, crossvein bm-cu absent; if M forked then M_1 not reaching wing margin; C continuous to M_1 or R_{4+5} ; body generally yellow or green metallic Dolichopodidae

4.2 CLASSIFICATION OF THE CLINOCERINAE

List of major references to the Clinocerinae

Clinocera group, Mik 1881: 6-13 (genera of Palearctic region).

Clinocera group, Melander 1902: 232-245 (species of Nearctic region).

Hemerodromiinae, Becker et al. 1903: 262-272 (list of Palearctic species).

Atalantinae, Kertész 1909: 111-129 (list of world species).

Atalanta group, Engel 1918: 1-80, 197-268 (species of Holarctic region).

Clinocerinae, Collin, 1928: 1-110 (species of New Zealand).

Clinoceratinae, Melander 1928: 210-248 (species of Nearctic region).

Clinocerinae, Collin 1933: 321-327 (species of Patagonia and South Chile).

Clinocerinae, Collin 1941: 237-241 (new Palearctic genera).

- Atalantinae, Engel 1956: 132-183 (species of Palearctic region, including keys).
- Atalantinae, Vaillant 1951a: 371-379 (immature stages).
- Clinoceratinae, Bährmann 1960: 485-540 (male genitalia).
- Atalantinae, Vaillant 1960a: 193-197 (adult mouth parts).
- Atalantinae, Vaillant 1960b: 117-123 (species of Appalachian Mtns.).
- Atalantinae, Vaillant 1960c: 170-186 (species of Russia).
- Clinoceratinae, Chillcott 1961: 419-428 (revision of Roederiodes).
- Clinoceratinae, Krystoph 1961: 824-872 (adult mouthparts).
- Hemerodromiinae, Collin 1961: 724-767 (species of Britian).
- Hemerodromiinae, Vaillant 1965: 143-173 (species of France, Spain and North Africa).
- Clinocerinae, Melander 1965: 466-470 (list of Nearctic species).
- Clinocerinae, Smith 1965: 98-109 (species of Nepal).
- Clinocerinae, Smith 1967: 44-45 (list of Neotropical species).
- Clinocerinae, Smith 1969: 285-296 (species of southern Africa).
- Clinocerinae, Ulrich 1971: 1-44 (sclerites and musculature of adult thorax).
- Clinocerinae, Ulrich 1972: 28-39 (male genitalia).
- Clinocerinae, Smith 1975: 200-202 (list of Oriental species).
- Clinocerinae, Steyskal and Knutson 1981: 613-614 (key to adult and immature stages of
Nearctic genera).
- Clinocerinae, Smith 1980: 440-441 (list of Afrotropical species).
- Hemerodromiinae, Vaillant 1981: 351-355 (tribal classification).
- Clinocerinae, Wilder 1981: 461-471 (revision of Oreothalia).

Clinocerinae, Wilder 1982: 166-178 (new Nearctic genera).

Clinocerinae, Chvála 1983: 13-85 (adult morphology and classification).

Clinocerinae, Teskey 1984: 462 (key to larvae of genera).

Clinocerini, Vaillant and Vinçon 1986: 261-275 (species of Pyrenees).

Clinocerinae, Saigusa 1986: 112-118 (new Eastern Asia genera).

Clinocerinae, Gorodkov and Kovalev 1988: 1016-1025 (key to species of the European part of USSR; translated from Russian, 1969: 662-670).

Clinocerinae, Chvála and Wagner 1989: 318-335 (list of Palearctic species).

Clinocerinae, Smith 1989: 387 (list of Australasian species).

Diagnosis of adults of Clinocerinae

Adults of Clinocerinae may be distinguished from other empidoid genera by the following combination of characters: Eyes pubescent (bare in Proclinopyga). Face often iridescent or with blue pruinescence. Pair of divergent ocellar setae. Antennae with first flagellomere globular to onion-shaped; arista two-segmented with short second flagellomere, third flagellomere filiform. An unpaired, thinly sclerotized, anterior ventrocervical sclerite often present or reduced to darkly pigmented membranous patch (lacking in Asymphyloptera and Proagomyia). Mouthparts with long, slender labral apodeme from inner margin of labrum (Fig. 105) (except Asymphyloptera and Proagomyia); labrum broadly triangular (except Roederiodes and Asymphyloptera); lacinia blade-like, partially to completely fused to labial paraphysis; hypopharynx generally with broad base, tapering to pointed apex (Fig. 104); labellum held at right

angles to premental plate, appearing sucker-like (except Asymphyloptera); pseudotracheae absent, except Proclinopyga.

Pleura and lateral margins of abdomen with faint to bright blue pruinescence; prosternum (= basisternum) fused laterally to proepisternum forming broad precoxal bridge; postnotum with setae; mesonotum with long setae confined to discrete regions or rows (e.g. dc, ppm, npl etc.) (Figs. 59-62).

Wing often narrow or at least anal angle obtuse; cell cup less than a quarter the length of wing; CuA₂ arched, meeting A₁ acutely; Sc usually complete (evanescent in Proclinopyga and Proagomyia only); costa with stout setae from R₁ to R₄₊₅ (Fig. 70).

Legs long, covered with dark setae. Second tarsomere usually subequal in length to tarsomeres 3 and 4 combined; fifth tarsomere often with dorsoapical extension; empodium usually pulvilliform; pulvilli forming elongate pads.

Tergite 8 narrow. Phallus arising apically from hypandrium; ejaculatory apodeme either lever-like (Proagomyia, Asymphyloptera, Oreothalia, Proclinopyga) or partially removed from base of phallus (Trichoclinocera, Clinocera, and remaining genera). Male cercus subdivided into cercal plate surrounding anus and dorsal clasping cercus (except Asymphyloptera). Spermatheca lengthened into long, slender, lightly sclerotized tube; lacking dark, heavily sclerotized, terminal receptacle; apex reduced to thinly sclerotized, glandular tissue (Fig. 87).

4.2.1 KEY TO ADULTS OF THE GENERA OF THE CLINOCERINAE

1	R_{4+5} simple (Figs 67,70)	2
1'	R_{4+5} branched (Fig. 69)	3
2	Wing lacking cell dm, R_{2+3} branched (Fig. 67)	<u>Asymphyloptera</u> Collin
2'	Wing with cell dm, R_{2+3} simple (Fig. 70)	<u>Oreothalia</u> Melander
3	Sc evanescent apically (Fig. 68)	4
3'	Sc ending in C (Figs. 69)	5
4	Fifth tarsomere with dorsoapical extension; palpus long, cylindrical, equal in length to proboscis; labrum elongate, with narrow apex	
	<u>Proagomyia</u> Collin (<u>insertae sedis</u>)	
4'	Fifth tarsomere lacking dorsoapical extension; palpus short, less than length of proboscis; labrum triangular, with broad apex	<u>Proclinopyga</u> Melander
5	Tarsomeres 2-4 of foreleg equal in length	6
5'	Tarsomeres 2-4 of foreleg of unequal length	8
6	Proboscis as long as head; labrum long and slender; labella narrow not sucker-like (Fig. 62)	<u>Roederiodes</u> Coquillett
6'	Proboscis shorter than head; labrum subtriangular; labellum sucker-like (Fig. 63)	

- 7
- 7 Width of gena half to two-thirds height of eye; clypeus prominent (Fig. 63)
 Hypenella Collin
- 7' Width of gena nearly half height of eye; clypeus not prominent
 Clinocerella Engel
- 8 Neck high on occiput, head extending obliquely forward (Fig. 64); wing infusate
 often with clear round areas termed irrorations; usually auxillary vein from base
 of R_4 to R_{2+1} (Fig. 73) Dolichocephala Macquart
- 8' Neck near centre of occiput; head vertical; wing usually lacking auxillary
 crossveins and irrorations 9
- 9 Presut and psut spal setae absent; tergite 7 of male with pair of dorsal, setose
 tubercles, tergite 8 subdivided into pair of cerci-like lobes (Fig. 28); female
 abdomen truncate Rhyacodromia Saigusa
- 9' Psut spal seta(e) present or absent; presut spal present; tergite 7 and 8 of male
 unmodified; female abdomen truncate or attenuated 10
- 10 R_1 with macrotrichia above; fore femur with stout setae beneath (Figs. 88-103);
 female abdomen truncate Trichoclinocera Collin
- 10' R_1 bare; fore femur lacking modified setae or only simple biserial row of short

- setae; female abdomen attenuated 11
- 11 Lower margin of face entire, lacking notch; lower third of face lacking median carina (Fig. 61) Clinocera Meigen
- 11' Lower margin of face with notch; lower third often with median carina; if notch lacking, phallus biarticulated and female abdomen truncate (B. nudipes) 12
- 12 Face with setulae along margin of eye; apical component of phallus not articulated; if biarticulated, apical component not a narrow filament Kowarzia Mik
- 12' Face lacking setulae along margin of eye; phallus biarticulated, apical filament long, narrow and reflexed (Figs. 53,57,150) 13
- 13 Pulvilli vestigial, empodia reduced to less than third length of tarsal claws Bergenstammia Mik
- 13' Pulvilli and empodia well developed, pad-like 14
- 14 Wings with distinct spots and clearly outlined, elliptical stigma; if spots lacking face with small notch along ventral margin Phacobalia Mik
- 14' Wings lacking spots, except for cloudy spots at wing tips; stigma either faint and elongate or dark and circular; large notch or carina extending one-third height of face (Fig. 66) Wiedemannia Zetterstedt

4.2.2 GENERA OF CLINOCERINAE

The genera of Clinocerinae, except Trichoclinocera, Clinocera and Wiedemannia (see 4.2.3, 4.2.4 and 4.2.5 respectively) are redescribed below.

GENUS ASYMPHYLOPTERA COLLIN

Asymphyloptera Collin 1933: 323. Type-species, A. discrepans Collin (original designation).

Type Material Examined. PARATYPES: A. quadriseta Smith: Australia: NSW: Katoomba, 6.X.1950, G.H. Hardy [on slide] (1♂, BMNH); Katoomba, 6.X.1950, 17.II.1950 [pinned] (1?, 1♀, BMNH).

In male terminalia of A. quadriseta, illustrated by Smith (1961, fig. 2), the apex of the phallus is undivided. Additional material from Australia was examined and illustrated (Fig. 21). This material appeared to be A. quadriseta, however the phallus was found to be biarticulated. These differences in the phallus suggest either that the additional Australian material represents a new species or the type material used by Smith (1961) was damaged when cleared and mounted on slides. Unfortunately, the abdomen of the holotype is missing (Bickel pers. comm.) and the phallus of the male paratype appears damaged. Since only two males were known from the type series, there is a need to collect and examine additional material from the type locality.

Recognition. This genus may be recognized by its very small size (1-1.5mm), long

mouthparts, extension of first flagellomere, distinct clypeus and very unusual wing venation (branched R_{2+3}) outlined in the key. Asymphyloptera is superficially similar to Roederiodes but differs by its distinctive wing venation and long pointed palpus.

Description. Male. Eyes small, with short dense pubescence; clypeus prominent, separated from face by suture (similar to Hypenella); gena wide (greater than half height of head in species from Venezuela). Antennae arising high on head, near ocellar triangle; scape short and cylindrical; pedicel oval; first flagellomere globular with long, slender apical or dorsoapical extension, from which extends two-segmented arista (similar to Gloma); second flagellomere short; third flagellomere filiform. Two stout anterior ocellar setae. Unpaired anterior ventrocervical sclerite lacking. Proboscis long (Fig. 59); labrum long and wide, apodeme lacking; hypopharynx elongate, apex round, lacking broad base; lacinia free, closely appressed to labial paraphysis; pseudotracheae absent; palpus equal in length to proboscis, apex pointed, closely appressed to labium; labellum not sucker-like.

Prosternum narrowly fused to proepisternum. Scutum brown, faintly bivittate; pleura with iridescent tinge. Acrostichals lacking; all setae stout and short; 4 dc; 1 ppn, slender; 1 presut spal; 2 npl, lower slender; 1 psut spal; 1 pal; 2-4 setl. Postnotum bare; anteprenotum with setulae.

Wing narrow, infusate; single, short basicostal seta; stigma lacking (Fig. 67). R_{4+5} , simple; dm-cu lacking; R_{2+3} , branched; crossvein h present (New World) or lacking (Australia); cell cup narrow, darkly clouded; A_1 lacking; costa with stout setae from R_1

to R_{4+5} .

Ventral surface of femora with long, pale setae. Fore legs much shorter than remaining legs; femur swollen, lacking anterior, preapical comb; tibia with anterior apical comb and biserial row of erect setae beneath. Hind tibia with posterior apical comb. Tarsomeres 2-4 short, subequal in length; fifth tarsomere with long, dorsoapical extension; empodium pulvilliform.

Tergite 8 narrow. Cercus with anal plates continuous with slender, lateral lobes; not modified for clasping. Epandrium elongate, with slender, sickle-shaped surstyli. Hypandrium elongate, with macrosetae, extending to apical margin of epandrium; anterodorsal margin with slender lobe(s). Phallus not positioned on apex of hypandrium, rather arising from within hypandrium; ejaculatory apodeme narrow, articulated ventrally with phallus. Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: face wider. Lacking long ventral setae on femora and fore tibia. Posterior margin of S8 invaginated, forming wide plate. Cercus narrow, with long setae; S10 narrow, continuous with cercus; T10 unsclerotized. Spermatheca long and slender; genital fork well developed in Australian species (Fig. 20).

Included Taxa and Geographical Distribution. This genus is known from Australia, South and Central America, and southwestern U.S. The type-species was collected in Verrugas Cañon, Lima, Peru (Collin 1933), a single, undescribed female specimen is

known from near La Aquada, S. Bolivar N.P. 3000m, Venezuela and two new species are described below. A single species is also known from New South Wales, Australia (Smith 1961).

Phylogenetic Relationships. This genus is the most basal genus of the Clinocerinae and is included in this subfamily primarily on the basis of a tubular spermatheca and stout, costal setae. The remaining features are all subject to homoplasy (e.g. loss of pseudotracheae, pubescent eyes, pulvilliform empodium). The discovery of the larva of Asymphyloptera and the whether the mandible is four or six-segmented would certainly test the validity of retaining this genus in the Clinocerinae.

At present it appears that this genus can be divided into two groups. The New World species group is characterized by the presence of a humeral cross-vein and lack a biarticulated phallus. The single Australian species lacks a humeral cross vein and the phallus is biarticulated.

Bionomics. Asymphyloptera quadriseta is found in temperate regions of New South Wales (Bickle, pers. comm.). In the Sydney region, this species has been collected in early Spring (late August-Sept.) on sandstone seepages, which dry up as the season progresses. A very early flight period is characteristic of cool adapted Gondwanan species (Bickle, pers. comm.).

The immature stages of this genus are unknown.

2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

List of described species included in Asymphyloptera.

- N chiricahua Sinclair sp.nov.
 S discrepans Collin, 1933: 324.
 S lutea Sinclair sp.nov.
 U quadriseta Smith, 1961: 245 [paratypes examined] (BMNH).

List of examined, undescribed species included in Asymphyloptera.

Asymphyloptera sp. 1: One female from Venezuela (CNC).

Asymphyloptera chiricahua sp.nov.

Holotype. Male labelled: "USA:A[ri]Z[ona]:Cochise Co./ Chiricahua M[oun]t[ai]ns./ 1-2.VI.1991 6500'/ East Turkey C[ree]k./ B.J. Sinclair BS9102" (CNC).

Allotype. Female. Same data as holotype.

Derivation of Species Name. Named after the type locality, the Chiricahua Mountains, the northern geographic limit of many more southernly distributed taxa.

Recognition. This species may be distinguished from A. lutea by dark legs and distinct differences in the male terminalia.

Description. Male. Very similar to generic description with following differences: First

flagellomere globular with long, slender apical extension, from which extends remainder of arista.

Scutellum with 2 apical marginal setae. Legs dark brown. Wing with crossvein h. Hypandrium with single apical slender lobe. Phallus slightly arched; apex with microsetae. Surstylus long, slender, slightly arched lobe; apex of epandrium pointed (Fig. 22).

Female. Similar to male except as follows: lacking long ventral setae on femora and fore tibia. Sternite 8 extended beneath cercus; posterior margin of S8 invaginated, forming wide plate with lateral sclerite extending to posteroventral margin of T8. Genital fork not observed (Fig. 24).

Geographical Distribution. Known only from the type locality in southeastern Arizona. This is the first record of this genus from the Nearctic region.

Chorological Affinities. The geographically nearest species is found in Costa Rica.

Phylogenetic Relationships. This species is most closely related to *A. lutea* (Costa Rica) on the basis of the configuration of the phallus.

Paratypes. USA. Arizona: Cochise Co., Chiricahua Mtns., 1-2.VI.1991, 6500', East Turkey Ck., B.J. Sinclair (5♂♂, 6♀♀, CNC).

***Axympyloptera lutea* sp. nov.**

Holotype. Male labelled: "COSTA RICA: Cartago: 1km. / W Santa Cruz de Turrialba/ 5500' by stream in gorge/ Grimaldi & Stark: 13/III/91" (AMNH).

Allotype. Female. Same data as holotype.

Derivation of Species Name. Latin for yellow, in reference to the yellowish coloured coxae and femora.

Recognition. Readily distinguished from Arizona species by yellowish-brown coxae and femora and distinct differences in the male terminalia.

Description. Male. Very similar to generic description with following differences: First flagellomere globular with long, slender, apical extension, from which extends remainder of arista.

Scutellum with 2 apical marginal setae. Halter, coxae and femora yellowish-brown, remaining leg dark. Wing with crossvein h.

Hypandrium lacking apical lobe. Phallus strongly arched; apex membranous. Surstylus short, slender and pointed (Fig. 23).

Female. Similar to male and generic description.

Geographical Distribution. This is the first record of this genus from Central America.

Chorological Affinities. See *A. chiricahua* (above).

Phylogenetic Relationships. See *A. chiricahua* (above).

GENUS PROCLINOPYGA MELANDER

Proclinopyga Melander, 1928: 220. Type-species, *P. amplexans* Melander (original designation).

Type Material Examined. Proclinopyga fistulator Melander, HOLOTYPE, male labelled: "MEGANTIC, Que[bec]./ 18.VI.1928, C.H. Curran"; "Holotype/ Proclinopyga/ fistulator/ Melander/ CNC No. 1465 [red label]" (CNC).

PARATYPE: *P. monogramma* Melander: [USA] Cal[ifornia]: Shasta Springs, VII.1915, A.L. Melander (1♂, USNM).

Recognition. Proclinopyga is readily distinguished by features given in the key. In addition, this species may be recognized by a protruding face, broad wings, dorsal margin of the epandrium expanded with setae, and truncate female abdomen.

Description. Male. Eyes bare. Face with median fold of thinly sclerotized cuticle; profile with facial protuberance (Fig. 60). Antennae arise above middle of head; scape

short and cylindrical; pedicel oval; first flagellomere onion-shaped to conical; arista two-segmented with short, bare apex, bearing terminal seta. Darkly pigmented, anterior ventrocervical sclerite present. Gena narrow divided by suture from base of palpus to ventral margin of eye. Labrum broadly triangular, dorsal margin with slender apodeme. Lacinia paddle-like, short, partially fused to labial paraphysis; palpus club-shaped; hypopharynx short, gradually tapering to apex; labellum held in horizontal position; pseudotracheae well developed.

Pruinescence of pleura and coxae variable in colour; scutum bivittate. Alternating biserial row of acrostichals, ending at prescutellar depression; 6-12 dc, foremost large and positioned toward pprn; 1 pprn and short, weak setae; 1-2 presut spal; oblique row of 3 npl; 2-3 psut spal; 1 pal; 4-8 sctl. Postnotum with short, black setae in vertical row; pair of pale setae on antepnotum.

Wing broad, infusate; anal angle developed, but not forming an acute angle; elongate, narrow stigma; single basicostal seta (Fig. 68). Costa with long spines from R_1 to R_4 ; Sc evanescent; CuA_2 reaching one-quarter way to base of cell cup; cell dm truncate, R_4 strongly divergent from R_5 .

Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform; claws short. Fore femur lacking anterior, preapical comb. Fore tibia with anterior apical comb. Mid femur with posteroventral row of long setae; mid tibia bearing long setae beneath. Hind tibia with posterior apical comb. All coxae with long, black setae.

Tergite 6 with transverse rows of erect, black setae. Tergite 8 reduced to narrow sclerite with shallow median notch. Hypandrium small cup-shaped, with macrosetae;

hypandrium continuous with heavily sclerotized, arched phallus; ejaculatory apodeme articulated ventrally with phallus (Fig. 26). Epandrium with expanded, lightly sclerotized posterodorsal margin, bearing long setae and setulae; epandrial lobe continuous with expanded region of epandrium, bearing long setae. Surstyli narrow, dark, shiny pointed lobes; closely associated with epandrial lobes. Clasping cercus with setal patches on inner surface; cercal plate continuous or partially isolated from clasping cercus; setae evenly distributed. Often two large, spherical, sclerotized accessory glands present in segments 3-6; as large as diameter of abdomen.

Female. Similar to male except as follow: middle leg unmodified. Tergite 6 lacking erect setae. Segment 8 retracted within segment 7. Anterior margin of T8 with central expanded region; posterior margin with wide, mid-dorsal, membranous cleft; posterior margin with sparse transverse row of short setae anterior. Tergite 10 deeply cleft, with desclerotized median region; posterior margin bearing group of stout setae or spines. Cerci lacking setae on dorsal surface; usually lateral margin with ridge. Spermatheca a long, convoluted, tapering tube, ending in a filament of thinly sclerotized glandular tissue (Fig. 25).

Included Taxa and Geographical Distribution. There are 10 described and approximately 9 undescribed species of Proclinopyga from the Nearctic, eastern Palearctic and Oriental regions. In North America, there are two species known from the Appalachian region and approximately 12 species from the western region. Proclinopyga

fistulator is very localized in distribution, known from southern Quebec to the southern Appalachians (pers. obs.). The second eastern species is undescribed and is believed to be confined to the southern Appalachians. The majority of species of Proclinopyga are confined to the western and northwestern regions of North America and include 5 described and approximately 7 undescribed species.

Phylogenetic Relationships. This genus is most closely related to Rhyacodromia and Trichoclinocera on the basis of female terminalia (see Sec. 5.1.2). Proclinopyga is one of the most basal clinocerine genera, with primitive male terminalia and thoracic chaetotaxy. Any polarity discussions within Clinocerinae or placement of this subfamily within the Empidoidea requires a detailed knowledge of this genus.

Bionomics. Adults are associated with running water habitats, most commonly collected in streams, creeks and cascades. The immature stages of this genus are unknown.

List of described species included in Proclinopyga.

- N amplectens Melander, 1928: 221.
- P bispinicauda Saigusa, 1963a: 93 [paratypes examined] (CNC).
- N exporrecta Melander, 1928: 222 [holotype examined] (USNM).
- N fistulator Melander, 1928: 222 [holotype examined] (CNC).
- N flavicoxa Melander, 1928: 223 (as variety of P. monogramma) [holotype examined] (USNM) New status.

- N monogramma Melander, 1928: 222 [holotype examined] (USNM).
 P pervaga Collin, 1941: 241 [examined].
 P seticosta Saigusa, 1963a: 91 [paratypes examined] (CNC).
 O ssp. occidentalis Smith, 1965: 104.
 N solivago Melander, 1928: 223 [holotype examined] (USNM).

List of examined, undescribed species included in Proclinopyga.

- Proclinopyga sp. 1: Males and females from Yukon, B.C. and Alberta, Canada (CNC).
Proclinopyga sp. 2: Males and females from Oregon, USA (OSUC).
Proclinopyga sp. 4: Males and females from southeastern USA (CNC).
Proclinopyga sp. 6: One male and one female from Oregon, USA (OSUC).
Proclinopyga sp. 8: Males and females from Yukon, Canada (CNC).
Proclinopyga sp. 9: One male from B.C., Canada (CAS).
Proclinopyga sp. 10: One male from New Mexico, USA (CAS).
Proclinopyga sp. 11: Two males and one female from New Mexico, USA (CNC).
Proclinopyga sp. 12: Two males and one female from Magadanskaya, Russia
 (CNC).

GENUS RHYACODROMIA SAIGUSA

Rhyacodromia Saigusa, 1986: 112. Type-species, R. flavicoxa Saigusa (original designation).

Type Material Examined. *Rhyacodromia evae* (Smith). HOLOTYPE, male labelled: "TAPLEJUNG DISTR: [Nepal]/ Dobhan.c 3500'"; "Spray-splashed rocks in/ River Maewa, 25.i.1962."; "BRIT. MUS./ East Nepal exp/ 1961-62./ R.L. Coe Coll./ B.M.1962-177" [genitalia cleared and in plastic microvial below specimen] (BMNH).

PARATYPES: Same data as holotype (1♂, 1♀, BMNH); Nepal: Taplejung Distr., Dobhan., spray-splashed rocks in R. Tamur. c 3300' 3.II.1962, R.L. Coe. (1♂ [genitalia mounted in Canada Balsam and wing mounted on card below specimen], 1♀ [genitalia cleared and in plastic microvial below specimen], BMNH).

Recognition. This genus is readily distinguished by features described in the key, including setose tubercles and male abdominal tergite 6 and/or 7, tergite 8 of male subdivided into pair of cercus-like lobes, and truncate female abdomen. *Rhyacodromia* could be mistaken for *Clinocera* but both male and female terminalia differ greatly.

Description. Male. Eyes densely haired. Face with blue pruinescence and median brown stripe, ventral margin with small central membranous cleft. Antenna with scape and pedicel short; first flagellomere conical with long, two-segmented arista. Anterior ventrocervical sclerite present. Gena narrow, separated from face by suture, which stretches from base of palpus to lower margin of eye. Pair of long divergent ocellar setae. Labrum short, convex in lateral view; dorsal margin with slender apodeme. Lacinia and stipes fused, apex of lacinia expanded, appressed or partially fused to labial paraphysis; hypopharynx needle-like, with broad base; pseudotracheae absent; labellum

sucker-like.

Pleura, coxae, pprn and npl with blue pruinescence; scutum faintly bivittate. Acrostichals lacking; 5 dc; 1 pprn; 0 presut spal; 1 npl, with several fine setulae; 0 psut spal; 1 pal; 2 sctl. Anteprenotum with long, pale setae; postnotum with patch of pale setae.

Wing infusate, narrow; single basicostal setae; stigma very faint or lacking. Costa with small spines from R_1 to R_4 ; R_4 strongly divergent from R_5 , ending closer to R_{2+3} than to R_5 ; R_{4+5} thick. Cell dm slightly produced apically; cell cup elongate, subequal to length of cell dm; anal vein short.

All legs with long setae. Fore femur lacking anterior, preapical comb; femur thick, apical third with anteroventral and posteroventral rows of short, stout, blunt spine-like setae; posteroventral surface with row of long pale setae along entire length; basal third with anteroventral row of short, pointed spine-like setae. Fore tibia with biserial row of erect setae beneath, becoming more stout apically. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Fifth tarsomere with long, dorsoapical extension; empodium pulvilliform.

Abdomen with blue pruinescence laterally and ventrally, dorsum brown. Tergite 6 unmodified (*R. evae*) or subdivided into setose tubercles (*R. flavicoxa*); T7 subdivided into setose tubercles; T8 split into two cercus-like lobes projecting upright (Fig. 28). Hypopygium held upright. Hypandrium lacking macrosetae, articulating with posterodorsal extension of S8. Epandrium small with large ear-like surstyli. Phallus stout, continuous with hypandrium; blunt rounded tip with subapical arching filament (Fig. 28).

Cercal plate faint bearing fine setae, evenly distributed; claspig cercus tapered apically, tips arched ventrally, Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: fore femur with setae less pronounced; fore tibia lacking biserial row of setae beneath, replaced by posteroventral row of short black tubercles. Posterior two abdominal segments retracted within segment 7; T8 deeply cleft with long setae along posterior margin; T10 deeply cleft, bearing stout setae with anteriorly curved tips. Cerci with lateral ridge; dorsal surface lacking setae (Fig. 29). Spermatheca a long, inconspicuous tapering tube, with smooth surface (Fig. 30).

Included Taxa and Geographical Distribution. Two species of the genus Rhyacodromia are known. Rhyacodromia flavicoxa Saigusa is common on the island of Kyushu, Japan (Saigusa 1986) and R. evae is known from the Himalayas of eastern Nepal (Smith 1965).

Phylogenetic Relationships. Rhyacodromia is the sister genus of Trichoclinocera sharing apomorphies of the adult mouthparts and male fore femur (see Sec. 5.1.2).

Bionomics. Rhyacodromia flavicoxa is very common in rocky streams (Saigusa 1986). The immature stages of this genus are unknown.

List of described species included in Rhyacodromia.

- O** evae (Smith), 1965: 106 (Clinocera) [holotype examined] (BMNH).
P flavicoxa Saigusa, 1986: 113.

GENUS OREOTHALIA MELANDER

Oreothalia Melander, 1902: 232. Type-species, O. pelops Melander (monobasic).

Type Material Examined. PARATYPES: O. spinitarsis Wilder: Canada: B.C., 50mi SW of Terrace, 24.VI.1960, J.G. Chillcott, vertical rock face under waterfall (1♂,CNC); B.C., Horseshoe Bay, 300', 30.V.1961, J.R. Vockeroth (1♀,CNC).

Recognition. This genus is very similar to Clinocera, but is readily distinguished by the simple R_{4+5} , apical half of fore femur with anteroventral row of inclined stout, spine-like setae, and phallus lacking apical filament.

Description. Male. Eyes densely haired. Head slightly narrowed ventrally, face narrower in male than female. Ocellar setae fine. Antenna with short, cylindrical scape and oval pedicel; first flagellomere oval, arista two-segmented. Anterior ventrocervical sclerite reduced to darkly pigmented membranous patch. Gena narrow, separated from face by suture, which stretches from base of palpus to lower margin of eye. Palpus much shorter than labrum and appressed to labrum; labrum with dull pruinescence, not shiny, subtriangular; dorsal margin of labrum with slender apodeme; lacinia fused to labial paraphysis; hypopharynx needle-like, with broad base; pseudotracheae absent; labellum

sucker-like.

Pruinescence of pleura and coxae variable in colour; scutum faintly bivittate. Several acrostichals anterior to first dc; 5 dc; 1 ppnn; 1 presut spal; 1-2 npl; 0.2 psut spa; (*Q. rupestris* lacking psut spal); 1 pal; 2 setl; scattered setae on npl depression and several marginal setae on setl. Postnotum with patch of pale setae; anteprenotum with setae.

Wing narrow; 1 (*Q. rupestris*) or 2 basicoastal setae; stigma elongate and narrow, usually faint (Fig. 70). Costa with small spines from R_1 to R_{4+5} ; R_{4+5} simple; cell dm slightly (*Q. rupestris*) to significantly produced apically.

Fore femur with anterior, preapical comb (reduced in *Q. rupestris*); apical half with anteroventral row of inclined thorn-like setae. Fore tibia with anterior apical comb; anteroventral region with row of short, stout setae. Hind tibia with posterior apical comb; apical half with dorsal and ventral erect setae. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform.

Tergite 8 narrow. Hypandrium with macrosetae (*Q. rupestris*) or lacking; in western species hypandrium short, continuous with phallus. Phallus strongly arched with membranous tubular tip; ejaculatory apodeme articulated ventrally with phallus (Fig. 31). Surstylus large, extending beyond epandrium, acting as an aedeagal guide (similar to *Clinocera*). Cercal plate with setae evenly distributed; clasping cercus broad, with modified setae. Two elongate, wrinkled sac-like accessory glands often observed in segments 3-6 of macerated specimens of *Q. rupestris*.

Female. Similar to male except as follows: sclerites 8 and 10 shiny; posterior margin of T8 membranous bearing microtrichia; T10 split, bearing short setae posteriorly; cerci unmodified (Fig. 32). In *Q. spinitarsis*, spermatheca a long twisted tube, ending in coiled ball (Fig. 33).

Included Taxa and Geographical Distribution. This genus is endemic to the Nearctic region and includes two eastern species (*Q. rupestris* Vaillant and an undescribed species) and 4 western species recently revised by Wilder (1981c). *Oreothalia rupestris* is found at elevations above 800m in the southern Appalachians of North Carolina and Tennessee (Vaillant 1960b; Wilder 1981c). It has also recently been collected from Cloudland Canyon in northwest Georgia (elev. 550m) (pers. obs.).

The four western species include *Q. chillcotti* Wilder, *Q. pelops*, *Q. sierrensis* Wilder and *Q. spinitarsis* Wilder. *Oreothalia chillcotti* is known from three alpine (+ 3200m) localities in Colorado (Wilder 1981c) and *Q. sierrensis* is primarily restricted to the Sierra Nevada Mountains of California at elevations between 2100 to 2600m (Wilder 1981c). *Oreothalia pelops* ranges from as far north as Banff (Alberta), and southwards to the Sierra Nevada Mountains at elevations between 1000-2600m. *Oreothalia spinitarsis* is the most widespread species of this genus, recorded from the coastal forests of southern Alaska to California, at elevations between 0-2080m (Wilder 1981c). It has also recently been collected from the Queen Charlotte Islands (pers. obs.).

The east/west disjunct distribution pattern of this genus is found in several insect groups associated with madicolous habitats (e.g. *Soyedina* Ricker (Plecoptera),

Ochrotrichia Mosely (Trichoptera) and Trichothaumalea Edwards (Diptera: Thaumaleidae)).

Phylogenetic Relationships. This genus is the sister group to Clinocera with which it shares a number of characters, for example: lower margin of face straight, lacking membranous cleft and surstylus large, wide, probably functioning as a phallic guide.

The four western species form a well supported monophyletic group based on the following synapomorphies: wing with two basicostal setae, fore femora with more than 8 spine-like setae and cell dm produced apically.

Bionomics. Oreothalia rupestris is restricted to headwater regions and madicolous habitats (Wilder 1981c; pers. obs.). Oreothalia pelops is largely confined to seepage areas, near waterfalls and rocky streams in wooded regions (Wilder 1981c). Oreothalia spinitarsis has a wide ecological tolerance being found in small to large streams, waterfalls, boggy areas, tundra, wet soil, and puddles along forest trails (Wilder 1981c; pers. obs.).

The immature stages of this genus are unknown.

Comments. In the male genitalic figures of Wilder (1981c, figs. 6-9,12), the membranous regions at the tip of the phallus and surstylus have apparently been distorted during maceration. Terminalia in this study were macerated in hot lactic acid which does not destroy membranes (see Sec. 2.2.1).

List of described species included in Oreothalia.

- N chillcotti Wilder, 1981c: 470 [holotype examined] (CNC).
 N melops Melander, 1902: 223 [examined].
 N rupestris Vaillant, 1960b: 118 (type locality is Tennessee not North Carolina as listed by Melander 1965) [examined].
 N sierrensis Wilder, 1981c: 469 [examined].
 N spinatarsis Wilder, 1981c: 467 [paratypes examined] (CNC).

List of examined, undescribed species included in Oreothalia.

- N Oreothalia sp. 1: One female from Florida, USA (CNC).

GENUS ROEDERIODES COQUILLET

Roederiodes Coquillett 1901: 585. Type-species, R. junctus Coquillett (original designation).

Roederioides (error) Curran 1934: 214; Frey 1940: 5; Chillcott 1961: 419; Saigusa 1963b: 187; Vaillant 1981: 353; Wagner 1981: 302.

Type Material Examined. PARATYPES: R. recurvatus Chillcott: Canada: Quebec: Old Chelsea, 13.IX.1956, J.R. Vockeroth (1♂, 2♀♀, CNC); Quebec: Old Chelsea, 3.X.1956, J.R. Vockeroth (1♂, 4♀♀, CNC).

PARATYPES: R. wirthi Chillcott: USA: New Mexico: Catron Co., 5 miE Glenwood, 24.VI.1953, W.W. Wirth (3♂♂, 3♀♀, CNC).

Recognition. Roederiodes is readily distinguished from all other clinocerines by a long slender labrum and small, rigid labellum.

Description. Male. Eye small, densely haired. Antennae attached high on head; scape short and cylindrical, pedicel oval; arista two-segmented, equal in length to remaining segments. Face greatly extended ventrally, with blue pruinescence. Gena wide, greater than half height of eye. Anterior ventrocervical sclerite reduced to darkly pigmented membranous patch. Proboscis three-fifths to equal height of head (Fig. 62); palpus broad, short, appressed, with strong apical and several short marginal setulae; labrum, hypoharynx and mentum greatly lengthened and narrow; dorsal margin of labrum with slender apodeme; lacinia fused to labial paraphysis; stipes long, extend back into head, closely articulated with lacinia; labellum rigid, heavily sclerotized, neither held horizontally, nor sucker-like; pseudotracheae absent.

Pleura with blue pruinescence. Several inconspicuous acrostichals anterior to first dc (except R. distincta, where acrostichals extend to prescutellar depression); 5-8 dc (usually 5); 1 ppm; 1 presut spal; 2 npl; 0 psut spal; 1 pal; 2-4 sctl, and numerous short setulae on disc. Postnotum with patch of pale setae; anteprepronotum with several setulae.

Wing narrow, infusate; single basicostal seta; stigma absent (Fig. 72). Anal vein reduced to brownish streak; stout setae on costa from R_1 to R_{4+5} , often lacking; R_4 and R_5 diverging; cell dm pointed apically, with M acutely branched, often coalesced for short distance before M_1 and M_2 branch (base of M_1 and M_2 widely separated in R. distinctus).

Legs often reddish brown and coxae light coloured. Lacking distinct ventral setae, only scattered chaetotaxy. Fore femur lacking anterior preapical comb. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Tarsomeres 2-4 of fore and mid legs short, subequal in length; fifth tarsomere laterally compressed, with dorsoapical extension; empodium pulvilliform, subequal in length to claw.

Tergite 8 narrow. Cercal plate with macrosetae confined to small apical plate; clasping cercus with dense short spine-like setae on inner surface. Surstyli small and pointed, not visible laterally. Phallus narrow with trifurcate membranous tip; lateral tips tapering and corrugated; ejaculatory apodeme slender, arched and separated from base of phallus. Hypandrium lacking macrosetae (Fig. 34). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: tergite 8 partially retracted within segment 7. Tergite 10 complete dorsally. Cerci geniculate dorsally, narrow (Fig. 35). Spermatheca an elongate, tapering tube, with whip-like anterior tip (Fig. 36).

Included Taxa and Geographical Distribution. This genus is very localized in distribution and often rarely collected, except by specialists. Species are described from the Nearctic region, Europe, Japan and Costa Rica. Undescribed species are known from Costa Rica, South Africa and Nepal (see below) and the Palearctic region (Wagner pers. comm.).

In several western North American and Costa Rican species, there appears to be

intraspecific variations in the shape of the clasping cercus. These variations should be examined more closely to see if they warrant species recognition or are just variations within species as concluded by Wilder (1981a) for R. wirthi.

Phylogenetic Relationships. This genus is possibly most closely related to Hypenella and Clinocerella on the basis of subequal tarsomeres 2-4 of the fore leg and a short, broad palpus (see Sec. 5.1.2).

Since most of the species of Roederiodes are widely separated and often rarely collected, little is known of the interrelationships on a world basis.

Bionomics. Adults of Roederiodes are often collected along shaded, cool areas of cascading streams and creeks. Adults rest very close to the water surface on emergent rocks and consequently are difficult to collect by sweeping. The larva and pupa of R. junctus were described by Needham and Betten (1901), but detailed figures are required for comparison to other genera of Clinocerinae.

Adults of R. junctus were observed feeding on dead and decaying blackfly pupae that were exposed along a stream (Peterson and Davies 1960). Adults of this species were also observed patrolling the surface of a stream, preying upon emerging simuliids (Peterson and Davies 1960).

List of described species included in Roederiodes.

N distinctus Chillcott, 1961: 425 [examined].

- P japonicus Saigusa, 1963b: 187 [paratype examined] (CNC).
- N junctus Coquillett, 1901: 585 [examined].
- P longirostris Frey, 1940: 4.
- P malickyi Wagner, 1981: 302.
- N recurvatus Chillcott, 1961: 424 [paratypes examined] (CNC).
syn. juncta Vaillant, 1960: 117 (misidentification).
- N petersoni Chillcott, 1966: 315 [paratypes examined] (CNC).
- N vockerothi Chillcott, 1961: 424 [holotype examined] (CNC).
- S wigginsii Wilder, 1981a: 417.
- N wirthi Chillcott, 1961: 426 [paratypes examined] (CNC).
syn. retroversa Coquillett, 1961: 427.

List of examined, undescribed species included in Roederiodes.

Roederiodes sp. 1: One male from Costa Rica (CNC).

Roederiodes sp. 2: Four males and one female from Costa Rica (CNC).

Roederiodes sp. 3: Two females from South Africa (CNC).

Roederiodes sp. 4: One male and three females from Nepal (CNC).

Roederiodes sp. 5: Two males from Nepal (CNC).

GENUS CLINOCERELLA ENGEL New status

Clinocerella Engel, 1918: 238 (as subgenus of Atalanta). Type-species, Atalanta sorex Engel (original designation).

Orthorhynchium Engel, 1918: 238. Nomen nudum. Cited as a manuscript name of Mik.

Type Material Examined. LECTOTYPE (here designated), male labelled: "[Germany] Dachau/ Gr.Amperwhr./ 9.VI.[19]14."; "Type von/ Clinocerella/ sorex Engel [hand written]"; "Clinocera [male and female symbol]/ Clinocerella/ sorex Eng." (ZSM). My lectotype label "LECTOTYPE/ Clinocerella [male symbol]/ sorex Engel/ des. B.J. Sinclair 1992 [red label]" has been attached to this specimen.

PARALECTOTYPE: A female specimen on the same pin as lectotype. My paralectotype label has additionally been attached to this specimen.

Engel (1918) described C. sorex from an unspecified number of specimens collected at Dachau near the River Amper in 15.V.1914 and several days later, but did not designate a holotype. I have only seen two syntypes from this series and all syntypes were originally housed in the ZSM. I have seen a single female labelled as cotype is housed in the USNM.

Recognition. Clinocerella is readily recognized by the wide gena and elongate proboscis. It is most similar to Roederiodes, but may be distinguished on the basis of a sucker-like labellum and short labrum. Clinocerella is also similar to Hypenella, but lacks a prominent clypeus. Although the phallus is biarticulated as found in Wiedemannia, Clinocerella may be distinguished by tarsomeres 2-4 of the foreleg equal in length.

Description. Male. Eyes densely haired. Antennae arising near vertex; scape cylindrical;

pedicel globular; first flagellomere conical; arista two-segmented, short. Face with long, median membranous cleft, extending parallel to base of eye. Width of gena nearly half height of eye. Length of proboscis nearly half height of head, narrow; palpus broad, short, oval; labrum subtriangular; labellum small and sucker-like (due to lack of specimens, mouthparts were not macerated) (Engel 1939, fig. 92).

Pleura and coxae with faint blue pruinescence; scutum bivittate. Acrostichals confined anterior to first dc (*C. oldenbergi*) or extending onto sc1l (*C. sorex*); 5-6 dc with short setae intermixed (*C. sorex*); 1 ppm, narrow; 1 presut spal; 2-3 npl; 0 psut spal; 1 pal; 2 sc1l, with several setulae on disc; numerous short, setae scattered on lateral region of scutum (*C. sorex*). Postnotum with patch of pale setae; anteprenotum with several setulae.

Wing infusate; single long basicostal seta, with long costal setae extending to R_1 ; stigma narrow and faint. Slender costal spines extend from R_1 to R_4 ; anal vein absent; cell dm with long distal extension.

Fore femur more stout than remaining femora, lacking anterior preapical comb. Legs with evenly scattered setae, lacking modified setae; fore tibia with anterior apical comb; hind tibiae with posterior apical comb. Fore tarsomeres 2-4 short, subequal in length; fifth tarsomere with short dorsoapical extension. Empodium pulvilliform, laterally compressed into wide, narrow pad, subequal to width of fourth tarsomere; claws large and strongly recurved.

Abdomen with pale, fine setae. Tergite 8 reduced to narrow sclerite. Cercal plate with macrosetae confined to small apical plate; clasping cercus with dense short setae on

inner surface; subepandrial sclerite extended to base of cercus. Surstyli short and pointed. Hypandrium with macrosetae. Phallus with articulated apex; ejaculatory apodeme slender, hook-shaped and separated from base of phallus (Fig. 38). Sclerotized accessory gland not observed in macerated specimens.

Female. Similar to male except as follows: segment 8 slender, with microtrichia; tergite 10 desclerotized into slender strips; cerci short, slender, held apically (Fig. 37). A short, slender, tubular spermatheca present.

Taxa Included and Geographical Distribution. There are two described species of Clinocerella, known from the western Palearctic region.

Phylogenetic Relationships. Clinocerella was originally described as a subgenus of Clinocera (Engel 1918) and subsequently considered a subgenus of Wiedemannia (Melander 1928, Chvála and Wagner 1989). Wagner and Horvat (in prep.) believe that Clinocerella is a junior synonym of Roederiodes; however, I disagree on the basis of differences in mouthparts and male and female terminalia. This genus is most closely related to Hypenella and together with Roederiodes form a well supported monophyletic group (see Sec. 5.1.2).

Bionomics. Like all clinocerines, Clinocerella has been collected along streams and rivers. The immature stages are unknown.

List of described species included in Clinocerella.

P oldenbergi (Engel), 1918: 241 (Atalanta (Clinocerella)) [females examined] New combination.

syn. tiefii (Engel), 1918: 241 (Orthorhynchium). Nomen nudum. Cited as a manuscript name of Mik.

P sorex (Engel), 1918: 239 (Atalanta (Clinocerella)) [lectotype designated] New combination (ZSM).

syn. brevimanum (Engel), 1918: 239 (Orthorhynchium). Nomen nudum. Cited as a manuscript name of Mik.

GENUS HYPENELLA COLLIN

Hypenella Collin, 1941: 239. Type-species, H. empodiata Collin (original designation).

Type Material Examined. Hypenella spumaria Smith, HOLOTYPE, male labelled: "TAPLEJUNG DISTR., [Nepal]/ Dobhan./ Spray-splashed/ rocks in R. Tamur./ c 3300' 3.ii.1962"; "BRIT. MUS./ East Nepal Exp./ 1961-62./ R.L. Coe Coll./ B.M. 1962-177" (BMNH).

PARATYPES: H. spumaria: Same data as holotype (1♂, 2♀♀, BMNH); **Nepal:** Taplejung Distr., Dobhan. c 3500', spray-splashed rocks in River Maewa, 25.I.1962, R.L. Coe (2♂♂, 1♀, BMNH).

Recognition. This genus is readily distinguished by its prominent clypeus and large,

laterally compressed empodia.

Description. Male. Eyes densely haired. Antennae arising near vertex; scape cylindrical; pedicel globular; first flagellomere conical; arista two-segmented, short. Face with blue pruinescence and central brown stripe; vertical row of long, pale setae below eye. Width of gena half to two-thirds height of eye (Fig. 63). Clypeus prominent. Length of proboscis equal to two-thirds height of head, narrow; palpus broad, short, oval; labrum subtriangular; dorsal margin of labrum with long, slender apodeme; lacinia fused to labial paraphysis; cibarium greatly lengthened, with large expanded cornua (= fulcralapophyses sensu Krystoph 1961); hypopharynx broad, gradually tapering to apex; pseudotracheae absent; labellum small and sucker-like.

Pleura, coxae, and npl with blue pruinescence; scutum faintly bivittate. Acrostichals lacking; 6 dc with 1-2 intermixed setae; 1 ppm, narrow; 1 presut spal; 2-3 npl; 0 psut spal; 1 pal; 2 sctl; numerous short, black setae scattered in presut spal region. Postnotum with patch of pale setae; anteprenotum with several setulae.

Wing hyaline; single long basicostal seta; stigma narrow and faint. Anal vein faint, reduced to fold; cell dm with short distal extension; subcosta complete; costa with stout setae from subcosta to R_5 .

Fore femur thick, lacking anterior preapical comb. Legs with evenly scattered setae; fore tibia with anterior apical comb; hind tibiae with posterior apical comb and 2 dorsal preapical setae. Tarsomeres 2-4 short, subequal in length; fifth tarsomere lacking dorsoapical extension. Empodium pulvilliform, laterally compressed into very wide,

narrow pad; claws large and strongly recurved.

Abdomen with pale, fine setae; ventrum blue, dorsum greenish-brown. Tergite 8 reduced to narrow sclerite. Hypandrium lacking macrosetae. Clasping cercus long, strongly curved club-shaped, with stout apical setae (*H. spumarius*) or wide, truncate, bearing thick setae on inner face (*H. empodiata*, Fig. 39); cercal plate with macrosetae confined to small dorsal plate. Surstylus narrow, bearing short apical setae on outer surface. Phallus narrow with weak, ventrally directed hook (*H. spumarius*) or bearing membranous tip, with posteriorly directed hook (*H. empodiata*); ejaculatory apodeme separated from base of phallus (Fig. 40). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: segment 8 retracted within segment 7. Tergite 8 rectangular, bearing row of long setae along posterior margin, in addition to scattered dorsal setae. Tergite 10 reduced to narrow transverse sclerite; short, stout setae with recurved tips on posterior membranous region. Cercus bare above, with lateral ridge and fine ventral setae (Fig. 42). Spermatheca a short, wrinkled tube, with round anterior tip (Fig. 41).

Taxa Included and Geographical Distribution. Described species of *Hypenella* are known from the Ussuri region of Russia and the Himalayas of eastern Nepal (Collin 1941; Smith 1965). Several undescribed species are known from Japan (Smith 1965).

Phylogenetic Relationships. Hypenella is included with those genera with the macrosetae of the cercal plate confined to a small plate or ridge. This genus is believed to be most closely related to Clinocerella and Roederiodes on the basis of the tarsomeres 2-4 of the fore leg subequal in length (see Sec. 5.1.2).

Bionomics. Hypenella spumaria was collected from emergent rocks along with species of Clinocera and Trichoclinocera (Smith 1965). The immature stages of this genus are unknown.

List of described species included in Hypenella.

- O bhura Smith, 1965: 100.
- P empodiata Collin, 1941: 240 [examined].
- O spumaria Smith, 1965: 100 [holotype examined] (BMNH).

GENUS KOWARZIA MIK

Kowarzia Mik, 1881: 325 (as genus). Type-species, C. barbatula Mik (des. Coquillett 1903: 251).

Archiclinocera Frey, 1945: 38 (as subgenus of Clinocera). Type-species, C. sexmaculata Frey (original designation).

? Hypoclinocera Frey, 1945: 39 (as subgenus of Clinocera). Type-species, C. storai Frey (original designation).

Notes on Synonymy. Frey (1945) erected a new subgenus of Clinocera, Archiclinocera, on the basis of the unique pattern of dark spots on the wings. On the basis of setulae on the face and modifications of the phallus, I believe Archiclinocera is congeneric with Kowarzia. Archiclinocera sexmaculata is simply an autapomorphic species of Kowarzia and does not warrant subgeneric status.

Frey (1945) also described Hypoclinocera as a new subgenus of Clinocera. Syntypes are currently not available for examination and thus I only tentatively propose that Hypoclinocera is congeneric with Kowarzia.

Type Material Examined. Archiclinocera sexmaculata Frey, SYNTYPES: "Azor: San Jorge/ Ribeira Funda/ 16.23.VI. Frey" (2♂♂, ZMH). Three additional syntypes of this species were on loan to Dr. Saigusa and unavailable for study.

The two syntypes of Hypoclinocera storai were on loan to Dr. Saigusa and unavailable for study.

Recognition. Readily distinguished from all other clinocerines except some Clinocera by the presence of setulae on the face. It can be distinguished from Clinocera on the basis of male terminalia (lacks apical whip-like filament and setae of cercal plate confined to dorsolateral ridge) and features stated in the key.

Description. Male. Eyes densely haired. Lower margin of face with V-shaped membranous cleft; 5-6 setulae along margin of each eye. Gena divided from base of

palpus to lower margin of eye. Antennae above middle of head; scape and pedicel short, subequal in length; first flagellomere onion-shaped; arista two-segmented. Anterior ventrocervical sclerite present. Proboscis short (see Vaillant 1960a); labrum short, triangular; dorsal margin of labrum with very long, slender apodeme; palpus slightly appressed, arched dorsally over labrum; tip of lacinia fused to inner labial sclerite and labial paraphysis; hypopharynx needle-like, with broad base; pseudotracheae lacking; labellum sucker-like.

Pruinescence of pleura and coxae variable in colour. Several short acrostichals anterior to first dc; 5 dc; 1 ppm; 1 presut spal; 2 npl; 0-1 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae; anteprenotum with several pale setulae.

Wing narrow, infusate; stigma narrow, elongate, faint; single basicostal seta. Costa with spines from R_1 to R_4 ; cell dm produced apically; cell cup narrow, often with short A_1 ; cell r_4 acute apically, R_4 and R_5 gradually diverging.

Legs lacking modified ventral setae. Fore femur with preapical comb (lacking in sexmaculata); hind tibiae with erect dorsal and ventral setae on apical third. Fore tibia with anterior apical comb; hind tibiae with posterior apical comb. Fifth tarsomere with dorsoapical extension; empodium pulvilliform, subequal in length to claw.

Tergite 8 narrow. Phallus usually with well developed distiphallus; surstylus narrow with macrosetae. Setae of cercal plate confined to dorsolateral region; clasping cercus often hook-shaped. Hypandrium with long macrosetae; ejaculatory apodeme narrow and separated from base of phallus (Figs. 43,48). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: sclerites of segment 8 equal in length to preceding segments; genital chamber formed by invagination of S8. Tergite 10 mid-dorsally divided into two triangular sclerites. Cercus short and narrow, bearing setae (Fig. 44). Spermatheca in shape of a long, loosely spiralled tube (Fig. 45).

Included Taxa and Geographical Distribution. Kowarzia is found in the Palearctic and Afrotropical Regions. It is not known from the New World or Australasian Region. This genus includes all species listed by Chvála and Wagner (1989), except C. stackelbergi (Vaillant) (see Clinocera). The South African species, C. capicola (Smith) should be transferred to Kowarzia on the basis of setulae on the face and male terminalia (the type of this species will have to be examined to verify this proposed transfer).

Phylogenetic Relationships. Mik (1881) erected Kowarzia to include Clinocera-like species with erect setulae on the face but has since been viewed as a subgenus of Clinocera. On the basis of similarities of the male terminalia, I believe Kowarzia is more closely related to Dolichocephala and Wiedemannia than Clinocera. Thus, elevation to generic level appears justified (see Sec. 5.1.2).

Bionomics. Kowarzia is restricted to the macrolous zone of seepages and streams (Vaillant 1960a). The larva and pupa of K. barbatula were described by Vaillant (1952b,c). Kowarzia bipunctata was observed to pupate in moss just above the water line in streams and if the water rises, the pupa wriggles up through the moss (Hinton 1950).

List of described species included in Kowarzia.

- P** amarantha Becker, 1908: 43 [examined].
- P** barbatula (Mik), 1880: 347 (Clinocera).
 syn. dorieri (Vaillant), 1968a: 88 (Clinocera).
- P** bipunctata (Haliday), 1833: 159 (Heleodromia) [examined].
- A** capicola (Smith), 1967: 231 (Wiedemannia) [examined] **New combination.**
- A** chania (Garrett Jones), 1940: 299 (Clinocera).
- P** dahli (Vaillant), 1964: 64 (Clinocera).
- P** dieuzedei Vaillant, 1953b: 60.
- P** haemorrhoidalis Becker, 1908: 189.
- P** jalonae (Wagner), 1984b: 121 (Clinocera).
- P** madicola (Vaillant), 1965: 152 (Atalanta).
- P** plectrum (Mik), 1880: 347 (Clinocera) [examined].
- P** rabacali (Frey), 1940: 6 (Clinocera).
- P** sandaliae (Wagner), 1984b: 121 (Clinocera).
- P** schnabli Becker, 1910: 646.
- P** sexmaculata (Frey), 1945: 39 (Clinocera (Archiclinocera)) [syntypes examined]
 (ZMNH) **New combination.**
- P** ? storai (Frey), 1945: 40 (Clinocera (Hypoclinocera)) **New combination.**
- P** subplectrum (Vaillant and Vinçon), 1986: 270.
- P** tenella (Wahlberg), 1844: 107 (Parmesia).
 syn. zetterstedti (Walker), 1851: 105 (Heleodromia).

securigera (Engel), 1918: 70 (Wiedemannia).

A thompsoni (Garrett Jones), 1940: 300 (Clinocera).

P tibiella (Mik), 1880: 348 (Clinocera).

GENUS DOLICHOCEPHALA MACQUART

Dolichocephala Macquart, 1823: 147. Type-species, D. maculata Macquart (monobasic) (= Tachydromia irrorata Fallén).

Ardoptera Macquart, 1827: 105. Type-species, Tachydromia irrorata Fallén (original designation).

Leptosceles Haliday, 1833: 160. Type-species, L. guttata Haliday (original designation).

Lamposoma Becker, 1889: 338. Type-species, L. cavaticum Becker (monobasic). New synonymy.

Eur Garrett Jones, 1940: 294. Type-species, E. fugitivus Garrett Jones (original designation). New synonymy.

Obstinocephala Garrett Jones, 1940: 296. Type-species, O. tali Garrett Jones (original designation). New synonymy.

Notes on Synonymy. Becker (1889) erected a new genus for a species with clear wings and lacking a crossvein between R_{2+3} and R_4 . Based on the position of attachment of the head and male genitalia, Lamposoma is considered congeneric with Dolichocephala.

Garrett Jones (1940) erected a new genus, Eur, for a stenopterous species. Based on the shape and position of the head, face with shallow depression delimiting the

clypeus and male genitalia. Fur is considered congeneric with Dolichocephala.

Garrett Jones (1940) erected a new genus, Obstinocephala, for a stenopterous species. However, based on the shape of the spermatheca, presence of a clypeus and wing pattern, this genus appears congeneric with Dolichocephala.

Type Material Examined. Dolichocephala argus Melander, LECTOTYPE (here designated), male labelled: "Mt. Constitution/ 31.VII.[190]8 Wash[ington]"; "PARATYPE/ Dolichocephala/ argus/ Mel [red label] [missing head, right wing, right fore leg and hind legs]" (USNM). My lectotype label "LECTOTYPE/ Dolichocephala/ argus Mel./ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Mt. Constitution, Wash., 31.VII., 7.VIII.[190]8 (2♀♀, USNM); Bellington, Wash., 15.V.[19]10 (1♂, USNM); Bellington, Wash., 29.VII. (2♂♂, 1♀, USNM). My paralectotype labels have additionally been attached to these specimens.

Melander (1928) described the new species D. argus from a series of seven specimens. Melander's type label was attached to a specimen in very poor condition (missing abdomen, wings), however since a holotype designation was not published, an alternative male specimen in better condition was chosen as lectotype.

Lamposoma cavaticum Becker, LECTOTYPE, male labelled: "Dalmatien [Bosnia and Herzegovina]/ 17/5 22480"; "Lamposoma/ casatiam/ n.g. n.sp."; "Typus"; "Sammlung/ Dr. Th. Becker" [dissected] (ZMHB). My lectotype label "LECTOTYPE/

Lamposoma/ cavaticum Becker/ des. B.J. Sinclair 1992 [red label]" has been attached to this specimen.

PARALECTOTYPES: Dalmatien, 17/5 22480, Sammlung, Th. Becker (1♀, ZMHB). My paralectotype label has additionally been attached to this specimen.

Fur fugitivus Garrett Jones, HOLOTYPE, male labelled: "Holotype [circle label with red border]"; "Namwamba Valley,/ 13-14,000ft./ F.W. Edwards."; "UGANDA:/ Ruwenzori Range./ XII.1934-I.1935./ B.M. E. Afr. Exp./ B.M. 1935-203." (BMNH).

ALLOTYPE: female labelled: "Allotype [circle label with red border]"; "Namwamba Valley,/ 13-14,000ft./ F.W. Edwards."; "UGANDA:/ Ruwenzori Range./ XII.1934-I.1935./ B.M. E. Afr. Exp./ B.M. 1935-203." (BMNH).

PARATYPES: Uganda: Ruwenzori Range, Namwamba Valley, 13-14,000ft., XII.1934-I.1935, F.W. Edwards (2♂♂?, BMNH [both missing abdomen]); Uganda: Ruwenzori Range, Namwamba Valley, 13,500ft., XII.1934-I.1935, E.G. Gibbons (1♂, 4♀♀, BMNH); Uganda: Ruwenzori Range, Nyamgasani Valley, 14-15,000ft., XII.1934-I.1935, D.R. Buxton (1♂, BMNH).

Garrett Jones (1940) listed three males and ten females from the type locality, collected by F.W. Edwards, and did not list the one male and four female specimens collected by E.G. Gibbons. All specimens are clearly labelled as paratypes and I consider the omission of E.G. Gibbons as simply an oversight. If the two specimens lacking abdomens are males, then a single female specimen of the original type series was not examined.

PARATYPES: Obstinocephala tali Garrett Jones: Uganda: Ruwenzori Range, Namwamba Valley, 13,500ft, XII.1934-I.1935, E.G. Gibbons (1♀, BMNH); Uganda: Ruwenzori Range, Nyamgasani Vally, 14-15,000ft., XII.1934-I.1935, D.R. Buxton (1♀, BMNH).

Recognition. This genus is readily identified by the position of attachment of the head and other features described in the key. Dolichocephala may also be recognized by a tightly convoluted spermatheca, presence of a clypeus and extension of the subepandrial sclerite beyond the base of the clasping cercus.

Description. Male. Eyes pubescent, not as dense as Clinocera. Head elongate, narrow; occipital foramen positioned high, near upper angle of head (Fig. 64). Antennae with scape and pedicel short, first flagellomere round with two-segmented arista. Anterior ventrocervical sclerite reduced to darkly pigmented membranous patch. Shallow depression on lower third of face delimits the clypeus (see Collin 1961, fig. 306). Gena divided by suture from base of palpus to lower margin of eye. Proboscis short; labrum subtriangular; dorsal margin of labrum with slender apodeme; stipes and lacinia fused and lacinia fused apically to labial sclerite and labial paraphysis; pseudotracheae lacking; hypopharynx slender, arising from wide base; labellum sucker-like.

Pruinescence of pleura and coxae variable in colour. Several acrostichal setulae anterior to first dc; 5 dc; 1 ppm; 1 presut spal; 2 npl, lower short and slender; 1 psut spal; 1 pal; 2 sclt. Anteprenotum bare; postnotum with several pale setulae.

Wing narrow; infusate, often with varying number of clear round areas termed irrorations; single, long basicostal seta (Fig. 73). Costa with small spines from R_1 to R_{4+5} ; R_4 with auxillary cross-vein to R_{2+3} (lacking in cavatica); cell cup narrow, lacking A_1 vein.

Ventral chaetotaxy of legs simple. Fore femur with anterior preapical comb. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Fifth tarsomere lacking dorsoapical extension; pulvilli and empodium small, latter pulvilliform.

Tergite 8 narrow. Cercal plate with macrosetae confined to small apical plate. Claspig cercus undivided; lobe of subepandrial sclerite extended beyond base of claspig cercus; surstylus short, not projecting beyond cerci. Hyandrium often with a transverse row of stout setae on the apex. Phallus usually with well developed distiphallus; ejaculatory apodeme narrow, separated from base of phallus (Figs. 46,51,52). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: length of segment 8 subequal to preceding segment; furca-like sclerite forming floor of genital chamber, apically attached to posterior margin of S8; shape of this sclerite appears species-specific (Fig. 49); T10 triangular, not divided mid-dorsally (Fig. 50). A long, wide, convoluted, twisted spermatheca present, characterized by tightly-ringed (spiral ridges) appearance, similar to tracheae (Fig. 47); anterior half of spermatheca often lost in maceration (Fig. 50).

Included Taxa and Geographical Distribution. Dolichocephala is found worldwide,

including undescribed species from the Neotropical region and New Guinea. The Nearctic fauna is in need of revision, with several undescribed species, including a stenopterous specimen.

Phylogenetic Relationships. This genus is believed to be most closely related to Kowarzia and Wiedemannia (see Sec. 5.1.2).

There appears to be a distinct species-group identified by stout setae near the apex of the hypandrium. This group includes K. bellstedti Joost, K. flamingo Smith, K. fuscilax Jones, K. irrorata Fallén, K. quadrispina Smith, and several undescribed species from Japan and North America.

Bionomics. Vaillant (1960c) has collected adults of this genus from moss and wet earth near madicolous habitats. Adults are believed to feed on collembola and small nematoceran adults (Vaillant 1960c). The larvae and pupae of D. ocellata (Costa) were collected from mats of moss and travertine deposits neighbouring madicolous habitats (Vaillant 1952c).

List of described species included in Dolichocephala.

- A afflicta Garrett Jones, 1940: 293 [paratype examined] (CNC).
- N argus Melander, 1928: 246 [lectotype designated] (USNM).
- ? austriaca Vaillant, 1968a: 88.
- P bellstedti Joost, 1985: 277.

- P** cavatica (Becker), 1889: 339 (Lamposoma) [lectotype designated] (ZMNH) New combination.
- A** combinata Becker, 1914: 122.
- A** duodecempunctata Smith, 1969: 287 [examined].
- O** flamingo Smith, 1965: 98.
- A** fugitiva (Garrett Jones), 1940: 294 (Eur) [holotype examined] (BMNH) New combination.
- A** fuscilanx Garrett Jones, 1940: 290.
- P** guttata (Haliday), 1833: 160 (Leptosceles)
 syn. exoleta (Haliday), 1833: 161.
 oblongoguttata (Dale), 1878: 264.
 nigrohalterata (Strobl), 1898: 399.
 fuscifera Oldenberg, 1924: 232.
- A** humanitatis Garrett Jones, 1940: 291.
- P** irrorata (Fallén), 1815: 13 (Tachydromia) [examined].
 syn. maculata Macquart, 1823: 148.
 anomala (Scholz), 1851: 59 (Ardoptera).
- A** maculatissima Garrett Jones, 1940: 292.
- P** mevi Joost, 1990: 77.
- P** monae Joost, 1981b: 193.
- P** ocellata (Costa), 1854: 76 (Ardoptera).
 syn. oculata (Loew), 1858a: 7 (Ardoptera).

novemguttata (Strobl), 1893: 98 (Ardoptera).

albohalterata (Strobl), 1898: 399 (Ardoptera).

barbarica Vaillant, 1952b: 65.

algira Vaillant, 1956c: 64.

A quadrispina Smith, 1969: 289.

A rarinota Garrett Jones, 1940: 289 [paratype examined] (CNC).

O septemnotata Brunetti, 1913: 35.

A sparsa Becker, 1914: 122.

A tali (Garrett Jones), 1940: 298 (Obstinocephala) (paratypes examined) (BMNH)

New combination.

P thomasi Wagner, 1983: 139.

Nomen nudum

engeli Vaillant, 1967b: 402; 1978: 467.

List of examined, undescribed species included in Dolichocephala.

Dolichocephala sp.: Undetermined sex from Tasmania (Hardy 1930: 244).

Dolichocephala sp. 1: Males and females from across North America (CNC).

Dolichocephala sp. 2: Males and females from B.C., Canada and two possible females from Colorado, USA (CNC).

Dolichocephala sp. 3: One stenopterous male from B.C., Canada (CNC).

Dolichocephala sp. 4: Males and females from Guatemala (CNC).

Dolichocephala sp. 5: One male from Venezuela (UGO).

Dolichocephala sp. 6: One female from Bolivia (CNC).

Dolichocephala sp. 7: One female from Bolivia (CNC).

Dolichocephala sp. 8: Males and females from Japan (CNC).

Dolichocephala sp. 9: Males and females from Japan (CNC).

Dolichocephala sp. 10: One female from New Guinea (BPBM).

Dolichocephala sp. 11: One female from Oaxaca, Mexico (CNC).

GENUS BERGENSTAMMIA MIK

Bergenstammia Mik, 1881: 326. Type-species, Clinocera nudipes Loew (monobasic).

Recognition. Readily distinguished from other clinocerines by its large size, vestigial pulvilli and reduced empodia. The only clinocerine with similar pulvilli is Trichoclinocera dolicheretma, but this species can be distinguished from Bergenstammia by macrotrichia on R₁.

Description. Male. Eyes densely haired. Face with shallow, membranous cleft along the lower margin, except B. nudipes where lower margin of face is entire. Antenna with cylindrical scape and oval pedicel; first flagellomere onion-shaped; arista short, two-segmented. Gena narrow, separated by incision opposite base of palpus reaching eye margin. Anterior ventrocervical sclerite present. Labrum broadly triangular; dorsal margin of labrum with slender apodeme; stipes and lacinia fused and lacinia fused

apically to labial sclerite and labial paraphysis; hypopharynx slender, needle-like with broad base; pseudotracheae absent; labellum sucker-like.

Pleura, coxae, ppm, npl, prescutellar depression and sc11 with blue pruinescence; scutum generally bivittate. Several short acrostichals present anterior to first dc; 12 dc; 1 ppm; 1 presut spal; 2-3 npl; 1 psut spal; 1-2 pal; greater than 8 sc11, setulae often present on disc; some additional setulae often scattered on scutum. Postnotum with patch of setae; antepronotum with long, pale setae.

Wing broad with distinct, elongate stigma; cell dm truncate; M_1 and M_2 broadly separated; costa spines from R_1 to R_{2+3} ; single basicostal seta.

Fore femur often with several anterior setae on apical third; anteroventral and posteroventral rows of long, pale setae; preapical anterior comb lacking. Fore tibia with anterior, apical comb; lacking modified setae beneath. Hind tibia with posterior apical comb. Fifth tarsomere lacking dorsoapical extension; pulvilli vestigial; empodium pulvilliform, reduced to one-third or less length of tarsal claws.

Tergite 8 narrow. Phallus biarticulated; hypandrium with macrosetae; ejaculatory apodeme with large, ventral keel-like plate, separated from base of phallus. Surstylus tooth-shaped. Clasping cercus divided into two lobes; cercal plate with setae confined to ridge near base of clasping cercus. Subepandrial sclerite separated from base of clasping cercus (Fig. 53). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: fore femur lacking long, pale setae beneath. Female terminalia unmodified, segments gradually tapering with small terminal

cerci (Fig. 55). Spermatheca in form of a lightly sclerotized tapering tube, becoming slightly convoluted apically (Fig. 54); apex reduced to loosely connected tissue in macerated specimens.

Included Taxa and Geographical Distribution. Bergenstammia is restricted to the western Palearctic region and includes seven described species.

Phylogenetic Relationships. Mik (1881) erected Bergenstammia to include Clinocera-like species with rudimentary pulvilli and empodia, but has since been viewed primarily as a subgenus of Clinocera. Bergenstammia has been elevated to generic level based on its distinctive male terminalia and reduced pulvilli (Vaillant and Vinçon 1986), but in the Palearctic catalogue it remained a subgenus of Clinocera (Chvála and Wagner 1989).

Based on similarities of the male terminalia, Bergenstammia is believed to be most closely related to Phaeobalia and Wiedemannia rather than Clinocera. Thus, elevation to generic level appears justified (see Sec. 5.1.2).

Bionomics. This genus is most often found on wet moss and rocks of high mountain streams (Vaillant and Vinçon 1986). The immature stages of this genus are unknown.

List of described species included in Bergenstammia.

P albanica Wagner, 1993: 39.

P frigida (Vaillant), 1965: 149 (Atalanta (Bergenstammia)).

- P** multiseta Strobl, 1893: 104 [examined].
- P** nudimana (Vaillant), 1973: 158 (Clinocera (Bergenstammia)).
- P** nudipes (Loew), 1858c: 386 (Clinocera) [examined].
- P** pulla Vaillant and Wagner, 1989: 200.
- P** pyrenaica Vaillant and Vinçon, 1986: 271.
- P** slovaca Wagner, 1984c: 460.

Nomina nuda

frigida anomala Vaillant, 1967b: 405.

gredosica Vaillant, 1978: 468.

pyrenaica Vaillant, 1978: 468.

GENUS PHAEOBALIA MIK

Phaeobalia Mik, 1881: 326. Type-species, Clinocera trinotata Mik (des. Coquillett 1903: 255).

Recognition. Readily distinguished from all other clinocerines by their darkly spotted wings, except some species of Clinocera. Although P. pokornyi Mik lacks wing spots, it should be readily distinguished from other clinocerines by a biarticulated phallus, shallowly notched face, and other features given in the key.

Description. Male. Eyes densely haired. Face with shallow notch along the lower

margin. Antenna with cylindrical scape and oval pedicel; first flagellomere onion-shaped; short arista two-segmented. Gena narrow, separated by incision opposite base of palpus reaching eye margin. Anterior ventrocervical sclerite present. Labrum broadly triangular; dorsal margin of labrum with slender apodeme; stipes and lacinia fused and lacinia fused apically to labial sclerite and labial paraphysis; hypopharynx slender, needle-like with broad base; pseudotracheae absent; labellum sucker-like.

Pleura, coxae, pprn, npl, prescutellar depression and sc1 with blue pruinescence; scutum generally bivittate. Several short acrostichals present anterior to first dc; 5-8 dc; 1 pprn; 1 presut spal; 2 npl; 0 psut spal; 0-1 pal, reduced to slender setulae or lacking; 2 sc1; additional setulae often scattered on scutum. Postnotum with patch of setae; antepnotum with pair of long setae.

Wing with cell dm long and narrow with upper end produced; stigma elongate, often distinct; single basicostal seta. Costa spines from R_1 to R_4 ; auxillary cross-vein between R_4 and R_{2+3} , occasionally present (*P. peniscissa*); cell dm truncate; M_1 and M_2 broadly separated. Circular dark spots at base of R_4 , apex of cell dm, R_{4+5} below stigma, crossvein r-m and apex of cell cup (spots lacking in *P. pokorny*).

Fore femur lacking modified setae beneath; preapical anterior comb present or absent. Mid femur the anteroventral and posteroventral rows of long, pale setae; mid tibia with long, erect setae beneath. Fore tibia with anterior, apical comb; lacking modified setae beneath. Hind tibia with posterior apical comb. Fifth tarsomere lacking dorsoapical extension; pulvilli well-developed; empodium pulvilliform extending beyond tarsal claws.

Tergite 8 narrow. Hypandrium with macrosetae. Phallus biarticulated; ejaculatory apodeme with large, ventral keel-like plate, separated from base of phallus. Surstylus tooth-shaped. Clasping cercus divided into two lobes; cercal plate with setae confined to ridge on apical third. Subepandrial sclerite separated from base of clasping cercus (Fig. 57). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: setae of legs reduced. Female terminalia unmodified, segments gradually tapering with small terminal cerci; sternite 8 invaginated, forming floor of genital chamber (Fig. 58). Spermatheca in form of a long, thinly sclerotized tapering tube, becoming slightly convoluted apically; apex reduced to loosely connected tissue in macerated specimens (Fig. 56).

Included Taxa and Geographical Distribution. Phaeobalia is restricted to the western Palearctic region and includes 16 described species.

Phylogenetic Relationships. Mik (1881) erected Phaeobalia to include Clinocera-like species with spotted wings and distinct stigma, but has since been viewed as a subgenus of Clinocera (Chvála and Wagner 1989). Based on similarities of the male terminalia, Phaeobalia is believed to be most closely related to Bergenstammia and Wiedemannia than Clinocera. Thus, elevation to generic level appears justified (see Sec. 5.1.2).

Bionomics. This genus is often collected in mountain streams along with Bergenstammia.

The immature stages of this genus are unknown.

List of described species included in Phaeobalia.

- P** dimidiata (Loew), 1869: 271 (Clinocera) [examined] New combination.
 syn. picta Strobl, 1893: 102 (Phaeobalia)
- P** elapha (Vaillant), 1968b: 4 (Clinocera (Phaeobalia)) New combination.
- P** elongata (Wagner), 1982b: 218 (Clinocera (Phaeobalia)) New combination.
- P** inermis (Loew), 1861: 349 (Clinocera) [examined] New combination.
- P** lynceborgi (Vaillant and Chvála), 1973: 60 (Clinocera (Phaeobalia)) New combination.
- P** maculata (Vaillant), 1965: 155 (Atalanta (Phaeobalia)) New combination.
- P** montana (Vaillant), 1973: 160 (Clinocera (Phaeobalia)) New combination.
- P** orophila (Vaillant), 1973: 160 (Clinocera (Phaeobalia)) New combination.
- P** peniscissa Becker, 1889: 336 [examined].
- P** pokorny Mik, 1886: 22 [examined].
- P** ramosa (Vaillant), 1965: 156 (Atalanta (Phaeobalia)) New combination.
- P** tetrastyla (Vaillant), 1973: 161 (Clinocera (Phaeobalia)) New combination.
- P** trinotata (Mik), 1869: 24 (Clinocera) [examined] New combination.
- P** vaillanti (Wagner), 1982b: 219 (Clinocera (Phaeobalia)) New combination.
- P** varipennis (Nowicki), 1868: 85 (Clinocera) [examined] New combination.
- P** zwicki (Vaillant and Vinçon), 1986: 270 (Clinocera (Phaeobalia)) New combination.

4.2.3 GENUS TRICHOCLINOCERA COLLIN

Trichoclinocera Collin, 1941: 237. Type-species, T. stackelbergi Collin (original designation).

Seguyella Vaillant 1960c: 179 nec Kelsey (1969: 294). Type-species, S. rostrata Vaillant (original designation). New synonymy.

Acanthoclinocera Saigusa, 1965: 53. Type-species, A. dasyscutellum Saigusa (original designation). New synonymy.

Notes on Synonymy. Vaillant (1960c) erected a new genus, Seguyella to receive 3 new species from eastern Palearctic and 2 species of Wiedemannia from eastern North America. I have examined the type series of 2 of 5 species and consider Seguyella as congeneric with Trichoclinocera.

Saigusa (1965) described a new genus and species (Acanthoclinocera dasyscutellum) from the island of Honshu (Japan). I have examined paratypes of this species and regard the genus as congeneric with Trichoclinocera. Acanthoclinocera also included a second species, A. glaucescens (Brunetti) [= A. saigusai (Smith 1965), a junior synonym (Smith 1975)]. On the basis of a biarticulated phallus, R₁ bare, M acutely branched, and fore femur lacking modified setae beneath, this species should be transferred to the genus Wiedemannia.

Type Material Examined. Acanthoclinocera saigusai Smith, HOLOTYPE, male labelled: "Holotype [red bordered circle]"; "TAPLEJUNG DISTR: [Nepal]/ Dobhan.c

3500''; "Spray-splashed rocks/ in River Maewa/ 25.i.1962."; "BRIT. MUS./ East Nepal Exp./ 1961-62./ R.L. Coe Coll./ B.M. 1962-177"; "HOLOTYPE/ *Acanthoclinocera saigusai* [hand written]/ K.G.V. Smith [wing mounted on card below specimen; genitalia cleared and mounted in Canada Balsam below specimen]" (BMNH).

Recognition. *Trichoclinocera* is phenetically most similar to *Wiedemannia*, but is readily distinguished by setae on vein R_1 , sickle-shaped ejaculatory apodeme, and truncate female abdomen.

Description. Male. Eye densely haired. Face wide, either with median carina and lateral ridge that extends from anteroventral edge of eye to base of palpus (Steyskal and Knutson 1981, fig. 47.26); or face with only a shallow membranous cleft on ventral margin of clypeus. Gena divided by suture from palpus to lower margin of eye in *T. dolicheretma*. Antenna with cylindrical scape and oval pedicel; first flagellomere onion-shaped; stout two-segmented arista. Anterior ventrocervical sclerite present. Labrum short, convex in lateral view (Fig. 105); dorsal margin with slender apodeme. Lacinia and stipes fused, apex of lacinia expanded, appressed to labial paraphysis; hypopharynx broadly triangular; labellum sucker-like; pseudotracheae absent (Fig. 104).

Pleura and coxae with blue pruinescence; scutum faintly bivittate. Acrostichals reduced to a few scattered setae anterior to first dc, or absent; 5-9 dc; 1-2 ppm; 0-1 presut spal; 2-6 npl; 2 psut spal; 1 pal; 2 sctl, often additional short setae scattered on margin or disc. Postnotum with patch of setae; anteprenotum with pale setulae.

Wing hyaline, infusate or with cloudy spots surrounding cross-veins (*T. stackelbergi*); stigma faint or absent; single basicostal seta. Costal spines from R_1 to R_4 ; upper surface of R_1 with setae, normally extending the full length of vein; R_4 and R_5 parallel (Fig. 69) or slightly diverging (*T. dasyscutellum*, *T. dolicheretma*, and *T. lapponica*); cell dm slightly produced apically.

Fore femur with stout setae and spines beneath. Fore tibia with biserial row of short, stout setae beneath. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Mid and hind femora with anteroventral and posteroventral 3-4 short, stout preapical setae. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform (pulvilli lacking and empodium reduced in *T. dolicheretma*).

Tergite 8 narrow. Hypandrium lacking macrosetae. Cercal plate with long setae evenly scattered; clasping cercus usually narrow and short. Surstylus shorter than clasping cercus, with thinly sclerotized tip. Phallus often strongly arched, with membranous apex; ejaculatory apodeme crescent-shaped, with posterior lobe; apodeme partially removed from base of phallus (Fig. 114). Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: modified ventral chaetotaxy of fore legs often reduced. Posterior two abdominal segments retracted within segment 7. Sclerites of segment 8 heavily sclerotized, shiny, lacking scattered setae; T8 divided by deep membranous cleft, with transverse row of long stout setae along posterior margin; posterior margin of S8 invaginated. Tergite 10 deeply cleft, triangular in lateral view;

bearing short, stout setae. Cercus with lateral ridge, lacking setae above (Fig. 116). Spermatheca a long, lightly sclerotized, winding tube, which may be easily overlooked; sclerotized genital fork not present (Fig. 87).

Included Taxa and Geographical Distribution. The genus contains approximately 22 species from the Palearctic and Nearctic regions, with a single described species from Nepal (Oriental region). There are approximately 30 additional undescribed species from Nepal, Burma, Thailand, Taiwan, Korea, Ussuri and Japan (Saigusa pers. comm.). In North America, there are 9 species confined to the eastern region and 4 species confined to the western region.

Phylogenetic Relationships. Trichoclinocera is most closely related to Proclinopyga and Rhyacodromia on the basis of several features of the female terminalia (see Sec. 5.1.2).

This genus is tentatively divided into approximately four large species groups, plus several groups containing a single species (see Sec. 5.1.3). In North America, there are four species groups represented. The proposed species groups and interrelationships are at present very tentative and must await a more detailed knowledge of the Asian fauna.

Bionomics. Adults of Trichoclinocera are found primarily in large creeks and rivers; for example, three species have been found locally in the Rideau and Ottawa rivers. In contrast to most clinocerines, adults of this genus are tolerant of elevated summer water

temperatures. Adults are found a few centimetres above the water on emergent rocks. They take short flights above the water surface, capturing emerging insects; for example, midges (Chironomidae) and mayflies (Ephemeroptera), and return to the same or neighbouring rocks. Often large numbers, up to 30-40, may be found on the vertical face of rocks, all individuals facing upwards. A specimen of *T. comata* (Melander) was observed feeding on a larval chironomid. A specimen of *T. rupestris* Sinclair sp.nov. was collected as prey of a male *Lasiopogon* Loew (Asilidae).

Mating also occurs in these large gatherings, similar to that described for *Wiedemannia* (Rogers 1981). Males have been observed crisscrossing the vertical rock face (always facing upwards), in search of a female. Females generally remain stationary and are quickly mounted by males. Males will step over the back of the female, curve their abdomen under the female abdomen and genital contact occurs nearly immediately. Often the female will reject the male's attempt at copulation by shaking and moving away. During copulation, the mating pair remains stationary and may last for over one minute in duration or until disturbed. No transfer of prey or any apparent precopulatory behaviour was observed.

Immature Stages. Larval Habitat. There is no published data on the immature stages of this genus. However, mature larvae were collected in late April and early May from creeks in southern Ontario. Larvae are most efficiently collected by kicking and disturbing the rocky substrate of fast-flowing regions in creeks. The larvae float into the current and caught in an aquatic "D"-net held downstream (see Methods section).

Larva. Recognition. Larvae of Trichoclinocera are very similar to larvae of Clinocera and Wiedemannia described by Brindle (1973) and Vaillant (1951a, 1952a). Larvae of Trichoclinocera key to Clinocera (couplet 58(57')) in Teskey (1984) on the basis of a single apical abdominal lobe. Trichoclinocera may be distinguished on the basis of dorsolateral lobes more than twice their width, while in Clinocera the lobes are equal to or less than twice their width.

Description. Mature larvae 4.5-6mm in length; pale white in colour; respiratory system apneustic. Antenna consists of a single long papilla (= baguette ventrale sensu Vaillant 1952a); several minute peg-like sensilla surrounding papilla (= papille dorsale sensu Vaillant 1952a); median papilla of antenna lacking (Fig. 81). Mandible comprises six components, external arm of basal sclerites slender, bearing a long apical seta (Figs. 79,80). Maxillary lobes bearing a series of narrow sclerites, apex of lobe with minute papillae. Single metacephallic rod present, deeply cleft posteriorly. Cranium broad, with long, slender lateral sclerites (Fig. 82).

Eight pairs of abdominal prolegs; length of proleg one-quarter width of abdomen; apex of each proleg bearing series of long claws. Terminal segment with two parallel, dorsolateral lobes and a single apical lobe, apex distinctly divided; lobes bearing long, apical setae (Fig. 78).

Pupal Habitat. Pupae were also collected by disturbing the rocky substrate along the more calm edges of creeks (5-15cm depth). The method of emergence of the adults remains speculative. It is hypothesized that the spines and caudal hooks hold the pupa fast

to the bottom mosses and algae, allowing the teneral adult to pull itself free and float up to the surface. In the calmer regions bordering creeks, adults probably pull themselves up onto emergent rocks and vegetation, remaining until their exoskeleton hardens. Wings appear to be ready for flight immediately upon emerging from the water.

Pupa. Recognition. The pupa of Trichoclinocera is also very similar to pupae of Clinocera and Wiedemannia (Brindle 1969, 1973; Vaillant 1951a). Pupa of Trichoclinocera may be distinguished from the latter two genera by the presence of 6 pairs of long setae on mesonotum and single transverse row of long, abdominal spines (Fig. 75).

Description. Antennal sheath ventrally arched beneath eye. Wing sheaths extend to posterior margin of abdominal sternite 2. Leg sheaths extend to middle of abdominal sternite 3 (Fig. 77). Respiratory organ reduced to raised circular ridge (Fig. 75). Mesonotum with anterior pair of long, widely separated setae; middle with transverse row of 2 pairs of long setae. Metathorax narrow, expanded laterally (Fig. 76).

Spiracles present on abdominal segments 2-7. Tergite 1 with posterior transverse row of short, slender spines. Abdominal segments 2-7 with transverse ring of long, stout spines; tergites 2-7 with anterior row of short, spine-like setae; sternites 4-7 with minute, transverse row of spine-like setae. Sternite 8 with mediolateral series of long spines; tergite 8 with transverse row of stout, long spines. Caudal hooks short, gently curved; hooks one-third length of segment (Fig. 75).

Source of Reared or Associated Material. Canada. Ontario: Halton Co., Lowville,

Bronte Ck., 28.IV.1991, B.J. Sinclair (5 larvae, CNC); Lanark Co., Almonte, Mill of Kintail Cons. Area, 17.V.1992, Indian River, B.J. Sinclair (6 larvae, CNC); Lanark Co., Almonte, Mill of Kintail Cons. Area, 8.VI.1992, Indian River, B.J. Sinclair (4 pupae, reared - in alc., CNC). Yukon: North Fork Pass, 20.VII.1982, D.M. Wood (2 pupae - pinned, CNC).

USA. Indiana: Tippe. Co., Battleground, Burnett's Ck., 22.IV.1983 (1 pupa, reared - in alc., PERC). South Carolina: Pickens Co., trib of Twelve Mile Ck., 1.3miN Central Town, 5.IV.1986, M.W. Heyn (1 pupa, reared - in alc., CUAC).

4.2.3.1 KEY TO ADULTS OF THE NEARCTIC SPECIES OF

TRICHOCLINOCERA

- 1 Face convex (Fig. 85) *T. lapponica* (Ringdahl)
- 1' Face flat 2
- 2 Face lacking median carina and lateral ridge (Figs. 83,84) 3
- 2' Face with median carina and lateral ridge (Fig. 86) 6
- 3 Pulvilli vestigial, reduced to slender filaments; empodia lacking on mid and hind tarsi; head attached high on occiput, well above middle of eye (Fig. 83); lacking pictured vertex *T. dolicheretma* (Melander)
- 3' Pulvilli and empodia well developed, pad-like; head attached above middle of eye (Fig. 84); vertex pictured with contrasting black and white velvety pruinescence

- (*T. comata* species group) 4
- 4 Postnotum with black, stout setae interspersed among pale setae
 T. cascadiensis sp.nov.
- 4' Postnotum with pale setae only, lacking black, stout setae 5
- 5 Notopleural depression with blue pruinescence; fore tibia of male lacking comb of
 long, slender setae on dorsoapical third (Fig. 91) *T. rupestris* sp.nov.
- 5' Notopleural depression lacking blue pruinescence; fore tibia of male with comb of
 long, slender setae on dorsoapical third (Fig. 90) *T. comata* (Melander)
- 6 Gena wide, approximately equal to half height of eye (Fig. 86).....
 T. minor (Melander)
- 6' Gena width less than half height of eye 7
- 7 Fore coxae with erect, dark setae along lateral margin; 6 dc and 3-5 additional long
 setae interspersed; pprn lobe with several long setulae ... *T. dasycoxa* sp.nov.
- 7' Fore coxae with pale, setae along lateral margin; 7 or fewer dc setae; pprn lobe with
 only short setulae 8
- 8 Face with blue pruinescence and wide, dark velvety carina medially 9
- 8' Face either with blue pruinescence and carina with narrow brown stripe; or face
 brown, lacking blue pruinescence 10

- 9 Anteroventral region of fore femur of male with single row of short, stout setae, dividing into 2-3 rows on basal third (Fig. 100); posteroventral region with row of slender, pale setae on basal half, becoming more stout and short apically; clasping cercus with round apex (Fig. 123). Anteroventral region of fore femur of female with row of short, stout setae *T. longipes* (Walker)
- 9' Anteroventral region of fore femur of male with single row of short, stout setae (Fig. 94); posteroventral row with 4-5 long, stout setae, equal in length to width of base of femur; clasping cercus with truncate apex (Fig. 118). Anteroventral region of fore femur of female with row of very short, stout setae
..... *T. ctenistes* (Melander)
- 10 Face with bright blue pruinescence 11
- 10' Face with brown or pale bluish-brown pruinescence 12
- 11 Fore femur of male with posteroventral row of short, stout setae with 3-4 lengthened setae near middle of femur (Fig. 103); clasping cercus strongly arched, with broadly, rounded apex (Fig. 126). Fore femur of female with posteroventral row of short, stout setae and 1-2 long, dark setae near middle of femur
..... *T. ozarkensis* sp. nov.
- 11' Fore femur of male with posteroventral row of slender, pale setae on basal fourth followed by 4-5 long, stout setae, equal in length to width of base of femur (Fig.

- 103); clasping cercus with broad square base and short finger-like lobe (Fig. 128). Fore femur of female with setae at mid-point of posteroventral region reduced to 2-3 widely spaced long, stout setae and several long slender, pale basal setae *T. pectinifemur* sp.nov.
- 12 Coxae and trochanter yellow-brown, remaining leg segments brown; fore femur with anteroventral row of widely separated, short, stout setae (Fig. 89); clasping cercus strongly arched, with expanded tip (Fig. 120) *T. fumosa* (Vaillant)
- 12' Coxae and trochanter with blue pruinescence only; fore femur variable; clasping cercus lacking expanded apex 13
- 13 Males 14
- 13' Females (the female of *T. agilis* is unknown) 16
- 14 Clasping cercus attenuated on apical half, curving medially to rounded apex (Fig. 122); anteroventral region of fore femur with single row of short, stout setae, dividing into 2 rows on basal third (Fig. 97) *T. hamifera* (Melander)
- 14' Clasping cercus strongly arched; anteroventral region of fore femur variable .. 15
- 15 Fore femur with posteroventral row of short, stout setae with 3-4 long, dark, stout setae on basal half; base of femur with long, pale setae beneath (Fig. 98); clasping cercus with slender, round tip (Fig. 121) *T. falcata* sp.nov.

- 15' Fore femur with posteroventral row of short, black setae (Fig. 93); clasping cercus with broadly, rounded apex (Fig. 117) *T. agilis* sp.nov.
- 16 Posteroventral region of fore femur with row of long, slender, pale setae on basal half, becoming more stout and short apically *T. hamifera* (Melander)
- 16' Posteroventral region of fore femur with row of short, stout setae with 3-4 very long, dark stout setae on basal half *T. falcata* sp.nov.

4.2.3.2 SPECIES OF TRICHOCLINOCERA

Trichoclinocera dolicheretma (Melander)

Clinocera dolicheretma Melander, 1902: 241.

Clinocera (Bergenstammia) brunnipennis Melander, 1928: 232. New synonymy.

Notes on Synonymy. Melander (1928) erected a new species, *C. brunnipennis*, on the basis of infumated wings compared to the hyaline wings of *C. dolicheretma*. I have examined the type series of both species and consider them conspecific.

Type Material Examined. Clinocera dolicheretma Melander, LECTOTYPE (here designated), male labelled: "Juliaetta/ Idaho"; "W.M. Wheeler,/ Collection."; "TYPE/ No./ A.M.N.H. [red label]"; "Am. Mus. Nat. Hist./ Dept. Invert. Zool./ 140. 810" (AMNH). My lectotype label "LECTOTYPE/ of Clinocera/ dolicheretma Mel./ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Juliaetta, Idaho, J.M. Aldrich coll. (2♂♂,1♀,AMNH; 2♂♂,3♀♀,MCZ; 3♂♂,5♀♀,USNM). My paralectotype labels have additionally been attached to these specimens.

Clinocera brunnipennis Melander, LECTOTYPE (here designated), male labelled: "Palo Alto, Cal[ifornia]./ 3 Aug. [18]91."; "TYPE/ Bergenstammia/ brunnipennis/ Mel[ander]. [red label]"; "ALMelander/ Collection/ 1961" (USNM). My lectotype label "LECTOTYPE/ of Clinocera/ brunnipennis Mel./ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Palo Alto, Cal[ifornia]. 3.VIII.[18]91. (3♂♂,1♀,USNM). My paralectotype labels have additionally been attached to these specimens.

Melander (1928) based his description of C. dolicheretma on an unspecified number of specimens. A total of 17 specimens from the type locality have been found and all are considered syntypes. As Melander did not designate a holotype, the specimen bearing his red "Type" label is herein designated lectotype. Melander (1928) based his description of C. brunnipennis on five specimens, however there are six syntypes bearing his red type labels. Four syntypes in the best condition were chosen as paralectotypes and the specimen bearing Melander's "Type" label is herein designated lectotype.

Recognition. This species is readily distinguished by the unusual head, preapical spine-like setae of the fore femur, reduction of pulvilli and empodia, and other features listed in the key.

Description. Male. Head attached high on occiput (above middle of eye); entire head with blue pruinescence, except vertex and ocellar triangle; lower margin of face lacking carina and notch; gena divided by suture from base of palpus to lower margin of eye (Fig. 83). Arista long and slender.

Pleura, coxae, ppm and npl with blue pruinescence; scutum with median brownish stripe. Acrostichals lacking; 6-8 dc; 1 ppm; 1 presut spal; 1 npl; 2 psut spal; 1 pal; 2 sctl and several marginal setae. Postnotum with patch of pale setae. Anteprenotum with several pale setae.

Wing narrow, hyaline to infusate; stigma faint and narrow; single, short basicostal seta. Cell dm slightly produced apically; R_4 and R_5 diverging gradually; R_1 with setae along entire length.

Fore femur with posteroventral and anteroventral rows of 5-6 spine-like setae on apical third; 2-4 preapical anterior setae; posteroventral region with row of long, slender, pale setae; basal half of fore femur with anterior row of short setae and anteroventral row of long, slender pale setae (Fig. 88). Fore tibia with anteroventral row of short, stout setae; posteroventral row of long, pale setae. Mid and hind femora with anteroventral and posteroventral rows of widely spaced, stout setae and anterodorsal row of widely spaced, stout setae. Pulvilli vestigial, reduced to thin filaments. Empodium of fore leg pulvilliform, reduced to half length of claw; empodium of mid and hind legs absent.

Ventrum, lateral margins of abdomen, hypandrium and epandrium with blue pruinescence, dorsum brown. Phallus weakly arched, with small, dorsal cap at base. Claspig cercus a finger-like lobe, bearing stout setae on inner upper face; lobe often

slightly curved ventrally; surface polished brown. Surstylus narrow, often with slender, curved apex; polished brown surface (Fig. 106).

Female. Similar to male except as follows: fore femur lacking posteroventral and anteroventral rows of long, slender, pale setae; anterior setae on basal half lacking. Fore tibia lacking modified setae beneath. Tergite 8 with dense transverse row of long setae; T10 with 2-3 enlarged stout apical setae.

Comments. Males of a New Mexico (Gila River) population lack long, erect, posteroventral setae of fore tibia; anteroventral region of fore femur with stout, short setae on basal third; entire lateral margin of scutum with blue pruinescence and scutum with 12 dorsocentral setae.

Geographical Distribution and Seasonal Occurrence. This species is confined to the western Cordillera, ranging from southern B.C. to southern New Mexico (Fig. 198). Adults are recorded from May to October.

Canada. British Columbia: Vancouver Is., Goldstream Prov. Pk., 19kmNW Victoria, Goldstream R., 8.VII.1974 (1♀,CAS).

USA. California: Fresno Co., Sierra N.F., Pitman Ck., 1500m, 2.VIII.1979 (13♂♂,13♀♀,CAS); Fresno Co., Westfall Ck., Big Ck., 5130', 25.VIII.1971 (1♀,CAS); Lake Co., Kelseyville, 29.V.1949 (1♂,CAS); Lake Co., St. Helena Ck., 17.VIII.1948 (3♂♂,7♀♀,USNM); Marin Co., Samuel P., Taylor S.P., Lagunitus Ck., 20.VI.1977

(1♀,CAS); Monterey Co., Los Padres N.F., Antonio R., 22.V.1977 (1♂,CAS); Palto Alto, 3.VIII.1891 (1♂,4♀♀, CAS,USNM); Placer Co., N.Fk. American R., Westville, 2.VIII.1975 (3♂♂,7♀♀,CAS); San Mateo Co., La Honda, 17.VIII.1974 (3♂♂,1♀,CAS); San Mateo, Purisima, Purisima, 28.IX.1988 (1♂,CAS); Santa Cruz Co., Big Basin S.P., Opal Ck., 14.VI.1978 (1♀,CAS); Shasta Co., 29kmSE Burney, Honn Ck Cpgd, Hat Ck., 30.VII.1974 (1♀,CAS); Shasta Co., W. boundary Castle, Craggs S.P., 17.VII.1980 (1♀,CAS); Siskiyou Co., Klamath N.F., E.Fk. of S.FK. Salmon R., 4.VII.1978 (6♂♂,3♀♀,CAS); Siskiyou Co., Klamath N.F., Knownothing Ck., 22.VII.1980 (24♂♂,34♀♀,CAS); Siskiyou Co., Klamath N.F., Matthews Ck. Cpgd, 5.VII.1976 (3♂♂,CAS); Siskiyou Co., Klamath N.F., Mule Ck., 2.VII.1978 (10♂♂,16♀♀,CAS); Siskiyou Co., Klamath N.F., N.Fk. Salmon R., 4.VII.1976 (1♂,3♀♀,CAS); Siskiyou Co., Klamath N.F., Wooley Ck., 3.VII.1978 (9♂♂,6♀♀,CAS); Siskiyou Co., Klamath N.F., Wooley Ck.Tr., 3.VII.1978 (5♀♀,CAS); S.Fk. St. Ana R., 29.VII.1942 (1♂,USNM); Trinity Co., Shasta N.F., Trinity R., 2.VII.1978 (2♂♂,4♀♀,CAS); Trinity Co., Shasta N.F., Scott Mtn. Ck., 20.VII.1980 (16♂♂,7♀♀,CAS); Tulare Co., Ash Mtn., 12.VII.1986, 23.VI.1987 (3♂♂,3♀♀ - in alc., PERC); Trinity Co., Shasta N.F., Three Rivers, Ash Mt. fume, 4.VIII.1984 (1♂ - in alc., PERC); Tulare Co., Sequoia N.F., 850m, Kern R., 18.IX.1979 (51♂♂,45♀♀,CAS); Tuolumne Co., Strawberry, 3.VII.1951 (2♂♂,1♀,UCB). **Colorado:** South St. Vrain Ck., 6miSW Raymond, 8700', 11.VIII.1961 (1♂, CNC). **Idaho:** Benewah Co., 2miS St. Maries, Thorn Ck., 24.VI.1978 (1♂,3♀♀,CAS); Culde Sac, 23.VI.1932 (8♂♂,8♀♀,USNM); Idaho Co., Major Fenn, 1.VIII.1981 (2♂♂,MEM); Kootenai Co., Beauty Ck., 31.VIII.1976

(3♂♂,2♀♀,UIM); Kootenai Co., Hayden Ck., 5.VIII.1965 (6♂♂,8♀♀,UIM); Latah Co., Palouse R., 15miE Potlatch, 6-7.VIII.1981 (40♂,43♀♀,WOOC,WSU); Latah Co., Potlatch R. at Juliaetta, 17.VII.1975 (4♂♂,4♀♀,WSU); Latah Co., St. Joe N.F., Emerald Ck., 24.VI.1978 (88♂♂,107♀♀,CAS); Latah Co., St. Joe N.F., 8miNE Harvard, 4.VIII.1981 (2♂♂,5♀♀,WSU); Lemhi Co., Salmon R., 3miS North Fk., 14.IX.1982 (1♀,HSU). New Mexico: Catron Co., 1.5miE Glenwood, Whitewater Ck., 30.V.1991 (2♂♂,3♀♀,CNC); Catron Co., 5miE. Glenwood, 24.VI.1953 (1♂,3♀♀,USNM); Grant Co., Gila N.F., E.Fk. Gila R., 6.V.1981 (5♂♂,16♀♀ in alc., PERC); Grant Co., Gila N.F., E.Fk. Gila R., 29.VI.1991 (4♂♂,3♀♀,CNC). Oregon: Benton Co., Alsea Falls Cpgd, 21.VI.1977 (1♂,1♀,CAS); Curry Co., Humbug Mtn.S.P., Brush Ck., 17.VII.1989 (5♂♂,2♀♀,CNC); Curry Co., 8kmW Sixes, Edson Ck., 16.VII.1989 (3♂♂,6♀♀,CNC); Curry Co., Siskiyou N.F., Pt. Orford, 14.5kmE Elk R. Rd., Elk R., 17.VII.1989 (6♂♂,4♀♀,CNC); Douglas Co., Canyonville, 20.VI.1977 (13♂♂,12♀♀,CAS); Hood R., 1.X.1917 (1♂,4♀♀,UCB,USNM); John Day R., 10.VII. (2♂♂,1♀,OSUC); Lane Co., Siuslaw N.F., Rock Ck., 10miS Yachats, 14-16.VII.1989 (11♂♂,17♀♀,CNC); Lane Co., Siuslaw N.F., Ten mi Ck., 14.VII.1989 (4♂♂,6♀♀,CNC); Lucki[a]mute R., 28-29.VI.1954 (2♀♀,UCD); Marion Co., Silver Falls S.P., S.Fk. Silver Ck., 12.VII.1989 (5♂♂,11♀♀,CNC); Umatilla Co., Ukiah-Dale Fro., Camas Ck., 24.VII.1974 (2♂♂,3♀♀,CAS). Utah: Duchesne Co., Duchesne R., Stockmore, 3.IX.1947 (4♂♂,1♀,CNC). Washington: Cashmere, 26.VII.1919 (1♀,USNM); Clallam Co., Olympic N.Pk., Blue Mt. 23.VII.1978 (2♀♀,CAS); Central Ferry, 3.IX.1921 (1♀,USNM); Clallam Co., Tumbling Rapids Rec. Area, Soleduck R.,

22.VII.1978 (5♂♂,2♀♀,CAS); Garfield Co., 8miS Pomeroy, Pataha Ck., 24.VI.1978 (31♂♂,36♀♀,CAS); Gifford Pinchot N.F., Ohanapecosh R., 1.X.1979 (26♂♂,53♀♀,CAS); Grays Harbor Co., Olympic N.P., Willaby Cpgd, 20.VII.1978 (8♂♂,10♀♀,CAS); Grays Harbor, Humptulips, 20.VII.1978 (52♂♂,59♀♀,CAS); Lewis Co., Gifford Pinchot N.F., Miller Ck., 1.X.1979 (11♂♂,21♀♀); Mt. Rainier N.P., White R., 3.X.1979 (2♂♂,1♀,CAS); Lilliwaup, 23.VII.1917 (8♂♂,11♀♀,USNM,CNC); Lilliwaup, 12.VIII.1921 (8♂♂,19♀♀,USNM); Mt. Baker, Nooksack R., 11.VIII.1925 (1♀,USNM); Mt. Baker N.F., Thompson Ck., 4.X.1979 (1♀,CAS); Olympic N.P., Ruby Beach, Cedar Ck., 7.VII.1989 (4♂♂,4♀♀,CNC); Pluvius, 16.VII.1922 (1♀,USNM); Skagit Co., Burlington, Friday Ck., 20.VIII.1986 (3♂♂,1♀,CAS); Spokane (1♂,3♀♀,WSU); Walla Walla, Mill Ck., 24.VI.1921, 16,18.VIII.1923 (36♂♂,55♀♀,USNM); Yakima Co., Naches R., 1 miNW Nile, 11.VIII.1979 (1♂,1♀,WOOC).

Chorological Affinities. This species is widely sympatric with species of the *T. comata* group.

Phylogenetic Relationships. Melander (1928) placed this species in the subgenus *Bergenstammia* on the basis of a very narrow gena, lack of pulvilli, and reduced empodium. Collin (1941) transferred *C. dolicheretma* to the new genus *Trichoclinocera* and *C. brunnipennis* was transferred to this genus by Sabrosky (1967).

This species is proposed as one of the most basal species of *Trichoclinocera* and

is part of an unresolved trichotomy with the *T. comata* group + *T. dasyscutellum* and the remaining species of *Trichoclinocera* (see Sec. 5.1.3).

***Trichoclinocera dasyscutellum* (Saigusa) New combination.**

Acanthoclinocera dasyscutellum Saigusa, 1965: 54.

Type Material Examined. PARATYPES: [Japan] Honshu, Kanayama, Yamanashi, 19.VIII.1962, T. Saigusa (2♂♂, 1♀, CNC).

Recognition. This species is readily distinguished from other Japanese species of *Trichoclinocera* by the reddish-brown coloured legs and large spine on the hind tibia.

Description. Male. Face with pale blue pruinescence, lower margin of face straight (clypeus) lacking carina; arista long and slender.

Pleura with blue pruinescence. Thoracic setae long; several acrostichal setulae anterior to first dc; 5 dc; 1 ppn; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 sctl and numerous pale setulae on disc. Postnotum with patch of pale setae; katapisternum with long, pale setae on anterior margin; anteprenotum with several pairs of setulae.

Wing narrow, infusate; stigma lacking; pair of long, basicostal setae. R_1 with setae along entire length; cell dm produced apically; R_4 and R_5 slightly divergent.

Legs (including coxae) reddish-brown, with long pale setae. Fore femur with 4-5 slender anterior setae on apical third; anteroventral region with row of long, slender

setae; 4 spine-like anteroventral setae on apical fourth; posteroventral region with row of long, slender setae; anterodorsal region with row of short, stout, black setae on basal third. Fore tibia with anteroventral row of short, stout setae; posteroventral row of slender setae. Mid femur with 2-3 stout anteroventral and posteroventral preapical setae; lacking anterodorsal setae. Hind femur with 1 stout anteroventral and posteroventral preapical seta; hind tibia with posterodorsal spine on basal third and 3 dorsal preapical spine-like setae. Empodium pulvilliform, subequal in length to claw.

Hypandrium long and slender. Phallus long and slightly undulated. Surstylus very slender and twisted. Claspig cercus a slender finger-like lobe, bearing stout setae on inner dorsal margin.

Female. Similar to male except as follows: chaetotaxy of legs very similar to male, except fore tibia lacking modified setae beneath. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is known from the Japanese island of Honshu.

Chorological Affinities. There are a total of 7 species of Trichoclinocera from Japan, of which 5 are undescribed (Saigusa, pers. comm.).

Phylogenetic Relationships. This species is tentatively believed to be most closely

related to the T. comata species group of western North America, on the basis of setulae on the disc of the scutellum (see Sec. 5.1.3).

The T. comata Species Group

Members of this group are characterized by the contrasting black and white tessellated pruinescence on the vertex of the head, 5-6 stout notopleural setae and apex of phallus with a small oblique sclerite. All members of this group are from the western Nearctic region, which includes the following three species. This group is believed to be most closely related to the Japanese species, T. dasyscutellum (see Sec. 5.1.3).

Trichoclinocera cascadiensis sp.nov.

Holotype. Male labelled: "U.S.A.: OREGON: Hood/ River Co. Starvation/ Creek State Park, at/ falls. 26 June 1978/ D.D. Wilder collector" (CAS).

Allotype. Female. Same data as holotype (CAS).

Derivation of Specific Name. Refers to the distribution of this species, which appears to be primarily limited to the Cascade Mountains of western North America.

Recognition. This species is readily distinguished from the other two species of the T. comata group by features given in the key.

Description. Male. Entire head with blue pruinescence; lower margin of face straight (clypeus) lacking carina; vertex tessellated with broad, black band of pruinescence, contrasting with white pruinescence surrounding ocellar triangle. Arista long with slender tip.

Pleura and coxae with blue pruinescence. Several short acrostichals anterior to first dc; 6 dc; 1 ppm and several fine setae; 0 presut spal; 5-6 stout npl; 2 psut spal; 1 pal; 2 long apical sctl and 2 short subapical sctl, with scattered short setulae on disc. Postnotum with long, black stout setae intermixed with pale setae; anepisternum lacking short black setae; anteprenotum with short, dark setae.

Wing wide, hyaline to infusate; stigma faint, slender and elongate; single long basicostal seta. R_1 with setae along entire length; cell dm produced apically.

Fore femur with anterior row of short setae along entire length; anteroventral region with single row of short, black setae; posteroventral region with row of long slender, pale setae. Fore tibia with posteroventral row of long, slender setae; anteroventral surface with row of erect setae, becoming very short on apical fifth (Fig. 89). Mid femur with anterodorsal row of widely spaced, erect, slender setae. Empodium pulvilliform, subequal to length of claw.

Ventrum, lateral margins of abdomen, hypandrium and epandrium with blue pruinescence, dorsum brown. Phallus with distinct sharp bend. Claspings cercus gradually arched with round apex, surface polished brown; inner dorsal margin with short, blunt spines. Surstylus a slender, short lobe (Fig. 107).

Female. Similar to male except as follows: ventral setae of fore tibia lacking modified setae. Setae of fore femur much less pronounced but with same distribution as male. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is confined to the Coast and Cascade mountains and commonly collected from late June to August (Fig. 192). Emergence trap data (1982) from Oregon indicates that eclosion of adults of this species occurs from late July to mid-August (Courtney, unpubl. data).

Chorological Affinities. This species is sympatric with T. comata in the Cascade mountains of Oregon.

Phylogenetic Relationships. Trichoclinocera cascadiensis is a member of the T. comata species group, but relationships within this group remain uncertain.

Paratypes. USA. California: Shasta Co., W. boundary Castle Crags State Park, 17.VII.1980, D.D. Wilder (8♂♂, 22♀♀, CAS); Siskiyou Co., Klamath N.For., along Fish Lake Creek, 21.VII.1980, D.D. Wilder (6♂♂, 5♀♀, CAS); Siskiyou Co., Klamath Nat. For., Mule Cr. at Hwy 3, T40N48W Sec.24, 2.VII.1978, D.D. Wilder (1♀, CAS); Trinity Co., Shasta N.F., Boulder Creek near Coffee Cr. Rd., 19.VII.1980, D.D. Wilder (3♂♂, CAS); Trinity Co., Shasta Nat. For. along Trinity R., T40N R6W Sec.31, 2.VII.1978, D.D. Wilder (4♀♀, CAS); Trinity Co., Shasta Nat. For., Scott Mt. Cr. at

Hwy 3, 20.VII.1980, D. D. Wilder (1♀,CAS). Oregon: Benton Co., Alsea Falls Cpgd, 21.VI.1977, D.D. Wilder (1♂,CAS); Hood River Co., Starvation Cr. State Park, at falls, 26.VI.1978, D.D. Wilder (25♂♂,29♀♀,CAS); Hood River Co., Mt. Hood N. Forest, Still Creek Campground, 1150m, 27.VI.1978, D.D. Wilder (17♂♂,28♀♀,CAS); Hood River Co., Starvation Ck. St.Pk., stream below falls, 10.VII.1989, B.J. Sinclair (5♂♂,9♀♀,CNC); Lane Co., 880m, 8miSE Cougar Dam, Grasshopper Ck., 11.VIII.1982, G.W. Courtney (7♂♂,3♀♀,OSUC); Lane Co., 490m, 2miN Blue R., Quartz Ck., 29.VI.1982, G.W. Courtney (1♀,OSUC); Lane Co., 800m, 11miNE Blue R., H.J. Andrews Expt. For., Mack Ck., 20,28.VII., 11.VIII.1982, G.W. Courtney (5♂♂,8♀♀,OSUC). Washington: Mt. Rainier Nat. Park along Cowlitz Divide Trail from Stevens Cyn Rd. to Silver Falls, 640m, 3.VIII.1977, D.D. Wilder (1♂,CAS).

Trichoclinocera comata (Melander) New combination.

Wiedemannia (Chamaedipsia) comata Melander, 1928: 232.

Type Material Examined. LECTOTYPE (here designated), male labelled: "Mt. Rainier, Wash[ington]. [USA]/ Above Longmire's/ 5000ft. Aug.3.[19]05"; "TYPE/ Chamaedipsia/ comata Mel. [red label] [missing mid and hind left tarsi]"; "ALMelander/ Collection/ 1961" (USNM). My lectotype label "LECTOTYPE/ of Wiedemannia/ comata Mel./ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Mt. Rainier, Wash[ington], above Longmire's, 5000ft., 3.VIII.[19]05 (1♂,2♀♀,USNM). My paralectotype labels have additionally been attached

to these specimens.

Melander (1928) based his description of W. comata on 4 specimens collected by J.M. Aldrich. Since Melander did not designate a holotype, the specimen bearing his red "Type" label is herein designated lectotype.

Recognition. This species is readily distinguished from the other two species of the T. comata group by features given in the key.

Description. Male. Entire head with blue pruinescence; lower margin of face straight (clypeus) lacking carina; vertex tessellated with contrasting black and white W-shaped pruinescence (Fig. 84). Arista long with slender tip.

Pleura and coxae with blue pruinescence. Several short acrostichals anterior to first dc; 6 dc; 1 ppm and 3-4 slender, long setae; 1 presut spal; 5 stout npl; 2 psut spal; 1 pal; 2 long apical sctl and 2 pairs of short subapical sctl, with scattered short setulae on disc. Postnotum with patch of pale setae; anepisternum with short black setae; anteprenotum with short, pale setae.

Wing wide, hyaline to infusate; stigma faint, slender and elongate; single long basicostal seta. R_1 with setae primarily confined to basal half; cell dm produced apically.

Fore femur with 2-3 anterior setae on apical third; anteroventral region with single row of short, black setae, basal third with dense patch of setae; posteroventral region with row of long, slender setae. Fore tibia with comb of long, slender setae on dorsoapical third; posteroventral surface with row of erect setae, increasing in length

apically; anteroventral surface with row of short, stout setae, increasing in length opposite to dense patch of setae on femur (Fig. 90). First tarsomere with alternating row of erect, slender setae. Mid femur with anterodorsal row of slender, erect setae. Empodium pulvilliform, subequal in length to claw.

Ventrum, lateral margins of abdomen, hypandrium and epandrium with blue pruinescence, dorsum brown. Phallus strongly arched ventrally on basal third, otherwise straight. Claspig cercus revolver-shaped with polished brown surface; inner dorsal margin with row of short, blunt spines. Surstylus a slender, short lobe (Fig. 108).

Female. Similar to male except as follows: fore tibia lacking long comb, with biserial row of setae beneath. Anteroventral region of fore femur with row of short, stout setae; posteroventral region with row of long, slender, black setae. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. Adults of *T. comata* are found along the Coast and Cascade Ranges from Alaska to California, from late June to October (Fig. 193).

Canada. British Columbia: Manning Prov. Pk., along Goodfellow Creek at Highway 3, 8.X.1979 (3♂♂, 2♀♀, CAS); Manning Prov. Pk., Coldspring Cpgd, along Buckhorn Creek, 7.X.1979 (1♂, 3♀♀, CAS); Summit Lake, mi392 Alaska Hwy, 4500', 13.VIII.1959 (1♂, 4♀♀, CNC); Summit Lake, mi392 Alaska Hwy, 4200', 19-21.VIII.1959 (3♂♂, 4♀♀, CAS, CNC); Tyee, 27miE Pr. Rupert, 24.VI.1960

(1♂,4♀♀,CNC).

USA. Alaska: Thane, 29.VII.1958. (3♀♀,WSU). **California:** Tuolumne Co., along Clark Fork R., 11.VII.1977 (1♂,3♀♀,CAS). **Idaho:** Boundary Co., Meadow Creek Cpgd near Bonners Ferry, 27.VIII.1975 (7♀♀,CAS). **Oregon:** Clackamas Co., Mt. Hood N.F., Toolgate Cpgd, 22.VI.1977 (2♀♀,CAS); Hood River Co., Mt. Hood N.F., Ash Ck. at E.Fk. Hood R., 27.VI.1978 (15♂♂,75♀♀,CAS); Hood River Co., Hood River N.F., Mitchell Ck. nr. Sahalie Falls, 1400m, 27.VI.1978 (3♂♂,17♀♀,CAS); Hood River Co., 2miE Parkdale, E.Fk.Hood R., 11.VII.1989 (1♂,6♀♀,CNC); Mt. Hood, Homestd Inn, 12.VII.1932 (1♂,1♀,USNM); Mt. Hood, Hood Rapids, 29.VII.1921 (1♂,1♀,USNM); Mt. Hood N.F., 11kmE Gov't Camp, White R., 11.VII.1989 (3♂♂,6♀♀,CNC); Mt. Hood N.F., 12kmE Gov't Camp-Rd 48, 11.VII.1989 (4♂♂,4♀♀,CNC). **Washington:** Clallam Co., Olympic N.P., Lake Ck., 650m, 24.VII.1978 (7♂♂,13♀♀,CAS); Jefferson Co., Olympic N.P., Hoh R., 6.VII.1989 (10♂♂,11♀♀,CNC); Jefferson Co., 8kmW Olympic N.P., Tower Ck., 6.VII.1989 (1♂,1♀,CNC); Jefferson Co., Olympic N.P., Hoh Rainforest, pan tp. 6.VII.1989 (1♂,1♀,CNC); Gifford Pinchot N.F., Ohanapecosh R., 1.X.1979 (2♀♀,CAS); Lake Chelan, Stehekin, 30.VII.1919 (1♀,USNM); Lake Chelan, Lucerne, 29.VII.1919 (1♂,USNM); Lewis Co., Mt. Rainier N.P., Stevens Crk. 24.VIII.1973 (4♂♂,3♀♀,WSU); Longmire Spr., 24.VIII.1925 (3♂♂,5♀♀,USNM); Mt. Baker, Nooksack R., 11.VIII.1925 (1♂,3♀♀,USNM); Mt. Baker, Silver Fir Cpgd, Hwy 542, 24.VII.1968 (1♂,1♀,CNC); Mt. Baker N.F., Thompson Ck., 400m, 4.X.1979 (10♂♂,20♀♀,CAS); Mt. Rainier, 4000ft., 25.VI.1935 (7♂♂,3♀♀,USNM); Mt. Rainier,

Christine Falls, 28.VI.1935 (1♂,9♀♀,USNM); Mt. Rainier N.P., Comet Falls Tr., 13.VIII.1977 (5♂♂,23♀♀,WSU); Mt. Rainier, Ohanapecosh, 11.VIII.1940 (4♂♂,12♀♀,USNM); Mt. Rainier, Paradise, VIII.1921 (1♀,USNM); Mt. Rainier, Summerland, 29.VIII.1934 (1♀,USNM); Mt. Rainier, Van Trump, 21.VII.1922 (4♀♀,USNM); Mt. Rainier, White R., 20.VII.1924, 28.VIII.1934 (4♀♀,USNM); Mt. Rainier N.Pk., Christine Falls, 8.VII.1989 (2♀♀,CNC); Mt. Rainier N.Pk., Comet Falls, 8.VII.1989 (1♀,CNC); Mt. Rainier N.Pk., 1650m, Edith Ck. at Paradise Pk., 2.VIII.1977 (1♂,2♀♀,CAS); Mt. Rainier N.Pk., 910m, Fish Ck. at West Side Rd., 1.VIII.1977 (3♂♂,6♀♀,CAS); Mt. Rainier N.Pk., Nisqually R. nr. Cougar Rock Cpgd, 7.VII.1989 (7♂♂,9♀♀,CNC); Mt. Rainier N.Pk., 720m, Panther Ck., 2.X.1979 (2♀♀,CAS); Mt. Rainier N.Pk., Paradise R. nr. Paradise, 8.VII.1989 (1♂,9♀♀,CNC); Mt. Rainier N.Pk., Paradise R. nr. Paradise, 20.VIII.1977 (4♂♂,7♀♀,WOOC); Mt. Rainier N.Pk., 1520m, Sunbeam Ck. above Louise Lk., 4.VIII.1977 (1♂,CAS); Mt. Rainier N.Pk., Van Trump Ck., 8.VII.1989 (4♂♂,3♀♀,CNC); Mt. Rainier N.Pk., 1220m, White R. nr. White R. Cpgd, 3.X.1979 (1♀,CAS); Pierce Co., Mt. Rainier N.Pk., 3.8miNE Sunshine Pt. Cpgd, 18.VII.1979 (1♀,WSU); Pluvius, 16.VII.1972 (1♀,USNM).

Chorological Affinities. This species is sympatric with *T. rupestris* in southern B.C. and *T. cascadiensis* in Oregon.

Phylogenetic Relationships. *Trichoclinocera comata* is a member of the *T. comata*

species group, but relationships within this group remain uncertain.

Trichoclinocera rupestris sp.nov.

Holotype. Male labelled: "USA:WYOMING, Park Co./ Shoshone Nat. For./ 20.VII.1989, Newton/ C[ree]k.C[am]pg[roun]d., Newton Ck./ BJ Sinclair" (CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. The Latin rupestris meaning of rocks or rocky, in reference to the Rocky Mountains where this species is primarily confined.

Recognition. This species is readily distinguished from the other two species of the T. comata group by features given in the key.

Description. Male. Entire head with blue pruinescence; lower margin of face straight (clypeus) lacking carina; vertex tessellated with contrasting black and white W-shaped pruinescence. Arista long with slender tip.

Pleura, coxae, pprn, npl and sc1l with blue pruinescence. Several snort acrostichals extend to second dc; 6 dc; 2 stout pprn and 2 slender, short setae; 1 presut spal; 6 stout npl, with short scattered setae; 2 psut spal; 1 pal; 2 long apical sc1l and 2 short subapical sc1l, with scattered short setulae on disc. Postnotum with patch of pale setae; anepisternum with short black setae; antepnotum with short, pale setae.

Wing wide, hyaline to infusate; stigma faint, slender and elongate; single long basicostal seta. R_1 with setae primarily confined to basal half; cell dm produced apically.

Fore femur with 2-3 anterior setae on apical third; anteroventral region with single row of short, black setae, basal third with additional row of slender setae; posteroventral region with row of short, black setae, row on basal quarter slender, pale setae. Fore tibia with anteroventral row of short, stout setae; posteroventral region with row of longer, slender setae (Fig. 91). Mid femur with anterodorsal row of widely spaced, erect, slender setae. Empodium pulvilliform, subequal in length to claw.

Ventrum, lateral margins of abdomen, hypandrium and epandrium with blue pruinescence, dorsum brown. Phallus straight, only slightly undulating. Claspings cercus straight, slender lobe with polished brown surface; apex with pointed ventral margin; inner dorsal margin with short, blunt spines on apical two-thirds; spines of basal third longer and pointed. Surstylus a slender, short lobe (Fig. 109).

Female. Similar to male except as follows: ventral setae of fore tibia less stout and erect. Fore femur with anteroventral region with single row of slender, black setae, lacking additional row of setae on basal third; posteroventral region with row of long, slender, black setae, becoming pale on basal third. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is known primarily from the Rocky Mountains and adults are commonly collected from late June to late

August (Fig. 192).

Chorological Affinities. This species is sympatric with *T. comata* in southern B.C and Washington.

Phylogenetic Relationships. *Trichoclinocera rupestris* is a member of the *T. comata* species group, but relationships within this group remain uncertain.

Paratypes. Canada. Alberta: Cadomin, base Prospect Mt., 18.VII.1987, S.A. Marshall (15♂♂, 7♀♀, UGO); Jasper Nat. Pk: Jasper, Cabin Ck., 27.VI.1989, B.J. Sinclair (1♂, CNC); Jasper Nat. Pk., Jasper, Athabasca R., 27.VI.1989, B.J. Sinclair (2♂♂, 3♀♀, CNC); Prospect Mt., 18-20.VII.1987, J. Troubridge (7♂♂, 5♀♀, UGO). **British Columbia:** Bromley Rock Prov. Pk., 19kmE Princeton, Similkameen R., 4.VII.1989, B.J. Sinclair (7♂♂, 7♀♀, CNC); Marysville, 18.VII., C. Garrett (2♂♂, 2♀♀, USNM); Three Valley, Victor Lake, 14.VII.1974, P.H. Arnaud (2♂♂, 4♀♀, CAS); Trans-Canada Highway 1, Key Falls, 11mi west 3 Valley Gap, 8.VIII.1986, P.H. Arnaud (1♂, 1♀, CAS); Wells Gray Provincial Park, Clearwater Valley, Lone Spoon Creek, 16.VIII.1986, P.H. Arnaud (1♂, 1♀, CAS); Yard Creek Provincial Park, 60kmW Revelstoke, 13.VII.1974, P.H. Arnaud (3♂♂, 1♀, CAS).

USA. Montana: Glacier National Park, Sun Point Trail, creek below Baring Falls, 26.VIII.1981, P.H. Arnaud (2♂♂, CAS). **Washington:** Chelan Co., 7miSW Leavenworth, Icicle Ck., 2800', 17.VIII.1990, W.J. Turner (6♂♂, 8♀♀, WSU).

Wyoming: Park Co., Shoshone Nat. For., Newton Ck. Cpgd, N.Fork Shoshone River, 21.VII.1989, B.J. Sinclair (13♂♂,6♀♀,CNC); Park Co., Shoshone Nat. For., Newton Ck. Cpgd, Newton Ck., 20.VII.1989, B.J. Sinclair (1♂,1♀,CNC); Shoshoni Nat'l. Forest, Pahaska Tepee, 11.VIII.1964, R.J. Lavigne & F. Holland (1♂,USNM); Yellow St.Pk., Summer 1921, Miss Cattell (2♂♂,1♀,USNM).

The T. cyanescens Species Group

Members of this group are characterized by a convex projecting face, fourth and fifth tarsomeres dorsoventrally compressed, much wider than preceding tarsomeres and T10 of female with transverse row of short, straight setae. Trichoclinocera lapponica (Ringdahl) is Holarctic in distribution and the only species of this group found in the Nearctic region. This species group also includes 3 species from Middle Asia (T. rostrata Vaillant, T. cyanescens Vaillant, and T. tadjikistana Vaillant). This species group is the sister group to T. stackelbergi group + T. fuscipennis + T. longipes group.

Trichoclinocera cyanescens (Vaillant) New combination.

Seguyella cyanescens Vaillant, 1960c: 180.

Type Material Examined. Type material was unavailable for study. Dr. Vaillant is currently donating his eastern Palearctic material to the Museum National d'Histoire Naturelle (Paris), after which I hope to examine the holotype.

Geographical Distribution and Seasonal Occurrence. This species is known only from the holotype collected in Tadjikistan.

Chorological Affinities. This species was collected from the same locality as *T. tadjikistana*.

Phylogenetic Relationships. This species is a member of the *T. cyanescens* species group, but relationships within this group remain uncertain.

Trichoclinocera lapponica (Ringdahl) New combination.

Atalanta lapponica Ringdahl, 1933: 281.

Type Material Examined. LECTOTYPE (here designated), male labelled: "[Sweden] Tjuonjatj./ [19]30.7-18"; "Atalanta/ lapponica [hand written]" (UZIL). My lectotype label "LECTOTYPE/ of Atalanta/ lapponica Ringd./ des. B.J. Sinclair 1992 [red label]" has been attached to this specimen.

PARALECTOTYPES: Same data as lectotype (4♂♂, 5♀♀, UZIL). My paralectotype labels have additionally been attached to these specimens.

Ringdahl (1933) based his description of Atalanta lapponica on 16 syntypes of which I have examined 9 specimens. Since Ringdahl did not designate a holotype, the specimen bearing a written species label is herein designated lectotype.

Recognition. This species is readily distinguished by its small size, convex-shaped face and small eyes. This species is also the only species of Trichoclinocera known from the far north of North America.

Description. Male. Arista short, tip blunt. Face, gena and occiput with blue pruinescence, ocellar triangle brown. Face convex, lacking distinctive median carina. Palpus short, with blunt apex (Fig. 85).

Pleura, coxae, prescutellar depression and sc1 with blue pruinescence. Acrostichals lacking; 5-6 dc; 1-2 ppm; 1 presut spal; 2-3 npl; 2 psut spal; 1 pal; 2 sc1 and 1-2 short outer marginal setae. Postnotum with patch of pale setae; anteprenotum lacking setae.

Wing infusate, slightly longer than abdomen; stigma lacking; single, short basicostal seta. Costal spine-like setae normal. R_1 lacking setae on apical third; R_4 variable in length and shape: either long and nearly parallel to R_5 or short and divergent from R_5 ; anal vein (A_1) present; cell dm blunt apically.

Fore femur with dense white pile beneath; anteroventral row of short, stout setae, often forming two rows basally; posteroventral row of long, pale seta; 2-3 preapical anterior setae (Fig. 92). Fore tibia with biserial row of stout, short setae beneath. Mid femur lacking anterodorsal setae. Tarsal claws short, less than half length of fifth tarsomere; tarsomeres 4 and 5 dorsoventrally compressed; empodium pulvilliform, subequal in length to claw.

Abdominal sternites, lateral margin of tergites and hypopygium with blue

pruinescence; surstyli, clasping cercus and apical half of phallus shiny, lacking pruinescence. Hypandrium long and slender; ejaculatory apodeme withdrawn into base of phallus; phallus straight. Epandrium with posteroventral membranous region, bearing microtrichia; surstylus long, slender, subequal in length to clasping cercus. Clasping cercus slender with stout setae on dorsal margin (Fig. 113).

Female. Similiar to male except as follows: ventral setae of fore femur often more stout than in males. Tergite 8 with wide, mid-dorsal membranous notch along posterior margin and transverse row of short setae. Posterior margin of S8 invaginated, extending as a narrow projection forming floor of genital chamber. Tergite 10 with short, stout, sparsely distributed setae, lacking curved tips (Figs. 110-111).

Geographical Distribution and Seasonal Occurrence. Trichoclinocera lapponica is Holarctic in distribution and represents the only species of this genus recorded from the western Palearctic. Although known from few localities, it is evidently widespread primarily throughout the arctic region of North America, north of treeline (Fig. 194). Ringdahl (1933) collected the type series of this species in small streams with moss covered rocks at 900m (alpine zone) near Tjuonajaure, a small lake near Abisko (Sweden). Despite few locality records, this species may be found to be circumpolar in distribution once the fauna of northern Russia is better known. Specimens from Victoria Island were collected from a narrow, trickling stream along with the blackfly, Gymnopaia (Simuliidae) (Wood pers. comm.). All specimens of T. lapponica were collected in July.

Canada. NWT: Chesterfield, 31.VII.1950 (2♂♂,26♀♀,CNC); Southampton Is[land]., Coral Harbour, in blackfly cage, 16,24,28.VII.1948 (9♂♂,29♀♀,CNC); Spence Bay, 30.VII.1951 (12♂♂,CNC); Victoria Is[land]., 71°17'N,114°W, 23-28.VII.1975 (7♂♂,12♀♀,CNC). **Quebec:** Payne Bay, 27.VII.1958 (1♂,CNC). **Yukon:** North Fork Pass, 20.VII.1982 (1♂,CNC).

USA: Alaska: Cape Thompson, 29.VII.1961 (2♂♂,13♀♀,CNC).

Chorological Affinities. At present, no other species of Trichoclinocera are known as far north as T. lapponica. However, one or two western species may eventually be found to be sympatric with T. lapponica in Alaska.

Phylogenetic Relationships. Although this species was originally described in the genus Atalanta, Ringdahl (1933) was uncertain into which subgenus it should be classified. This species was classified as a "Doubtful species in Clinocera" in the Palearctic catalogue (Chvála and Wagner 1989). Besides inclusion of this species in the T. cyanescens species group, the relationships appear unclear.

Trichoclinocera rostrata (Vaillant) New combination.

Seguyella rostrata Vaillant, 1960c: 181.

Type Material Examined. SYNTYPES: "Seguyella/ rostrata/ VAILLANT/ male or female sign' F. VAILLANT det.[yellow hand-written label]"; "Ushch. Kondara, Dol./

R[iver]. Varzob, Tadj[ikistan]./ Stackelberg 20.IV.[19]44 [in Russian]"
(2♂♂, 2♀♀, ZISP).

Since there were no type labels on this material, I am currently treating them as possible syntypes. A lectotype was not designated since only 4 of 17 syntypes have been located. I suspect that F. Vaillant has retained several specimens and the remaining specimens may have been lost. Vaillant is currently in the process of donating his eastern Palearctic material to the Museum National d'Histoire Naturelle (Paris), after which I hope to examine these specimens and determine whether a holotype had been designated.

Description. Male. Face, gena and occiput with blue pruinescence, ocellar triangle brown. Face convex, with blue pruinescence; median carina lacking. Arista short with blunt tip. Palpus with broad apex.

Pleura, coxae, pprn, npl, pal, sctl and prescutellar depression with blue pruinescence. Acrostichals lacking; 5 dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 apical sctl. Postnotum with patch of pale setae; antepnotum lacking setae.

Wing broad, hyaline; stigma lacking; single short basicostal seta. Costal spines reduced; R_1 with setae along entire length; R_4 with spurious extension at base; cell dm blunt apically.

Fore femur with 3 anterior bristles on apical third; anteroventral region with row of short, stout, spine-like setae; posteroventral region with row of long, slender, pale setae on basal two-thirds. Fore tibia with anteroventral row of short, stout setae; posteroventral row of short, slender setae. Mid femur lacking anterodorsal, erect setae.

Tarsomeres 4 and 5 dorsoventrally compressed. Claws and empodium long, subequal in length.

Abdominal sternites, lateral margin of tergites and hypopygium with blue pruinescence; surstyli, clasping cercus and apical two-thirds of phallus shiny, lacking pruinescence. Hypandrium long and slender; phallus long and straight, ejaculatory apodeme drawn up into base of phallus. Epandrium with posteroventral membranous region, bearing microtrichia; surstylus narrow and straight. Slender finger-like clasping cercus, bearing stout setae on inner dorsal margin.

Female. Similar to male except as follows: lacking modified setae of fore tibia. Fore femur lacking posteroventral row of long setae; anteroventral row with short, blunt spine-like setae on apical third; 2 short, stout basal setae. Tergite 8 with dense transverse row of long setae; T10 with short, stout setae.

Geographical Distribution and Seasonal Occurrence. This species is known from a single locality in Tadjikistan (Middle Asia), collected in April.

Chorological Affinities. This species is likely more widespread, and sympatric with the other two species of Trichoclinocera known from Tadjikistan.

Phylogenetic Relationships. This species is a member of the T. cyanescens species group, but relationships within this group remain uncertain.

Trichoclinocera tadjikistana (Vaillant) New combination.

Seguyella tadjikistana Vaillant, 1960c: 184.

Type Material Examined. SYNTYPES: "Seguyella/ tadjikistana/ VAILLANT/ male or female sign/ F. VAILLANT det.[yellow hand-written label]"; "Tavil-Dara I/ Skl. Darvaz 9.X/ Stackelberg [1]942 [in Russian]" (1♂,1♀,ZISP); "Seguyella/ tadjikistana/ VAILLANT/ male sign/ F. VAILLANT det.[yellow hand-written label]"; "Stalinabad [=Dushanbe]/ Tadjik[istan]. Predgor'ch/ Goussakovosky 18.IV.[19]43 [in Russian]" (1♂,ZISP); "Seguyella/ tadjikistana/ VAILLANT/ female sign/ F. VAILLANT det.[yellow hand-written label]"; "Viskharvy NA R[iver]./ Pyandzh, Tadjik[istan]. 21.X./ Stackelberg [1]942 [in Russian]" (1♀,ZISP).

Since there were no type labels on this material, I am currently treating them as possible syntypes. A lectotype was not designated since only 4 of 11 syntypes have been located. I suspect that F. Vaillant has retained several specimens and the remaining specimens may have been lost. Vaillant is currently in the process of donating his eastern Palearctic material to the Museum National d'Histoire Naturelle (Paris), after which I hope to examine these specimens. Vaillant (1961c) chose Viskharvy as the type locality.

Description. Male. Face, gena and occiput with blue pruinescence, ocellar triangle brown. Face convex, with blue pruinescence; median carina lacking. Arista short with blunt tip. Palpus with broad apex.

Pleura, coxae, pprn, npl, pal, sctl and prescutellar depression with blue

pruinescence. Several minute acrostichals anterior to first dc; 5 dc; 1 ppn and 4 short, black setae; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 apical setl and 1 pair subapical setae. Postnotum with patch of pale setae; anteprenotum with several pairs of black setae.

Wing broad, hyaline; stigma lacking; single long basicostal seta. Costal spine-like setae normal. R_1 with setae on basal half only; R_4 with spurious extension at base; cell dm blunt apically.

Fore femur with 2-3 anterior bristles on apical third; anteroventral region with row of short, stout, spine-like setae increasing in length apically; posteroventral region with row of long, slender, pale setae; base of femur with several long, slender pale setae. Fore tibia with biserial row of short, stout setae beneath. Mid femur lacking anterodorsal, erect setae. Tarsomeres 4 and 5 dorsoventrally compressed. Empodium pulvilliform, subequal to claw.

Abdominal sternites, lateral margin of tergites and hypopygium with blue pruinescence; surstyli, claspig cercus and apical half of phallus shiny, lacking pruinescence. Hypandrium long and slender; phallus stout, apical half membranous with three apical pointed lobes. Epandrium with posteroventral membranous region, bearing microtrichia; surstylus boot-shaped. Claspig cercus slender with stout setae on dorsal margin; apex expanded.

Female. Similar to male except as follows: chaetotaxy of fore legs similar to males. Tergite 8 with sparse transverse row of short setae; T10 with short, straight, stout setae. A darkly sclerotized U-shaped genital fork present (Fig. 112).

Geographical Distribution and Seasonal Occurrence. Adults of this species are recorded from two localities in Tadjikistan (Middle Asia), collected in April and October (Vaillant 1960b) and a single locality from Uzbekistan, collected in May (Wagner 1984).

Chorological Affinities. This species was collected from the same locality as *T. cyanescens*.

Phylogenetic Relationships. This species is a member of the *T. cyanescens* species group, but relationships within this group remain uncertain.

The *T. stackelbergi* Species Group

The members of this group are characterized by long, stout anterodorsal and posterodorsal setae on the mid and hind femora and the apex of the phallus with a narrow sclerite. All known members of this group are from the eastern Palearctic region and include *T. stackelbergi* and many undescribed species (Saigusa pers. comm.). This species group is part of an unresolved trichotomy with *T. fuscipennis* and *T. longipes* species group.

***Trichoclinocera stackelbergi* Collin**

Trichoclinocera stackelbergi Collin, 1941: 238.

Type Material Examined. LECTOTYPE (here designated), male labelled: "[Russia]

Tigrovaja, Sutshan District/ Ussuri region 3.VIII./ Stackelberg [1]927 [in Russian]" (ZISP). My lectotype label "LECTOTYPE/ of *Trichoclinocera/ stackelbergi* Collin/ designated 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Tigrovaja, Sutshan District, Ussuri region. 3.VIII.1927, Stackelberg (1♂, ZISP); Same data, except collected 5.VIII. (2♀♀, ZISP). My paralectotype labels have additionally been attached to these specimens.

Collin (1941) based his description of *T. stackelbergi* on a series of 6 males and 14 females. In addition to the 3 designated paralectotypes, 11 specimens not examined have my paralectotype label attached. The location of the 5 remaining syntypes is unknown.

Recognition. This species is distinguished from all other described species of *Trichoclinocera* by the cloudy margins of the wing veins.

Description. Male. Face with blue pruinescence and wide, dark carina medially; arista long.

Pleura, coxae, ppn, npl, sctl and prescutellar depression with blue pruinescence. Acrostichals lacking; 6-7 dc; 1 ppn and several dark setulae; 1 presut spal; 2 npl and 1 setulae; 2 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae.

Wing broad, infusate; single long basicostal seta; stigma lacking; cell dm blunt apically; R_1 with setae along entire length; recurrent stump vein at base of R_4 . Base of R_1 , distal edge of cell dm and r-m vein with cloudy brown margins.

Fore femur with 2-3 anterior setae on apical third; anteroventral region with row of stout, black setae, decreasing in length apically; posteroventral region with row of slender, pale setae and 3 evenly spaced long, stout setae on apical third. Mid and hind femora with widely spaced anteroventral, posteroventral, anterodorsal, and posterodorsal stout, erect, setae. Empodium pulvilliform, subequal to length of claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Clasping cercus wide, broadly rounded, inner face with short, blunt spine-like setae (Fig. 115). Surstylus short and narrow. Phallus with distinct curve at apical third; apex with a narrow, ventral sclerite (Fig. 114).

Female. Similar to male except as follows: anteroventral region of fore femur with row of 5-6 evenly spaced, stout setae with slender setae intermixed; posteroventral region with row of three stout setae on apical half and pale setae on basal half. Tergite 8 with dense transverse row of long setae; T10 with 2-3 enlarged stout apical setae (Fig. 116).

Geographical Distribution and Seasonal Occurrence. This species is known only from the type locality.

The T. longipes Species Group

Members of this group are characterized by the lack of stout setae on the inner face of the clasping cercus and the apex of the phallus with a narrow folded, pointed

sclerite. Members of this group are confined almost exclusively to the eastern Nearctic region and includes 10 species. This species group is part of an unresolved trichotomy with *T. fuscipennis* and *T. stackelbergi* species group.

***Trichoclinocera agilis* sp.nov.**

Holotype. Male labelled: "USA: T[en]N[essee]: Van Buren Co./ Fall C[ree]k. Falls St[ate].P[ar]k./ Cane C[ree]k. below falls/ 19.VI.1990/ B.J. Sinclair BS9029/ ex. emergent rocks" (CNC).

Derivation of Specific Name. Latin for quick or nimble, in reference to the behaviour of adults of this genus, which often eluded my collecting efforts by quickly dropping down from emergent rocks, and escaping across the stream.

Recognition. This species is readily distinguished by features given in the key.

Description. Male. Face light brown with median carina dark; gena with pale blue pruinescence. Arista long and slender.

Pleura, coxae, pprn and npl with pale blue pruinescence. Acrostichals lacking; 6-7 dc; 1 pprn and several setulae; 1 presut spal; 3 npl, lower slender; 2 psut spal; 1 pal; 2 setl. Postnotum with patch of pale setae; anteprepronotum with short, pale setae.

Wing narrow, infusate; stigma absent; single long basicostal seta. R₁ with setae along entire length; cell dm slightly produced apically.

Fore femur with 1-3 anterior setae on apical third; anteroventral row of short, black setae, becoming more stout apically; posteroventral row of short black setae on apical two-thirds, basal third with row of long, pale setae. Fore tibia with biserial row of short, stout setae beneath (Fig. 93). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with pale, blue pruinescence, dorsum brown. Clasper shiny brown, strongly arched, with broadly, rounded apex; very similar to *T. ozarkensis*. Surstylus slender, with microtrichia along dorsal margin. Phallus with slight undulations (Fig. 117).

Female. Unknown.

Geographical Distribution and Seasonal Occurrence. This species is known only from the type locality, which is found along the Cumberland Plateau of Tennessee, west of the Appalachian Mountains.

Chorological Affinities. This species was collected together with *T. fumosa*.

Phylogenetic Relationships. This species is believed to be most closely related to *T. falcata*, *T. fumosa* and *T. ozarkensis* on the basis of the shape of the clasper.

Paratypes. USA. Tennessee: Van Buren Co., Fall Creek Falls State Park., Cane

C[ree]k., 19.VI.1990, B.J. Sinclair (5♂♂,CNC)

Trichoclinocera ctenistes (Melander)

Wiedemannia (Chamaedipsia) ctenistes Melander, 1928: 234.

Type Material Examined. LECTOTYPE (here designated), male labelled: "Hanover/ VII.6.[19]08 N[ew]H[ampshire, U.S.A.]"; "TYPE/ Chamaedipsia/ ctenistes/ Mel. [red label]"; "AL Melander/ Collection/ 1961" (USNM). My lectotype label "LECTOTYPE/ of Wiedemannia/ ctenistes Mel./ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: N.H.: Hanover, 6.VII.[19]08, C.W. Johnson (1♂,2♀♀,MCZ; 1♀,USNM). My paralectotype labels have additionally been attached to these specimens.

Melander (1928) based his description of W. ctenistes on 5 syntype specimens. Since Melander did not designate a holotype, the specimen bearing his red "Type" label is herein designated lectotype.

Recognition. This species is easily identified by markings of the face. It can only be mistaken for T. longipes, but is readily distinguished by features outlined in the key.

Description. Male. Face with blue pruinescence and dark velvety carina medially; gena with blue pruinescence. Arista long and slender.

Pleura and coxae with blue pruinescence. Acrostichals lacking; 6 dc; 1 ppn; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 setl. Postnotum with patch of pale setae; anteprenotum with several slender setae.

Wing narrow, infusate; single long basicostal seta; stigma lacking; cell dm slightly produced apically; R_1 with setae along entire length.

Fore femur with 2 anterior setae on apical fourth; anteroventral region with single row of short, stout setae, becoming more stout apically; posteroventral region with row of slender, pale setae on basal two-thirds and 2-3 stout, setae on apical third. Fore tibia with biserial row of short, stout setae beneath (Fig. 94). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Claspig cercus slender, straight with broad base and truncate apex. Surstylus narrow. Phallus with shallow undulations (Fig. 118).

Female. Similar to male except as follows: fore tibia with biserial row of ventral setae less stout. Anteroventral region of fore femur with row of very short stout setae; posteroventral region with apical setae less stout. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is known from only four localities (Fig. 195), consequently its distribution and seasonal occurrence are poorly understood.

Canada. Ontario: Nipissing Co., Whitney, Madawaska R., 19.VII.1991 (1♂, 6♀♀, CNC). **Quebec:** Gatineau Park, Lac Philippe Cpgd, stream nr. Parent Beach, 7.VII.1990, 29.VII.1992 (1♂, 2♀♀, CNC).

USA. Michigan: Newaygo, 15.VII.1950 (3♂♂, 2♀♀, CNC, MSU). **New Hampshire:** Hanover, 6.VII.1908 (1♀, NYSM).

Chorological Affinities. This species was collected together with T. minor, T. falcata, and T. hamifera from emergent rocks in a small stream in Gatineau Park (Quebec).

Phylogenetic Relationships. This species was transferred to Trichoclinocera by Sabrosky (1967) and is most closely related to T. longipes on the basis of facial colour patterns. Both species are believed to be closely related to T. dasycoxa and T. hamifera on the basis of similar chaetotaxy of the male fore femur.

Trichoclinocera dasycoxa sp.nov.

Holotype. Male labelled: "Along Sherman Creek/ 1 mi. W. Dromgold/ Perry Co., Pennsylvania. [USA]/ 11 July 1972/ D. S. Shetlar"; "D. Dee Wilder/ Collection [yellow label]" (CAS).

Allotype. Female. Same data as holotype, except collected by D. Dee Wilder (CAS).

Derivation of Specific Name. From the Greek dasys meaning hairy, in reference to the

markedly setose nature of the fore coxa of adults of this species.

Recognition. This species is morphologically most similar to *T. hamifera*, but may be readily distinguished by features outlined in the key.

Description. Male. Face dull brown with dark carina medially; lateral margins of carina pale; arista long and slender.

Pleura and coxae with pale blue pruinescence. Acrostichals lacking; 6 dc and 3-5 additional long setae interspersed; 1 pprn and several long setulae; 1 presut spal; 3 npl and scattered setulae; 2 psut spal; 1 pal; 2 setl. Postnotum with patch of pale setae; anteprenotum with 5-6 pairs of pale setae.

Wing slender and infusate, with long basicostal seta; stigma lacking; cell dm slightly produced apically; R_1 with setae along entire length.

Fore coxa with erect, dark setae on lateral margins. Fore femur with 2-3 anterior setae on apical fourth; anteroventral region with single row of short, stout setae, dividing into 2 rows on basal half; posteroventral region with row of widely spaced long, slender, pale setae on basal third, becoming more stout and shorter apically. Fore tibia with biserial row of short, stout setae beneath (Fig. 96). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with pale blue pruinescence, dorsum brown. Claspig cercus strongly arched with lobe on middle of inner surface. Surstylus narrow. Phallus with shallow undulation (Fig. 119).

Female. Similar to male except as follows: fore tibia with biserial row of ventral setae less stout. Anteroventral region of fore femur with fewer short, stout setae. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is rarely collected compared to the majority of species of Trichoclinocera. It is apparently very localized in distribution in the northern Appalachian Mountains and oddly enough is also known from a small series in Washington, which were likely collected from the Wenatchee River (Fig. 197). This east-west disjunct pattern is similar to distributions of stoneflies discussed by Ricker (1964). He believed they were the result of postglacial or interglacial dispersal across the continent followed by extinction when the prairie spread northwards during the Hypsithermal 5-8000 yr.B.P. An alternative scenario could be that this species was more widespread prior to the Pleistocene and this western locality represents a relict population. Since the existence of this western population of T. dasycoxa has not been verified, these specimens may have been mislabelled.

A specimen of this species was reared from a pupa collected (8.VI.1992) from the Indian River near Almonte, Ontario (See "Source of Reared Material" under generic description).

Chorological Affinities. In the Ottawa River this species was collected with T. longipes and T. pectinifemur and in Pennsylvania collected with T. minor.

Phylogenetic Relationships. This species is believed to be closely related to *T. longipes*, *T. ctenistes*, and *T. hamifera* on the basis of similar chaetotaxy of the male fore femur.

Paratypes. Canada. Ontario: Ottawa, 11.IX.1947, G.E. Shewell (4♂♂, CNC); Ottawa, Ottawa R., Remic Rapids, 23-24.VI., 2.IX.1991, B.J. Sinclair (1♂, 8♀♀, CNC); Ottawa River, Remic Rapids, 18.VI.1949, G.E. Shewell (1♀, CNC); Ottawa, Rideau R., Carleton Univ., 22.VI.1991, B.J. Sinclair (1♀, CNC). **Nova Scotia:** Truro, 8.VII.1913 (1♂, 1♀, CNC).

USA. Connecticut: Cornwall, 13.VI.1935, R.B. Friend (2♂♂, 2♀♀, CAES). **Pennsylvania:** Center Co., State College, 23.VII.1972, D.D. Wilder (1♂, CAS); State Stream Survey, A.N.S.P., Station 129, 13.VIII.1948 (1♂, 2♀♀, USNM); Monroe Co., Henryville, Broadhead Ck., 15.VI.1910 (3♂♂, 3♀♀, CMNH); Perry Co., Along Sherman Creek, 1miW Dromgold, 11.VII.1972, D.D. Wilder (5♂♂, 46♀♀, CAS); Perry Co., Along Sherman Creek, 1miW Dromgold, 11.VII.1972, D.J. Shetlar (9♂♂, 57♀♀, CAS); Union Co., Glen Iron, Penn Ck., V.1949, (5♂♂, 4♀♀, CMNH); Wilawana, 6.VI.1932, R.H. Crandall (1♂, 1♀, AMNH). **New York:** Horton, 28.VII.1935, H.K. Townes (2♂♂, 3♀♀, USNM); [Fulton Co.] Ingham Mills, 24.VII.1934, H.K. Townes (1♂, 6♀♀, USNM); Ithaca, VIII. [E.T. Cresson?] (2♂♂, 1♀, CU, USNM). **Virginia:** Giles Co., #107, Sinking Crk., 5.2miE Pembroke, 17.VI.1975, G.W. Byers (10♂♂, 23♀♀, SMEK). **Washington:** Cashmere, 26.VII.1919, A.L. Melander (1♂, 9♀♀, USNM). **West Virginia:** Morgan Co., Cacapon River near Great Cacapon, 1.VI.1986, W.E. Steiner & J.M. Swearingen (1♂, 16♀♀, USNM).

3

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

Trichoclinocera falcata sp.nov.

Holotype. Male labelled: "CANADA: Quebec/ Gatineau Park, Lac/ Philippe C[am]pg[roun]'d/ 7.VII.1990, stream/ at Lusk Cave/ BJ Sinclair BS9033" (CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. From the Latin falcatus meaning sickle-shaped or curved, in reference to the strongly curved clasping cercus of the male terminalia.

Recognition. This species is readily distinguished by its small size, dark colour and by features given in the key.

Description. Male. Face brown to pale blue pruinescence; median carina dark with lateral faint blue pruinescence. Arista long and slender.

Pleura, coxae, pprn, npl and base of sc11 with faint blue pruinescence. Acrostichals lacking; 6 dc; 1 pprn; 1 presut spal; 2-3 npl; 2 psut spal; 1 pal; 2 sc11. Postnotum with patch of pale setae; anteprenotum with short, pale setae.

Wing narrow, infusate; stigma absent; single long basicostal seta. R₁ with setae along entire length; cell dm slightly produced.

Fore femur with 2-3 preapical anterior setae; anteroventral row of short, stout setae; posteroventral row of short stout setae with 3-4 long, dark stout setae on basal half; base of femur with long, pale setae beneath. Fore tibia with biserial row of short,

stout setae beneath (Fig. 98). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Surstylus short, slender. Claspig cercus strongly arched, with slender, round tip. Phallus with gradual undulations (Fig. 121).

Female. Similar to males including chaetotaxy of fore femur. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This is the most widespread eastern species of Trichoclinocera, known from the Great Whale River in Quebec to the southern Appalachians of Georgia (Fig. 200). Collection records indicate that adults of this species first appear in early May and have been collected throughout the summer to mid-August.

Chorological Affinities. This species is largely sympatric with T. fumosa.

Phylogenetic Relationships. This species is believed to be most closely related to T. agilis, T. fumosa, and T. ozarkensis on the basis of the shape of the claspig cercus.

Paratypes. Canada. Ontario: Eugenia, 11.VIII.1985, S.A. Marshall (1♀,UGO); S. Kapuskasing, Beaver Falls, Kapuskasing R., 17.VI.1992, B.J. Sinclair (1♀,CNC); Sault

Ste. Marie, Crystal Falls, 29.VII.1989, M.&R. Hurley (1♂,HSU). Quebec: Gatineau Park, stream at Dunlop Picnic Area, 14.VII.1991, B.J. Sinclair (1♂,CNC); Gatineau Park, Lac Philippe Cpg'd, stream at Lusk Cave, 7.VII.1990, B.J. Sinclair (8♂♂,9♀♀,CNC); Gatineau Park, Lac Philippe Cpg'd, stream nr. Parent Beach, 7.VII.1990, 29.VII.1992, B.J. Sinclair (3♂♂,1♀,CNC); Great Whale River, 13.VII.1949, J.R. Vockeroth (13♂♂,20♀♀,CNC).

USA. Connecticut: Avon, Avon Old Farms, 27.VI.1929, C.H. Curran (1♂,AMNH); Redding, 8.VI.1930, 30.V.1931, A.L. Melander (2♂♂,1♀,USNM). Georgia: Dawson Co., Amicalola Falls St. Pk., 18miW Dahlonega, Little Amicalola Crk., 25.IV.1989, J.M. Cumming (11♂♂, 8♀♀,CNC); White Co., Chattahoochee Nat. For., near Helen, Chattahoochee R., 21.VI.1990, B.J. Sinclair (1♀,CNC). New York: Bear Mt., 18.V.1941, A.L. Melander (1♀,USNM); Ludlowville, 27.VI.1973, L.L. Pechuman (2♂♂,1♀,CU); W. Nyack, 31.V.1936, 5.VI.1938, A.L. Melander (2♂♂,USNM). Pennsylvania: Perry Co. Notch Rd., 4.5kmW Hwy 11-15, 34kmN Harrisburg, 5.V.1987, J.M. Cumming (3♂♂,2♀♀,CNC).

Trichoclinocera fumosa (Vaillant) New combination.

Wiedemannia (Roederella) fumosa Vaillant, 1960b: 119.

Type Material Examined. Type not available for study. Dr. Vaillant is in the process of donating his Nearctic material to the Museum National d'Histoire Naturelle (Paris), after which I hope to examine the type series of this species.

Recognition. This species is readily distinguished by the yellow-coloured coxae and other features given in the key.

Description. Male. Face brown; median carina with faint blue pruinescence on lateral margins. Arista long and slender.

Pleura, coxae, ppm and npl with faint blue pruinescence. Acrostichals lacking; 6 dc; 1 ppm; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae; anteprenotum with short, pale setae.

Wing narrow, infusate; stigma absent; single long basicostal seta. R_1 with setae along entire length; cell dm slightly produced.

Coxae and trochanter yellow-brown, remaining leg segments brown. Fore femur with 2-3 preapical anterior setae; anteroventral row of short, stout setae, more widely separated than in *T. falcata*; posteroventral row of short stout setae on apical third, increasingly more slender and longer basally. Fore tibia with biserial row of short, stout setae beneath (Fig. 99). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal to length of claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Surstylus short and arched. Claspig cercus strongly arched, with expanded tip. Phallus with gradual undulations (Fig. 120).

Female. Similar to males except as follows: ventral setae of fore femur and tibia much less pronounced. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. *Trichoclinocera fumosa* is confined to the Appalachian Mountains and is recorded from Vermont to northern Georgia (Fig. 200). Adults of this species occur from late May to late August. A specimen of this species was reared from a pupa collected from a tributary of Twelve Mile Creek in South Carolina (See "Source of Reared Material" under generic description).

USA. Georgia: Lumpkin Co., Chattahoochee N.F. nr. Desota Falls Scenic Area, Frogtown Ck., 20.VI.1990 (12♂♂,6♀♀,CNC); White Co., Chattahoochee N.F., Anna Ruby Falls, Smith Ck., 21.VII.1990 (3♂♂,1♀,CNC); White Co., Chattahoochee N.F. nr. Helen, Chattahoochee R., 21.VI.1990 (4♂♂,3♀♀,CNC); White Co., Chattahoochee N.F., Raven Cliff Falls, Dodd Ck., 21.VI.1990 (1♂,CNC). **North Carolina:** Haywood Co., Great Smoky Mtns N.P., Cataloochee Ck. + trib., 12.VI.1990 (8♂♂,3♀♀,CNC). **South Carolina:** Oconee Co., Sumter N.F., Brasstown Falls, 22.VI.1990 (4♂♂,9♀♀,CNC); Pickens Co., trib. of 12mi Ck., 1.3miN Central Town, 5.IV.1986 (1♂, reared - in alc., CUAC). **Tennessee:** Sevier Co., Great Smoky Mtns N.P., Elkmont, Little R. + Jakes Ck., 14.VI.1990 (9♂♂,17♀♀,CNC); Sevier Co., Great Smoky Mtns. N.P., Elkmont, 2300', 27.VIII.-3.IX.1986 (1♂,1♀,MEM); Smokies, Chimneys, 29.VI.1941 (4♂♂,4♀♀,USNM); Smokies, L. Pigeon River, 27.VI.1941 (14♂♂,21♀♀,USNM); Van Buren Co., Fall Ck. Falls S.P., Fall Ck., 19.VI.1990 (4♂♂,1♀,CNC). **Vermont:** Rutland, Mendon, Mendon Br., 21.VIII.1988 (1♂,1♀,CNC). **Virginia:** Augusta Co., Briery Branch, 3,17.VII.1955 (5♂♂,13♀♀,USNM); Giles Co., Stony Ck., 2000', 26.V.1962 (2♂♂,CNC).

Chorological Affinities. This species is largely sympatric with *T. fulcata*.

Phylogenetic Relationships. This species is believed to be most closely related to *T. agilis*, *T. falcata*, and *T. ozarkensis* on the basis of the shape of the clasping cercus.

Trichoclinocera hamifera (Melander)

Wiedemannia (Chamaedipsia) hamifera Melander, 1928: 233.

Wiedemannia (Roederella) saltans Vaillant, 1960b: 122. New synonymy.

Notes about Synonymy. The type of saltans was not available for examination, and the synonymy is based on the description (see "Notes about Synonymy" under *T. fumosa*).

Type Material Examined. Wiedemannia hamifera Melander, LECTOTYPE (here designated), male labelled: "Beaverkill N[ew]Y[ork] [USA]/ 4.VIII.[19]09/ ET Cresson Jr."; "TYPE/ Chamaedipsia/ hamifera/ Mel[ander]. [red label]"; "AL Melander/ Collection/ 1961" (USNM). My lectotype label "LECTOTYPE/ of Wiedmannia/ hamifera Melander/ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Middletown, C[onnecticu]t, 17.VI.[19]09, C.W. Johnson (1♂, ANSP; 4♂♂, USNM) [conspecific with lectotype]; Ithaca, N[ew].Y[ork]., 9.VI.[19]01 (2♂♂, 1♀, USNM) [conspecific with lectotype]; Beaverkill, N[ew]Y[ork], 4.VIII.[19]09 (1♀, ANSP) [conspecific with lectotype]; Moosehead, M[aine],

18.VII.[19]07, C.W. Johnson (3♀♀,USNM; 2♂♂,1♀,MCZ; 1♀,ANSP; 1♂,2♀♀,NYSM) [= T. longipes]; Ithaca, N[ew]Y[ork], .VIII. (1♂,CU; 1♂,1♀,USNM) [= T. dasycoxa]; Ithaca, N[ew]Y[ork], 9.VI.[19]01, O.A. Johannsen (1♀,CU) [= T. pectinifemur]. My paralectotype labels and determination labels have additionally been attached to these specimens.

Melander (1928) based his description of W. hamifera on 30 specimens, of which 23 specimens have been located. The syntype series contains four different species. Since Melander did not designate a holotype, the specimen bearing his red "Type" label is herein designated lectotype.

Recognition. This large species is readily distinguished by features given in the key. It is one of the most commonly collected species in the Appalachian region.

Description. Male. Face dull brown with dark carina medially; lateral margins of carina pale; arista long and slender.

Pleura and coxae with pale blue pruinescence. Acrostichals lacking; 5-7 dc; 1 ppm and several setulae; 1 presut spal; 3 npl; 2 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae; antepnotum with 5-6 pairs of pale setae.

Wing slender and infusate, with long basicostal seta; stigma lacking; cell dm slightly produced apically; R₁ with setae along entire length.

Fore femur with 2-3 anterior setae on apical fourth; anteroventral region with single row of short, stout setae, dividing into 2 rows on basal third; posteroventral region

with row of long, slender, pale setae on basal half, becoming more stout and short apically. Fore tibia with biserial row of short, stout setae beneath (Fig. 97). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Claspig cercus attenuated on apical half, curving medially to rounded apex. Surstylus narrow. Phallus with shallow undulations (Fig. 122).

Female. Similar to male except as follows: fore tibia with biserial row of ventral setae less stout. Anteroventral region of fore femur with row of short stout setae, but not dividing into distinct additional rows. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species ranges from southern Ontario and Quebec to the southern Appalachians (Fig. 201). Adults have been recorded from late May or early June to August.

Canada. Ontario: Algonquin P.Pk., Highland Trail., outflow from Provoking L., 18.VII.1991 (1♂,1♀,CNC); 5kmNW Almonte, Mill of Kintail Cons. A., 29.VII.1990 (2♂♂,13♀♀,CNC); Bellfountain, 24.VI.1974, 15.VI.1976 (3♂♂,UGO); Dundas, 7.VI.1975 (1♂,1♀,UGO); Forks Credit, 26.VI.1973 (10♂♂,3♀,UGO); Forks of the Credit P.Pk., Credit R., 28.VI.1991 (14♂♂,29♀♀,CNC); Grey Co., Owen Sound, Inglis Falls Cons. A., Sydenham R., 29.VII.1990 (8♂♂,13♀♀,CNC); Halton Co., Hilton Falls Cons. Area, 27.VI.1991 (8♂♂,11♀♀,CNC); Halton Co., Lowville, Bronte Ck., 24.VII.1989, 26.VI.1991 (11♂♂,16♀♀,CNC); Limehouse, Manon Ck., 15.VI.1974

(1♂,UGO); Nipissing Co., Algonquin P.Pk., Oxtongue R., 19.VII.1991 (20♂♂,17♀♀,CNC); Nipissing Co., Whitney, Madawaska R., 19.VII.1991 (3♂♂,2♀♀,CNC); Varney, 20.VI.1975 (1♀,UGO); Wellington Co., 1968-70 (24♂♂,30♀♀ - in alc., UMQ). Quebec: Gatineau Pk., Meach L., 20.VII.1959 (1♂,7♀♀,CNC); Gatineau Pk., L. Philippe Cpgd, 7.VII.1990, 29.VII.1992 (2♂♂,4♀♀,CNC); Hemmingford, 30.VI.1923 (1♂,2♀♀,CNC); Hull, 8.VII.1923 (1♂,2♀♀,CNC,USNM); Mt. Tremblant N.P., Riv. du Diable, 30.VI.1958 (2♂♂,1♀,CNC); Old Chelsea, 29.VII.1956, 31.VIII.1958, 25.VI., 9,21.VII.1959, 23.VII.1985(42♂♂,77♀♀,CNC); Perkins, 18.VII.1967(3♂♂,4♀♀,CNC); Perkins Mills, 11.VI.1949 (1♂,4♀♀,CNC); Riv. du Diable, PMT, VI.VII.VIII.1958 (9 alc.vials, UMQ).

USA. Connecticut: Avon, 26.VI.1929 (23♂♂,22♀♀,AMNH); Redding, 1.VI.1929, 8.VI.1930, 30.V.1931 (16♂♂,21♀♀,BPBM,CU,USNM). **District of Columbia:** Rock Creek, 5.VI.1925 (5♂♂,10♀♀,USNM). **Georgia:** Lumpkin Co., Chattahoochee N.F., Frogtown Ck., 20.VI.1990 (1♀,CNC); White Co., Chattahoochee N.F., Chattahoochee R., 21.V.1990 (6♂♂,3♀♀,CNC). **Maryland:** Frederick Co., 1.5miN Thurmont, 25.VII.1971 (1♂,USNM); Montg. Co., Clarksburg, 20-22.V.1988 (6♂♂,8♀♀,USNM); Plummers Id, 14.V.1914 (3♀♀,USNM). **Massachusetts:** Mt. Toby, 21.V.1951 (1♂,4♀♀,MSU). **New York:** Horton, 16.VII.1935 (1♂,1♀,USNM); Hoversville, 20.VI.1923 (4♂♂,8♀♀,NYSM); Ingham Mills, 24.VII.1934 (1♀,USNM); Ludlowville, 7.VII.1966 (2♂♂,CNC); Tompkins Co., Salmon Ck., 16.VI.1981 (13♂♂,CNC); Tuxedo, Sta Study Insects, 25.VI.1928 (3♂♂,6,AMNH); W. Nyack,

5.V.1938 (23♂♂,17♀♀,USNM). **North Carolina:** Haywood Co., W.Fk. Pigeon R., 13.V.1976 (1♂,1♀,CUAC); Smokemont, 2.VII.1941 (3♂♂,USNM). **Pennsylvania:** B. Moshannon, 11.VI.1950 (1♂,1♀,PSU); Centre Co., State College, 13.V.1953 (1♀,PSU); Chester Co., Phoenixville, 17.V.1964 (1♂, CNC); Crawford Co., Woodcock Ck. above Woodcock Lk. Dam, 16.VII.1974 (1♂, PERC); Erie Co., Wattsburg, French Ck., 18.VI.1974 (5♂♂,15♀♀, PERC, in alc.); Lawrence Mills, Darey Ck., 9.VI.1917 (1♂,1♀,ANSP); Lewiston, 7.VI.1940 (5♀♀,USNM); Monroe Co., Henryville, Broadhead Ck., 15.VI.1910 (2♂♂,6♀♀,CMNH). **South Carolina:** Oconee Co., Sumter N.F., Brasstown Falls, 22.VI.1990 (1♀, CNC). **Tennessee:** Sevier Co., Great Smoky Mtns. N.P., Elkmont Cpgd, Little R., 14.VI.1990 (5♂♂,8♀♀, CNC). **Vermont:** Rutland Co., Mendon, Mendon Br., 21.VIII.1988 (1♂, CNC). **Virginia:** Augusta Co., Briery Branch, 3.VII.1955 (5♂♂,13♀♀,USNM); Fairfax Co., Dead Run, 14.V.1914, 30.V.1927 (1♂,12♀♀,USNM); Giles Co., Stony Ck., 2000', 26.V.1962 (7♂♂,12♀♀, CNC). **West Virginia:** Randolph Co., Harmon, Dry Fk. Cheat R., 5.VI.1990 (11♂♂,5♀♀, CNC).

Chorological Affinities. This species is sympatric with *T. longipes* in southern Ontario and Quebec, but rarely in the same creek or river.

Phylogenetic Relationships. This species was transferred to *Trichoclinocera* by Collin (1941). This species is believed to be closely related to *T. longipes*, *T. ctenistes*, and *T. dasycoxa* on the basis of similar chaetotaxy of the male fore femur.

Trichoclinocera longipes (Walker)

Heliodromia longipes Walker, 1849: 504.

Type Material Examined. HOLOTYPE, female labelled: "Hudson's [Hudson] Bay [Canada: Ontario]/ St. Martin's Falls [Albany River]/ longipes, [G.]Barnston" (BMNH).

Recognition. This species is one of the most easily identified species of Trichoclinocera due to markings of the face. It can only be mistaken for T. ctenistes, but is readily distinguished by features outlined in the key.

Description. Male. Face with blue pruinescence and wide, dark velvety carina medially; gena with blue pruinescence. Arista long and slender.

Pleura and coxae with blue pruinescence. Acrostichals lacking; 6 dc; 1 ppn and several setulae; 1 presut spal; 2 npl and 1 setulae; 2 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae; antepnotum with 5-6 pairs of pale setae; anepisternum with pale setulae.

Wing narrow, infusate; single long basicostal seta; stigma lacking; cell dm slightly produced apically; R₁ with setae along entire length; specimens from type locality with recurrent stump vein at base of R₄ (Smith 1971, fig. 5).

Fore femur with 2-3 anterior setae on apical fourth; anteroventral region with single row of short, stout setae, dividing into 2-3 rows on basal third; posteroventral region with row of slender, pale setae on basal half, becoming more stout and short

apically. Fore tibia with biserial row of short, stout setae beneath (Fig. 100). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal in length to claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Claspig cercus slender, straight with broad base and round apex. Surstylus narrow. Phallus with shallow undulations (Fig. 123).

Female. Similar to male except as follows: fore tibia with biserial row of ventral setae less stout. Anteroventral region of fore femur with row of short stout setae, but not dividing into distinct additional rows. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is found as far north as the Great Whale River and extends southward to approximately 42°N latitude (Fig. 201). Most records of adults are from July, but specimens have been collected from late May to October.

CANADA. Ontario: Bruce Co., Southampton, Derry's Dam, Saugeen R., 26.VII.1989 (4♂♂, 7♀♀, CNC); Hog's Back, Ottawa, 13.VII.1959 (2♂♂, 2♀♀, CNC); S. Kapuskasing, Beaver Falls, Kapuskasing R., 17.VI.1992 (1♂, 1♀, CNC); Marmora, 14.VI.1952 (1♀, CNC); Ogoki, 1.VII.1952 (24♂♂, 41♀♀, CNC); Ottawa, 11.IX.1947, 18.IX.1978 (35♂♂, 20♀♀, CNC); Ottawa, Ottawa R., Remic Rapids, 28.IX., 18.X.1991 (30♂♂, 25♀♀, CNC); Ottawa River, Remic Rapids, 18.VI.1949 (20♂♂, 19♀♀, CNC); Ottawa, Rideau River, 29.V.1992 (2♂♂, 4♀♀, CNC). Quebec: Baie James, L. Attila [53°34'N 77°33'W], L. Nathalie [53°27'N 77°25'W], 15/25.VII.1973 (12♂♂, 16♀♀ - in

alc., UMQ); Great Whale River, 13.VII.1949 (1♀, CNC); Hull, 8.VII.1923 (1♀, USNM); Rupert House, 27.VI.1949 (3♂♂, 1♀, CNC).

USA. Maine: Moosehead, 18.VII.1907 (3♂♂, 6♀♀, ANSP, MCZ, NYSM, USNM). **Michigan:** Gogebic, McDonald Lake, 22.VI.1964 (1♂, MSU). **Minnesota:** Pine, Mouth Snake R., 30.V.1951 (2♂♂, 6♀♀, UMSP). **New York:** St. Lawrence Co., Lotus Is. 21.IX.1922 (1♀, USNM).

Chorological Affinities. This species is often collected with T. minor, T. pectinifemur, and/or T. dasycoxa.

Phylogenetic Relationships. This species was placed as a questionable junior synonym of Clinocera simplex Loew by Osten Sacken (1878), which was later accepted by Melander (1902). After examining the holotype, Smith (1971) transferred longipes to the genus Trichoclinocera. This species is most closely related to T. ctenistes on the basis of facial colour patterns. Both species are believed to be closely related to T. dasycoxa and T. hamifera on the basis of similar chaetotaxy of the male fore femur.

Trichoclinocera minor (Melander)

Wiedemannia (Chamaedipsia) minor Melander 1928: 233.

Type Material Examined. HOLOTYPE, male labelled: "Ithaca, N.Y. [USA]/ VII.[19]01. [v. . . Johannsen] ", "TYPE/ Chamaedipsia/ minor/ Mel. [red label];

[genitalia cleared and placed in microvial beneath specimen]" (USNM).

Recognition. This species is distinguished by a wide gena and the shape of the clasping cercus in the male terminalia.

Description. Male. Face brown, with median carina; arista long and thin. Gena wide, with blue pruinescence, approximately equal to half height of eye (Fig. 86).

Pleura and coxae with blue pruinescence. Acrostichals absent; 6-7 dc; 1 ppm and short setae; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 sctl. Anteprenotum with pale setae; postnotum with patch of pale setae.

Wing narrow, infusate; single long basicostal seta; stigma absent; R_1 with setae along entire length; A_1 faint and long.

Fore femur with anteroventral row of short, stout setae, increasing in length apically; posteroventral row with long pale setae on basal third, becoming stout, long setae on apical two-thirds; 2-3 preapical anterior setae. Fore tibia with biserial row of short, stout setae beneath (Fig. 101). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal to length of claw.

Abdominal sternites, lateral margin of tergites and hypopygium (except phallus and clasping cercus) with blue pruinescence. Phallus arched. Clasping cercus hook-shaped, with apex curved dorsally. Surstylus slender and reduced (Fig. 124).

Female. Similar to male except as follows: tergite 8 with transverse row of very

long, stout setae (Fig. 125).

Geographical Distribution and Seasonal Occurrence. This species is confined primarily to the Appalachian region, with localities as far to the west as southern Ontario (Fig. 196). Label data indicate that adults of this species are known primarily from June to August, with one series from October. Two specimens of this species have been reared from pupae collected (8.VI.1992) in the Indian River near Almonte, Ontario (See "Source of Reared Material" under generic description).

Canada. New Brunswick. Campbellton, Sugarloaf Prov. Pk., 17.VII.1986 (1♂, CNC). **Ontario:** 5kmNW Almonte, Mill of Kintail Cons. Area, ex. Indian River, 29.VII.1990 (3♂♂, 4♀♀, CNC); Deep Creek, ex. Cedar Ck., 11.X.1986 (3♂♂, 1♀, UGO); Forks of the Credit Prov. Pk., Credit R., 28.VI.1991 (1♀, CNC); Halton Co., Lowville, Lowville Pk., 24.VII.1989 (2♂♂, 4♀♀, CNC); Guelph, 5.VII.1975 (1♀, UGO); Nipissing Co., Algonquin P.Pk., Oxtongue R., 19.VII.1991 (1♂, CNC). **Quebec:** Gatineau Pk., Lac Philippe Cpg'd, stream nr. Parent Beach, 7.VII.1990, 29.VII.1992 (6♂♂, 3♀♀, CNC); Hemmingford, 30.VI.1923 (1♂, 3♀♀, CNC); Perkins, 18.VII.1967 (2♂♂, CNC); Wakefield, 1.VII.1959 (2♂♂, CNC).

USA. Connecticut: Redding, 8.VI.1930 (1?, USNM). **New York:** Ludlowville, 27.VI.1973 (1♀, CU). **North Carolina:** Smokemont [Great Smoky Mtns N.P.], 2.VII.1941 (5♂♂, 1♀, USNM). **Pennsylvania:** Crawford Co., Woodcock Creek above Woodcock Lake Dam, 16.VII.1974 (2♀♀, PERC); Perry Co., along Sherman Creek, 1mi.W. Dromgold, 11.VII.1972 (6♂♂, 9♀♀, CAS). **Tennessee:** Van Buren Co., Fall Ck.

Falls St.Pk., Cane Ck. below falls, 19.VI.1990 (6♂♂,15♀♀,CNC). Virginia: Augusta Co., Briery Branch, 17.VII.1955 (1♀,USNM).

Chorological Affinities. Often collected with *T. hamifera* in large creeks.

Phylogenetic Relationships. This species was transferred to *Trichoclinocera* by Sabrosky (1967). At present the relationships of this species to the remaining species of the *T. longipes* group remains uncertain.

***Trichoclinocera ozarkensis* sp.nov.**

Holotype. Male labelled: "USA:AR[kansas]:Johnson Co./ Ozark Nat[ional]. For[est]. Haw/ C[rec]k. Falls 8.VI.1991/ ex. Haw Ck. BS9105/ B.J. Sinclair" (CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. Refers to the distribution of this species, which appears to be restricted to the Ozark Plateau of the Interior Highlands of eastern North America.

Recognition. This species is readily distinguished by features given in the key. The only other species of this genus found in the Interior Highlands is *T. pectinifemur*.

Description. Male. Face and gena with blue pruinescence; median carina dark. Arista

long and slender.

Pleura and coxae with blue pruinescence. Acrostichals lacking; 6 dc; 1 ppm and several setulae; 1 presut spal; 3 npl, lower slender; 2 psut spal; 1 pal; 2 setl. Postnotum with patch of pale setae; anteprenotum with short, pale setae.

Wing narrow, infusate; stigma absent; single long basicostal seta. R_1 with setae along entire length; cell dm slightly produced apically.

Fore femur with 2-3 anterior setae on apical third; anteroventral region with row of short, stout setae; posteroventral region with row of short stout setae with 3-4 lengthened setae near middle of femur, base with 2-3 long, pale setae. Fore tibia with biserial row of short, stout setae beneath (Fig. 102). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal to length of claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Claspig cercus shiny brown, strongly arched, with broadly, rounded apex (Fig. 127). Phallus with slight undulations (Fig. 126).

Female. Similar to male except as follows: modified chaetotaxy of forelegs not as pronounced; antero- and posteroventral rows of stout setae reduced in size; only 1-2 long, dark setae near middle of femur. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is endemic to the Interior Highlands of North America, confined to the Ozark Plateau of Arkansas, southern Indiana and southern Illinois (Fig. 196). It is both interesting and surprising that

there are very few, if any, records of Diptera endemic to the Interior Highlands, which was likely the reason that a recent analysis of the relationships of the insects of the Interior Highlands (Allen 1990), did not use any examples of Diptera.

Chorological Affinities. This species may be found to be sympatric with western populations of *T. pectinifemur*.

Phylogenetic Relationships. This species is believed to be most closely related to *T. agilis*, *T. falcata*, and *T. fumosa* on the basis of the shape of the claspings cercus.

Paratypes. USA. Arkansas: Johnson Co., Ozark Nat. For., Haw Ck. Falls, Haw Ck., 22.V., 8.VI.1991, B.J. Sinclair (18♂♂,29♀♀,CNC); Johnson Co., Ozark Nat. For., Haw Ck. Falls, 8.VI.1991, B.J. Sinclair (1♂,2♀♀,CNC); Logan Co., Ozark Nat. For., Shoal Ck., 23.V.1991, B.J. Sinclair (1♂,4♀♀,CNC); Pope Co., Ozark Nat. For., Falling Water Ck. and trib., 22.V.1991, B.J. Sinclair (4♂♂,35♀♀,CNC); Stone Co., Ozark Nat. For. at Hwy 5, trib. of West Livingston Creek, 21.V.1991, B.J. Sinclair (4♂♂,3♀♀,CNC); Stone Co., Ozark Nat. For., Blanchard Springs, stream nr. spring, 21.V.1991, B.J. Sinclair (2♂♂,CNC); Stone Co., Ozark Nat. For., Blanchard Springs, N. Sylamore R., 21.V.1991, B.J. Sinclair (4♂♂,4♀♀,CNC). Illinois: Pope Co., Shawnee Nat. For., Bell Smith Springs Rec. Area, sweeping creek, 20.V.1991, B.J. Sinclair (2♂♂,7♀♀,CNC); Pope Co., Shawnee Nat. For., Burden Falls, sweeping creek and falls, 20.V.1991, B.J. Sinclair (8♂♂,15♀♀,CNC). Indiana: Crawford Co., Hoosier

Nat. For., 13kmS English, rocky creek, B.J. Sinclair (27♂♂, 12♀♀, CNC); Hoosier N. For., 8kmS Eckerty, stony stream, 29.IV.1989, J.M. Cumming (15♂♂, 33♀♀, CNC); Perry Co., 22.V.1978, R.W. Meyer (1♂, PERC).

Trichoclinocera pectinifemur sp.nov.

Holotype. Male labelled: "Phoenixville/ Chester Co., P[ennsylvania]. [USA]/ 17.V.1964/ J.G. Chillcott" (CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. From the Latin pecten meaning comb or rake, in reference to the row of long spine-like setae on the posteroventral surface of the fore femur.

Recognition. This species is readily distinguished by the long spine-like setae of the fore femur and the blue pruinescence of the face. It is most similar to T. ozarkensis, but is readily distinguished by the features given in the key.

Description. Male. Face with blue pruinescence; brown-coloured median carina. First flagellomere laterally expanded. Arista long and slender.

Pleura and coxae with faint blue pruinescence. Acrostichals lacking; 5 dc; 1 ppm; 1 presut spal; 3 npl; 2 psut spal; 1 pal; 2 setl. Postnotum with patch of pale setae; antepnotum bearing pale, slender setae.

Wing narrow, infusate, with single basicostal seta; stigma lacking. Cell dm slightly produced apically; R₁ with setae along entire length.

Fore femur with 1-2 anterior setae on apical third; anteroventral region with single row of short, stout setae, becoming more stout apically. Posteroventral region of fore femur with row of slender, pale setae on basal fourth followed by 4-5 long, stout setae, equal in length to width of base of femur; apical half with row of short, stout setae. Fore tibia with biserial row of short, stout setae beneath (Fig. 103). Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal to length of claw.

Ventrum and lateral margins of abdomen with blue pruinescence, dorsum brown. Surstylus short and broad. Claspig cercus with broad square base and short finger-like lobe. Phallus with shallow undulations (Fig. 128).

Female. Similar to male except as follows: fore tibia with biserial row of ventral setae less stout. Anteroventral region of fore femur similar to male; setae at mid-point of posteroventral region reduced to 2-3 widely spaced long, stout setae and several long slender, pale basal setae. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is primarily found in the northern Appalachian mountains, but also extends as far west as Indiana (Fig. 199). In Ontario, *T. pectinifemur* is the first species of *Trichoclinocera* to appear in the spring, with adults collected in the months of May and June.

Emergence trap collections from Pennsylvania generally indicate that eclosion of

adults of this species occurs from mid to late May (Masteller, unpubl. data). A specimen of this species was reared from a pupa collected from a creek near Battleground, Indiana (See "Source of Reared Material" under generic description).

Chorological Affinities. In the Ottawa River, this species was collected along with *T. longipes* and *T. dasycoxa*.

Phylogenetic Relationships. At present the relationships of this species to the remaining species of the *T. longipes* group remains uncertain.

Paratypes. Canada. Ontario: Bruce Pen[insula]., Oliphant, 30.V.1946, G. Steyskal (3♀♀,USNM); Elora, 10.VII.1982, B. Sinclair (1♂,UGO); Guelph, 19.V.1968, L.L. Tibbles (1♂,UGO); Guelph, 30.V.1977, A.A. Konecny, (1♂,1♀,ROGC,UGO); Guelph, 7.VI.1977, E.A. Innes (2♀♀,UGO); Halton Co., Lowville Pk., Bronte Ck., 12.V.1990, 17.V.1991, B.J. Sinclair (11♂♂,14♀♀,CNC); Havlock, 11.VI.1977, J.W. McCreadie, (2♀♀,UGO); Ottawa, 23.V.1927, C.H. Curran (1♀,CNC); Ottawa, 17.VI.1956, J.R. Vockeroth (1♀,CNC); Ottawa, Ottawa R., Remic Rapids, 22-24.VI.1991, B.J. Sinclair (8♂♂,4♀♀,CNC); Ottawa River, Remic Rapids, 18.VI.1949, G.E. Shewell (5♂♂,19♀♀,CAS,CNC); Ottawa, Rideau R., Carleton Univ., 12.V.1991, B.J. Sinclair (2♂♂,12♀♀,CNC); Stitsville, 31.V.1938, G.E. Shewell (16♂♂,3♀♀,CNC); Wellington Co., 1968-1970, P. Harper (32♂♂,43♀♀,UMQ: in alc.). Quebec: Blanche Riv., Power House, 28.V.1949, G.E. Shewell (6♀♀,CNC); Chandler, 2.VII.1971, B.V. Peterson,

15♂♂,4♀♀,CNC); Hemmingford, 29.VI.1923, C.H. Curran (4♂♂,1♀,CNC,USNM); St. Chrysostome, 28.VI.1927, G.S. Walley (1♀,CNC).

USA. Connecticut: Redding, 30.V.1931, 10.VI.1933, A.L. Melander (2♂♂,1♀,USNM). **Indiana:** Jennings Co., nr. San Jacinto, 16.V.1984, R. Meyer (4♂♂,PERC); Jennings Co., Bigger Twp., Big Graham Creek, 29.IV.1975, R.W. Meyer (1♂,2♀♀,PERC); Tippe[canoe]. Co., Battleground, Burnett's Cr., 22.IV.1983 (1♂ - reared, in alc., PERC); Warren Co., River Bank: Green Hill, 14.V.1987, R.W. Meyer (2♂♂,1♀,PERC). **Maryland:** Montg. Co., Clarksburg, 20-22.V.1988, W.E. Steiner & J.M. Swearingen (4♂♂,8♀♀,USNM). **Massachusetts:** So[uth]. Hadley, 14.V.1936, M. Chapman (1♀,USNM). **New York:** Ithaca, 9.VI.[19]01, O.A. Johannsen (1♀,CU); W. Nyack, 5.VI.1938, A.L. Melander (1♂,1♀,USNM). **Ohio:** Adams Co., Cave Run, 3miSW Dunkin[s]ville, 29.V.1983, R. Hurley (1♀,HSU). **Pennsylvania:** Centre Co., Whipple Dam St. Park, 21.V.1980, D. Wilder (17♂♂,14♀♀,CAS); Chester Co., Phoenixville, 17.V.1964, J.G. Chillott (13♂♂,3♀♀,CNC). **Virginia:** [Dinwiddle Co.], Difficult Run [38°58'N 77°14'W], 24.V.1932, E. Meyers (3♂♂,USNM). **West Virginia:** Randolph Co., Harmon, Dry Fk. Cheat River, 5.VI.1990, B.J. Sinclair (3♂♂,2♀♀,CNC).

Comments. In the CNC, specimens of this species were labelled with Melander's red type and paratype labels as Wiedemannia (Chamaedipsia) currani Melander. This species was apparently not published and remains simply a manuscript name.

Unplaced Species of Trichoclinocera

Trichoclinocera fuscipennis Saigusa

Trichoclinocera fuscipennis Saigusa, 1965: 55.

Type Material Examined. PARATYPES: [Japan] Kyushu, Magaribuchi, Fukuoka, 2.V.1962, T. Saigusa (1♂, USNM); [Japan] Kyushu, Magaribuchi, Sagara, Fukuoka, 2.V.1962 (2♂♂, 1♀, CNC).

Recognition. Distinguished from other Japanese species by dark legs, bright blue pruinescence of the face, spine on hind tibia lacking, and stout anterodorsal and posterodorsal setae on mid and hindlegs lacking.

Description. Male. Face with blue pruinescence and medial carina light brown in colour. Arista long and slender.

Pleura and coxae with blue pruinescence and ppm, npl and sctl with pale blue pruinescence. Acrostichals lacking; 6 dc; 1 ppm and several setulae; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 sctl. Postnotum with patch of pale setae; antepronotum with several pairs of setulae.

Wing narrow, infusate; stigma lacking; single basicostal seta. R₁ with setae along entire length; cell dm slightly produced apically.

Fore femur with 1-2 preapical anterior setae; anteroventral region with row of

short, stout setae, along entire length; posteroventral region with row of 5-6 dark, stout setae (equal in length to width of femur) on basal two-thirds; base with 5-6 long, pale setae. Fore tibia with biserial row of short, stout setae beneath. Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform, subequal to length of claw.

Abdominal sternites, lateral margin of tergites and hypopygium (except phallus and clasping cercus) with blue pruinescence. Phallus long and slightly undulated. Surstylus narrow. Clasping cercus slender finger-like lobe, bearing stout setae on inner dorsal margin.

Female. Similar to male except as follows: long, dark seta of posteroventral region of fore femur widely distributed along leg, intermixed with short, stout setae. Terminalia as described in generic description.

Geographical Distribution and Seasonal Occurrence. This species is known from the Japanese islands of Kyushu and Honshu, with adults collected in April and May (Saigusa 1965).

Chorological Affinities. There are a total of 7 species of Trichoclinocera from Japan, of which 5 are undescribed (Saigusa, pers. comm.).

Phylogenetic Relationships. This species is part of an unresolved trichotomy with the T. stackelbergi group and the T. longipes group.

Trichoclinocera maewa Smith

Trichoclinocera maewa Smith, 1965: 103.

Type Material Examined. HOLOTYPE, male labelled: "HOLOTYPE [red bordered circle]"; "Spray-splashed rocks/ in River Maewa./ 25.i.1962."; "[Nepal] TAPLEJUNG DISTR./ Dobhan.c 3500'"; "BRIT. MUS./ East Nepal Exp./ 1961-62./ R.L. Coe Coll./ B.M. 1962-177"; "HOLOTYPE/ Trichoclinocera/ maewa/ K.G.V. SMITH" [genitalia cleared and mounted in Canada Balsam below specimen] (BMNH).

Recognition. This is the only known species of Trichoclinocera from Nepal. Any further details enabling quick recognition must await Saigusa's revision of the Asian and Oriental species of this genus.

Description. Male. Face with bright blue pruinescence; head collapsed, so it is difficult to view modifications of face.

Pleura, coxae, pprn and npl with pale blue pruinescence. Acrostichals lacking; 5 dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 pal (slender); 2 scrl. Postnotum with patch of dense, long, pale setae; anepisternum with short, dark setae; katapisternum with long, white setae.

Wing narrow, hyaline; stigma lacking; single basicostal seta. R₁ with setae along entire length; cell dm slightly produced apically.

Anteroventral region of fore femur with row of short, slender, pointed setae,

increasing in length apically, forming to 2-3 rows on basal half; posteroventral region with row of pale slender setae. Fore tibia with biserial row of short, stout setae beneath. Mid femur lacking erect, anterodorsal setae. Empodium pulvilliform.

Hypandrium long and slender; phallus long and straight, with sharp subbasal fold. Epandrium narrow; surstylus narrow and straight. Slender finger-like clasping cercus, bearing stout setae on inner dorsal margin.

Female. Not examined.

Geographical Distribution and Seasonal Occurrence. This species is known only from the type locality.

Phylogenetic Relationships. The relationships of this species in Trichoclinocera remains uncertain and is currently unplaced pending a greater knowledge of the Asian and Oriental faunas.

List of described species included in Trichoclinocera.

- N agilis Sinclair sp.nov.
- N cascadensis Sinclair sp.nov.
- N comata (Melander), 1928: 232 (Wiedemannia (Chamaedipsia)) [lectotype designated] (USNM) New combination.
- N stenistes (Melander), 1928: 234 (Wiedemannia (Chamaedipsia)) (USNM)

[lectotype designated].

- P cyanescens (Vaillant), 1960c: 180 (Seguyella) New combination.
- N dasycoxa Sinclair sp.nov.
- P dasyscutellum (Saigusa), 1965: 54 (Acanthoclinocera) [paratypes examined] New combination.
- N dolicheretma (Melander), 1902: 241 (Clinocera) [lectotype examined] (USNM).
 syn. brunnipennis (Melander), 1928: 232 (Clinocera (Bergenstammia))
 [lectotype designated] (USNM) New synonymy.
- N falcata Sinclair sp.nov.
- N fumosa (Vaillant), 1960b: 119 (Wiedemannia (Roederella)) (type locality is Tennessee not New York as listed by Melander 1965) New combination.
- P fuscipennis Saigusa, 1965: 55 [paratypes examined].
- N hamifera (Melander), 1928: 233 (Wiedemannia (Chamaedipsia)) [lectotype designated] (USNM).
 syn. saltans (Vaillant), 1960b: 122 (Wiedemannia (Roederella)) (type locality is Tennessee not New York as listed by Melander 1965)
 New synonymy.
- N,P lapponica (Ringdahl), 1933: 281 (Clinocera) [lectotype designated] (UZIL) New combination.
- N longipes (Walker), 1849: 504 (Heliodromia) [holotype examined] (BMNH).
- O maewa Smith, 1965: 103 [holotype examined] (BMNH).
- N minor (Melander), 1928: 233 (Wiedemannia (Chamaedipsia)) [holotype examined]

(USNM).

N ozarkensis Sinclair sp.nov.

N pectinifemur Sinclair sp.nov.

P rostrata (Vaillant), 1960c: 181 (Seguyella) [syntypes examined] (ZISP) New combination.

N rupestris Sinclair sp.nov.

P stackelbergi Collin, 1941: 238 [lectotype designated] (ZISP).

P tadjikistana (Vaillant), 1960c: 184 (Seguyella) [syntypes examined] (ZISP) New combination.

List of examined, undescribed species included in Trichoclinocera.

Two additional species of Trichoclinocera may yet be described. However, due to lack of material I have chosen not to designate them as formal species. These possible additional species are known from the following localities:

Trichoclinocera sp. 1: One female from Alabama, USA (USNM).

Trichoclinocera sp. 2: Three males and two females North Carolina and Washington, DC (USNM,CAS).

4.2.4 GENUS CLINOCERA MEIGEN

Clinocera Meigen, 1803: 271. Type-species, C. nigra Meigen, 1804 (subsequent mon.).

Atalanta Meigen, 1800: 31. Suppressed by I.C.Z.N., 1963: 339.

Paramesia Macquart, 1835: 656. Type-species, P. wesmaeli Macquart (des. Coquillett 1903: 255).

Hydrodromia Macquart, 1835: 658. Type-species, Heleodromia stagnalis Haliday (des. Coquillett 1903: 251).

Notes on Synonymy. Macquart (1835) erected a new genus, Hydrodromia, to include two former species of Heleodromia (stagnalis and bipunctata). Hydrodromia was first classified as a subgenus of Clinocera by Kertész (1909) and Engel (1918) and subsequently has been recognized as such. With the establishment of the monophyly of the genus Clinocera, the recognition of subgenera is no longer considered taxonomically useful, or appropriate, unless several new subgenera are recognized (see Sec. 4.2.4.2).

Recognition. Clinocera is most similar to Oreothalia and Kowarzia, but is readily distinguished by lack of setulae on face, or presence of apical phallic filament, and other features given in the key.

Description. Male. Eyes densely haired. Face usually with pruinescence; lower margin lacking median membranous cleft; setulae occasionally present. Antenna with short, cylindrical scape and oval pedicel; first flagellomere oval; arista two-segmented. Gena

narrow, with suture from base of palpus to margin of eye (Fig. 61). Anterior ventrocervical sclerite reduced to darkly pigmented membranous patch. Labrum broadly triangular; dorsal margin with long, slender apodeme. Lacinia fused to stipes apically, tip fused to labial sclerite and labial paraphysis; palpus short (appressed to labrum in lineata group); hypopharynx needle-like, with broad base; labellum sucker-like; pseudotracheae absent.

Pruinescence of plura and coxae variable in colour; scutum bivittate. Several acrostichals anterior to first dc; 5 dc (occasionally as many as 10); 1 ppm; 1 presut spal; 2-3 npl; 1-2 psut spal; 1 pal; 2 scll. Postnotum with patch of setae; anteprenotum with setulae.

Wing infusate with cloudy spots (Fig. 71) or lacking; stigma present, faint or absent; costa with stout setae from R_1 to R_{4+5} ; auxillary crossvein between R_{2+3} and R_4 sometimes present.

Fore femur and tibia with stout setae beneath; preapical anterior comb of fore tibia often present. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Fifth tarsomere with dorsoapical extension present in C. stagnalis and C. gubernans groups; empodium pulvilliform.

Tergite 8 narrow. Hypandrium usually lacking macrosetae (present in stackelbergi). Phallus with whip-like apical filament, arching anteriorly; ejaculatory apodeme small, inconspicuous and removed from base of phallus. Surstylus large, wide, usually extending beyond epandrium (Fig. 136). Cercal plate with long setae evenly distributed; clasping cercus large, with modified setae on inner face. Sclerotized accessory

glands not observed in macerated specimens.

Female. Similar to male except as follows: length of segment 8 equal to or less than preceding segment; T10 and S10 split medially; cerci narrow, straight (Fig. 138). Spermatheca a loosely to tightly coiled tube, often with thinly sclerotized, oval glandular tissue at apex; small, triangular genital fork often present (Fig. 137).

Included Taxa and Geographical Distribution. There are approximately 40 described species of Clinocera worldwide. However there are many undescribed species, including more than 30 from the Nearctic region alone.

There are 4 species of Clinocera restricted to eastern North America and 25 species restricted to the western region.

Phylogenetic Relationships. This genus is the sister group to Oreothalia and they share a number of characters, for example; lower margin of face straight, lacking membranous cleft and surstylus large, wide, probably functioning as a phallic guide.

This genus may be divided into seven species groups as described in Sec. 4.2.4.2. The phylogenetic relationships of these groups are discussed further in Sec. 5.1.4.

Bionomics. This genus is generally confined to cool, headwater streams, springs and seepages. In rheocrene springs in southern Ontario, adults may be found throughout the winter months on the underside of emergent rocks (Sinclair and Marshall 1986). In

Europe, C. wesmaeli has also been observed to overwinter as adults (Chvála 1983).

Adults of Clinocera have been observed feeding on larvae of Thaumaleidae (Sinclair and Marshall 1986). On the vertical rock face of a roadcut seep C. olivacea Melander was observed feeding on larval Chironomidae and C. fuscipennis Loew was observed feeding on an adult midge. Vaillant (1956a) listed seven species of Clinocera that were predacious (both adult and larval stages) on larvae living in madicolous habitats. Adults of C. stagnalis have been observed feeding on flies trapped in the surface film (Lindroth (1931) in Downes and Smith 1969). Adults of C. binotata were observed apparently attempting to feed on blackfly larvae which were found on rocks covered by a thin film of water (Peterson 1960). Clinocera nr. trunca was observed grasping a simuliid adult netted from a blackfly swarm (Peterson 1960).

This genus has been collected from emergence traps used in stream surveys in Quebec (Harper 1980; Landry and Harper 1985) and Germany (Wagner 1980, 1982c; Caspers and Wagner 1982) and madicolous habitat surveys (Bertrand 1948; Vaillant 1956a; Lindegaard and Thorup 1975; Sinclair and Marshall 1986).

Immature Stages. Larval Habitat. Larvae and pupae of C. stagnalis were collected on broken and partially decomposing vegetation in shallow margins of a lake (Brindle 1973). Larvae and pupae of this species were also observed in mats of filamentous algae growing on rocks in a slow moving stream (Brindle 1973). In southern Ontario, larvae of Clinocera were more numerous in summer than winter months and collected from mats of algae hanging from vertical rock faces in seepage habitats (Sinclair 1987).

Recognition. A variety of larvae of Clinocera have been briefly described and/or figured (Brindle 1964, 1973; Steyskal and Knutson 1981). However, only Vaillant (1952a) provided useful and detailed descriptions, which included the head capsules. Larvae of Clinocera may be distinguished from Wiedemannia and Trichoclinocera by the terminal abdominal segment which bears two short, dorsolateral lobes and a partially divided apical lobe.

Pupal Habitat. Pupae of Clinocera have been collected from saturated mats of filamentous algae growing along cascading spring-streams and seeps (Sinclair 1987).

Recognition. The pupae have also been briefly described and figured (Brindle 1973; Steyskal and Knutson 1981), but again only Vaillant (1952a) provided a detailed description. Pupae of Clinocera are characterized by a single transverse ring of abdominal spines, short caudal hooks and indistinct mesonotal setae.

List of described species included in Clinocera.

P appendiculata (Zetterstedt), 1838: 559 (Wiedemannia) [examined].

 syn. aucta (Zetterstedt), 1849: 3019 (Brachystoma).

storchi Mik, 1880: 348 (as a var. of appendiculata).

simplicinervis Frey, 1913: 62 (as a var. of aucta).

A aquatica (Becker), 1914: 122 (Atalanta).

N binotata Loew, 1876: 325 [holotype examined].

 syn. bicincta (error) Tucker, 1907: 97.

P,N bivittata Loew, 1864: 258 [holotype examined] (ZMHB).

syn. longifurca Melander, 1928: 231 [holotype examined] (USNM)

New synonymy.

bivittata (error) Vaillant, 1978: 467.

N brevitibia Melander, 1928: 235 [lectotype designated].

O chilamche Smith, 1965: 107 [examined].

N conjuncta Loew, 1860: 80 [holotype examined].

syn. taos Melander, 1902: 469 [holotype examined] New
synonymy.

undulata Melander, 1928: 230 [holotype examined] New
synonymy.

S cubatao Smith, 1962: 264 (C. (Hydrodromia)).

S cucama Smith, 1962: 265 (C. (Hydrodromia)).

S ditaeniata Bezzi, 1909: 387 (C. (Heleodromia)) [examined].

S empodiata Collin, 1933: 322 [examined].

O feuerborni Engel, 1931: 487.

O fluviatilis Brunetti, 1913: 34.

P fontinalis (Haliday), 1833: 160 (Heleodromia) [examined].

N fuscipennis Loew, 1876: 324 [holotype examined].

U gressitti Smith, 1964: 327.

N gubernans (Melander), 1928: 234 (Wiedemannia (Chamaedipsia)) [holotype
examined] New combination.

N lecta Melander, 1902: 243 [lectotype designated].

- N lineata Loew, 1862: 207 [lectotype designated].
- P maroccana (Séguy), 1941, 29 (Hydrodromia).
 syn. algira (Vaillant), 1952b: 65 (Atalanta (Hydrodromia)).
- N maculata Loew, 1860: 79 [holotype examined].
- P megalatlantica (Vaillant), 1956c: 65 (Atalanta (Atalanta)).
- P minutissima (Vaillant), 1960c: 172 (Atalanta (Atalanta)).
- O nadi Smith, 1965: 108.
- P nigra Meigen, 1804: 292. [examined].
 syn. unicolor (Curtis), 1834: plate 513 (Heleodromia).
 roberti (Macquart), 1835: 657 (Paramesia).
 ssp. orientalis Vaillant, 1965: 148.
- P,N nivalis (Zetterstedt), 1838: 545 [examined].
- N olivacea Melander, 1928: 233 [holotype examined].
- S oriunda Collin, 1933: 323 (C. (Hydrodromia)) [examined].
- O pani Smith, 1965: 108.
- N prasinata Melander, 1928: 232 [holotype examined].
- P rufipes Bezzi, 1899: 147 (as a ssp. of nigra).
- P schremmeri (Vaillant), 1965: 149 (Atalanta (Atalanta)) [examined].
- P schumanni Joost, 1981a: 184.
- P stackelbergi (Vaillant), 1960c: 174 (A. (Kowarzia)) [examined].
- P,N stagnalis (Haliday), 1833: 159 (Heleodromia) [examined].
 syn. westermanni (Zetterstedt), 1838: 558 (Brachystoma).

genualis Coquillett, 1910: 124 [holotype examined] New
synonymy.

A tripunctata Smith, 1969: 291 (C. (Hydrodromia)) [examined].

N trunca Melander, 1928: 230 [holotype examined].

O velutina (Engel), 1931: 488 (Kowarzia).

P wesmaeli (Macquart), 1835: 656 (Paramesia) [examined].

syn. nebulosa (Zetterstedt), 1838: 559 (Brachystoma).

sabulosa (error for nebulosa) (Engel), 1940: 155 (Atalanta
(Hydrodromia)).

Nomina nuda

carpatica Vaillant, 1978: 467.

musciola Vaillant, 1978: 467.

restonica Vaillant, 1978: 468.

rhodani Vaillant, 1978: 468.

segregata Vaillant, 1978: 468.

vesubiana Vaillant, 1978: 468.

List of examined, undescribed species included in Clinocera.

Clinocera spp. from Nearctic region (include approx. 30 species).

Clinocera sp. 1: One male and one female from Tasmania, Australia (CNC).

Clinocera sp. 2: Males and females from NSW, Australia (AMS, USNM).

Clinocera sp. 3: One male from Chile (CNC).

Clinocera sp. 4: One male and one female from Costa Rica (CNC).

Clinocera sp. 5: Six females from Venezuela (CNC).

Clinocera sp. 6: One male and two females from Mexico (CNC,USNM).

Clinocera sp. 7: Three males and three females from Mexico (USNM).

Clinocera sp. 8: Males and females from Costa Rica (CNC).

Clinocera sp. 9: Two males and two females from Costa Rica (CNC).

Clinocera sp. 10: Two males and one female from Costa Rica and Venezuela (AMNH,CNC).

4.2.4.1 KEY TO ADULT MALES OF THE SPECIES-GROUPS OF

CLINOCERA

- 1 Fifth tarsomere with dorsoapical extension; wings with spots at base of R_4 , apex of cell dm, r-m crossvein and apex of cell bm (Fig. 71); phallus subapically split at base of phallic filament (Fig. 136) C. stagnalis species group
- 1' Fifth tarsomere lacking, if present facial tubercle present; wing spots present or absent; phallus slender, lacking subapical split at base of phallic filament 2
- 2 Clasping cercus pointed apically (except C. nigra), with dense setulae on inner surface (Fig. 135); if clasping cercus truncate, ppm seta slender and short C. nigra species group

- 2' Clasping cercus variable, if pointed lacking setulae or if truncate ppm seta(e)
unmodified 3
- 3 Apical margin of the clasping cercus truncate, bearing stout spines on apical third of
inner face; surstylus often with subapical notch (Fig. 131)
..... *C. conjuncta* species group
- 3' Clasping cercus not truncate apically, surstylus variable 4
- 4 Surstylus truncate apically, not extending freely beyond epandrium; 1 postsutural
supraalar seta (Figs. 133, 134) 5
- 4' Surstylus not truncate apically, extending freely beyond epandrium (Figs. 129,130);
2 (rarely 1) postsutural supraalar seta 6
- 5 Apical phallic filament flexible, strongly geniculate at base; membranous region at
base of phallic filament dorsoventrally expanded; surstylus subrectangular, often
with slender apex (Fig. 134) *C. lineata* species group
- 5' Apical phallic filament heavily sclerotized with reduced flexibility (except sp.#2 which
has long coiled filament); base of filament not expanded; surstylus rectangular,
apical margin straight (except sp. #2) (Fig. 133) *C. sp.#22* species group
- 6 Pronounced facial tubercle present; fifth tarsomere with dorsoapical extension (except
sp.#17) *C. gubernans* species group

- 6' Facial tubercle lacking or weakly developed; fifth tarsomere lacking dorsoapical extension C. fuscipennis species group

4.2.4.2 SPECIES-GROUPS OF CLINOCERA

Traditionally, seven subgenera of Clinocera have been recognized (Chvála and Wagner 1989). The subgenus Kowarzia, has been elevated to generic level and Archiclinocera and Hypoclinocera are believed to be junior synonyms of Kowarzia. The subgenera Phaeobalia and Bergenstammia have also been removed from Clinocera and elevated to generic rank. These two genera are believed to be most closely related to Wiedemannia. Thus, only the subgenera Clinocera (s.s.) and Hydrodromia remain.

The subgeneric concepts were originally derived from European species and consequently it has often been difficult to classify species from outside of this region (see Melander 1902). Historically, Hydrodromia included all species with distinct wing spots and undivided clasping cercus and Clinocera (s.s) included any species that did not fit into the other six subgenera. After surveying species of Clinocera from all biogeographic regions, I consider these two subgenera of no further taxonomic value and currently recognize seven species groups. The continued recognition of these two subgenera would require the naming of at least four new subgenera, which I consider an unnecessary proliferation of names, which would lead to further confusion.

The following species groups of Clinocera are tentatively proposed. Types of several described species require examination to facilitate correct species group placement and two groups (fuscipennis and gubernans) are presently not clearly defined. The

phylogenetic justification for these species groups of Clinocera are presented in Sec. 5.1.4.

The C. gubernans Species Group

The C. gubernans group is characterized by a large facial tubercle on the lower two-thirds; 2 psut spal; slender phallus with long flexible phallic filament (Fig. 129); fifth tarsomere with dorsoapical extension (except sp.#17); apical half of spermatheca loosely coiled, with terminal tissue remnants only.

This species group is currently restricted to the western Nearctic region and includes C. gubernans and several new species (spp. #?17, 28,29).

The C. fuscipennis Species Group

The monophyly of this group is currently not clearly defined. Several species of the C. fuscipennis group have an indistinct facial tubercle which suggests a close relationship with the C. gubernans species group. This group is also characterized by a narrow clasping cercus with small anteroapical projection; phallus slender with long flexible phallic filament (Fig. 130); normally 2 psut spal; apical half of spermatheca loosely coiled, with terminal tissue remnants only.

This group is also confined to the Nearctic region and includes C. fuscipennis, C. lecta, C. brevitibia and two new species (spp. #?3,1A).

The C. conjuncta Species Group

The C. conjuncta group is characterized by a truncate apical margin of the clasping cercus, bearing stout spines on apical third of inner face; surstylus with subapical notch; phallus often with slender, sclerotized margin of subapical membranous region at base of filament (Fig. 131). Female terminalia with posterior margin of S8 invaginated; S8 extended posteriorly beneath S10; dorsolateral margin of S8 darkly pigmented; spermatheca lacking terminal sclerotized receptacle.

This species group is presently restricted to the western Nearctic region (except C. conjuncta) and includes C. conjuncta, C. olivacea, C. prasinata, C. trunca and several new species (spp. #12A,12B,13 (?#11, #33)).

The C. sp.#22 Species Group

This species group is characterized by a small truncate head; short truncate surstylus; slender clasping cercus with short, stout setae on inner face (Fig. 132); phallic filament usually heavily sclerotized, reducing flexibility (except sp.#2); hypandrium small in comparison to epandrium (Fig. 133); apical half of spermatheca loosely coiled, with terminal tissue remnants only.

This group includes four undescribed species primarily from the western Nearctic region (spp. #2,22,23,24). Despite lacking a terminal spermathecal receptacle, this species group could be most closely related to C. lineata group on the basis of a truncate surstylus and small hypandrium.

The C. lineata Species Group

Members of this group are characterized by an apical phallic filament strongly geniculate at base, membranous region at base of phallic filament dorsoventrally expanded; hypandrium small in comparison to epandrium; surstylus subrectangular, often with slender apex (Fig. 134); scutum often with dark, median vittae. The female spermatheca is a loosely to tightly coiled, tapering tube with small, thinly sclerotized, apical spherical-shaped structure.

The lineata group includes C. stackelbergi, C. velutina and several undescribed species from the Oriental region and Japan, which were previously classified in Kowarzia on the basis of facial setulae. The C. lineata group also includes C. chilamche from Nepal, C. minutissima from mid-Asia and probably C. megalatlantica from North Africa; C. lineata and several new Nearctic species (spp.# 14,26); several undescribed species from Central America (spp.#8,9); and several undescribed species from the Australasian region (spp. #1,2).

The C. nigra Species Group

The C. nigra group is characterized by the clasping cercus normally pointed apically (except nigra), with dense setulae on inner surface; apical filament of phallus broadly flattened (Fig. 135); anterior subapical comb of fore femur lacking in C. nigra and C. empodiata; spermatheca a loosely to tightly coiled, tapering tube with small, thinly sclerotized, apical spherical-shaped structure.

This group includes C. appendiculata, C. nigra, C. rufipes, C. schremmeri, C.

schumanni and C. bivittata from the Palearctic region; C. longifurca and an undescribed species (sp.#25) from the Nearctic region; and C. empodiata and C. pani from the Neotropical and Oriental regions respectively.

The C. stagnalis Species Group

Members of the C. stagnalis group are characterized by distinct round spots on the wings, usually at base of R_4 , apex of cell dm, r-m cross-vein and apex of cell bm; cell dm truncate; auxillary vein between R_4 and R_{2+3} , rare (present in binotata); fore femur often with stout, long, basal setae; legs reddish in colouration with pale apex ("knees"); fifth tarsomere with dorsoapical extension; face and thoracic pleura with silvery-blue pruinescence; phallus subapically split at base of phallic filament; phallic filament broadly flattened; genital fork present (Fig. 136); spermatheca a loosely to tightly coiled, tapering tube with small, thinly sclerotized, apical spherical-shaped structure (Fig. 137).

Many species of this group were traditionally placed in the subgenus Hydrodromia. This group includes C. fontinalis, C. maroccana, C. nivalis, C. stagnalis, C. wesmaeli from the Palearctic region; C. binotata, C. maculata and new sp.#21 from the Nearctic; C. oriunda, possibly C. ditaeniata, and several undescribed species from the Neotropical region (sp. #5).

Unplaced species of Clinocera (types not yet examined).

cubatao Smith

cucama Smith

feuerborni Engel

fluvialis Brunetti

nadi Smith

tripunctata Smith

gressitti Smith (nigra species group ?)

4.2.5 GENUS WIEDEMANNIA ZETTERSTEDT

Wiedemannia Zetterstedt, 1833: 207. Nomen nudum.

Wiedemannia Zetterstedt, 1837: 32. Nomen nudum.

Wiedemannia Zetterstedt, 1838: 559. Type-species, W. borealis Zetterstedt (des. Coquillett 1903: 258) (= Heleodromia bistigma Curtis).

Agyrtomyia Gistel, 1848: XI. New name for Wiedemannia.

Macellaria Gistel, 1848: 153. New name for Wiedemannia.

Wiedmannia (error) Bigot, 1856: 55,70,90.

Roederia Mik, 1881: 326. Type-species, Clinocera longipennis Mik (= B. escheri Zetterstedt) (monobasic).

Camelopsis Engel, 1918: 14,232 (as subgenus). Type-species, C. phantasma Mik (original designation).

Recognition. This genus encompasses a large diversity of forms, which have a distinct notch or carina on the lower margin of the face and often the acrostichals are well

developed. Males are readily recognized by the position of the subepandrial sclerite, biarticulated phallus of the male terminalia and one-component clasping cercus. Females are difficult to identify unless associated with males, but should be readily distinguished on the basis of features given in the key.

Description. Male. Eyes densely haired. Face with deep membranous cleft, extending at least one-third height of face. Antenna with cylindrical scape and oval pedicel; first flagellomere onion-shaped; short arista two-segmented. Gena wide with ridge extending from base of palpus to notch on face (Figs. 65,66). Anterior ventrocervical sclerite present. Labrum broadly triangular; dorsal margin with slender apodeme. Lacinia fused to stipes apically, tip fused to labial sclerite and labial paraphysis; hypopharynx tridentate, with broad base gradually tapering to sharp point; labellum sucker-like; pseudotracheae absent.

Pruinescence of pleura and coxae variable in colour; scutum usually faintly bivittate. Acrostichals may be well developed or lacking; 5-7 dc, often with setulae intermixed; 1-2 ppm; 1 presut spal; 2-3 npl; 0-1 psut spal; 1 pal; 2 sctl, setulae often present on disc and margin; additional setulae often scattered on scutum. Postnotum with patch of setae; anteprenotum with short setae of variable number and thickness.

Wing with cell dm long and narrow with upper end produced; stigma present, often faint; either elongate or circular (Fig. 74). Costa spines from R_1 to R_4 ; M acutely branched, often coalesced for a short distance before M_1 and M_2 branch; or M widely branched.

Fore femur and tibia lacking modified setae beneath; preapical anterior comb of fore femur lacking. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Fifth tarsomere often with dorsoapical extension; empodium pulvilliform.

Tergite 8 narrow. Phallus with articulated distiphallus; hypandrium with macrosetae; ejaculatory apodeme separated from base of phallus. Surstylus tooth-shaped, meeting corresponding surstylus of opposite epandrium, holding phallus firmly. Cercal plate with setae confined to ridge on apical third; clasping cercus large and bearing modified setae. Subepandrial sclerite separated from base of clasping cercus (Fig. 150). The terminalia of W. hughesi (Fig. 140) is highly modified. Sclerotized accessory glands not observed in macerated specimens.

Female. Similar to male except as follows: female terminalia unmodified, segments gradually tapering with small terminal cerci. Spermatheca in form of a lightly sclerotized tapering tube, becoming slightly convoluted apically; apex reduced to loosely connected tissue in macerated specimens (Fig. 152).

Included Taxa and Geographical Distribution. This genus includes approximately 85 described species distributed throughout the Palearctic (78 described species), Nearctic, and Afrotropical regions. Wiedemannia is also recorded from Nepal and an undescribed species is known from Papua New Guinea. In North America, Wiedemannia is confined to the arctic region, the western Cordillera, and an isolated population on an island in Lake Superior (see W. simplex). This genus is not found in the Appalachian region.

Phylogenetic Relationships. Wiedemannia appears to be most closely related to Phaeobalia and Bergenstammia on the basis of a biarticulated phallus (see Sec. 5.1.2).

This genus may be divided into approximately seven or eight species groups. The phylogenetic relationships of these groups are outlined in Sec. 5.1.5).

Bionomics. Adults of Wiedemannia may be collected from emergent rocks in cool, fast-flowing streams, creeks and rivers. In western North America, W. simplex (Loew) was collected on large emergent rocks, together with species of Trichoclinocera, Roederiodes and Proclinopyga. Adults have also been collected in emergence traps (Wagner 1980, 1982c). Adults are generally believed to feed on emerging Chironomidae, Ephemeroptera and Plecoptera (Vaillant 1967a). They search for prey in a manner similar to that described for Trichoclinocera. Two species of Wiedemannia (W. bistigma, W. lota) have been observed feeding on dead insects caught in mats of algae (Laurence 1953). Adults of an unknown species of Wiedemannia were also observed feeding on simuliid larvae from the water's edge in mountain streams of California (Wirth and Stone 1956).

Vaillant (1967a) studied the ecological requirements of Wiedemannia in streams and rivers of France. He found many species distributed along the same water course, but they were limited to specific regions according to elevation, water temperature, flow rate and food resources. The greatest diversity of species were found between approximately 300-1000m, where the daytime water temperatures reached above 15°C during the summer.

The mating behaviour of two species of Wiedemannia (W. bistigma, W. lepida)

have been described (Laurence 1953, Rogers 1981). Mating occurs in large numbers, clustered on the vertical face of emergent rocks, in rapidly flowing streams (Rogers 1981). This mating behaviour is very similar to that observed for Trichoclinocera.

Immature Stages. Larval Habitat. Larvae are found on submerged rocks in fast-flowing regions, among filamentous algae and mosses (Vaillant 1967a). They are believed to feed almost exclusively on larvae of Chironomidae, although W. (Roederella) ouedorum Vaillant was observed to actively feed on larvae of Simuliidae (Vaillant 1951a).

Recognition. A variety of larvae of Wiedemannia have been briefly described and/or figured (Brindle 1964, 1969, 1973; Smith 1969; Vaillant 1967a). However, only Vaillant (1951a) provided a useful and detailed description, which included the head capsule. Larvae of Wiedemannia may be distinguished from Clinocera and Trichoclinocera by the terminal segment which bears four diverging lobes of equal length.

Pupal Habitat. Pupae have been found in the same habitat as larvae (Vaillant 1967a). Eclosion occurs within the water and its nonwetable cuticle enables the adult to reach the surface, however eclosion has not been observed. Pupae of W. bistigma have been observed in moss on completely submerged rocks in swift regions of streams (Hinton 1950). In contrast, pupae of W. rhynchops have been observed in mosses just above the water level (Brindle 1969).

Recognition. The pupae have also been briefly described and figured (Brindle 1969, 1973; Smith 1969), but again only Vaillant (1951a) provided a detailed description.

Pupae of Wiedemannia are characterized by two transverse rings of abdominal spines, long caudal hooks and distinct mesonotal setae.

4.2.5.1 KEY TO ADULTS OF THE NEARCTIC SPECIES OF WIEDEMANNIA

- 1 Acrostichals biserial, extending to the scutellum 2
- 1' Acrostichals inconspicuous, confined anterior to first dorsocentral seta 4
- 2 Base of apical filament of phallus with flag-like structure, bearing stout spines (Fig. 149) W. vexillum sp.nov.
(Females of W. vexillum are unknown and females of W. undulata and W. simplex are generally indistinguishable, but may be tentatively separated on the basis of geographic distribution and association with males. Refer to descriptions.)
- 2' Base of apical filament of phallus lacking flag-like structure, bearing stout spines 3
- 3 Anterior and posterior lobes of clasping cercus of similar length; setae of inner surface straight (Fig. 150) W. simplex (Loew)
- 3' Anterior lobe of clasping cercus half length of posterior lobe; inner surface of posterior lobe with very long, sinuous setae (Fig. 151) .. W. undulata sp.nov.
- 4 Anteroapical margin of wing with a distinct dark spot between R_{2+3} and R_4

- W. apicalis sp.nov.
- 4' Anteroapical margin of wing with faint cloudy spot between R_{2+3} and R_4 (Fig. 74) or
lacking 5
- 5 Width of gena equal to half height of eye; acrostichals extend to almost second dc;
apical margin of wing lacking cloudy spot; 5-7 dc W. lepida (Melander)
- 5' Width of gena less than half height of eye; acrostichals confined anterior to first dc;
apical margin of wing with faint cloudy spot, or inconspicuous; 5 dc
..... W. uncinata sp.nov.

4.2.5.2 SPECIES OF WIEDEMANNIA

The W. lepida Species Group

This group includes three Nearctic species distinguished by long, narrow heads, reduced facial carina, sclerotized epandrial bridge ventral to cercus very slender or absent and reduced thoracic chaetotaxy.

Wiedemannia apicalis sp.nov.

Holotype. Male labelled: "Taylor Canyon Colo[orado, USA]/ Gunnison Co. 8000'/
29.VII.1961/ B. Poole" (CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. This species is named for its distinctive dark wing tips.

Recognition. This species may be distinguished from W. uncinata by a very dark apical wing spot and its much larger size. Males are most easily separated by their distinctive sickle-shaped clasping cercus.

Description. Male. Face brown, median carina reduced; gena with blue pruinescence. Width of gena one-third height of eye. Ocellar setae short and narrow. Arista short with blunt tip.

Pleura and coxae with blue pruinescence; scutum faintly bivittate. All thoracic bristles thin and short. Several scattered, short acrostichals anterior to first dc; 6-7 dc; 1 ppm; 1 presut spal, with scattered setulae; 2 npl; 0 psut spal; 1 pal; 2 setl. Anteprenotum with numerous setae; postnotum with patch of pale setae.

Wing lightly infusate; anteroapical margin of wing with a distinct dark spot between R_{2+3} and R_4 ; single basicostal seta; stigma absent. Anal vein reduced to brown streak; R_4 slightly arched; cell dm extended apically such that M acutely branched (sometimes M_1 and M_2 widely separated).

Fore femur with anteroventral row of long fine setae and single preapical, anterior seta. Apical third of hind tibia with dorsal and ventral, erect setae. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform, subequal in length to claw.

Abdominal sternites and lateral margin of tergites with blue pruinescence. Phallus biarticulated, distiphalus lacking central swelling; ejaculatory apodeme reduced to small

triangular sclerite. Clasping cercus sickle-shaped (Fig. 144); tip nipple-shaped in Utah and Colorado populations (Fig. 143). Cercal plate with setae confined to dorsolateral ridge. Epandrium lacking narrow sclerotized bridge ventral to cercal plate. Surstylus short, geniculate.

Female. Similar to male except as follows: terminalia similar to W. lepida.

Geographical Distribution and Seasonal Occurrence. This species is rarely encountered when compared to other species of Wiedemmania from the western United States. Known localities of this species are scattered along the Rocky and Sierra Nevada Mountain ranges (Fig. 202). Adults are present from June to September.

Chorological Affinities. This species is sympatric with W. lepida.

Phylogenetic Relationships. This species is most closely related to W. uncinata on the basis of the following two characters: shape of clasping cercus; epandrium lacks narrow sclerotized bridge ventral to cercal plate. Adult males of these two species are generally difficult to distinguish simply on the basis of terminalia.

Paratypes. USA. California: Inyo Co., Rock Creek, 6.VI.[19]48, W. Wirth (6♂♂, 2♀♀, USNM). Colorado: Chaffee Co., Garfield, South Arkansas River, 2290m, 13.VIII.1973, P.H. Arnaud (1♂, CAS); Gunnison Co., Taylor Canyon, 8000',

29.VII.1961, B. Poole (2♂♂, 1♀♀, CNC). Idaho: F[ran]kl[i]n. Co., Cub River Canyon, 7.VIII.-17.IX.1985, W.J. Hanson (1♀, USU). Nevada: Washoe Co., Galena Creek, Hwy 27, 2mi b[e]l[o]w Mt. Rose Ski Area, 19.V.1983 Baumann-Mower (1♂, BYU). Utah: Pine Valley, 13.VI.1961, D. Dami (1♀, USU); Utah Co., S.Fk. Amer[ican] Fk. Riv., 10.VIII.1987, C.R. & J.R. Nelson (1♂, BYU); Utah Co., S.Fk. American Fork River, 1 mi N.Fk., 11.IX.1987, C.R. Nelson & Franklin (2♀♀, BYU).

Wiedemannia lepida (Melander)

Clinocera lepida Melander, 1902: 241.

Type Material Examined. HOLOTYPE, female labelled: "Julietta/ Idaho [U.S.A.]" [collected by J.M. Aldrich]; "W.M. Wheeler/ Collection"; "TYPE/ No./ A.M.N.H. [red label]"; "Am. Mus. Nat. Hist./ Dept. Invert. Zool./ No. 815" (AMNH).

Recognition. Females are generally similar in appearance to W. uncinata, but may be separated by features given in the key. Males are readily distinguished by their distinctively shaped clasping cercus (Fig. 145).

Description. Male. Face with faint blue pruinescence. Arista short with blunt tip. Ocellar setae fine and short. Gena with faint blue pruinescence; width equal to half height of eye.

Pleura with blue pruinescence, coxae faintly blue; scutum faintly bivittate.

Acrostichals biserial, extending to almost second dc; 5-7 dc; 1 ppm; 1 presut spal; 2 npl and scattered short setae; 0 psut spal; 1 pal; 2 scti; scattered setulae on presut spal region. Postnotum with patch of pale setae; anteprenotum with 1-2 pairs of setae.

Wing very narrow, infusate; stigma inconspicuous; short basicostal seta. Anal vein lacking; cell dm pointed; M acutely branched or M_1 and M_2 widely separated; R_4 and R_5 straight and diverging.

Fore femur with biserial row of long, narrow setae beneath; single anterior pre-apical seta. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform, subequal in length to claw.

Abdominal sternites and lateral margin of tergites with blue pruinescence. Phallus biarticulated, lacking median swelling on distiphallus; ejaculatory apodeme reduced to small triangular sclerite. Surstylus a short, pointed lobe. Epandrium with narrow bridge ventral to cercal plate. Cercal plate with macrosetae confined to dorsal tubercle; clasping cercus triangular to oval-shaped, bearing setae along lateral margin (Figs. 145-148).

Female. Similar to male except as follows: ventral surface of S7 thinly sclerotized. Segment 8 equal in length to segment 7; dorsal surface of T8 thinly sclerotized; S8 thinly sclerotized; T10 split mid-dorsally. Cercus small and narrow. Spermatheca a long, tapering tube; equal in length to two abdominal segments.

Comments. There is significant variation in the shape of the clasping cercus and number of dorsocentral (dc) setae in this species. Populations in California and Oregon have a

triangular clasping cercus (Figs. 145,148) and 5 dc setae. A typical example of this form was illustrated by Rogers (1981, figs. 2-3). Populations in Oregon and Washington have 6 dc setae and the dorsal margin of the clasping cercus is rounded (Fig. 146). Populations in Wyoming and Colorado often have about 7 dc setae and the clasping cercus is almost oval in shape (Fig. 147). The first two groups have also been found occurring in the same locality in several sites in California. In addition, variations in these three forms have been found that make confident separation difficult.

Variation in the shape of the clasping cercus has been noted in the European species W. escheri (Zett.) (Niesiolowski 1988). Variations in the shape were also noted for specimens collected at the same locality and the differences were not considered due to geographic separation (Niesiolowski 1988). Since variation in the shape of the clasping cercus has been noted in other species of Wiedemannia, I believe it best at this time to interpret the differences in W. lepida as being due to intraspecific variation and not warranting species distinction at this time.

Geographical Distribution and Seasonal Occurrence. This species is found along the streams and rivers of the Coast and Cascade ranges from California to southern B.C. and also found in the Rockies of Wyoming and Colorado (Fig. 203). Adults are present from late May to mid-August.

Canada. B.C.: Marysville, 18.VII. (4♂♂,9♀♀,USNM); 15kmW Revelstoke, Victor Lake Prov. Pk., 3.VII.1989 (1♀,CNC); Three Valley, Victor Lake, 14.VII.1974 (2♀♀,CAS); Wells Gray Prov. Pk., Clearwater Valley, Lone Spoon Ck., 16.VIII.1986

(1♂,CAS); Yard Ck. Prov. Pk., 60 kmW Revelstoke, 13.VII.1974 (2♀♀,CAS).

USA. California: Alpine Co., Little Teton Ck., 12.VII.1977 (5♂♂,14♀♀,CAS); Disaster Ck., 11.VII.1977 (2♂♂,2♀♀,CAS); Douglas Co., Canyonville, 20.VI.1977 (2♂♂,1♀,CAS); Eldorado Co., Somerset, 31.V.1954 (1♂,1♀,UCD); Eldorado Co., Kyburz, 19.VII.1953 (1♂,1♀,UCD); El Dorado Co., Kyburz, 14.VII.1981 (1♀,ROGC); Hood River Co., 2mi.E Parkdale, E. Fk. Hood R., 11.VII.1989 (3♀♀,CNC); Humboldt Co., Six Rivers N. F., Ikes Ck., Klamath R., 3.VII.1976 (2♀♀,CAS); Jackson Co., Union Ck. Cpgd, 975m, Rogue R., 17kmN Prospect, 27.VII.1974 (1♀,CAS); Lane Co., Siuslaw N. F., 10miS Yachats, 15.VII.1989 (4♂♂,3♀♀,CNC); Siuslaw N. F., Ten Mile Ck., 14.VII.1989 (1♂,CNC); Lane Co., Willamette N.F., McKenzie Bridge Cpgd, McKenzie R., 21.VI.1978 (8♂♂,17♀♀,CAS); Marin Co., Mt. Tamalpais, Little Carson Trail, Kent L., 15.VII.1978 (1♀,CAS); Monterey Co., Indians Guard Sta., 17 air Mi.NW Jolon, 2100', 9.V.1975 (7♂♂,10♀,CAS); Monterey Co., Los Padres Nat. For., Antonio R. below Escondido, 22.V.1977 (1♂,3♀♀,CAS); Mt. Hood, Hood Rapids, 29.VII.1921 (1♀,USNM); Plumas Co., Massack, Greenhorn Ck., 24.VI.1970, (2♂♂,6♀♀,HSU); Shasta Co., W. boundary Castle Crags St. Pk., 17.VII.1980 (8♂♂,10♀♀,CAS); Sierra Co., Sierra City, 16.VI.1940 (2♀♀,AMNH); Siskiyou Co., Klamath N.F., E.Fk. Cpgd. C.Fk. Salmon R., 4.VII.1978 (13♂♂,24♀♀,CAS); Siskiyou Co., Klamath N.F., Russian Ck., China Gulch, 4.VII.1976 (25♂♂,25♀♀,CAS); Siskiyou Co., Klamath N.F., Wooley Ck., Murderer's Bar, 3.VII.1976 (1♂,5♀♀,CAS); Siskiyou Co., Klamath N.F., Knownothing Ck., S.Fk. Salmon R., 22.VII.1980 (122♂♂,229♀♀,CAS); Siskiyou Co., Klamath N.F., Wooley Ck. Tr., 3.VII.1978

(2♂♂,1♀,CAS); Trinity Co., Shasta N.F., Boulder Ck., 419.VII.1980 (4♂♂,1♀,CAS); Trinity Co., Shasta N.F., Trinity R., 2.VII.1978 (6♂♂,15♀,CAS); Tuolumne Co., along Clark Fk. R., 11.VII.1977 (8♂♂,9♀♀,CAS); Tuolumne Co., Strawberry, 8.VII.1957 (1♂,UCD); Tuolumne Co., Dardanelle, 1768m, 1.VII.1977 (1♂,CAS). **Colorado:** Boulder Co., Boulder Falls, 2135m, 11kmW Boulder, 8.VIII.1973 (1♂,2♀♀,CAS). **Idaho:** Benewah Co., Thorn Ck., 2miS St. Maries, 24.VI.1978 (7♂♂,17♀♀,CAS); Idaho Co., 9miE Lowell, along Selway R., 30.VI.1991 (5♂♂,11♀♀,WSU); Latch Co., 15mi ENE Potlatch, Strychnine Ck., 8.VI.1982 (3♂♂,15♀♀,WSU); Troy, 31.V.1908 (1♀,ANSP). **Washington:** Cashmere, 26.VII.1919 (1♂,USNM); Grays Harbor Co., Olympic N.F., Willaby Cpgd, 20,21.VII.1978 (25♂♂,47♀♀,CAS); Husum, 26.VII.1921 (26♂♂,27♀♀,USNM); Jefferson Co., Olympic N.Pk., Hoh R., 6.VII.1989 (3♂♂,6♀♀,CNC); Mt. Rainier, Ohanapecosh, 11.VIII.1940, (1♀,USNM). **Wyoming:** Park Co., Shoshone N.F., Newton Ck. Cpgd, Newton Ck., 20.VII.1989 (6♂♂,11♀♀,CNC); Park Co., Shoshone N.F., Newton Ck. Cpgd, N.Fk. Shoshone R., 21.VII.1989 (3♂♂,2♀♀, CNC); Yellstn Park, Cascades Y.R., 22.VII.1923 (2♂♂,17♀♀,USNM).

Chorological Affinities. This species is widely sympatric with W. uncinata and W. undulata (Wyoming).

Phylogenetic Relationships. This species is closely related to W. uncinata + W. apicalis.

Wiedemannia uncinata sp.nov.

Holotype. Male labelled: "U.S.A.: OREGON: Hood/ River Co. Starvation/ Creek State Park, at/ falls. 26 June 1978/ D.D. Wilder collector"; "D. Dee Wilder/ Collection [yellow label]" (CAS).

Allotype. Female. Same data as holotype (CAS).

Derivation of Specific Name. From the Latin uncinatus meaning hooked, in reference to the shape of the male clasping cercus.

Recognition. Readily distinguished by small size and wing spot on apical margin of wing. However, if spot faint or absent, females may be distinguished by features given in the key. Males are most easily separated by their distinctive L-shaped clasping cercus, which most closely resembles W apicalis.

Description. Male. Face brown; arista short, with blunt tip; ocellar setae narrow and short. Gena with faint blue pruinescence; width less than half height of eye.

Pleura and coxae with faint blue pruinescence; scutum faintly bivittate. Acrostichals inconspicuous, anterior to first dc; 5 dc; 1 ppm; 1 presut spal; 2-3 npl; 0 psut spal; 1 pal; 1 sctl; scattered short setulae in presut spal region. Antepnotum with several short setae; postnotum with patch of pale setae.

Wing narrow, infusate; faint spot at tip between R_{2+3} and R_5 , often inconspicuous

or lacking; single basicostal seta; stigma faint, elongate. R_1 and R_2 straight and diverging; cell dm pointed; M acutely branched or M_1 and M_2 widely separated.

All legs with fine chaetotaxy. Hind tibia with erect, dorsal setae on apical third. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform, subequal in length to claw.

Abdominal sternites and lateral margin of tergites with blue pruinescence. Epandrium lacking narrow sclerotized bridge ventral to cercal plate. Phallus biarticulated, lacking median swelling on distiphallus; ejaculatory apodeme reduced to small triangular sclerite. Surstylus a short lobe. Cercal plate with macrosetae confined to dorsal tubercle; clasping cercus L-shaped (Figs. 141,142).

Female. Similar to male except as follows: female terminalia similar to W. lepida.

Geographical Distribution and Seasonal Occurrence. This species ranges from southern B.C. to California (Fig. 202) and adults appear from late June to September.

Chorological Affinities. This species is widely sympatric with W. lepida.

Phylogenetic Relationships. See discussion under W. apicalis.

Paratypes. Canada. B.C.: Manning Provincial Park, small creek vic. Manning Park

Lodge, 5.VIII.1986, P.H. Arnaud (1♂,CAS); Mt. Revelstoke Nat. Pk., Giant Cedars Trail, 700m, 2.VII.1989, ex. cascading stream, B.J. Sinclair (2♀♀,CNC).

USA. California: Alpine Co., along Little Teton Creek, T6N R19E Sec 12, 12.VII.1977, D. Wilder (16♂♂,22♀♀,CAS); Falls Valley, 10.VII.1940, A.L. Melander (5♂♂,7♀♀,USNM); [Humboldt Co.] Forest Home, 25.V.1936, 26.VIII.1944, A.L. Melander (2♂♂,2♀♀,USNM); Fresno Co., Sierra N.F., E.&W. Forks Camp 61 Cr. nr. Forebay Lk. 2200m, T7S R26E Sec. 19, 31.VII.1979, D.D. Wilder (6♂♂,11♀♀,CAS); Fresno Co., Sierra N.F., Along Pitman Cr. near Big Cr. 1500m, T8S R25E Sec. 28, 2.VIII.1978, D.D. Wilder (6♂♂,6♀♀,CAS); Fresno Co., Sierra N.F., unnamed cr. nr. Kaiser Pass, T7S R26E Sec. 26, 2700m, 2.VIII.1978, D.D. Wilder (7♂♂,3♀♀,CAS); Fresno Co., Sierra N.F., along Bear Cr., T8S R26E Sec. 6, 2100m, 1.VIII.1979, D.Wilder (2♂♂,2♀♀,CAS); Fresno Co., Sierra N.F., unnamed cr. nr. Kaiser Pass, 2700m, D.D. Wilder (4♂♂,5♀♀,CAS); Fresno Co., Huntington L., Midge C. 2200m, 13.VII.1984, J. MacDonald (1♂,1♀,PERC); Huntington L., Kaiser C. 2700m, 23.VII.1984, J. MacDonald (1♀,PERC); Huntington L., Ranceria C. 2600m, 20.VII.1984, J. MacDonald (1♂,PERC); Los Angeles Co. N.Fk. San Gabriel R. along Hwy 39, 2mi.S. Coldbrook Stn., 25.IV.1977, D. Wilder (5♂♂,6♀♀,CAS); Sequoia Nat.Pk., Lodge Pole, 21.VII.1984 D.J. Burdick (2♂♂,PERC); Sequoia Nat.Pk., Wolverton, 9.VI.1985 D.J. Burdick (1♂,PERC); S. Fork, S[an]ta Ana, 2.VIII.1942, 15.VI.1945, A.L. Melander (1♂,1♀,USNM); Shasta Co., W. Boundary Castle Crags State Park, 17.VII.1980, D.D. Wilder (3♂♂,9♀♀,CAS); Shasta Co., McArthur Burney Falls Mem. St.Pk., 2900', 1.VIII.1970, P.H. Arnaud (5♀♀,CAS); Siskiyou Co., Klamath N.For., along Fish Lake

Cr., 21.VII.1980, D.Wilder (1♂,CAS); Trinity Co., Shasta N.F., Boulder Creek near Coffee Cr. Rd., 19.VII.1980, D.D. Wilder (5♂♂,1♀,CAS). Idaho: Priest Lake, 1.VIII.1916, A.L. Melander (1♂,USNM). Oregon: Benson Park, 24.VI.1935, A.L. Melander (1♂,2♀♀, USNM); Hood River Co., Starvation Ck. St.Pk., cascading stream below falls, 10.VII.1989, B.J. Sinclair (3♂♂,5♀♀,CNC); Hood River Co., Starvation Creek State Park, at falls, 26.VI.1978, D.D. Wilder (5♂♂,20♀♀,CAS); Lane Co., 11mi.NE Blue R., H.J. Andrews Expt. For., 800m, Mack Ck., 11.VIII.1982, G.W. Courtney (3♀♀,OSUC); Mt. Hood, el.4000', 25.VI.1935, A.L. Melander (1♀,USNM). Utah: Cache Co., Blacksmith Fork Can., 26.VI.1967, 1.VII.1976, H.J. Hanson (11♂♂,17♀♀,USU). Washington: L. Keechelus, 5.IX.1917, A.L. Melander (1♂,1♀,USNM); Mt.Rainier, Ohanapecosh, 11.VIII.1940, A.L. Melander (1♂,5♀♀,USNM).

The W. koeppeni Species Group

Members of this group are characterized by the mitten-shaped clasping cercus and twisted distiphallus. This group includes W. koeppeni Joost known from Eastern Siberia, W. mauersbergeri Joost from Mongolia (Joost 1980, 1984) and W. vexillum Sinclair sp.nov. from the Nearctic region. This group may also include, only on the basis of the shape of the clasping cercus, W. chvali Joost and W. klausnitzeri Joost from the Caucasus Mountains (Joost 1981a).

Wiedemannia vexillum sp.nov.

Holotype. Male labelled: "NWT [Canada: Northwest Territories]: Martin River/ FWI. Pipeline Proj./ 20.VI.1972/ MR1.35 DE"; "Wiedemannia/ sp./ Det. H.J. Teskey 1972 [dissected]" (CNC).

Derivation of Specific Name. Latin for flag, in reference to the the distinctive flag or pennant-like structure on the phallus.

Recognition. This species is readily distinguished by features given in the key. The male terminalia are unlike any other Nearctic species.

Description. Male. Face and gena with blue pruinescence; vertex brown; width of gena one-quarter height of eye. Arista short and blunt. Palpus with brown setae. Ocellar and occipital setae stout.

Scutum brown; pleura and coxae with blue pruinescence. Acrostichals biserial, extending onto sctl; 5 dc; 1 pprn; 1 presut spal; 2 npl; 1 psut spal; 1 pal; 2 sctl and 2 outer marginal setae; scattered, short setulae on presut spal region. Anteprepronotum with pair of stout setae; postnotum with patch of pale setae.

Wing broad, infusate; single long basicostal seta; stigma faint, elongate. Cell dm produced apically; M_1 and M_2 widely separated; R_4 and R_5 straight and diverging.

All legs with long setae, evenly distributed. Base of fore femur widely expanded with 2-3 anterior setae on apical fifth. Fifth tarsomere with dorsoapical extension;

empodium pulvilliform, subequal in length to claw.

Tergite 8 wide. Phallus biarticulated; distiphallus strongly curved; base of distiphallus with flag-like structure, bearing stout spines; ejaculatory apodeme long and narrow. Surstylus a small pointed lobe. Cercal plate with macrosetae confined to dorsal tubercle; clasping cercus mitten-shaped; anterior lobe short and round; posterior lobe wide; short, stout setae on inner surface (Fig. 149).

Female. Unknown.

Geographical Distribution and Seasonal Occurrence. This species is known only from the holotype collected near Fort Simpson, as part of the MacKenzie River Valley survey (Fig. 204). This survey was to monitor the effects of pipeline construction.

Chorological Affinities. This species is sympatric with W. simplex.

Phylogenetic Relationships. Possibly most closely related to W. mauersbergeri.

The Philolutra Mik Species Group

Philolutra was originally described as a new genus by Mik (1881), but is currently recognized as a subgenus of Wiedemannia (Chvála and Wagner 1989). This group presently includes species with acrostichals extending to the scutellum, a narrow stigma, and femora lacking preapical bristles. Despite its apparent paraphyly, Philolutra will be

used for convenience until the phylogenetic relationships are better understood among species of this subgenus with other species of Wiedemannia.

Within this group the following two Nearctic species, along with W. fallaciosa (Loew), W. hygrobia (Loew), and possibly W. bifida Vaillant (from subgenus Chamaedipsia) form a monophyletic group on the basis of club-shaped setae on the male clasping cercus.

Wiedemannia simplex (Loew)

Clinocera simplex Loew, 1862: 207.

C. appendiculata Frey *nec* Zett., 1913: 61. Misidentification (Collin 1961: 767).

Type Material Examined. Clinocera simplex Loew, LECTOTYPE (here designated), male labelled: "H. B. T. [Hudson Bay Territory, Canada]"; "Loew/ Coll."; "simplex [hand written]"; "Type/ 1181 [red label with upper white border] (MCZ). My lectotype label "LECTOTYPE/ of Clinocera/ simplex Loew/ des. B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: H.B.T. [Hudson Bay Territory] (1♀,CNC; 2♀♀,MCZ); Portage and Slave Lake [hand written], H.B.T. [Hudson Bay Territory] (1♂,1♀,MCZ). My paralectotype labels have additionally been attached to these specimens.

The following specimen labelled as cotype was found in the USNM: "Labr[ador]"; "COTYPE/ Clinocera/ simplex/ Lw. [red label] [abdomen, legs and one wing missing: damaged and remounted]" (USNM). Due to the condition of this

specimen, species identification remains tentative; however, the geographic locality indicates that it is likely to be W. simplex. Since Loew (1862) did not indicate a specimen from this region in the type series, I have not labelled it as a paralectotype.

Recognition. Females are presently indistinguishable from W. undulata. Males are easily separated from W. undulata by features of the terminalia given in the key.

Description. Male. Face, gena and postocciput with blue pruinescence, vertex brown; ocellar setae long and narrow. Width of gena one-third height of eye. Arista short, tip blunt. Setae on palpus dark.

Pleura, coxae, prescutellar depression and sc1 with blue pruinescence (occasionally specimens with pruinescence on pprn and npl); scutum faintly bivittate. Acrostichals biserial, diverging around prescutellar depression, extending onto sc1; 6 dc, many short, setae interspersed; 1-2 pprn and several short setae; 1 presut spal; 2-3 npl; 0 psut spal; 1 pal; 2 sc1 and inner and outer marginal setae; scattered setae on npl and presut spal regions. Postnotum with patch of pale setae; anteprenotum with pale setae.

Wing broad, faintly infusate; stigma faint, elongate; single basicostal seta. Anal vein reduced to streak; cell dm elongate, M acutely branched or M₁ and M₂ widely separated; R₄ and R₅ straight and diverging.

All legs with evenly distributed setae. Anterior surface of fore femur lacking macrosetae. Fifth tarsomere with dorsoapical extension; empodium pulvilliform, subequal to length of claw.

Abdominal sternites, lateral margin of tergites and hypopygium with blue pruinescence. Tergite 8 bilobed. Phallus straight, distiphallus with median swelling; ejaculatory apodeme long and narrow. Surstylus small and pointed. Cercal plate with macrosetae confined to dorsal tubercle. Clasping cercus mitten-shape, anterior and posterior lobes of similar length; anterior lobe short, shiny, lacking blue pruinescence; posterior lobe expanded apically bearing lateral setae; setae of inner surface short, pale, with expanded tips (Fig. 150).

Female. Similar to males except as follows: segments 8 and 10 conical, laterally compressed. Segment 8 one-third longer than preceding segment; T8 triangular shaped; S8 long and narrow; T10 triangular, short. Cerci narrow, pointed lobes. Narrow short tubular spermatheca, with genital fork not distinguishable (Fig. 152).

Females appear indistinguishable from females of W. undulata.

Geographical Distribution and Seasonal Occurrence. Wiedemannia simplex is widely distributed in the far north and ranges from the Ungava region of Quebec, west to Alaska and southwards down the Rockies to Jasper. A long series is known from Isle Royale National Park (Michigan, USA), and also from localities in southwestern New Mexico and Arizona (Fig. 204). In northern localities, adults are present from mid-June to mid-August and from early-May to June or July in southern localities.

CANADA. Alberta: Jasper Nat. Pk., Jasper, Athabasca R., 27.VI.1989 (5♂♂, 7♀♀, CNC). Manitoba: Churchill, 9.VII.1947 (1♂, CNC). NWT: Keewatin, N.W.

corner Nueltin Lk., mouth of Windy R., 29.VII.1947 (5♀♀, 1? ANSP, USNM); Barlow L. outlet, 62°05'N, 102°53'W, 17.VII.1966 (14♂♂, 14♀♀, CNC); Boyd L. outlet, 61°39'N, 103°40'W, 13.VII.1966 (5♂♂, 4♀♀, CNC); Dubawnt L., 62°54'N, 102°07'W, 30.VII.1966 (6♂♂, 14♀♀, CNC); Grant L., 63°41'N, 100°33'W, 8-10.VIII.1966 (3♂♂, 5♀♀, CNC); Markham L. 62°32'N, 102°38'N, 25.VII.1966 (4♂♂, 8♀♀, CNC); Marjorie L. 64°04'N, 99°25'W, 19.VIII.1966 (4♂♂, 6♀♀, CNC); Nicholson L. 62°45'N, 102°40'W, 26-27.VII.1966 (8♂♂, 12♀♀, CNC); Ptarmigan Rap. 61°13'N, 103°30'W, 10.VII.1966 (3♂♂, 4♀♀, CNC). Quebec: Leaf River, Ungava, 16, 31.VII.1968 (3♂♂, 3♀♀, UMQ - in alc.); Pt. Harrison, 28.VII.1949 (40♂♂, 27♀♀, CNC). Yukon: Little Salmon RL. 62°10'N, 134°46'W, 9.VIII.1959 (3♂♂, 6♀♀, CNC); Starr Ck. 61°46'N, 131°51'W, 3.VIII.1981 (2♂♂, 1♀, UBC); Whitehorse, Lewes R., 4.VII.1949 (1♂, 1♀, CNC); Whitehorse, Yukon R., 18.VI.1987 (21♂♂, 38♀♀, UGO).

USA. Alaska: King Salmon, Naknek R., 6.VII.1952 (8♂♂, 8♀♀, CAS, CNC). Arizona: Navajo Co., White R., W. Fort Apache, 3.VI.1982 (1♂, BYU). Michigan: Isle Royale, 10.VII.1957 (17♂♂, 31♀♀, MSU). New Mexico: Catron Co., 1.5mi E Glenwood, Whitewater Ck., 30.V.1991 (1♂, 1♀, CNC); Grant Co., E. Fk. Gila R., 6.V.1981, 29.VI.1991 (17♂♂, 17♀♀, CNC, PERC).

Chorological Affinities. This species is sympatric with W. vexillum.

Phylogenetic Relationships. I have examined a determined specimen of W. impudica (Mik), which is known in Europe from Norway, Great Britain (Chvála and Wagner

1989), Finland, and western Russia (Frey 1913). It appears that W. impudica may be conspecific with W. simplex. The shape of the clasping cercus of these two species varies only slightly over North America and Europe. Any further decisions must await examination of the type specimens of W. impudica housed in the Naturhistorisches Museum in Vienna.

Wiedemannia impudica was often believed to be conspecific with W. fallaciosa, but is clearly distinguished by characters listed by Collin (1961). In addition, the clasping cercus of the latter species bears long, thick wavy setae on the inner apical surface of the posterior lobe, which are lacking in W. impudica.

Zoogeographic Considerations. The zoogeographic pattern displayed by W. simplex (Fig. 204) is also found in other species of arctic-alpine flora and fauna. For example, there are several species of beetles, stoneflies and many species of plants that are widespread in the high latitudes of North America, with a disjunct population along the north shore of Lake Superior (Ashworth 1977, Ricker 1964, Soper and Maycock 1963).

During the growth and advance of the Wisconsinan ice sheets, arctic and subarctic beetle populations are hypothesized to have survived proximal to the southern ice margin (Schwert and Ashworth 1988). Climatic warming subsequently decimated these populations, except for populations in isolated tundra-like microhabitats along the shores of cold lakes. During the Holocene, arctic-subarctic beetle species recolonized the northern regions of North America from Beringia (Schwert and Ashworth 1988).

Although W. simplex is not strictly a cold-adapted species, a similar scenario is

hypothesized to explain the present distribution pattern of W. simplex. During the late Wisconsinan, populations of this species occurred along the ice margin and southern Cordillera. This species survived within the midcontinent on Isle Royale, surrounded by Lake Superior. It was possibly prevented from dispersing further northwards, where appropriate habitat exists, through competition with species of Trichoclinocera. The southwestern populations in New Mexico and Arizona also likely represent relict populations that may also have been prevented from dispersing northwards due to competition with W. undulata and species of Trichoclinocera. Additional collecting north of Lake Superior and the southern Cordillera is required to verify whether these populations are truly isolated or are artifacts due to lack of collections in these areas. Alternatively, the southern population of W. simplex may represent a cryptic species presently not morphologically distinguishable.

Wiedemannia undulata sp.nov.

Holotype. Male labelled: "USA: WYOMING: Bighorn/ Nat.For., BighornCo./ 10kmE Shell 21.VII.1989/ Shell C[ree]k./ BJ Sinclair"
(CNC).

Allotype. Female. Same data as holotype (CNC).

Derivation of Specific Name. Latin for wavy, in reference to the long, wavy setae on the inner face of the male clasping cercus.

Recognition. Females are indistinguishable from W. simplex. Males are easily separated from W. simplex by features of the terminalia given in the key.

Description. Male. Face, gena, postocciput with blue pruinescence, vertex brown; ocellar setae narrow; arista short with blunt tip. Width of gena one-third height of eye. Setae on palpus generally light brown.

Pleura, coxae, pprn, npl, sctl and prescutellar depression with blue pruinescence; scutum faintly bivittate. Acrostichals biserial, diverging around prescutellar depression and extending onto sctl; 5 dc with shorter setae mixed between; 1-2 pprn; 1 presut spal; 2-3 npl; 0 psut spal; 1 pal; 2 sctl with several outer marginal setae and pair of inner marginal setae. Postnotum with patch of pale setae; anteprenotum with 2-3 pairs of stout setae.

Wing broad, faintly infusate; long basicostal seta; stigma elongate and faint. Anal vein reduced to streak; cell dm extended apically, M_1 and M_2 widely separated, only occasionally M acutely branched; R_4 and R_5 straight and diverging.

All legs with evenly distributed setae. Anterior surface of fore femur lacking macrosetae. Fifth tarsomere with dorsoapical extension; empodium pulvilliform, subequal to length of claw.

Abdominal sternites, lateral margin of tergites and hypopygium with blue pruinescence. Tergite 8 narrow. Phallus biarticulated, straight; distiphallus with central swelling. Epandrium greatly inflated and spherical. Cercal plate with macrosetae confined to dorsal tubercle. Claspig cercus mitten-shaped; anterior lobe shiny, lacking blue

pruinescence, half length of posterior lobe, setae on inner surface short with expanded tip; inner surface of posterior lobe with very long, sinuous setae (Fig. 151).

Female. Similar to male except as follows: terminalia identical to that described for W. simplex, which is presently indistinguishable from females of this species.

Geographical Distribution and Seasonal Occurrence. This species is widely distributed from southern B.C. to northern New Mexico (Fig. 204). Adults are present from June to October.

Chorological Affinities. This species has been collected in the same streams and rivers as W. lepida.

Phylogenetic Relationships. This species appears to be most closely related to W. simplex.

Paratypes. Canada. B.C.: Bromley Rock Prov. Pk., 19kmE Princeton, 4.VII.1989, B.J. Sinclair (1♂, 4♀♀, CNC).

USA. New Mexico: Jemez Springs, 4.VII.1953, W.W. Wirth (17♂♂, 20♀♀, USNM). Utah: Duchesne Co., Duchesne R. at Stockmore, 3.IX.1947, G.F. Edwards (1♂, 4♀♀, CNC); Cache Valley nr. base Porcupine Dam, 14.VIII.1947, D.J. Burdick (1♂, PERC); Manilla, 13.VII.1938, G.F. Knowlton, F.C. Harmston

(2♀♀,USU); Logan, 16.VII.1933, T.O. Thatcher (1♂,1♀,AMNH); Logan Canyon, 14.VII.1938, D.E. Hardy & G.S. Stains (1♂,2♀♀,USU); Logan Canyon, 2.VII.1940, A.C. Valcarce (2♂♂,2♀♀,USU); Wash[ington] Co., Zion Natl. Park, Slide area, 15.IX.1981, C.R. Nelson (1♀,USU); Wash. Co. Zion Natl. Park, Big Cott, 9.VI.1981, C.R. Nelson (7♂♂,5♀♀,USU); Washington Co., Zion Nat. Pk., Desert Swamp, Zion Narrows Tr[ail]., 30.X.1982, R.W. Baumann (1♀,BYU); Washington Co., Zion Nat. Pk., N.Fk. Virgin River, Temple of Sinawava, 30.III.1981, Baumann & Stranger (4♂♂,7♀♀,BYU). Washington. Cashmere, 26.VII.[19]19, A.L. Melander (15♂♂,21♀♀,BPBM, CNC,CU,USNM); Entiat, 26.VII.1919, A.L. Melander (1♀,USNM); Hanford, 23.VIII.1950, C.L. Cooper (1♂,1♀,MSU); Spokane, R.W. Doane (2♀♀,USNM); Spokane Co., Bowl and Pitcher, Riverside St. Pk., 27.VIII.1977, W.J. Turner (16♂♂,38♀♀,WSU). Wyoming: Bighorn Co., Bighorn Nat. For., 10kmE Shell, 21.VII.1989, Shell Ck., B.J. Sinclair (7♂♂,24♀♀,CNC); Park Co., Shoshone Nat. For., Newton Ck. Cpgd., 21.VII.1989, N.Fork Shoshone River, B.J. Sinclair (5♂♂,3♀♀,CNC); Yell[ow]st[o]n[e] Park, Cascades Y.R., 22.VII.1923, A.L. Melander (1♀,USNM); Yellowst. Pk, Summer 1921, Miss Cattell (1♂,1♀,USNM).

Comments. Four females from "California: Mono Co., Bridgeport (Virginia Ck.), collected 7.VI.1948 by W.W. Wirth (USNM)" were not included in the type series. A male from this locality is required for positive species identification of this population.

List of described species included in Wiedemannia.

Roederella group:

- P czernyi (Bezzi), 1905: 362 (Clinocera) [examined].
- P ssp. rufipes (Oldenberg), 1915: 92 (Roederia (Atalanta),
 as var. of czernyi).
- P ouedorum Vaillant, 1951a: 371.
 syn. ovedorum (error) Vaillant, 1978: 469.

Eucelidia group:

- P pirata (Mik), 1880: 350 (Clinocera) [examined].
- P zetterstedti (Fallén), 1826: 7 (Empis) [examined].
 syn. hirtiloba (Speiser), 1924: 13 (Atalanta, as var. of
 zetterstedti).
- escheri (Zetterstedt), 1838: 558 (Brachystoma).
- longipennis (Mik), 1880: 349 (Clinocera).

Pseudowiedemannia group:

- P armata (Engel), 1918: 244 (Atalanta (Pseudowiedemannia)) [syntypes examined]
 (ZSM).
- P lamellata (Loew), 1869: 276 (Clinocera) [examined].
- P microstigma (Bezzi), 1904: 201 (Clinocera (Wiedemannia)).

Wiedemannia (s.s.) group:

- P andreevi Joost, 1982: 122.
- P bistigma (Curtis), 1834: plate 513 (Heleodromia) [examined].
 syn. borealis Zetterstedt, 1838: 559.
 juvenilis Zetterstedt, 1842: 366.
- P braueri (Mik), 1880: 352 (Clinocera).
- P caucasica Joost, 1981a: 186.
- P dinarica Engel, 1940: 170.
- P maxima Wagner, 1984c: 462.
- P similis Vaillant, 1960c: 178.
- P stylifera Mik, 1889b: 150.
- P tricuspidata (Bezzi), 1905: 365.

rhynchops group:

- P arvernensis Vaillant, 1965: 167 (as a ssp. of rhynchops).
- P austriaca Vaillant, 1965: 166 (as a ssp. of rhynchops).
- P balkanica Wagner, 1981: 300.
- P bilobata Oldenberg, 1910: 349 [examined].
- P brevilamellata Wagner, 1985: 86 (new name for W. alpina Vaillant).
 syn. alpina Vaillant, 1953b: 62.
- P debilis Collin, 1961: 761 (as ssp. of W. rhynchops).
- P dolichocephala Vaillant, 1965: 165 (as ssp. of W. oxystoma).

- P dyonysica Wagner, 1990: 232.
- P falcifera Vaillant, 1967a: 275.
- P graeca Vaillant and Wagner, 1990: 96.
- P kroatica Wagner, 1981: 301.
- P mirousei Vaillant, 1956b: 11.
- P nevadensis Wagner, 1990: 230.
- P oxystoma (Bezzi), 1905: 364 (Clinocera (Wiedemannia)).
- P rhynchops (Nowicki), 1868: 89.
 syn. insularis Collin, 1927: 98 (as ssp. of W. rhynchops).
- P rivulorum Wagner, 1990: 234.

koeppeni group:

- P koeppeni Joost, 1980: 89 (W. (Philolutra)).
- P mauersbergeri Joost, 1984: 123 (W. (Philolutra)).
- N vexillum Sinclair sp.nov.

lepida group:

- N apicalis Sinclair sp.nov.
- N lepida (Melander), 1902: 241 (Clinocera) [holotype examined] (AMNH).
- N uncinata Sinclair sp.nov.

Chamaedipsia group:

- P** aquilobata Mandaron, 1964: 81.
- P** aerea Vaillant, 1967a: 271.
- P** alpina (Engel), 1918: 220 (Clinocera (Chamaedipsia)).
- P** beckeri (Mik), 1889a: 71 (Chamaedipsia) [examined].
- syn. jugorum (Strobl), 1893: 105 (Chamaedipsia).
- crinita Engel, 1918: 217 (as var. of beckeri).
- alticola Vaillant, 1950a: 54.
- glaciola Wagner, 1985: 86 (as a ssp. of beckeri; new
name for W. beckeri alpina Vaillant).
- alpina Vaillant, 1967a: 274 (as a ssp. of beckeri).
- P** berthelemyi Vaillant and Vinçon, 1986: 272.
- P** bicolorata Vaillant, 1960c: 175.
- P** bicuspidata (Engel), 1918: 217 (Atalanta (Chamaedipsia)) [examined].
- P** bifida Vaillant, 1965: 157.
- P** carpathia Vaillant, 1967a: 274.
- P** corſicana Vaillant, 1965: 158.
- P** digitata Vaillant and Vinçon, 1986: 272.
- P** foliacea Vaillant, 1960c: 176.
- P** hastata (Mik), 1880: 349 (Clinocera).
- P** longicornis (Mik), 1887: 162 (Chamaedipsia).
- P** lota Walker, 1851: 107.

syn. pusilla (Loew), 1858b: 243 (Clinocera).

- P mgounica Vaillant, 1956c: 69.
- P mikiana (Bezzi), 1899: 149 (Chamaedipsia).
- P oredonensis Vaillant, 1967a: 276.
- P ornata (Engel), 1918: 219 (Atalanta (Chamaedipsia)).
- P pyrenaica Vaillant, 1967a: 274.
- P syriaca Wagner, 1982a: 16.
- P thienemanni Wagner, 1982c: 502.
- P thomasi Vaillant, 1968a: 91.
- P wachtli (Mik), 1880: 351 (Clinocera).

syn. languedocica Vaillant, 1965: 159 (W. (Chamaedipsia)).

- P zwicki Wagner, 1982b: 219.

Philolutra group:

- P angelieri Vaillant, 1967a: 273.
 - P aquilex (Loew), 1869: 272.
- syn. gracilis Vaillant, 1950a: 55.
- P azurea (Vaillant), 1951b: 3 (Philolutra).
 - P bohemani (Zetterstedt), 1838: 558 (Brachystoma) [examined].
 - P chvalai Joost, 1981a: 186.
 - P erminea (Mik), 1887: 161 (Philolutra).
 - P fallaciosa (Loew), 1873: 44 (Clinocera) [examined].

syn. agilis Vaillant, 1950a: 56.

ssp. litardierei Vaillant, 1956c: 67.

orientalis Vaillant, 1965: 163 (as a ssp. of fallaciosa).

P hygrobia (Loew), 1858b: 248 (Clinocera) [examined].

P jazdzewskii Niesiolowski, 1987: 519.

P klausnitzeri Joost, 1981a: 188.

P lagunae (Becker), 1908: 43 (Philolutra).

P phantasma (Mik), 1880: 350 (Clinocera) [examined].

P pseudovaillanti Joost, 1981a: 188.

P quercifolia (Engel), 1918: 235 (Camelopsis).

P queyarasiana Vaillant, 1956b: 14.

N,P simplex (Loew), 1862: 207 (Clinocera) [lectotype designated] (MCZ).

syn. impudica (Mik), 1880: 351 (Clinocera) New synonymy.

N undulata Sinclair sp.nov.

P vaillanti Joost, 1981a: 189.

P veletica Vaillant and Chvála, 1973: 63.

Unplaced species:

A edendalensis Smith, 1969: 295.

O glauescens (Brunetti), 1917: 80 (Clinocera) New combination.

syn. saigusai (Smith), 1965: 102 (Acanthoclinocera) [Holotype

examined] (BMNH).

- A gorongoza Smith, 1969: 293.
- A hughesi Smith, 1969: 294 [paratypes examined] (NM).
- A reducta Garrett Jones, 1940: 303.
- A rudebecki Smith, 1967: 230.
- A submarina Garrett Jones, 1940: 302.

Nomina nuda

botosaneanui Vaillant, 1978: 468.

bucegica Vaillant, 1978: 468.

hispanica Vaillant, 1978: 469.

lavandieri Vaillant, 1978: 469.

macedonica Vaillant, 1978: 469.

minutissima Vaillant, 1978: 469.

nevadica Vaillant, 1978: 469.

sarranetica Vaillant, 1978: 469.

schmidi Vaillant, 1978: 469.

4.3 GENUS INCERTAE SEDIS IN CLINOCERINAE

The following genus has traditionally been included in the Clinocerinae. However, I believe the placement has been based on symplesiomorphic and homoplastic characters (e.g. narrow wing, pulvilliform empodium, pubescent eyes). I have not been able to place this genus confidently into any other major empidoid lineage and consequently consider Proagomyia as incertae sedis in Clinocerinae.

GENUS PROAGOMYIA COLLIN

Proagomyia Collin, 1933: 325. Type-species, P. torrentium Collin (original designation).

Type Material Examined. P. torrentium Collin, HOLOTYPE, male labelled: "Argentina: Terr. Rio Negro./ F & M Edwards/ BM 1927-63"; "L[ake]. Gutierrez./ 3-14.XI.1926"; "On wet rocks by/ waterfall" [missing all except one hind leg, antennae and thorax damaged] [dissected]" (BMNH).

Recognition. This genus is distinguished from all other Clinocerinae by the long proboscis, long, straight palpus and highly modified male terminalia. Proagomyia should be identified as a clinocerine by features outlined in the key to the major empidoid lineages.

Description. Male. Face narrower than frons. Eyes with short, sparse pubescence (or absent). Antennae arising above middle of head; scape twice as long as pedicel (P.

torrentium), or slightly longer than pedicel; first flagellomere elongate; two-segmented arista slender. Anterior ventrocervical sclerite absent. Ridge extends from palpus along anterior margin of eye. Proboscis long; palpus long, straight, cylindrical, equal in length to proboscis; labrum long and slender, with wide base; labral apodeme lacking; labellum held in horizontal position, sucker-like, lacking pseudotracheae; hypopharynx slender, extending beyond labellum.

Pruinescence and coxae variable in colour. Acrostichals long, alternating and divergent, ending opposite last psut spal; 5 dc, with setulae among setae; 1 ppm; 1 presut spal; 2 npl; 2 psut spal; 2 apical sctl, 1 pair of subapical lateral setae. Postnotum bare; anteprenotum with several setulae; prosternum fused laterally with proepisternum.

Wing wide, with obtuse anal angle; 1-2 basicostal setae; infusate; stigma distinct, elongate and slender. Stout setae along upper surface of costa (not on outer margin of costa) from R_1 to R_{4+5} ; subcosta evanescent; R_{4+5} branched; cell dm slightly produced apically; CuA_2 reaching one-third to base of cell cup; A_1 faint and straight.

Empodium pulvilliform; fifth tarsomere with dorsoapical extension. All legs except hind were missing from holotype (see Collin (1933) for description of P. torrentium).

Long setae on lateral margins of tergites. Terminalia enlarged, arched dorsally over abdomen. Since the terminalia of both known species are very different, only the type species will be described here. Refer to P. tridentata for comparison. Tergite 8 with mid-dorsal notch. Sternite 8 with narrow, pruinulent dorsolateral lobes (Fig. 154). Hypandrium enclosed posteriorly with pair of diverging, pointed phallic guides; short

gonocoxal apodemes present; phallus arising anterodorsally, greatly expanded apically (Fig. 155). Surstyli subdivided into 3 components; anterior component bearing 2 long, yellow, stout setae; middle component comprised of thumb-like lobe bearing tuft of long yellow setae; posterior component comprised of small lobe with setal bearing ventral projection (Fig. 153). Cerci subdivided into setose anal plates and slender sclerotized lobes, bearing short, stout spines along posterior margin.

Female. Unknown for type species, refer to *P. tridentata*.

Included Taxa and Geographical Distribution. This genus is known from southern Argentina, Chile and an undescribed species from near Melbourne, Australia.

Bionomics. The type species was collected on wet rocks near a waterfall (Collin 1933). The immature stages of this genus are unknown.

List of described species included in *Proagomyia*.

S torrentium Collin, 1933: 325 [holotype examined] (BMNH).

S tridentata Sinclair sp.nov.

List of examined, undescribed species included in *Proagomyia*.

Proagomyia sp. 1: One female from Australia (BPBM).

Proagomyia tridentata nov.sp.

Holotype. Male labelled: "CHILE: N. Correntoso/ N.E. Puerto Montt/ June - July 1989/
L.E. Pena" (CNC).

Allotype. Female. Same data as holotype.

Derivation of Species Name. Latin for trident or fork with three tines, in reference to the three phallic filaments of the male terminalia.

Recognition. This species is distinguished from *P. torrentium* by bare eyes, a scutellum with modified apical setae and distinctly different male terminalia.

Description. Male. Very similar to generic description with following differences: Eyes bare. Antenna with scape slightly longer than pedicel; first flagellomere shorter than arista. Pseudotracheae weakly developed; short, blunt, blade-like lacinia, appressed to paraphysis of the lacinia.

Scutum faintly bivittate. Acrostichals apparently confined anterior to first dc. Scutellum with 2 pairs of short, stout, flattened apical setae and 2 pairs of unmodified subapical setae. Wing with single basicostal seta.

All leg chaetotaxy dark. Femora with short, white pile beneath. Fore femur with anteroventral and posteroventral row of long, slender setae; mid femur with anteroventral and posteroventral row of long, black, stout setae; hind femur with posteroventral row

of slender setae. Fore tibia with ventral row of short, erect setae and anteroapical comb; hind tibia with posterior apical comb.

Lateral margins of sternites 7 and 8 with short, stout, appressed setae; T8 narrow with two anterior sclerotized patches. Cercus with stout lateral margins, not modified for clasping. Phallus comprises two long, straight filaments with curved apex and a short posterior filament; ejaculatory apodeme articulated with base of phallus. Hypandrium closed posteriorly, phallus arising subapically; anterior margin with pair of long slender phallic guides (Fig. 156).

Female. Similar to male except as follows: scutellum lacking modified apical setae. Abdominal sclerites telescoping, unmodified; T8 desclerotized mid-dorsally, bearing a membranous, flattened tubercle; posteroapical margin of S8 folded back, forming floor of genital chamber; genital fork faint, inconspicuous; T10 desclerotized and divided mid-dorsally; cerci long and cylindrical (Fig. 157). Darkly sclerotized spherical spermatheca at end of long duct (Fig. 158).

Geographical Distribution and Seasonal Occurrence. This species is known only from the type locality, with adults collected from April to July.

Paratype. Chile. N. Correntoso, N.E. Puerto Montt, April - May 1989, L.E. Pena (1♂, CNC).

4.4 GENERA REMOVED FROM CLINOCERINAE

4.4.1 CLASSIFICATION OF THE TRICHOPEZA GROUP OF GENERA

The results of the phylogenetic analysis (Sec. 5.1.1) suggest that the Trichopeza group of genera is most closely related to the Brachystomatinae and Ceratomerinae. Thus it appears to be appropriate to elevate this group to subfamily rank to reflect the hierarchial information illustrated in Figure 205. In the following section, I will redefine and describe the subfamily Trichopezinae and redescribe all the former clinocerine genera currently placed in this lineage.

4.4.1.1 TRICHOPEZINAE NEW STATUS

Type genus: Trichopeza Rondani, 1856.

This subfamily includes the following genera: Apalocnemis Philippi, Boreodromia Coquillett, Ceratempis Melander, Ephydrempis Saigusa, Gloma Meigen, Heleodromia Haliday, Heterophlebus Philippi, Hyperperacera Collin, Niphogenia Melander, Rubistella Garrett Jones, Sabroskyella Wilder, Trichopeza Rondani.

Recognition. This subfamily is a very heterogeneous group and presently only distinguished from other empidoid subfamilies on the basis of a truncate female abdomen, with an internal apodeme arising from the anterior margin of tergite 8 (except Boreodromia).

Description. Male. Eyes holoptic in Gloma, Apalocnemis, and Heterophlebus, with upper facets enlarged. Eyes closely approximated below antennae in Trichopeza and male specimens of Hyperperacera. The proboscis is usually long, with stout labrum and long, fleshy palpus; labral apodeme lacking; pseudotracheae present.

Thorax strongly arched; prosternum either isolated or fused to proepisternum; chaetotaxy long and in distinct rows; acrostichals usually well-developed; postnotum often lacking setae.

Basal angle developed, except in Heleodromia and Rubistella; subcosta complete or evanescent; R_{4+5} simple in Heleodromia, Hyperperacera and some Rubistella. Legs slender, often bearing long, erect setae.

Terminalia highly variable; epandrium and hypandrium separate sclerites with simple cerci or epandrium and hypandrium fused and asymmetrical.

Female. Similar to male except as follows: eyes dichoptic; tip of abdomen truncate, terminal segments retracted within segment 7; posterior margin of T7 with fringe of long, stout setae. Apodeme arising from anterior margin of T8 extending into segment 7; S8 slender, articulated to anteroventral margin of T8. Tergite 10 divided mid-dorsally, bearing short, stout setae or spines (= acanthophorites). Cercus directed upright, bearing modified setae (except Boreodromia). Spermatheca spherical or tubular.

Geographical Distribution. The genus Gloma is known from western North America and Europe and includes 4 described species. Heleodromia includes 13 described species

distributed in the Holarctic and Oriental regions. Heterophlebus contains 26 described species distributed in the Neotropical and Australasian regions. Hyperperacera is a monotypic Neotropical genus and Rubistella is an Afrotropical genus and includes 10 described species (includes all species described under Brachystoma by Smith (1969)). Apalocnemis includes 29 described species, distributed in the Nearctic, Neotropical and Australasian regions.

Boreodromia, Ceratempis, Niphogenia, and Sabroskyella are endemic to the Nearctic region, confined to the western Cordillera. The genera, Trichopeza and Ephydrempis are confined to the Palearctic and Oriental regions.

Phylogenetic Relationships. The Trichopeza family group name was first coined by Vaillant (1981) as a new tribe within the Hemerodromiinae and included the single genus Trichopeza. I have redefined this lineage, which is characterized by a large internal apodeme arising from the anterior margin of female abdominal tergite eight. The similarities of the female abdomen of Trichopeza, Gloma, and Heleodromia were first noted by Collin (1961). Trichopeza, Sabroskyella, Ephydrempis, Niphogenia, Ceratempis, and Boreodromia were formerly classified in the subfamily Clinocerinae. Despite lacking acanthophorites or other modifications of the female terminalia, Boreodromia is classified in the Trichopezinae on the basis of similarities of the male terminalia with Nearctic species of Apalocnemis and Trichopeza. It should be noted that there are significant differences, in both male and female terminalia, between Nearctic and Neotropical Apalocnemis. Consequently a revision to evaluate the monophyly of this

genus is warranted.

Rubistella was originally believed to be an aberrant genus of the Clinocerinae (Garrett Jones 1940). This genus was later synonymized with Brachystoma on the basis of modified abdominal sclerites (Smith 1969). The female terminalia of Rubistella distinctly differs from Brachystoma, consequently the former genus should be re-elevated to generic rank.

Phillipi (1865) described ten species of Chilean empidids under the genus Brachystoma, of which five were placed in a new subgenus, Heterophlebus. This subgenus was erected to include species with R_4 ending in R_{2+3} , rather than the costa (Collin 1933). Collin (1933) later transferred nine of Phillipi's species to the genus Oreogeton. On the basis of female terminalia, the Chilean species are not congeneric with the Holarctic concept of Oreogeton. Consequently, I propose that Heterophlebus should be removed from synonymy and elevated to the rank of genus, in order to receive all the species listed by Collin (1928, 1933) under Oreogeton. Examination of all species will be conducted at a later date to verify this proposal. The remaining species (H. nemoralis (Phillipi)) was placed into a new genus Hyperperacera, in which R_{4+5} was simple (Collin 1933). This genus is possibly a junior synonym of Heterophlebus.

4.4.1.2 TRICHOPEZA SUBGROUP OF THE TRICHOPEZINAE

The following four genera, formerly placed in Clinocerinae (redescribed below), plus Nearctic Apalocnemis (currently classified in Oreogetoninae) appear to form a monophyletic subgroup within the Trichopezinae on the basis of an elongate, slender

phallus and fusion of the hypandrium and epandrium.

GENUS BOREODROMIA COQUILLET

Boreodromia Coquillett 1903: 247, 260. Type-species, Synamphotera bicolor Loew (original designation).

Boreomyia (error) Aldrich, 1905: 316.

Type Material Examined. LECTOTYPE (here designated), male labelled: "524"; "Loew."; "Type/ 13088 [red label with upper white border] [only thorax and abdomen remaining] (MCZ). My lectotype label "LECTOTYPE/ of Synamphotera/ bicolor Loew/ des. B.J. Sinclair 1992 [red label]" has been attached to this specimen.

PARALECTOTYPE: Same data as lectotype [only thorax and abdomen remaining] (1♀, MCZ). My paralectotype label has additionally been attached to this specimen.

Recognition. This monotypic genus is readily distinguished by its shiny abdomen, bicoloured antenna, truncate cell cup and simple R_{4+5} .

Description. Male. Eyes with very short hairs, lower facets becoming larger; ocellar setae pale and slender. Antennae inserted in middle of head; scape and pedicel yellow, flagellomeres brown; first flagellomere long and tapering, bearing setulae; arista two-segmented, basal flagellomere small, apical flagellomere half length of first flagellomere.

Gena very narrow, not divided. Proboscis long; labrum long and stout, with 5 apical teeth; lacking internal apodeme from proximal margin of labrum; labium long; labellum not held in horizontal position, bearing pseudotracheae; lacinia free, equal in length to palpus; hypopharynx long, slender, equal in length to labrum. Palpus half length of proboscis.

Prosternum fused to proepisternum. Pleura light brown, coxae pale, with sparse pruinescence; scutum dark brown, mostly covered by pruinescence. All thoracic setae pale; acrostichals uniserial, extending to prescutellar depression; approximately 10 dc; setulae only on pprn; 1 short presut spal; 2 npl, lower slender; 2 short psut spal; 1 pal; 4 setl. Postnotum bare; anteprenotum with several pale setulae.

Wing clear with microtrichia; stigma faint, elongate; single short basicostal seta. R_{4+5} simple; Sc evanescent; cell cup truncate; A_1 faint, long; cell dm produced apically. Calypters with fringe of pale setae.

Entire leg, including coxae, yellow. Empodium bristleform; pulvilli pad-like, not elongate as in Clinocera. Fore femur with long, white pile beneath; mid femur with posteroventral row of long setae. Fore tibia with anterior apical comb; hind tibia with posterior apical comb. Fifth tarsomere lacking dorsoapical extension.

Abdomen dark brown, shiny. Tergite 8 well developed, narrowed mid-dorsally. Epandrium enclosing and fused to hypandrium. Hypandrium reduced, narrow, with pointed apex; bearing pair of phallic guides, extending half length of abdomen. Phallus filamentous, extending length of abdomen, emerging at apex of hypandrium; base of phallus with double articulation points, moved by set of stout adductor muscles. Cercus

not subdivided, held erect. Surstylus large, ear-like, positioned at posterodorsal margin of epandrium (Figs. 159,160).

Female. Similar to male except as follows: all femora with long, white pile beneath; fore and mid tibia with stout, dark erect setae beneath. Segment 10 and cerci retracted within T8. Spermatheca a very elongate, lightly sclerotized tube, longer than abdomen; surface covered by erect pubescence. Genital fork strongly sclerotized, U-shaped and darkly pigmented (Fig. 161).

Included Taxa and Geographical Distribution. Boreodromia was originally described from Sitka, Alaska, from material collected by Sahlberg (Loew 1863). This genus occurs along the Pacific coast of North America, from Alaska to California (Melander 1928), including the Queen Charlotte Islands (specimens in USNM).

Phylogenetic Relationships. Boreodromia has been a very difficult genus to place into the existing subfamilies of the Empidoidea. While surveying the genera of the Oreogetoninae, I noted striking similarities between the male terminalia of Boreodromia and Nearctic species of Apalocnemis described by Melander (1946). Both genera share the following apomorphies: hypandrium and epandrium fused; elongate, thread-like phallus; erect, unmodified male cerci; ear-like surstyli (Figs. 160,162); elongate, tube-shaped spermatheca (a narrow tubular spermatheca, lacking terminal sclerotized receptacle, was partially visible in Nearctic species of Apalocnemis; however,

verification in additional specimens is required).

Two male specimens collected in California, which may represent a new genus, are also considered to belong to this group on the basis of male terminalia (Fig. 163). Although female specimens are currently unassociated, I would predict that the female terminalia would probably be modified similar to that of Nearctic species of Apalocnemis. The wing of this species also has a truncate cell cup and wing with reduced anal angle, character states used to place Boreodromia in the Clinocerinae.

Bionomics. This genus is commonly collected over streams and riparian regions. The immature stages of this genus are unknown.

GENUS EPHYDREMPIS SAIGUSA

Ephydrempis Saigusa, 1986: 114. Type-species, E. setiventris Saigusa (original designation).

Type Material Examined. PARATYPES: E. Nepal: Topke Gola, 3700m, 27°38'N, 87°35'E; Thurukpa, 2600m, 27°36'N, 87°36'E, 9.VII.1972, J. Emoto (1♂, 1♀, CNC).

Recognition. This monotypic genus may be distinguished by its hairy eyes, broad face and fused prosternum. It is most similar to Sabroskyella but setose lobes are present on tergites 6 and 7 of the male abdomen and the cercus-like lobes of tergite 8 of females are broad.

Description. Male. Eyes with short pubescence; separated on frons and face. Antennae inserted above middle of head; scape one and one-half times as long as globular pedicel; first flagellomere prolonged into arista-like filament, lacking further subdivisions of flagellum, bearing pruinescence. Gena very narrow, ridge extending from palpus along anterior margin of eye. Proboscis long, slender; palpus half as long as labium; labrum long and narrow, apex bearing four short points (Saigusa 1986); labral apodeme lacking, lacinia free; labium narrow bearing setae; labellum large, not sucker-like as described by Saigusa (1986); pseudotracheae present.

Prosternum fused to proepisternum. Single row of acrostichals extend to prescutellar depression; 7-10 dc; 1 pprn; 1 presut spal; 2 npl; 2-3 psut spal; 1 pal; 4 scrl. Pleura bare, with thin, pale pruinescence; postnotum lacking setae; anteprenotum with several pale setae.

Wing long and broad, lightly infusate; stigma narrow, elongate; anal lobe weakly produced; single basicostal setae. Sc evanescent; cell dm slightly produced apically; R_{4+5} branched; R_4 very long, basal angle often with auxillary crossvein to R_{2+3} ; CuA_2 reaching one-quarter to base of cell cup; A_1 represented by crease in wing; calypters with fringe of setae.

Legs long and slender, fore coxae one-half length of fore femur; femora and tibiae with long, slender setae. Mid femur swollen with anteroventral and posteroventral rows of stout setae on apical fifth. Fore tibia with anteroapical comb; hind tibia with with posteroapical comb; midlength with posterodorsal row of short, stout setae; basal third distinctly narrowed. Fifth tarsomere of fore and hind legs with dorsoapical extension;

empodium pulvilliform, much longer than pulvilli; fifth tarsomere of mid leg blunt apically, twisted, slightly flattened, with subbasal anterior projection, which receives a lengthened and curved claw.

Tergite 6 with pair of dorsolateral lobes bearing dense, stout setae apically. Tergite 7 with asymmetrical pair of dorsolateral lobes; left lobe bare, right lobe short bearing setae apically; lateral margin of sclerite densely setose (Saigusa 1986, fig. 11). Sclerites of segment 8 fused, forming a ring. Hypopygium asymmetrical, various parts fused making it extremely difficult to homologize. Hypandrium and epandrium fused, divided apically into narrow lobes; phallus elongate and thread-like. Paired cerci displaced to left side of terminalia; a single right surstylus present (Fig. 165).

Female. Similar to male except as follows: mid tarsomere unmodified. Tip of abdomen truncate, terminalia as found in Trichopezinae; T7 with short, median notch and posterior margin lined with long, stout setae. Tergite 8 with broad, posterolateral cercus-like lobe, densely covered with long setae; anterior apodeme of T8 slender. Acanthophorites subdivided into 2 pairs of sclerites; anterior pair bare, rectangular; posterior pair bearing more than 10 pairs of heavily sclerotized spine-like setae; cercus short, dorsally arched (Fig. 164). A spherical, heavily sclerotized spermatheca present (Fig. 166); genital fork in shape of a wide ring.

Included Taxa and Geographic Distribution. A monotypic genus known only from the Himalayas of Nepal (Saigusa 1986).

Phylogenetic Relationships. See discussion under Trichopeza. This genus is most closely related to Sabroskyella on the basis of a modified mid femur and cercus-like lobes on T8 of the female terminalia.

Bionomics. Adults were found between 2100-4700m, collected along streams and puddles (Saigusa 1986). The immature stages of this genus are unknown.

GENUS SABROSKYELLA WILDER

Sabroskyella Wilder, 1982: 167. Type-species, S. rancheria Wilder (original designation).

Type Material Examined. PARATYPES: U.S.A. California: Fresno Co., Sierra N.F., Badger Flat Cpgd. along Rancheria Creek, 2500m, T7S R26E Sec. 3, 31.VII.1979, D.D. Wilder (1♀,CNC); U.S.A. California: Fresno Co., Huntington Lake along Bear Creek, 2100m, 7.VIII.1978, D.D. Wilder (1♀,CNC).

Additional material examined: U.S.A. California: Huntington Lake, Rancheria Ck., 2600m, Fresno Co., 9,23,30,31.VII.1984, J. MacDonald (2♂♂,3♀♀,CNC).

Recognition. This genus may be distinguished by the evanescent subcosta, broad face and hairy eyes. It is most similar to Ephydrempis but tergites 6 and 7 of male abdomen are unmodified and the cercus-like lobes of tergite 8 of females are narrow.

Description. Male. Eyes with short pubescence; separated on frons and face. Antennae inserted above middle of head; scape equal in length to globular pedicel; first flagellomere prolonged into arista-like filament, lacking further subdivisions of flagellum, bearing pruinescence. Gena very narrow, ridge extending from palpus along anterior margin of eye. Proboscis long, slender; labrum long and narrow, apex bearing four short points; labral apodeme lacking; hypopharynx equal in length to labrum; blade-like, blunt-tipped lacinia, fused to stipes; labium narrow, bearing setae; labellum small, not sucker-like, bearing well developed pseudotracheae.

Prosternum fused to proepisternum. Single row of acrostichals extend to prescutellar depression; 6-8 dc; 1 pprn; 1 presut spal; 2 npl; 1-2 psut spal; 1 pal; 2 scrl. Pleura bare, with pale pruinescence; postnotum lacking setae; anteprenotum with short setae.

Wing long and broad, infusate; stigma narrow, elongate; anal lobe weakly produced; single basicostal seta. Sc evanescent; cell dm blunt apically; R_{4+5} branched; CuA_1 reaching one-third to base of cell cup; A_1 represented by crease in wing; calypters with fringe of setae.

Legs long and slender; fore coxae one-half length of fore femur. Mid femur swollen with anteroventral and posteroventral rows of stout setae on apical third. Fore tibia with anterior apical comb; hind tibia with posteroapical comb. Apex of fifth tarsomere blunt. Claws and pulvilli short, empodium setiform.

Eighth abdominal tergite and sternite fused to form a broad ring. Hypopygium asymmetrical, various parts fused making it extremely difficult to homologize.

Hypandrium and epandrium fused, divided apically into narrow lobes, central lobe forming a phallic guide; phallus elongate and thread-like, looped back beyond eighth segment. Cerci positioned together on left side and a long, slender surstylus present on right side (Wilder 1982, figs. 3,4).

Female. Similar to male except as follows: tip of abdomen truncate, terminalia as found in *Trichopezinae*; T7 with deep U-shaped notch, posterior margin lined with long, stout setae. Tergite 8 with narrow, posterolateral cercus-like lobe, densely covered with long setae; anterior apodeme of T8 slender. Acanthophorites subdivided into 2 pairs of sclerites; anterior pair bare, rectangular; posterior pair bearing more than 10 pairs of heavily sclerotized spine-like setae; cercus short, dorsally arched (Fig. 167). An elongate-oval, heavily sclerotized spermatheca present, positioned in sixth segment (Fig. 169).

Included Taxa and Geographic Distribution. Monotypic genus, apparently confined to the Sierra Nevada Mountains of California (Wilder 1982).

Phylogenetic Relationships. See discussions under *Trichopeza* and *Ephydrempis*.

Bionomics. Occurs along stream margins at high elevations, from July to August (Wilder 1982). The immature stages of this genus are unknown.

4

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

GENUS TRICHOPEZA RONDANI

Trichopeza Rondani, 1856: 150. Type-species. Brachystoma longicornis Meigen (original designation).

Type Material Examined. Trichopeza albicincta Frey, LECTOTYPE (here designated), male labelled: "Lojo [Lohja, Finland]"; "Frey"; "363"; "Mus. Zool. H:fors/ Spec. typ. No 4422/ Trichopeza/ albicincta Frey [hand written]" (ZMH). My lectotype label "LECTOTYPE/ Trichopeza/ albicincta Frey/ des. B.J. Sinclair 1992 [red label]" has been attached to this specimen.

PARALECTOTYPES: Finland: Ab. Karislojo (J. Sahlb., Forsius, R. Frey) (4♂♂, 4♀♀, ZMH); Ab. Lojo, R. Frey (5♂♂, 3♀♀, ZMH); St. Yläne, J. Sahlb. (2♂♂, 2♀♀, ZMH); Sb. Tuovilanlaks, Lundström (1♂, ZMH); Kh. Nurmis, J. Sahlb. (2♀♀, ZMH). Russia: Ik. Metsäp[irtti]. J. Sahlb. (1♀, ZMH); Kl. Ruskeala, J. Sahlb. (1♀, ZMH). My paralectotype labels have additionally been attached to these specimens.

Recognition. This genus may be distinguished from the other genera of this group by evanescent subcosta, long, erect setae on the legs and eyes sparsely haired, closely approximated below antennae.

Description. Male. Eyes sparsely pubescent; separated on frons and closely approximated below antennae; facets on front region below antennae enlarged. Antennae placed well above middle of head; scape twice to three times as long as globular pedicel;

first flagellomere prolonged into arista-like filament, lacking further subdivisions of flagellum, bearing pruinescence. Gena very narrow, ridge extending from palpus along anterior margin of eye. Proboscis long, slender; labrum long and narrow, apex bearing four short points; labral apodeme lacking; hypopharynx equal in length to labrum; lacinia short, slender rod, articulated to stipes; labium narrow bearing setae; labellum small, not sucker-like, bearing well developed pseudotracheae.

Prosternum isolated, not fused to proepisternum. Scutum strongly arched in profile. Several long, slender acrostichals anterior to first dc; 4-6 dc; 1 ppm; 1 presut spal; 2 npl; 1-2 psut spal; 1 pal; 2 setl. Pleura bare, with pale pruinescence; postnotum lacking setae; anteprenotum lacking setulae.

Wing long and broad, infusate; stigma narrow, elongate; anal lobe weakly produced; single basicostal setae. Sc evanescent; cell dm blunt apically; R_{4+5} branched; CuA_1 reaching one-third to base of cell cup; A_1 represented by crease in wing; calypters lacking fringe of setae.

Legs long and slender, bearing long setae; fore coxae one-third length of fore femur. Fore tibia with anterior apical comb; posterior tip of hind tibia dilated, bearing apical comb. Claws and pulvilli short, empodium setiform. Third tarsomere on midleg modified in *T. longicornis*. Apex of fifth tarsomere blunt.

Abdomen long, sclerites shiny. Eighth tergite and sternite fused to form a broad ring. Hypopygium asymmetrical, various parts fused making it extremely difficult to homologize. Hypandrium and epandrium fused, divided apically into narrow lobes, central lobe forming a phallic guide; phallus elongate and thread-like, looped back

through abdomen (Fig. 168). A single, short cercus and a long, slender, setose surstylus (*T. longicornis*) or pair of setose surstyli (*T. albocincta*) present.

Female. Similar to male except as follows: tip of abdomen truncate, terminalia as found in Trichopezinae; T7 with deep U-shaped notch, posterior margin lined with long, stout setae; S7 extending beneath eighth. Anterior apodeme of T8 slender. Acanthophorites subdivided into 2 pairs of sclerites; anterior pair bare, rectangular, fused laterally with S10; posterior pair bearing two transverse rows of heavily sclerotized spine-like setae. Cercus comprises two stout, pointed lobes (Fig. 170). An oval, heavily sclerotized spermatheca present, positioned in seventh segment; spermathecal duct strongly coiled (Fig. 171).

Included Taxa and Geographic Distribution. This genus is found in the Palearctic and Oriental regions, including a Baltic Amber species and undescribed species from Japan (Meunier 1908; Brunetti 1913; Chvála and Wagner 1989). The distribution of *T. longicornis* and *T. albocincta* Boheman in Europe has been illustrated by Wagner (1984d).

Miller (1923) described *T. longipennae* from New Zealand, but after examining female paratypes, I believe that this species should be removed from *Trichopeza*. On the basis of simple female terminalia, modified mouthparts and stout anterior setae on the fore coxae, this species appears to be most closely related to *Zanclostus* and may represent a new genus. Smith (1989) published a new name (*T. milleri*) for *T.*

longipennae (listed in Australasian Catalog as T. longipennis) since he believed the species name was preoccupied; however, this represents an unjustified emendation.

The Baltic Amber species, T. sucina Melander is also likely not congeneric. The first flagellomere of the antenna of this species is subdivided (Meunier 1908, fig. 7.3), while in extant species of Trichopeza the first flagellomere is prolonged and not subdivided (c.f. Chvála 1983, fig. 14).

Phylogenetic Relationships. Trichopeza, Sabroskyella, and Ephydrempis form a monophyletic group within the Trichopezinae on the basis of asymmetrical male terminalia and sclerites of segment 8 fused to form a ring.

The above three genera, plus Boreodromia and Apalocnemis (Nearctic species only), appear to form a monophyletic group on the basis of an elongate, slender phallus and fusion of the epandrium and hypandrium.

Bionomics. Trichopeza longicornis has been observed feeding on small nematocerans, holding the prey between the fore femur and tibia (Ulrich 1981). Large numbers of T. longicornis have been collected from emergence traps over streams in Germany (Caspers and Wagner 1982). The immature stages of this genus are unknown.

List of described species included in Trichopeza.

P albocincta (Boheman), 1864: 80 (Brachystoma).

syn. albicincta Frey, 1913: 66 [Lectotype designated] (ZMH).

- O fusca Brunetti, 1913: 31 [type apparently partially destroyed (Parui, pers. comm.)] .
- P longicornis (Meigen), 1822: 12 (Brachystoma) [examined].
- P sucina Melander, 1928: 220 (for longicornis Meunier).
 syn. longicornis Meunier, 1908: 108 [Preocc. Meigen 1822] [Baltic Amber].

List of examined, undescribed species included in Trichopeza.

Trichopeza sp. 1: Males and females from Japan (CNC).

Trichopeza sp. 2: One male and three females from Japan (CNC).

4.4.1.3 NIPHOGENIA SUBGROUP OF THE TRICHOPEZINAE

The following two genera of the Trichopezinae are believed to be most closely related on the basis of an elongate, densely pubescent first flagellomere and modifications of the epandrium.

GENUS CERATEMPIS MELANDER

Ceratempis Melander, 1928: 218. Type-species, C. longicornis Melander (original designation).

Type Material Examined. LECTOTYPE (here designated), male labelled: "Nasel R[iver]. W[ashingto]N [USA]/ 15.VII.[19]22/ AL Melander"; "TYPE/ Aprerempis/

longicornis/ Mel [red label]" (USNM). My lectotype label "LECTOTYPE/ of Ceratempis/ longicornis/ des B.J. Sinclair 1991 [red label]" has been attached to this specimen.

PARALECTOTYPES: Nasel River, W[ashingto]N, 2.VII.[19]25, A.L. Melander (1♂, USNM); Ilwaco, WASH[ington], 28.VI.[19]25, A.L. Melander (2♂♂, USNM). My paralectotype labels have additionally been attached to these specimens.

Melander (1928) described this species based on males from a series of 8 syntypes. Four syntypes are known, the location of the remaining specimens is unknown.

Recognition. This genus may be distinguished by its yellow colour, bare eyes, lack of distinct acrostichals and dense grey pubescence on the first flagellomere.

Description. Male. Body entirely yellow except first flagellomere, ocellar triangle and fifth tarsomere. Eyes bare. Gena narrow, separated from eye. Antennae inserted above middle of head; scape twice length of globular pedicel; first flagellomere three-times length of head, slightly tapering, clothed by dense grey pubescence; apical arista lacking. Proboscis lightly pigmented; labral apodeme lacking; palpus directed forward, bearing stout setae; labrum half length of labium, subequal to hypopharynx; labellum not sucker-like, bearing pseudotracheae.

Prosternum small and isolated. All setae dark. Several minute acrostichals confined to anterior fifth of notum; 5-6 dc; 2-3 pprn; 1 presut spal; 2 psut spal; 1 pal; 2 sctl. Several setae on anteprepronotum; postnotum with patch of pale setae.

Wing hyaline; anal lobe not produced; apical half of wing broad; stigma lacking, single basicostal seta. Sc complete; R_4 and R_5 diverging; cell dm with short projection apically; cup cell elongate and narrow; anal vein reduced to fold of membrane. Calypters with fringe of brown setae.

Legs slender; pulvilli broad, pad-like (as opposed to elongate as in clinocerines); empodium not pulvilliform, bearing minute setae along ventral margin. Femora with 1-2 antero and posteroventral, preapical setae. Fore tibia lacking anteroapical comb. Mid tibia with single anteroventral row of preapical short, stout setae; mid femur with corresponding ventral row of setae at base. Apical half of hind tibia with erect, dorsal setae; posterior apical comb lacking. Apex of fifth tarsomere blunt.

Abdomen with scattered setae. In dried specimens, hypopygium held at right angle to horizontal (erect) (Fig. 172). Cercus unmodified; surstyli lacking. Epandrium deeply cleft, partially encircling hypandrium; with 3 stout setae arising from tubercle; tip with dark spur. Hypandrium a shallow sclerite, with two pairs of posterior processes; phallus a straight tube (Fig. 173).

Female. The location of the females included in the type series is unknown. Additional female specimens are presently unavailable for study.

Included Taxa and Geographical Distribution. There is only one species of Ceratempis, known from southwestern Washington (Melander 1928).

Phylogenetic Relationships. Despite the lack of females, this genus is included in the Trichopezinae due to its apparent close relationship to the genus Niphogenia. Both genera possess a small, dorsoapical, epandrial, hook-shaped lobe.

Bionomics. Male specimens have been recently collected by Dr. Turner (WSU) sweeping coastal forest in Washington. The immature stages of this genus are unknown.

GENUS NIPHOGENIA MELANDER

Niphogenia Melander, 1928: 217. Type-species, Q. eucera Melander (original designation).

Type Material Examined. PARALECTOTYPES (by designation of Wilder 1981b): N. eucera, Mt. Rainier [National Park], W[ashingto]n.[USA], Paradise Park, August 1917, A.L. Melander (11♀♀,USNM,1♀,CNC); Mt. Rainier, Eagle Peak, 19.VII.1917, A.L. Melander (1♀,USNM); Mt. Rainier, Wn, Van Trump Crk, 1.IX.1917, A.L. Melander (1♀,USNM).

Niphogenia eucera determined by D.D. Wilder, USA: Oregon; Clackamas Co., Mt. Hood Nat. For., Still Creek Cpgd, 23.VI.1977, D.D. Wilder (6♂♂,2♀♀,CAS).

Melander (1928) based the description of N. eucera on 1 male and 25 females specimens; however, a holotype was not designated. Wilder (1981b) subsequently listed the male specimen as the holotype. According to Section 74(b) of the I.C.Z.N., Wilder (1981b) has actually designated the male specimen the lectotype by inference. I have

subsequently attached a yellow paralectotype label to the above listed specimens. A red lectotype label will also be attached to the single male syntype, housed in the USNM.

Recognition. This genus is readily distinguished by the long first flagellomere clothed in dense pubescence, bare eyes, short proboscis and row of distinct acrostichals.

Description. Male. Eyes bare. Antennae positioned above middle of head; scape twice length of globular pedicel; first flagellomere greater than length of scutum, clothed by long dense pubescence; tip of flagellomere with minute two-segmented style. Gena narrow, ridge extending from palpus along anterior margin of eye. Proboscis short; labrum short, often bearing setae (*N. eucera*); labral apodeme lacking; pseudotracheae present; lacinia fused to labial sclerite and labial paraphysis, stipes separate from lacinia. Palpus equal to length of labrum.

Pleura with pale pruinescence. Prosternum isolated; proepisternum with several dark, stout setae above coxae; anteprenotum with 4 pairs of setae. All thoracic setae short, lateral setae stout; single row of acrostichals; 11 + dc; 2-3 ppm; 1 presut spal; 2-3 npl; 2 psut spal; 1 pal; 2 widely separated sctl. Postnotum with patch of black setae.

Wing infusate; anal angle slightly produced; single basicostal seta; stigma faint, elongate. Anal vein reduced to fold; R_4 and R_5 strongly diverging; cell dm slightly produced apically; Sc complete; cup cell elongate and narrow. Calypters with fringe of dark setae.

All legs yellow, coxae with black setae; pulvilli small, empodium bristleform,

with short setae beneath. Apical half of mid tibia with anteroventral spine-like setae; mid femur with biserial row of setae at base. Hind tibia with erect dorsal setae. Fore tibiae with small anterior, apical comb; hind tibia with small, posterior, apical comb. Apex of fifth tarsomere blunt.

Tergite 8 narrow; hypopygium not rotated dorsally. Cercus unmodified; surstylus lacking. Epandrium deeply cleft, partially encircling hypandrium; with pair of pointed lateral filaments; tip with dark spur. Hypandrium a shallow sclerite, paired dorsal projections fused posteriorly; phallus apparently a narrow filament (Fig. 174).

Female. Similar to male except as follows: ventral seta of midleg lacking. Spermatheca not visible in macerated specimens. Apex of abdomen truncate, terminalia as found in Trichopezinae; T7 with dense posterior fringe of long setae; dorsal surface with longitudinal, desclerotized central region on posterior two-thirds. Segment 8 narrow; dorsal region of posterior half of T8 membranous; anterior margin with wide, short apodeme extending into segment 7; S8 narrow strip, articulated at anteroventral edge of T8. Acanthophorite narrow, bearing short, blunt, spine-like setae. Cerci heavily sclerotized, arched dorsally, bearing short setae (Figs. 175-176).

Included Taxa and Geographical Distribution. There are two species of Niphogenia, both described from western North America (Wilder 1981b). Niphogenia eucera is known from California, Oregon and Washington and commonly collected in moist areas. Niphogenia turneri Wilder is known from two localities in Idaho.

Phylogenetic Relationships. This genus, on the basis of male terminalia, appears most closely related to the genus Ceratempis.

Bionomics. Niphogenia is not believed to be associated with lotic habitats, since it has been frequently observed in alpine meadows (Wilder 1981b). Adults feed, rest and mate on moist soil or low vegetation. They have been observed feeding on insect larvae unearthed from the soil (Wilder 1981b). The immature stages of this genus are unknown.

List of described species included in Niphogenia.

N eucera Melander, 1928: 217 [paratypes examined] (CNC).

N turneri Wilder, 1981b: 427.

4.4.2 OTHER TAXA REMOVED FROM CLINOCERINAE

The following three genera, Dipsomyia Bezzi, Dryodromia Rondani, and Zanclotus Wilder are removed from the Clinocerinae.

The genus Dipsomyia is poorly defined, particularly because of the lack of associated males. Consequently, I have chosen to address each species of this genus separately. The long, stout labrum and shape of the spermatheca is similar in all species, which may help to characterize Dipsomyia until males are associated. Unfortunately, the holotype female of D. spinifera Bezzi, housed in the Staatliches Museum in Dresden, is currently on loan to Mr. J.A. Rafael (Brazil). Dipsomyia is removed from the Clinocerinae on the basis of the spermatheca with a terminal, sclerotized receptacle and

orcogetonine-like male terminalia.

Dipsomyia mutabilis Collin

Dipsomyia mutabilis Collin, 1928: 60

Type Material Examined. HOLOTYPE, female labelled: "TYPE/ ♀ [circle label with red border]"; "New Zealand:/ Glenorchy/ 3.i.1923/ C.C. Fenwick./ B.M.1923 - 150"; "Dipsomyia/ mutabilis [dark circle label"; Dipsomyia/ mutabilis/ TYPE ♀ Collin"; "Wing of ♀ TYPE/ figured in text of/ author's description" (BMNH).

Recognition. This species of Dipsomyia is distinguished from D. stigmosa by a long setose palpus, which lacks stout apical setae, double row of acrostichals and 4 scutellar setae.

Description. Female. Eyes bare; separated on frons and face. Antennae inserted above middle of head; scape equal in length to globular pedicel; remaining antennae missing. Palpus very long and slender, bearing scattered setae; labrum greatly lengthened, longer than height of head, slightly incurved; labium much shorter than labrum, probably an artifact due to drying.

Pleura, coxae, pprn and npl with pale blue pruinescence. Prosternum fused to proepisternum. Acrostichals unise-ial in front, slightly longer and biserial behind, extending to prescutellar depression; 6 dc, intermixed with short, slender setae; 1 pprn;

1 presut spal, with 2-3 short setae; 2 npl, lower slender and short; 2 psut spal with 2-3 short setae; 1 pal; 4 setl and outer pair slender. Postnotum with patch of pale setae; antepronotum with several pairs of short setulae.

Wing broad, infusate; stigma broad, elongate; anal lobe produced, yet remaining obtuse; single long basicostal setae (see Collin 1928, fig. 17). Sc evanescent; cell dm slightly produced apically; R_{4+5} branched; CuA_1 reaching one-quarter to base of cell cup; A_1 represented by crease in wing; calypters with fringe of dark setae.

Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform, equal in length of pulvilli. Coxae with pale setae. Fore femur with anterodorsal row of short, stout setae. Hind femur with long, erect setae. Fore tibia with anteroapical comb; hind tibia with posteroapical comb.

Terminal two segments retracted within seventh segment in dried specimen; posterior margin of T8 with small membranous, mid-dorsal cleft; sclerite bare, except for transverse row of small, setae increasing in size towards lateral margins; sternite 8 broad, extending beneath segment 10. Tergite 10 divided mid-dorsally into two rectangular sclerites; each sclerite with mid-dorsal row of 4-5 short setae; cercus narrow and short, fused to S10 (Fig. 177). A small, narrow, sclerotized spermatheca present at apex of long duct which leads to small genital fork (Fig. 178).

Male. Unknown.

Geographical Distribution. This species is known only from the type locality.

Phylogenetic Relationships. In D. mutabilis, the spermatheca is characterized by a spherical, terminal receptacle, which justifies removing this species from the Clinocerinae.

Dipsomyia stigmosa (Smith)

Empidadelphina stigmosa Smith, 1964: 325

Type Material Examined. PARATYPES: New Zealand: Campbell Is., Tucker Cove, 4m, Malaise Trap, 1-3.XII.1961, J.L. Gressitt (1♂, BMNH); New Zealand: Campbell Is., Lookout Bay, beach, 16,19.XII.1961, J.L. Gressitt (1♀, BMNH).

Recognition. This species of Dipsomyia is distinguished from D. mutabilis by the stout setae on the apex of the palpus, single row of acrostichals and 2 scutellar setae.

Description. Male. Eyes bare; separated on frons and face. Antennae inserted above middle of head; scape twice as long as globular pedicel; first flagellomere prolonged into arista-like filament, with long, thick apical one-segmented arista bearing pruinescence. Proboscis short and fleshy; palpus broad, flattened with several stout apical setae.

Pleura, ppn, npl and sctl with pale blue pruinescence. Prosternum fused to proepisternum. Single row of acrostichals extend to prescutellar depression; 6 dc, intermixed with short, slender setae; 1 ppn and several short setae; 1 presut spal; 3 npl;

3 psut spal; 1 pal; 2 setl and outer pair of setulae. Postnotum with several short, black setae; antepronotum with several pairs of short, dark setae.

Wing broad, infusate; stigma broad, elongate; anal lobe produced, yet remaining obtuse; single long basicostal setae. Sc evanescent; cell dm slightly produced apically; R_{4+5} branched; CuA_2 reaching one-quarter to base of cell cup; A_1 represented by crease in wing; calypters with fringe of dark setae.

Legs brown. Fifth tarsomere lacking dorsoapical extension; empodium pulvilliform, equal in length of pulvilli. Fore femur with anteroventral and posteroventral rows of short, stout setae (mid and hind legs absent in specimen examined, refer to Smith (1964) for further details). Fore tibiae with short, erect setae beneath; anteroapical comb present. Hind tibiae with posteroapical comb.

Cercus unmodified; pair of short surstyler lobes projecting from lateral margin of epandrium; posterior apex of epandrium with slender, curved processes (Fig. 180). Hypandrium narrow with expanded anterior margin; phallus stout, strongly arched (Fig. 181).

Female. Similar to male except as follows: palpus long and narrow, bearing several stout, apical setae; labrum greatly lengthened, longer than height of head. Lacking modified setae of fore femur. Terminal two segments retracted within seventh segment in dried specimen; posterior half of T8 with mid-dorsal membranous region; sclerite bare, except for transverse row of small, setae across middle; sternite 8 broad extending beneath segment 10; T10 divided mid-dorsally into two rectangular sclerites

each with posterior, transverse row of 4-5 short, stout setae; cercus narrow and short (Fig. 182). A small, spherical, sclerotized spermatheca present at apex of long duct which leads to small genital fork (Fig. 179).

Geographical Distribution. This species is restricted to Campbell Island, a subantarctic island (Smith 1964).

Phylogenetic Relationships. This species was originally described under the genus Empidadelpha Collin and later transferred to Dipsomyia by Smith (1989).

The male terminalia of D. stigmosa is very similar to Oreogeton, the anal angle of the wing is acute and the spermatheca is spherical. On the basis of these three character states, D. stigmosa is clearly not a clinocerine.

Based on modifications of the male cercus, Dryodromia should be removed from the Clinocerinae and classified in the Empidinae + Hemerodromiinae lineage.

GENUS DRYODROMIA RONDANI

Dryodromia Rondani, 1856: 150. Type-species, D. testacea Rondani (monobasic).

Synamphotera Loew, 1858d: 453. Type-species, S. pallida Loew (monobasic).

Material Examined. Moravia [Czech Republic] mer., Pavlov, 19.V.1976 (1♂, CNC); Slovakia centr., Kremnické phorie Mts., Turček env., 850m, J. Roháček leg. (1♂, CNC);

CS [Czechoslovakia]: Šumava-S slope of Pamčír, meadow, 49°09'N, 13°16'E, 1000m, Barták, 24.VIII.1989 (1 ♀, BARC); [Germany?] Charlottenbrum, 5. 34/75. (1 ♂, USNM).

Recognition. This genus is readily distinguished by its yellow colour, bare eyes, reduced thoracic chaetotaxy and truncate cell cup.

Description. Male. Body entirely yellow, except claws and articulation between trochanter and femur. Eyes bare; ocellar triangle and eyes dark. Antennae arise in middle of head; first flagellomere ovate, somewhat pointed, with short three-segmented arista, apical joint bare (see Chvála 1983, fig. 13); tip of first flagellomere and arista dark. Proboscis long, cylindrical and straight; lacinia free, lancet-like blades (Krystoph 1961, fig. 10c); pseudotracheae present (Krystoph 1961); palpus long, two-thirds length of proboscis. Chaetotaxy of head inconspicuous, short and yellow.

Thoracic chaetotaxy of minute, yellow setulae; uniserial row of dc; biserial row of acrostichals extend to prescutellar depression; sc1l with more than 8 short, marginal setulae. Postnotum with 2-3 setae; anteprenotum with several short setae; prosternum fused to proepisternum.

Wing hyaline, anal lobe slightly developed; stigma indistinct; costa continuous around wing. Auxiliary crossvein between R_{2+3} and R_4 (occasionally lost); cell cup truncate, with A_1 extending to wing margin (Collin 1961, fig. 304); cell dm produced apically.

Chaetotaxy of legs short and yellow. Fore tibia with anterior, apical comb; hind

tibia with posteroapical comb. Mid and hind tibiae with small cylindrical, subapical, slightly hairy appendage projecting at right angles, length equal to width of tibia. Empodium setiform, pulvilli pad-like. Apex of fifth tarsomere blunt.

Hypopygium arched anterodorsally over abdomen; T8 narrow, transverse band. Hypandrium stout, tubular; phallus arising from tubular hypandrium, bent at right angles subapically, bearing a pair of terminal curved filaments (Fig. 183). Cercus modified for clasping, stout, with broad base; lacking cercal plate (Fig. 184). Epandrium with curved dorsal lobe with darkened tip, bearing numerous setae with dark sockets (Fig. 185). Wide membranous region between subepandrial sclerite (at base of cercus) and base of hypandrium; bacilliform sclerites indistinct.

Female. Similar to male except as follows: mid and hind tibiae lacking subapical appendage. Tergites 8 and 10 fused, lightly sclerotized and indistinct; S8 long, extended beneath cerci. Cercus small with rounded tips. Spermatheca a small, dark sphere (Fig. 186).

Included Taxa and Geographical Distribution. Only a single species of this genus is known, confined to the western Palearctic.

Phylogenetic Relationships. *Dryodromia* has traditionally been placed in the Clinocerinae on the basis of a narrow wing and lack of raptorial fore legs. Despite similarities with some hemerodromines as suggested by Saigusa (1986) (e.g.

Xanthodromia Saigusa), confident placement of this genus has remained an enigma. I believe Dryodromia is most closely related to the Nearctic genus Hesperempis Melander, on the basis of the following characters states: very reduced thoracic chaetotaxy; 8 or more short scutellar setae; antennae with three-articulated arista, apical component bare (c.f. Chvála 1983, figs. 3,13), positioned in middle of head; cell cup truncate; palpus yellow, slightly compressed. The South African genus, Afroempis Smith (Smith 1969) may also be closely related to these two genera, however specimens were not readily available for study.

The male cercus of Dryodromia and Hesperempis appears to be modified for clasping, which would place these genera in the Empidinae + Hemerodromiinae lineage (sensu Cumming and Sinclair 1990) (see Sec. 5.1.1).

Bionomics. Numbers of specimens of Dryodromia have been collected on blossoms (Collin 1961). While dissecting female specimens of Hesperempis, pollen grains were noted in the gut, indicating that this genus also visits flowers and feeds on pollen.

Zanclotus is here removed from the Clinocerinae and is believed to be most closely related to one of the most basal empidid genera, Hormopeza, on the basis of similarities in mouthparts, chaetotaxy of the legs, and male terminalia.

GENUS ZANCLOTUS WILDER

Zanclotus Wilder, 1982: 172. Type-species, **Z. dioktes** Wilder (original designation).

Type Material Examined. PARATYPES: **Z. dioktes**: Canada: B.C., Manning Prov. Pk. along unnamed creek crossing Rd. to Lookout, 8.X.1979, D. Wilder (1♂, CNC); U.S.A.: Washington: Mt. Rainier Nat. Park, Edith Cr. at Paradise Park, 1650m, 11.1979, D. Wilder (1♂, 2♀♀, CNC, USNM); [WA] Mt. Rainier, Yakima Park, 19.VIII.1934, A.L. Melander (1♀, USNM).

Recognition. This genus is readily recognized by the strongly arched labrum and stout setae on the fore femur.

Description. Male. Eyes pubescent in **Z. dioktes**. Antennae inserted just above middle of head; scape cylindrical, equal in length to globular pedicel; first flagellomere oval, drawn out to narrow apex, with two-segmented arista. Clypeus prominent, occupying most of face; gena narrow, divided by suture from palpus to eye. Labrum stout, curved; hypopharynx long, slender, curved, pointed; labium equal in length to labrum, bilobed enclosing labrum; pseudotracheae present. Palpus half as long as proboscis, apically expanded. Ventral surface of head (subgena) with many stout, spine-like setae.

Pleura with faint pruinescence. Prosternum not fused to proepisternum; postnotum bare; anteprenotum with single pair of setae. Chaetotaxy short, increasing in length posteriorly; 4-5 widely spaced pairs of acrostichals, extending to prescutellar depression;

5 dc; 1 ppm, slender; 1 presut spal; 1 npl; 1 psut spal; 1 pal; 2 setl, with short outer pair.

Wing infusate; anal angle obtuse; basal costal seta lacking; large, dark circular stigma between ends of R_1 and R_{2+3} (in *Z. dioktes*); R_{4+5} branched with auxillary crossvein at base of R_4 to R_{2+3} ; margins of crossveins clouded in *Z. dioktes*.

Fore coxae and trochanter armed with strong spines. Femora and tibiae with short, slender setae; mid femur with stout ventral setae, mid tibia with erect setae beneath. Fore tibia with anterior, apical comb; hind tibia with posterior, apical comb. Apex of fifth tarsomere blunt; empodium pulvilliform, longer than pulvilli.

Tergite 8 narrowed dorsally. Terminalia projecting horizontally from apex of abdomen, except California species where terminalia held erect. Cerci unmodified, fleshy; hypoproct heavily sclerotized, often thickly matted with setae. Epandrium U-shaped, with subapical process (Figs. 187,188). Hypandrium narrow, ventral surface lightly sclerotized; pair of apical, dorsally directed 'gonostyli'-like processes, often fully articulated; small gonocoxal apodemes present (Fig. 189). Short tube-like phallus, with membranous apical filament (not illustrated by Wilder (1982)); ejaculatory apodeme long and narrow.

Female. Similar to male except as follows: mid femur and tibia lacking modified setae beneath. Terminalia with well-developed sclerites, not retracted. Long, fleshy cercus fused with undifferentiated T10 (Fig. 190). Spermatheca oval, lightly sclerotized; spermathecal duct with ribbed texture along mid-length (Fig. 191).

Included Taxa and Geographical Distribution. Zanclostus dioktes is distributed from southern B.C. to Oregon and collected most often in autumn or early spring (Wilder 1982). An undescribed species (Z. sp. 1) with faint wing markings and distinct chaetotaxy of the mid leg was found at Mt. Baker (Washington) and a much smaller third species is known from California (Z. sp. 2).

Phylogenetic Relationships. This genus appears to be closely related to an undescribed species from Chile (found in CNC) and Trichopeza longipennae Miller (1923) (see discussion under Trichopeza; types in NZAC). All three taxa share the following apomorphies: labrum curved posteriorly; labium forming sheath over labrum; fore coxae with stout, erect spine-like setae; mid femur of male with modified setae beneath; epandrium with subapical process; phallus with flexible apical filament. It is interesting to note that the genus Ragas Walker (not examined) apparently also shares the above synapomorphies (Melander 1945, Collin 1961).

The male terminalia of the above taxa also display similarities to Hormopeza (Fig. 18) (see also Steyskal 1969, figs. 14,18). Common features such as a membranous filament from the apex of the phallus and subapical hypandrial processes suggest a close relationship (see Comments below). In addition, the labrum is also stout and arched posteriorly in Hormopeza, similar to the labrum of Zanclostus.

Bionomics. The type species has been observed feeding on Collembola, using long spines on the fore coxae and trochanter to hold the prey (Wilder 1982). Adults have been

collected on rocks along streams. The immature stages of this genus are unknown.

Comments. The articulated 'gonostyli'-like lobes positioned subapically on the hypandrium appear to be secondarily derived. In the primitive state, as shown in Hormopeza, the processes are fused to the hypandrium and not flexible. The hypandrial processes are also fused in Z. sp. 2, but articulated in Z. dioktes and Z. sp. 1.

List of described species included in Zanclotus.

N dioktes Wilder, 1982: 174 [paratypes examined] (CNC).

List of examined, undescribed species included in Zanclotus.

Zanclotus sp. 1: One male from Washington, USA (CAS).

Zanclotus sp. 2: Two males from California, USA (CNC).

5. EVOLUTIONARY HISTORY

5.1 PHYLOGENETIC INTERPRETATION

5.1.1 MONOPHYLY OF CLINOCERINAE AND RELATIONSHIPS TO REMAINDER OF EMPIDOIDEA

Traditionally the superfamily Empidoidea consists of two families: Empididae (which was widely believed to be paraphyletic) and Dolichopodidae. Chvála (1983) recently subdivided the Empididae into four families: Empididae (including Clinocerinae), Hybotidae, Atelestidae, Microphoridae. These four, together with the Dolichopodidae form the superfamily Empidoidea. His reclassification brought together a variety of characters, including those of wing venation, adult mouthparts and genitalia. However, the taxa he examined were primarily from the Holarctic region and omitted several key southern hemisphere taxa.

Chvála's monograph has strongly influenced empidoid workers, especially with the support of such internationally respected systematists / morphologists as Hans Ulrich and Graham Griffiths. However, Chvála's statements and figures should be carefully interpreted. Woodley (1989) and Cumming (1989) have both generally criticized the apparent resolution of Chvála's cladogram of the Empidoidea (fig. 140). Some of these and other criticisms of this cladogram are listed below:

1. The monophyly of his family Empididae in the new restricted sense is not supported by any derived characters.
2. The Oreogetoninae appears to be simply a collection of genera based on

symplesiomorphies.

3. The Ceratomerinae was thought be the sister group to Clinocerinae, but this is only supported by perceived similarities of the male terminalia. No synapomorphies were described.
4. The Atelestidae were believed to "probably share a common ancestor with the Cyclorrhapha", which means that Chvála's Empidoidea was actually paraphyletic. However, no convincing synapomorphies were proposed for this relationship. It appears that the placement of Atelestidae was based on the suggestions of Griffiths (1972).
5. Chvála's cladistic analysis appears to have been biased by his acceptance of the periandrial hypothesis.
6. Many of his figures of male and female genitalia are poorly drawn, inaccurate and include several misinterpretations (e.g. the epandrium is actually the cercus in figs. 120,121). I recommend that the species he illustrated should be re-examined and compared to his figures.

In his analysis of the orthorrhaphous Brachycera, Woodley (1989) proposed two character states which supported the monophyly of the Empidoidea. Reviewing opposing arguments concerning the relationships of the Empidoidea, Woodley (1989) concluded by strongly refuting Chvála's hypothesis of the Atelestidae as the sister group to the Cyclorrhapha.

More recently, further evidence has been presented which also supports the

monophyly of the Empidoidea. In a new interpretation of male genitalic homologies, Cumming and Sinclair (1990) hypothesized that the loss of gonostyli in the male terminalia of Empidoidea was synapomorphic (see Fig. 210). In a survey of the homologies of the larval mandible, Sinclair (1992) hypothesized that a mandible subdivided into 4 components was also synapomorphic for the Empidoidea.

The five family concept of the Empidoidea (*sensu* Chvála 1983) has not been used in this analysis. I prefer to maintain the traditional two families, Empididae and Dolichopodidae, despite the apparent paraphyly of the former family, until more conclusive evidence is presented concerning the monophyly and relationships of the major lineages. However, the Hybotidae appear to be a well supported group and its family status may remain in favour. Detailed phylogenetic analyses are urgently required to help establish the monophyly of the Oreogetoninae, Empidinae, and Ocydromiinae and ground plan characters of the Empidoidea.

Fifty-five morphological characters are used in the phylogenetic analysis of the Empidoidea. These characters are used in establishing the monophyly of the Empidoidea and resolving some of the relationships of the major lineages within this superfamily. In the following discussion of characters, the italicized words following a character number describe the apomorphic state of the characters being considered. The characters are numbered 1-55 throughout the text and numbers correspond to those used in the hand-generated cladogram (Fig. 205) and the character matrix (Table 4). Extant genera currently listed in regional catalogues are listed under each major taxon throughout the

analysis.

The hand-generated cladogram of the higher classification of the Empidoidea (Fig. 205) has a tree length of 63, a consistency index of 0.83, retention index of 0.87 and rescaled consistency index of 0.72 (calculated using MacClade *sensu* Maddison and Maddison 1992). The shaded triangles refer to clades which are not supported by apomorphies and probably represent lineages based on symplesiomorphies. The phylogenetic relationships suggested by using the parsimony program, PAUP, are discussed in Appendix II.

Monophyly of the Eremoneura

The Cyclorrhapha and Empidoidea form a well supported monophyletic lineage known as the Eremoneura (Griffiths, 1972; Cumming & Sinclair, 1990), supported by characters 1-3.

1. Larval maxilla reduced to an elongate, primarily membranous lobe

In the lower Brachycera, the larval maxilla consists of well defined sclerites, articulated posteriorly with the basal mandibular sclerite. In the Eremoneura, the maxilla is an elongate, primarily membranous lobe (Figs. 3,82; Teskey, 1981a, figs 3.12-13). This character is considered a possible synapomorphy of the Eremoneura (Sinclair 1992).

2. Larval labial hypopharyngeal sclerite "V"-shaped

The plesiomorphic condition occurs in the Tabanomorpha and Asiloidea, where the larval labium consists of a large rectangular submental plate. The apomorphic state, a "V"-shaped labial hypopharyngeal sclerite, is present in the Empidoidea (Vaillant, 1948, fig. 16) and retained in primitive Cyclorrhapha (e.g. Melanderomyia, Megaselia). This character was first proposed as a possible synapomorphy of the Eremoneura by Hennig (1952) and adopted by Griffiths (1972) and Sinclair (1992).

3. Subepandrial membrane completely sclerotized, divided laterally into pair of sclerites extending to outer apical margin of epandrium

From the anterior margin of the hypoproct to the base of the phallus extends an intersegmental membrane, termed the subepandrial membrane. In Asiloidea, sclerites are formed in this membrane, but only in Apsilocephala do the sclerites extend anteriorly to articulate with the base of the phallus.

In Eremoneura, the subepandrial membrane is completely sclerotized to the base of the phallus at a point Hennig (1976) termed "point y". The subepandrial sclerite extends to the hypoproct and is divided laterally into two slender bacilliform sclerites, which extend to the outer apical margins of the epandrium.

This character state is considered autapomorphic for the Eremoneura and similar modifications outside this taxon are only known in Apsilocephala (Therevidae) and Leptomorphus subcaeruleus (Coquillett) (Mycetophilidae).

Cyclorrhapha

Characters 4 and 5 support the monophyly of the Cyclorrhapha. Two additional character states discussed by Sinclair (1992), also support the monophyly of this clade.

4. Pupa completely enclosed by hardened cuticle of the last instar larva

In Cyclorrhapha, pupation occurs within the hardened cuticle of the final instar larva (McAlpine 1989). The cuticle undergoes marked changes in shape and chemical composition. This character state is autapomorphic for the lineage. Pupation also occurs within the final instar larval cuticle of Stratiomyidae and Xylomyidae, but the cuticle remains unchanged in shape and composition. However, since the pupa is free in their sister group, the Pantophthalmidae, it is assumed that pupal enclosure in Stratiomyidae and Xylomyidae has evolved independently within the Stratiomyomorpha.

5. Ejaculatory apodeme and sperm pump separated from base of phallus

In lower Brachycera and Empidoidea, the ejaculatory apodeme and sperm pump are inserted into the base of the phallus. In Cyclorrhapha, the ejaculatory apodeme and sperm pump are separated from the base of the phallus (Hennig 1976). This is a distinguishing feature of the Cyclorrhapha and hence apomorphic (Cumming and Sinclair 1990). A sperm pump separated from the base of the phallus is also present in the Stratiomyomorpha and Anisopodidae and has presumably evolved there independently.

Discussion. Based on a survey of more basal Brachycera, Sinclair (1992) considered that the mouthhooks of larvae of Cyclorrhapha were mandibular in origin. In contrast,

Jürgens *et al.* (1986) clearly showed through the use of blastoderm fate maps, that the mouthhooks were derived from the lower portion of the maxillary lobe of the embryo. From this evidence Griffiths (pers. comm.) concludes that the mouthhooks are maxillary in origin. The opposing conclusions of morphological and embryological studies remain a difficult problem. It appears that whenever there is a controversy concerning the segmental origin of a structure, embryological studies are given greater weight.

If the mouthhooks are to be considered maxillary in origin, the segmental origin of several other mouthparts should also be questioned given the fate map presented by Jürgens *et al.* (1986). For example, the pharyngeal filter and ventral cornu were considered to be derived from the mandibular lobe. Should we conclude from this that these structures are mandibular in origin?

Given this controversy, the mouthhooks of Cyclorrhapha could be interpreted either as mandibles or new maxillary structures. The larval mandible of Empidoidea is clearly homologous to more basal lineages of the Brachycera (Sinclair 1992). I disagree with the interpretation of Griffiths (pers. comm.), that given the apparent maxillary origin of the cyclorrhaphan mouthhooks, the dorsal hook and basal mandibular sclerite of lower brachyceran larvae must also be of maxillary origin.

Empidoidea

Characters 6-9 support the monophyly of the Empidoidea.

6. Mandible of final instar larva comprising four components

The larval mandible of lower Brachycera is subdivided into two components, a distal hook and basal sclerite. From this plesiomorphic condition, the derived condition of the larval mandible comprises 4 components: distal hook, two connecting sclerites and a ventral sclerite (Sinclair 1992, character 21). A four component mandible is believed to be a synapomorphy of the Empidoidea (Sinclair 1992).

7. Gonostylus absent

The gonostylus is articulated to the gonocoxite or gonocoxite + hypandrium in the Nematocera, Orthorrhaphous Brachycera and Cyclorrhapha (Wood 1991; Sinclair *et al.*, in prep; Cumming *et al.*, in prep). The gonostylus is absent in Empidoidea (Cumming and Sinclair 1990). Associated with the loss of gonostyli, the musculature is reduced and not readily distinguished; for example, no muscles that could be gonostylar muscles associated with the apex of the hypandrium were identified by Ulrich (1972).

The gonostylus is also absent in the Acroceridae and Mydidae, but its absence is believed to be due to homoplasy. Subapical hypandrial processes in the genus Zanclostus secondarily exhibit articulation in several species.

8. Ejaculatory apodeme lever-like

In the ground plan of the Brachycera, the ejaculatory apodeme performs like a piston, moving freely in and out of the base of the phallus. In the ground plan of the

Empidoidea, the ejaculatory apodeme articulates ventrally with the phallus, moving lever-like. This modification of the ejaculatory apodeme is considered apomorphic for the Empidoidea. Within the Empidoidea, this apodeme may become fused with the phallus (e.g. Gloma, Atelestus). In addition, the ejaculatory apodeme is somewhat separated in several clinocerine genera, such as Clinocera, Kowarzia, and Wiedemannia.

9. Adult female with a single spermatheca

The plesiomorphic number of spermathecae in Diptera is believed to be three, and this number is found in most orthorrhaphous Brachycera and Cyclorrhapha (Woodley 1989, McAlpine 1989). In Empidoidea, the number of spermathecae is reduced to one, including the problematic genera Atelestus Walker, Meghyperus Loew (Wiegmann 1989) and Nemedina Chandler (Chandler 1981). It is generally believed that the spermatheca is lost in Ocydromiinae, Hybotinae and Tachydromiinae, but a single unpigmented, membranous spermatheca may be observed when properly prepared (see Sec. 3.2.4).

**Oreogetoninae + Empidinae + Hemerodromiinae + Clinocerinae + Atelestinae +
Ocydromiinae + Hybotinae + Tachydromiinae**

Character 10 tentatively supports the monophyly of this lineage.

10. Acanthophorites absent

In many Asiloidea (sensu Woodley 1989), tergite 10 is divided into two lobes, bearing spine-like setae, termed acanthophorites. Although acanthophorites have been lost

frequently in the Asiloidea (e.g. Mythicomyiinae, Hilarimorpha Schiner, and Scenopinidae), Adisoemarto and Wood (1975) regarded acanthophorites as a ground plan feature of this superfamily due to their widespread occurrence within the basal lineages.

Prior to this study, acanthophorites appeared seemingly throughout the Empidoidea and were believed to be not very useful in elucidating phylogenetic relationships (Chvála 1983). Woodley (1989) considered the similarities of empidoid acanthophorites, their widespread occurrence and the presence among the most primitive of empidoid lineages, as evidence supporting a sister group relationship with the Asiloidea.

I also consider empidoid acanthophorites to be homologous with those of asiloids. The recognition of the Trichopezinae has eliminated the widespread distribution of acanthophorites within this superfamily. Thus, acanthophorites are restricted to the Trichopezinae, Brachystomatinae, Ceratomerinae, Microphorinae, and Dolichopodidae. The absence of acanthophorites is tentatively considered apomorphic for Oreogetoninae + Empidinae + Hemerodromiinae + Clinocerinae + Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae. I also believe that acanthophorites have been lost independently in the Cyclorrhapha.

A loss should be interpreted with caution and given low weight (Hecht and Edwards 1976), since it is difficult to determine the degree of homoplasy associated with it. Confidence in the apomorphic loss of acanthophorites is further weakened by the lack of additional characters supporting the monophyly of this clade.

Acanthophorites appear to be lacking in the fossil microphorine Microphorites.

The female terminalia of this genus are apparently slender, uniformly tapered and lacking spines (Hennig 1971). But since the abdomen was quite dirty, the terminalia may actually be either unmodified or modified similarly to those of Microphor. This specimen must be re-examined.

Oreogetoninae

Chvála (1976) erected the subfamily Oreogetoninae based on several plesiomorphic characters (e.g. prosternum free, not fused to proepisternum). I include the following genera in the Oreogetoninae: Anthepiscopus Becker, Brochella Melander, Hormopeza, Iteaphila Zetterstedt, Ragas Walker, Holarctic species of Oreogeton, and Homalocnemis (see Brachystomatinae). I also include in this group two former clinocerine genera, Dipsomyia and Zanclotus (including "Trichopeza" longipennae Miller and associated undescribed taxa), that on the basis of male terminalia appear most closely related to Oreogeton and Hormopeza respectively. At present there are no characters supporting the monophyly of this subfamily and consequently there is a great need for a phylogenetic analysis.

Empidinae + Hemerodromiinae

The Empidinae and Hemerodromiinae form a monophyletic group on the basis of a single character state.

11. Cercus of male heavily sclerotized, modified for clasping

A fleshy, setose cercus not modified for clasping occurs in most Empidoidea, Asiloidea, and basal lineages of the Cyclorrhapha. A heavily sclerotized cercus modified for clasping is believed to be apomorphic for the Empidinae + Hemerodromiinae (Ulrich 1975; Cumming and Sinclair 1990). On the basis of a modified male cercus, Dryodromia, formerly of the Clinocerinae, and Hesperempis, formerly of the Oreogetoninae, should also be included in this lineage. The former Oreogetoninae genus Philetus Melander should also be included in this lineage on the basis of a modified male cercus.

Empidinae

At present there are no characters supporting the monophyly of this subfamily.

The following genera are included in the Empidinae: Afroempis Smith, Allochrotus Collin, Amictoides Bezzi, Aplomera Macquart, Atrichopleura Bezzi, Clinorhampha Collin, Deuteronista Philippi, Empidadelphina Collin, Empis Linnaeus, Gynatoma Collin, Hilara Meigen, Hilarempis Bezzi, Hilarigona Collin, Hystichonotus Collin, Lamprempis Wheeler and Melander, Macrostomus Wiedemann, Opealocerata Melander, Pasitrichotus Collin, Rhamphella Malloch, Rhamphomyia Meigen, Sphicosa Philippi, Toreus Melander, and Trichohilara Collin (Smith 1967, 1980, 1989).

Hemerodromiinae

Characters 12 and 13 support the monophyly of the Hemerodromiinae.

12. Subcosta incomplete, ending before reaching costa

In the ground plan of the Empidoidea, the subcosta is complete, ending in the costa. An evanescent subcosta is believed to have been derived independently in Hemerodromiinae, most Empidinae, some genera of the Trichopezinae, and the clinocerine genera Proclinopyga and Proagomyia. (See character 12 under Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae)

13. Fore coxa more than twice the length of mid or hind coxae

In Empidoidea, the fore coxa is distinctly longer than the mid or hind coxae. In Hemerodromiinae, the fore coxa is further lengthened to more than twice the length of the mid or hind coxae. Its presence in some ceratomerines is regarded as convergent. This character state is believed to be apomorphic for the Hemerodromiinae.

The following genera are included in the Hemerodromiinae: Afrodromia Smith, Apterodromia Oldroyd, Cephalodromia Becker, Chelifera Macquart, Chelipoda Macquart, Chelipodozus Collin, Cladodromia Bezzi, Colabris Melander, Doliodromia Collin, Drymodromia Becker, Hemerodromia Meigen, Metachela Coquillett, Monodromia Collin, Neoplasta Coquillett, Phyllodromia Zetterstedt, Ptilophyllodromia Bezzi, Sematopoda Collin, and Xanthodromia Saigusa (Chvála and Wagner 1989,

Cumming 1990, Saigusa 1986, Smith 1967, 1975, 1980, 1989).

Clinocerinae

Characters 14-19 support the monophyly of the Clinocerinae as recognized here.

14. Eyes pubescent

This feature is present in all Clinocerinae (except Proclinopyga), but also occurs in some members of the Trichopezinae, Drapetini (Tachydromiinae), Parathalassini and Dolichopodidae. However, it is possible that only in the Clinocerinae is the pubescence extremely dense and may be considered an adaptation to aquatic habits. Since this character is very homoplastic, the phylogenetic usefulness is questionable. Pubescent eyes are lacking in Proclinopyga, which is considered a reversal.

15. Lacinia appressed or fused to labial paraphysis

In the ground plan of Empidoidea, the maxilla consists of a slender stipes, which is found within the head capsule and extends to the base of the palpus where it is weakly fused to a thin stylet-like lacinia. In the ground plan of Clinocerinae, the lacinia is short, blade-like, tightly appressed to the labial paraphysis (a strengthening rod on the inner wall of the labium). Upon maceration (in lactic acid), the lacinia becomes partially separated from the paraphysis. The lacinia appressed to the paraphysis is considered apomorphic for the Clinocerinae. The complete fusion of the lacinia to the labial paraphysis is considered apomorphic for all Clinocerinae, except Asymphyloptera.

Proagomyia, Proclinopyga, Rhyacodromia, and Trichoclinocera. The lacinia is also fused to the labial paraphysis in the genus Niphogenia (Trichopezinae).

This interpretation of the lacinia is contrary to Krystoph (1961), who believed that the lacinia was lost and the labial paraphyses were fused to the remnants of the maxillae. The laciniae are also apparently lost or fused to the maxillae in the Ocydromiinae, Hybotinae and Tachydromiinae (see character 26). In groups in which the laciniae are 'lost', the paraphyses are stout, rigid rods; in contrast, the paraphyses are slender in those groups in which the laciniae are free. I believe the increase in size of the paraphyses is a result of fusion with the laciniae.

The musculature may also support this interpretation. Laurence (1953) described three sets of muscles (apodemal-clypeal, apodemal-tentorial, and mental) from the inner apodemes (stipes and laciniae) of the mouthparts of Clinocerinae and Dolichopodidae. He believed them to be homologous to those described for the Tabanidae (Gouin 1949 cited in Laurence 1953), and thus considered that the inner apodemes in these empidoid groups were maxillary in origin. Bletchly (1954) agreed with Laurence's interpretation concerning the former two sets of muscles. Bletchly believed the apodemal-tentorial and apodemal-clypeal muscles were homologous to muscles of the lacinia in Empis (Bletchly 1954). However, he interpreted the mental muscle as homologous to muscles of the labium and hence considered that the apical apodeme in clinocerines was homologous to the labial paraphysis.

16. Labellum lacking pseudotracheae

Pseudotracheae are present in all empidoid lineages except Tachydromiinae, most Hybotinae (Krystoph 1961), Ceratomerinae, Microphorella (Chvála 1983) and Clinocerinae. I consider the absence of pseudotracheae in Clinocerinae (including Proagomyia) the result of independent loss. The presence of pseudotracheae in Proclinopyga is considered a reversal. Wiegmann (1989) stated that the lack of pseudotracheae in Hemerodromiinae was evidence of a close relationship with Clinocerinae. However, I have observed pseudotracheae in Chelipoda sicaria Melander and species of Neoplasta. Consequently, loss of pseudotracheae may have occurred independently in genera such as Hemerodromia, which possess more specialized mouthparts. Since this character is very homoplastic, the phylogenetic usefulness is questionable.

17. Costa with stout, erect setae intermixed among longitudinal rows of simple setae

In the Empididae, the costa bears longitudinal rows of simple, appressed setae. In addition to these rows of setae, there are intermixed stout, erect setae in the Clinocerinae (Fig. 70). The presence of these modified costal setae is considered apomorphic for this subfamily, including Asymphyloptera. The apomorphic condition was first identified by Hackman and Väisänen (1985). In Proagomyia, stout setae were observed along the upper margin of the costa rather than the outer margin. I am uncertain whether the condition observed in this genus is homologous with that of the Clinocerinae. The presence of stout costal setae is considered to have evolved

independently in Heterophlebus and a new genus nr. Apalocnemis.

18. Empodium pulvilliform

In the Asiloidea and Eremoneura, the empodium is setiform (or bristleform). The empodium is modified into a narrow, pubescent pad in all genera of Clinocerinae (Fig. 95), Ceratomerinae, some species of Hilara, some species of Rhamphomyia (e.g. Megacyttarus) and some genera of Trichopezinae and Dolichopodidae (e.g. Liancalus). This character state appears very homoplastic, and is usually found in groups in which adults often stand on or near water. The presence of a pulvilliform empodium is considered to have evolved independently in the Clinocerinae and Ceratomerinae.

19. Spermatheca lengthened into an elongate tube

Spherical spermathecae are present in Oreogetoninae, Empidinae, Hemerodromiinae, Ceratomerinae, Trichopezinae, Microphorinae, Atelestinae, Cyclorrhapha, and throughout the Asiloidea. An elongate, tapering, tubular spermatheca is considered apomorphic for Clinocerinae (exclusive of Proagomyia). The spermatheca is straight to gradually winding, with the apex reduced to thinly sclerotized glandular tissue (Fig. 87). The entire tube is considered the spermatheca and the apical glandular material provides nutrients for the stored sperm.

An elongate spermatheca is also present in Boreodromia (Trichopezinae), Nearctic species of Apalocnemis, and Brachystomatinae, but they are considered independently evolved (see character 46).

The following genera are included in the Clinocerinae: Asymphyloptera, Bergenstammia, Clinocera, Clinocerella, Dolichocephala, Hypenella, Kowarzia, Oreothalia, Phacobalia, Proclinopyga, Rhyacodromia, Roederiodes, Trichoclinocera, and Wiedemannia. Collin classified the genus Proagomyia in the Clinocerinae on the basis of homoplastic characters such as the pulvilliform empodium. I consider Proagomyia in Clinocerinae as incertae sedis due to the plesiomorphic state of the spermatheca.

This is a new restricted concept for Clinocerinae, similar to Vaillant's (1981) "Clinocerini". The concept of the "Trichopezini" is rejected, and many of its genera are placed in a new lineage, the Trichopezinae, which is believed to be more closely related to the Brachystomatinae and Ceratomerinae (see below). The Clinocerinae was traditionally defined on the basis of highly homoplastic characters which created a polyphyletic group. This new concept of Clinocerinae is monophyletic and should greatly benefit future analyses of the higher classification of the Empidoidea.

Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae

Characters 12, 20 and 21 support the monophyly of this lineage. Since these characters are highly homoplastic, support for the sister group relationship between the Atelestinae and Ocydromiinae + Hybotinae + Tachydromiinae is considered very weak.

12. Subcosta incomplete, ending before reaching costa

An incomplete subcosta was considered by Hennig (1970, 1971) as apomorphic for the Ocydromiinae + Hybotinae + Tachydromiinae + Microphorinae +

Dolichopodidae and Atelestinae. In all extant Dolichopodidae, the subcosta ends in R_1 . This condition is regarded as non-homologous to the loss of the apex of the subcosta in the above mentioned Empididae. In the Late Cretaceous dolichopodid, Archichrysotus Negrobov (Negrobov 1978), the subcosta is complete (see character 12 under Hemerodromiinae above).

20. Costa not circumambient, ending at M_1 or R_{4+5}

In the basal lineages of the Asiloidea, Protempis Usachev (the oldest known ancestor of the Empidoidea (Chvála 1983)), Clinocerinae, and most oreogetonine genera, the costa extends along the entire wing margin. Reduction of the costa to M_1 or R_{4+5} was considered by Hennig (1970, 1971) as apomorphic for the Ocydromiinae + Hybotinae + Tachydromiinae + Microphorinae + Dolichopodidae and possibly also the Atelestinae. The reduction of the costa is considered to have evolved independently in Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae and the Dolichopodidae (costa circumambient in Microphorinae).

Reduction of the costa is also believed to have evolved independently several times within other Empidoidea lineages (Empis, Rhamphomyia, Gloma, and Hormopeza). The costa is also reduced in most Cyclorrhapha, except Opetia and Lonchopteridae (McAlpine 1989). Its apparent homoplastic nature renders this character unreliable in phylogenetic analyses.

21. R₄₊₅ unbranched

In the ground plan of the Empidoidea including Protempis, R₄₊₅ is branched. Hennig (1970, 1971) and Chvála (1983) considered an unbranched R₄₊₅ apomorphic for Ocydromiinae + Hybotinae + Tachydromiinae + Atelestinae + Microphorinae + Dolichopodidae. I consider that this character state has developed independently in the Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae lineage and in the Microphorinae + Dolichopodidae lineage, because of the existence of several conflicting characters.

This character state may also have been derived independently in Cyclorrhapha (McAlpine 1989) as well as in some or all of the following empidoid genera: Asymphyloptera, Oreothalia, Rhamphomyia, Anthepiscopus, Monodromia, Icasma, Heleodromia, and Nemedina. Its apparent homoplastic nature renders this character unreliable in phylogenetic analyses.

Atelestinae

Characters 22-25 support the monophyly of the Atelestinae.

22. Sclerites of apical segments of female abdomen narrow, lightly sclerotized, retracted within preceding segment

The female abdomen of the empidoid ground plan is a series of subrectangular sclerites, at most only partially retracted within the preceding segment. In Atelestinae, all apical segments are retracted within segment 4 and the sclerites are reduced to

slender, darkly pigmented bands. In the basal genera of Ocydromiinae (e.g. Trichina, Bicellaria) the segments are only partially retracted and sclerites are rectangular. Completely retracted apical segments with reduced sclerites are considered apomorphic for Atelestinae.

23. Tergite 8 of male "C"-shaped

In Empidoidea, tergite 8 of the male abdomen ranges from a broad sclerite, nearly equal in length to tergite 7, to a slender transverse band (Bährmann 1960). Wiegmann (1989) proposed a "C"-shaped tergite 8 as a possible synapomorphy of the Atelestinae. This character state appears unique among the Empidoidea and autapomorphic for the Atelestinae.

24. Subepandrial sclerite with mid-lateral lobe

In the Atelestinae, a lobe arises mid-laterally from the subepandrial sclerite. This lobe appears to be unique among the Empidoidea and autapomorphic for this subfamily. I am uncertain of the homology of this lobe, although it could possibly be a modified surstylus.

25. Gonocoxal apodeme greatly lengthened

In the ground plan of Empidoidea, the gonocoxal apodeme is a short, truncate process arising anterodorsally from the hypandrium (Fig. 18). In all three genera of Atelestinae, the gonocoxal apodeme has become greatly lengthened (see Hennig 1976,

fig. 28, "Basim. apod."). I believe that this character state has evolved secondarily within the Empidoidea and consider it apomorphic for the Atelestinae.

Paired apodemes arising from the hypandrial bridge are homologous to gonocoxal apodemes of lower Brachycera and contrary to Griffiths (1984), are not apomorphic for the Empidoidea.

The following genera are included in the Atelestinae: Acarteroptera Collin, Atelestus Walker, and Meghyperus Loew (Chvála 1983).

Ocydromiinae + Hybotinae + Tachydromiinae

Characters 26-30 support the monophyly of this lineage.

26. Lacinia absent

See discussion of fusion of laciniae with labial paraphyses (character 15) in the Clinocerinae. The absence or loss of a 'free' lacinia appears to be a synapomorphy of Ocydromiinae + Hybotinae + Tachydromiinae. The loss of a "free" lacinia is also believed to have evolved independently in the Parathalassini + Dolichopodidae.

Since an intermediate stage in the fusion of the lacinia to the paraphysis is lacking in Ocydromiinae + Hybotinae + Tachydromiinae and Parathalassini + Dolichopodidae, the loss of the lacinia in Clinocerinae is not considered homologous here.

27. Tormae distant from labrofulcral articulation point

Among the basal lineages of the Empidoidea, Chvála (1983) showed that the tormae are articulated with the labrum and cibarium at the labrofulcral articulation point. Krystoph (1961) believed that separation of the tormae from this articulation point was a distinctive synapomorphy of the Ocydromiinae + Hybotinae + Tachydromiinae. I believe that this character state has also developed independently in the Microphorinae + Dolichopodidae lineage (see character 27 below).

In Asiloidea and basal lineages of the Cyclorrhapha, the tormae appear to be articulated with the labrofulcral articulation point (Peterson 1916), as observed in more basal empidoids.

28. Palpus separate from stipes, connected to an external sclerite or palpifer

In most Empidoidea, the base of the palpus is membranously attached to the lacinia. In contrast, the base of the palpus in Ocydromiinae, Hybotinae and Tachydromiinae is attached to a small sclerotized palpifer (Krystoph 1961). This character state is unique to this group and is a well documented synapomorphy (Krystoph 1961, Tuomikoski 1966, Hennig 1971, Chvála 1983).

29. Fore tibia with tubular gland

A gland near the base of the fore tibia is a well documented synapomorphy of Ocydromiinae + Hybotinae + Tachydromiinae (Tuomikoski 1966, Smith 1969, Hennig 1971). The function of this gland remains unknown and various differences in structure

have been discussed by Tuomikoski (1966) and Smith (1969).

30. Male terminalia rotated between 45-90°

The male terminalia of Ocydromiinae, Hybotinae and Tachydromiinae are rotated between 45-90° to the right. Since the rotation does not include pregenital segments (segments 7 and 8), the similarities in the rotation of the male terminalia with those of the microphorine + dolichopodid lineage are considered to have developed independently.

Ocydromiinae

This subfamily is likely paraphyletic in relation to the Hybotinae and Tachydromiinae (Tuomikoski 1966) and thus it is in need of revision. Since there are no apomorphies defining this subfamily, the 3 tribes were analysed separately.

Ocydromiini

Character 31 supports the monophyly of the Ocydromiini.

31. M₁ absent

In the ground plan of Empidoidea including Protempis, M vein is forked (M₁ and M₂) and three veins extend from cell dm. In the Ocydromiini, two veins extend from cell dm. Tuomikoski (1966) convincingly showed that M₂ was retained in the genera of this tribe and that M₁ was lost, hence the two vein condition in Ocydromiinae is not

homologous to that described for Hybotinae + Tachydromiinae. The loss of M_1 is considered an apomorphy of the Ocydromiini.

The Ocydromiini include the following genera: Aboccipta Plant, Austropeza Plant, Haplopeza Bezzi, Leptodromiella Tuomikoski, Leptopeza Macquart, Ocydromia Meigen, Oropezella Collin, Pseudoscelolabes Collin, Scelolabes Philippi, and Stylocydromia Saigusa (Chvála 1983, Plant 1989, Saigusa 1986, Tuomikoski 1966).

Oedaleini

Character 32 supports the monophyly of the Oedaleini.

32. Antennal style or arista short or absent, always shorter than first flagellomere

In the ground plan of the Empidoidea, the terminal style or arista is nearly subequal in length to the first flagellomere (Chvála 1983). In the Oedaleini, the style is short or absent, always much shorter than the first flagellomere (Tuomikoski 1966, Chvála 1983). This distinctive antenna, considered apomorphic for this tribe, readily distinguishes it from the remaining Ocydromiinae.

The Oedaleini include the following genera: Allanthalia Melander, Anthalia Zetterstedt, Euthyneura Macquart, Oedalea Meigen, and Stuckenbergomyia Smith (Chvála 1983). The modifications of the female ovipositor (elongate segment 8) and mouthparts directed obliquely forwards may also be additional synapomorphies for this

tribe (Tuomikoski 1966).

Trichinini

The Trichinini include the following genera: Bicellaria Macquart, Hoplocyrtoma Melander, Leptocyrtoma Saigusa, Trichina Meigen, and Trichinomyia Tuomikoski (Saigusa 1986, Tuomikoski 1966). This is a heterogeneous, paraphyletic group. The first three genera lack cell dm and form a distinct group. Trichinomyia and Bicellaria are considered the most basal genera on the basis of symmetrical male terminalia. The genus Edenophorus Smith is believed to be a member of the Ocydromiinae (Chvála 1981), and I have tentatively included this genus in the Trichinini, since it lacks the apomorphies defining the other two tribes.

Hybotinae + Tachydromiinae

Characters 16 and 33 tentatively support the sister group relationship of these two subfamilies. Since these two characters are known to be homoplastic, this lineage is not supported with a great deal of confidence. These two subfamilies may not be sister taxa and possibly evolved independently from within the Ocydromiinae (Tuomikoski 1966).

16. Labellum lacking pseudotracheae

Pseudotracheae are present in all Ocydromiinae, but are lost in Hybotinae (except Euhybus) and Tachydromiinae (Krytoph 1961). The absence of pseudotracheae is hypothesized as synapomorphic for Hybotinae + Tachydromiinae, and to have developed

independently from other lineages (see Clinocerinae).

33. M₂ absent

In the ground plan of Empidoidea, M vein is forked (M₁ and M₂). In the derived state, it is believed that M₂ is lost, resulting in two veins extending from cell dm. Chvála (1983) proposed this character state as a synapomorphy of Hybotinae + Tachydromiinae. Reduction in the number of branches of the medial vein has occurred independently in several taxa, including Atelestus, Acarteroptera, Nemedina, and Dolichopodidae (see character 31).

Tachydromiinae

Characters 34 and 35 support the monophyly of the Tachydromiinae. Tuomikoski (1966) listed the following additional characters defining this subfamily which should be evaluated for their phylogenetic significance: arista long, outer surface of labellum sclerotized, palpifer devoid of setae, stigma lacking, and modifications of male cercus.

34. Palpus short, broad and flattened

The palpus is long and cylindrical in the ground plan of the Empidoidea. A short, broad flattened palpus is found in Tachydromiinae (Tuomikoski 1966) and Dolichopodidae, but is regarded here as non-homologous.

35. Cell dm absent

In the ground plan of Empidoidea including Protempis, cell dm is present. In Tachydromiinae, cell dm is absent through loss of crossvein dm-cu. The derived state is considered apomorphic for this subfamily, although it has also been lost probably independently in Nemedina and Atelestus.

The following genera are included in the Tachydromiinae: Allodromia Smith, Austodrapetis Smith, Chaetodromia Chillcott, Charadrodromia Melander, Chersodromia Walker, Crossopalpus Bigot, Drapetis Meigen, Dusmetina Gil, Dysaletria Loew, Elaphropeza Macquart, Isodrapetis Coquillett, Megagrapha Melander, Micrempis Melander, Platypalpus Macquart, Stilpon Loew, Symballophthalmus Becker, Tachydromia Meigen, Tachyempis Melander, and Tachypeza Meigen (Chvála and Wagner 1989, Cumming 1990, Cumming and Cooper 1992, Melander 1965).

Hybotinae

The following genera are included in the Hybotidae: Acarterus Loew, Afrohybos Smith, Chillcottomyia Saigusa, Ceratohybos Bezzi, Euhybus Coquillett, Hybos Meigen, Lactistomyia Melander, Lamachella Melander, Parahybos Kertész, Stenoproctus Loew, Syndyas Loew, and Syneches Walker (Saigusa 1986, Smith 1967, 1975, 1980).

This subfamily is not supported by any apomorphies (Tuomikoski 1966, Chvála 1983). Although most genera are characterized by an elongate cell cup, the polarity of this character compared to the outgroups of the Empidoidea remains uncertain. The

genera Lamachella, Stenoproctus, and Acarterus each have a short, truncate cell cup (Smith 1969), thus the concept of this subfamily must be re-evaluated. A promising character state is holoptic eyes in females (except Lamachella) (Chvála 1983).

**Trichopezinae + Brachystomatinae + Ceratomerinae + Microphorinae +
Dolichopodidae**

Characters 36 and 37 support the monophyly of this lineage.

36. Sternite 8 of female articulated or fused to anteroventral corner of tergite 8

In the Asiloidea and all empidoids which lack acanthophorites, sternite 8 of the female is separated from tergite 8 by a membrane. In the derived condition, the anterodorsal margin of sternite 8 is articulated or fused to the anteroventral margin of tergite 8. This derived state is apomorphic for the Trichopezinae + Brachystomatinae + Ceratomerinae + Microphorinae + Dolichopodidae.

37. Cercus of female heavily sclerotized, bearing stout setae

In the Asiloidea, the female cercus is a lightly sclerotized, setose lobe. In primitive empidoids, the female cercus is slender, projecting apically and bearing setulae. In the derived state, the cercus is heavily sclerotized and bearing stout setae. This modification of the cercus is considered apomorphic for the Trichopezinae + Brachystomatinae + Ceratomerinae + Microphorinae + Dolichopodidae.

Trichopezinae + Brachystomatinae + Ceratomerinae

Characters 38 and 39 support the monophyly of this lineage.

38. Tergite 7 of female with fringe of setae along posterior margin

In the Empidoidea ground plan, tergite 7 of the female abdomen is sparsely covered with slender setae. A fringe of setae along the posterior margin of tergite 7 is tentatively proposed as a synapomorphy of the Trichopezinae + Brachystomatinae + Ceratomerinae. This fringe may be lost several times, but appears to be part of the ground plan of each lineage. A fringe of setae is lacking in the Microphorinae + Dolichopodidae lineage.

39. Cercus of female held upright

Throughout the lower Brachycera and Empidoidea, the female cercus is held horizontally, bearing setulae. In the Trichopezinae, Brachystomatinae, and Ceratomerinae, the female cercus is held upright, bearing stout setae or spines similar to those of tergite 10. This character is proposed as a possible synapomorphy of this lineage. The structure of the cercus suggests that it assists the acanthophorites in oviposition. The highly modified cercus of this group has led to several misinterpretations (see Sec. 3.2.4). The cercus is held horizontally in the Microphorinae + Dolichopodidae lineage.

Ceratomerinae

Characters 16, 18 and 40-42 support the monophyly of the Ceratomerinae.

16. Labellum lacking pseudotracheae

The loss of pseudotracheae appears to have developed independently in the Ceratomerinae. See character 16 under Clinocerinae for discussion of distribution of this character state.

18. Empodium pulvilliform

The presence of a pulvilliform empodium in Ceratomerinae is considered to have evolved independently from other lineages (see character 18 under Clinocerinae for discussion).

40. Pedice] with thumb-like condyle (conus) inserted into first flagellomere

The pedicel with a thumb-like condyle or conus is considered to be independently derived in the subfamily Ceratomerinae (Chvála 1983, fig. 17) and the dolichopodid genera Dolichopus Latreille (unpubl. obs.) and Syntormon Loew (Plan: 1991; but may not be homologous) among the Empidoidea. A similar feature is present in almost all Cyclorrhapha, except Platypezidae and Opetia (Hennig 1976), but the condition in Ceratomerinae is most certainly due to convergence (McAlpine 1989).

41. Mouthparts positioned anteriorly on head

The mouthparts usually arise mid-ventrally from the head. In the Ceratomerinae, the mouthparts arise anteroventrally from the head. The derived state is comparable to some Bombyliidae with long, slender mouthparts.

42. CuA₂ vein absent, cell cup lacking

The cell cup, present in most Empidoidea, has been lost in the Ceratomerinae. The cell cup is also absent in some genera of Tachydromiinae and Hemerodromiinae, but is present in the ground plan of these two subfamilies. The lack of the cell cup is considered apomorphic for Ceratomerinae.

The following two genera are included in the Ceratomerinae: Ceratomerus Philippi (Tomia Paramonov was recently synonymized with Ceratomerus by Colless and McAlpine 1991) and Icasma Collin (Smith 1989).

Trichopezinae

Character 43 supports the monophyly of the Trichopezinae.

43. Tergite 8 of female with a large projecting apodeme

The Trichopezinae is distinctively characterized by the presence of a large median apodeme extending from the anterior margin of tergite 8 of the female and projecting into segment 7. This character state is apparently unique among the Empidoidea.

The Trichopezinae is a redefined monophyletic empidoid lineage which includes the following genera: four former genera of Oreogetoninae [Apalocnemis, Gloma, Heterophlebus (for all Neotropical and perhaps Australasian species of Oreogeton), and Hyperperacera], one former genus of Hemerodromiinae (Heleodromia), one former genus of Brachystomatinae (Rubistella including all southern Africa species of Brachystoma), and 6 former genera of Clinocerinae (Boreodromia, Ceratempis, Ephydrempis, Niphogenia, Sabroskyella, and Trichopeza).

Brachystomatinae

Characters 44-46 support the monophyly of the Brachystomatinae as recognized here.

44. Phallus with paired basal processes

In the ground plan of Empidoidea, the phallus consists of a long, slender tube lacking basal processes. In Brachystomatinae, there are paired processes arising from the base of the phallus considered to be apomorphic for this lineage. Paired phallic processes are also known in Chelipoda and Chelifera (Hemerodromiinae), but are not considered homologous.

45. Genital fork connected to sternite 10 by narrow sclerite

Female terminalia of Brachystomatinae are characterized by a narrow sclerite extending from sternite 10 to the posterior margin of the genital fork. The derived state

is apparently unique among the subfamilies with acanthophorites.

46. Spermatheca lengthened into an elongate, coiled tube

In the ground plan of the Empidoidea, the female spermatheca consists of a dark sphere at the apex or a long, straight duct. In the Brachystomatinae, the spermatheca is reduced to a long, tightly coiled tube. The derived state is considered apomorphic for the Brachystomatinae. The similar shaped and modified spermatheca in Clinocera (Clinocerinae) is not considered to be homologous (see character 19).

The Brachystomatinae, as defined here, include two genera, Brachystoma Meigen and Anomalempis Melander. The genus Homalocnemis, has been removed from this subfamily on the basis of lack of acanthophorites and other modifications of the female terminalia and tentatively placed in the Oreogetoninae. Chvála (1983, 1991) believed that Homalocnemis shares many synapomorphies with the Brachystomatinae; for example, the similar male terminalia, long first flagellomere and wing venation (elongate cell cup). On the contrary, the male terminalia of this genus are very unusual and do not show any similarities or synapomorphies with those of the Brachystomatinae. A long first flagellomere is symplesiomorphic. Although an elongate cell cup is present in the Asiloidea and Protempis, Hennig (1970) considered the elongate cell cup in Homalocnemis (and Hybotinae) as secondarily derived. If correct, similarities in the shape of the cell cup of Homalocnemis and the brachystomatine genera are probably due to homoplasy.

Microphorinae + Dolichopodidae

Characters 21,27 and 47-50 support the monophyly of this lineage.

21. R₄₊₅ unbranched

An unbranched R₄₊₅ is considered to have evolved independently in the Ocydromiinae + Hybotinae + Tachydromiinae + Atelestinae and in the Microphorinae + Dolichopodidae (see character 21 under Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae for discussion).

27. Tormae distant from labrofulcral articulation point

I believe that this character state has developed independently in the Microphorinae + Dolichopodidae lineage (see character 27 under Ocydromiinae + Hybotinae + Tachydromiinae).

47. Unpaired anterior ventrocervical sclerite present

In the cervical region of adult empidoids there are a pair of ventrocervical sclerites (= cornicula of Ulrich 1984) and paired laterocervical sclerites (Marina 1985). In addition to these sclerites, Microphorinae and Dolichopodidae are characterized by an unpaired, thinly sclerotized, anterior ventrocervical sclerite (Marina 1985; Ulrich 1984, 1988). An anterior ventrocervical sclerite is also present in Clinocerinae (except Asymphyloptera and Proagomyia), but its presence in many clinocerines is probably due

to convergence (Ulrich 1984).

48. Apical 4 or 5 segments of female abdomen retracted within segment 5 or 6

The apical segments of the female abdomen are retracted within segment 5 or 6 in the Microphorinae + Dolichopodidae (Chvála 1987, fig. 43; 1988, fig. 23). The sclerites of this lineage are only partially reduced, except those of Microphor and Dolichopodidae, in which the sclerites are reduced to slender rods. Consequently it appears that in the ground plan of the Microphorinae + Dolichopodidae, the sclerites are only partially reduced and thus not homologous to those of the Atelestinae (see character 22). A similar type of abdomen has evolved independently among some genera of Tachydromiinae (e.g. Platypalpus).

49. Male terminalia rotated between 90-180°

In the ground plan of most empidoid lineages, the male terminalia are unrotated. In all members of the microphorine + dolichopodid lineage, the male terminalia are rotated to the right, beginning with the pregenital segments and including the hypopygium, to between 90-180°, and then lateroflexed to the right (Cumming and Sinclair 1990). As a result of this rotation, the hypopygium lies along the right side of the abdomen with the phallus and cerci directed anteriorly.

50. Bacilliform sclerite extending beyond phallus to fuse with the hypandrium

In the ground plan of Eremoneura, the bacilliform and subepandrial sclerites

articulate with the base of the phallus (Cumming and Sinclair 1990). In Microphorinae + Dolichopodidae, the bacilliform sclerites extend beyond the articulation point and fuse with the hypandrium. The apomorphic state is unique among the Empidoidea.

Microphorinae

At present there is no synapomorphy defining the Microphorinae and this lineage appears to be paraphyletic in relation to the Dolichopodidae. However, the Microphorinae should be recognized until the relationships of all the microphorine genera with those of the Dolichopodidae can be more fully understood. On the basis of female terminalia, Schistostoma could be considered the most basal lineage of this subfamily. The following trends and transformations of male terminalia and pregenital segments within the Microphorinae have been observed, and these appear to be independent of those of the Dolichopodidae.

1. Apical hypandrial processes present in Microphor, Schistostoma and Parathalassius.
2. Hypandrium larger, and epandrium smaller than corresponding structures in Dolichopodidae. In the latter lineage, the epandrium is large and the hypandrium is reduced in size and slender.
3. In Microphor, tergite 8 is distinct. In genera of the Parathalassini, tergite 8 becomes reduced, but apparently not fused to sternite 8. In Dolichopodidae, syntergite 8 (fusion of T8 and S8) is part of the ground plan.

Ulrich (1991) reviewed the characters supporting the Microphorinae, Parathalassini and Parathalassini + Dolichopodidae, but was hesitant to draw any definitive conclusions about the relationships of these lineages. The following characters (51-53) are highlighted here to draw attention to their distribution and possible value in elucidating phylogenetic relationships.

Microphorini

Character 51 tentatively supports the monophyly of the Microphorini.

51. Hypandrium with 1-3 pairs of long, stout setae

The hypandrium of the male terminalia of Microphorini possess 1-3 pairs of long, stout setae (Chvála 1986, 1987; Ulrich 1988). This character state is tentatively proposed as a synapomorphy of this tribe. The Microphorini includes the most basal genera of the Microphorinae (Schistostoma and Microphor), but has previously only been defined on the basis of symplesiomorphies (Chvála 1983, 1988).

Parathalassini + Dolichopodidae

Characters 14,26 and 52 tentatively support the monophyly of the Parathalassini + Dolichopodidae.

14. Eyes pubescent

Pubescent eyes are found in the Parathalassini and some genera of the

Dolichopodidae. This character state appears to be very homoplastic, and thus not very useful in phylogenetic analyses. Refer to character 14 under Clinocerinae for discussion of the distribution of this character state.

26. Lacinia absent

See discussion of fusion of laciniae with labial paraphyses under character 26 in the Clinocerinae. The absence or loss of a "free" lacinia appears to be a synapomorphy the Parathalassini + Dolichopodidae. The morphology of the lacinia in Thalassophorus (Microphorinae) is unknown. The loss of a 'free' lacinia is believed to have also evolved independently in the Ocydromiinae + Hybotinae + Tachydromiinae.

52. Cell dm partially to completely coalesced to cell bm by reduction or loss of crossvein bm-cu

In all other empidoid lineages, crossvein bm-cu is complete, separating cells dm and bm (Ulrich 1991). In all genera of the Parathalassini, except Thalassophorus (Saigusa 1986), crossvein bm-cu is reduced, incompletely separating cells dm and bm (Hennig 1971, Chvála 1988, Ulrich 1991). In the Late Cretaceous fossil Cretomicrophorus Negrobov, crossvein bm-cu is also partially reduced (Negrobov 1978).

In the Dolichopodidae, bm-cu is absent and cells dm and bm are fused. In Empidoidea, this character state is unique to this family. Fusion of cells dm and bm occur independently within the Cyclorrhapha.

The phylogenetic value of this character state is put into question by the Late

Cretaceous fossil dolichopodid, Archichrysotus, which has crossvein bm-cu partially reduced, as in the Parathalassini (Negrobov 1978). However, Archichrysotus has M unbranched and a two-segmented arista, as in extant Dolichopodidae. Consequently, Archichrysotus may possibly be considered the sister group to the Parathalassini + Dolichopodidae.

Parathalassini

Character 53 tentatively supports the monophyly of the Parathalassini.

53. Arista one-segmented

In the ground plan of Empidoidea, the arista is believed to be two-segmented (Chvála 1983). Lack of aristal segmentation is found in all Parathalassini genera, including Microphorella, Parathalassius (Hennig 1971, Chvála 1983), Plesiothalassius, Amphithalassius (Ulrich 1991), and Thalassophorus (Saigusa 1986). A one-segmented arista is also found in some Hemerodromiinae, Trichopezinae (Heleodromia) and Ocydromiinae. As emphasized by Ulrich (1991), this character appears to be subject to homoplasy and hence should be interpreted with caution.

The Late Cretaceous fossil Cretomicrophorus possesses a single articulated arista as do members of the Parathalassini; however, it also shares apomorphies with the Dolichopodidae. For example, the costa ends at R_{4+5} ; and the mid tibia has long anterodorsal and posterodorsal setae (Negrobov 1978). Although Cretomicrophorus appears similar to the Dolichopodidae, M is branched (M_2 present). Given these

conflicting characters, Chvála (1983) suggested that this genus lies at the boundary between the Microphorinae and Dolichopodidae.

Thus, given the distribution of characters 52 and 53 within the Microphorinae and Dolichopodidae, the microphorines probably should be classified in the family Dolichopodidae.

The Parathalassini includes the genera: Amphithalassius, Microphorella, Parathalassius, Plesiothalassius, and Thalassophorus (Chvála and Wagner 1989, Saigusa 1986, Smith 1980, Ulrich 1991). The genus Edenophorus Smith (Smith 1969), is tentatively excluded from this subfamily and is possibly a member of the Ocydromiinae (Chvála 1981).

Dolichopodidae

Characters 20,33,34,54 and 55 support the monophyly of the Dolichopodidae.

20. Costa not circumambient, ending at M_1 or R_{4+5}

Reduction of the costa is considered to be apomorphic for Dolichopodidae (see character 20 under Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae for discussion).

33. M_1 reduced or absent

In extant Dolichopodidae, M_1 is normally unbranched. When branched, M_1 does

not reach the wing margin. See character 33 under Hybotinae + Tachydromiinae for discussion and distribution of this character state.

34. Palpus short, broad and flattened

A short, broad flattened palpus is regarded as apomorphic for the Dolichopodidae (see character 34 under Tachydromiinae for discussion).

54. Epipharynx sharp, heavily sclerotized

In the ground plan of Empidoidea, the epipharynx is produced apically into distinctive blades (Krystoph 1961). From the plesiomorphic condition, the epipharynx has become heavily sclerotized and sharply pointed in Dolichopodidae (Cregan 1941, Satô 1991). The derived state is believed to be autapomorphic for the family (Woodley 1989, character 37).

55. Large apodeme arising from epipharynx

The adult mouthparts of Dolichopodidae are also characterized by a large internal apodeme, arising from the epipharynx (Peterson 1916, fig. 528; Cregan 1941, Satô 1991). This character state is apparently widely distributed within the Dolichopodidae, including the basal subfamily Sciapodinae. It is proposed here as an autapomorphy of the Dolichopodidae.

The Dolichopodidae includes over 150 genera and nearly 6000 species world wide

(Robinson and Vockeroth 1981).

Phylogenetic Conclusions.

Cladistic analysis of the above characters has partially resolved the basal polychotomy of the hypothesis of Cumming and Sinclair (1990, see Fig. 210) for the Empidoidea (Fig. 205). The monophyly of the Clinocerinae has been established, although the sister group relationship remains unresolved. The monophyly of the Oreogetoninae, Empidinae, Ocydromiinae, Hybotinae and Microphorinae remains unresolved.

The loss of acanthophorites tentatively supports the monophyly of the Oreogetoninae + Empidinae + Hemerodromiinae + Clinocerinae + Atelestinae + Ocydromiinae + Tachydromiinae + Hybotinae. A loss of a structure is often subject to homoplasy. Thus, it should be interpreted with caution until additional characters are found which also support the monophyly of this clade.

The Atelestinae has tentatively been placed as the sister group of the Ocydromiinae + Tachydromiinae + Hybotinae. The character states supporting this lineage pertain to wing venation and each displays some homoplasy (see discussion under each character). The configuration of the ejaculatory apodeme in relation to the phallus may provide additional support for this lineage. In Atelestus, and in the ocydromiine genus Trichinomyia, the ejaculatory apodeme is fused directly to a rod-shaped phallus. In contrast, the ejaculatory apodeme of another atelestine, Meghyperus, and of many other Ocydromiinae and Hybotinae, appears to articulate within the phallus. The

configuration in *Atelestus* and *Trichinomyia* may either represent the ground plan of this lineage (Atelestinae + Hybotinae + Tachydromiinae + Ocydromiinae) or may be the result of convergent evolution in their respective subfamilies. A careful, detailed study of the homologies of the various sclerites and apodemes in the phallus of the genera of these subfamilies is required. There is probably much more valuable phylogenetic information to be found in both the male and female terminalia of these four subfamilies.

The implications of new interpretations of homologies of the empidoid female terminalia proposed in this study have also significantly altered previously held concepts concerning the higher classification of the Empidoidea and are listed as follows: (1) the Trichopezinae (including 6 former clinocerine genera and 6 genera from 3 other subfamilies) is proposed as a newly recognized empidoid lineage based on the apomorphic development of an apodeme projecting anteriorly from tergite 8; (2) the Trichopezinae, together with the subfamilies Brachystomatinae and Ceratomerinae are removed from the basal polychotomy of Cumming and Sinclair (1990, see Fig.210) and form a new empidoid clade; (3) these three taxa are tentatively believed to be the sister group to the Microphorinae + Dolichopodidae. The characters used by Chvála (1983) and Cumming and Sinclair (1990) that suggested a close relationship between the latter two taxa and the hybotid subfamilies (Ocydromiinae + Hybotinae + Tachydromiinae) are considered highly homoplastic and must be used with caution in phylogenetic interpretations.

This analysis also suggests that the Parathalassini are more closely related to the Dolichopodidae than to the Microphorinae. Consequently, the Microphorinae appear to

be paraphyletic in relation to the Dolichopodidae. However, the characters supporting the Parathalassini + Dolichopodidae are all subject to homoplasy. Thus, the relationships of these three lineages requires further analysis. Given the divergent trends in the male terminalia of the Microphorinae from the Dolichopodidae, detailed studies of the small, complex male terminalia of the Microphorinae are urgently needed in order to incorporate them into phylogenetic studies.

5.1.2 RECONSTRUCTED PHYLOGENY OF THE GENERA OF CLINOCERINAE

As stated in Sec. 5.1.1, members of the Clinocerinae are characterized by the following synapomorphies: pubescent eyes; appressed lacinia; pseudotracheae absent; stout costal setae; empodium pulvilliform; and tubular spermatheca. The sister group of the Clinocerinae has not been established and remains part of an unresolved polychotomy with the Oreogetoninae, Empidinae + Hemerodromiinae, and Atelestinae + Ocydromiinae + Hybotinae + Tachydromiinae.

Forty-six morphological characters are used in the phylogenetic analysis resolving the relationships of the genera of the Clinocerinae. In the following discussion of characters, the italicized words following a character number describe the apomorphic state of the characters being considered. The characters are numbered 1-46 throughout the text and the numbers correspond to those used in the hand-generated cladogram (Fig. 206) and the character matrix (Table 5).

The hand-generated cladogram of the relationships of the genera of the

Clinocerinae (Fig. 206) has a tree length of 56, a consistency index of 0.8, retention index of 0.78 and rescaled consistency index of 0.62 (calculated using MacClade). The phylogenetic relationships suggested by using the parsimony program PAUP are discussed in Appendix II.

Asymphyloptera

Characters 1-7 support the monophyly of the genus Asymphyloptera.

1. Gena wide, undivided

In the ground plan of the Clinocerinae, the gena is narrow and divided by the frontoclypeal suture, which runs from the base of the palpus and anterior tentorial pit along the lower margin of the eye toward the antenna (Fig. 64; Steyskal and Knutson 1981, fig. 47.27, 47.28). The gena of several genera within this subfamily is approximately as wide as half the height of the eye and not completely divided by the frontoclypeal suture (Fig. 59). The apomorphic condition is believed to have arisen independently four times: in Asymphyloptera, among some species of Trichoclinocera, in the clade Roederiodes + Hypenella + Clinocerella and in Wiedemannia. Due to its homoplastic nature, this character state must be interpreted with caution.

2. Clypeus convex, separated as a distinct sclerite

In the ground plan of Empidoidea, the clypeus is not differentiated from the face. Within Clinocerinae, the clypeus is a convex sclerite, partially separated from the face

(Figs. 59,63). This character state is considered to have evolved independently in Hypenella and Asymphyloptera. The clypeus is quite variable in both convexity and separation from the face in Parathalassini (Microphorinae) (Ulrich 1991) and Dolichopodidae (Robinson and Vockeroth 1981). Hence the shape and form of the clypeus in the latter two lineages may not be homologous to the condition in Asymphyloptera or Hypenella.

3. First flagellomere with long, slender extension

In the ground plan of the Empidoidea, the first flagellomere is believed to be conical, with a long two-segmented arista or style (Chvála 1983). A long, slender extension arising from the first flagellomere is considered here to be a derived character state. This character state has been derived independently in the genera Asymphyloptera and Giloma (Chvála 1983, fig. 4).

4. Palpus appressed to labrum, lacking setae

In the ground plan of Empidoidea, the palpus is cylindrical and covered by long setae. In Asymphyloptera, the palpus is apically pointed, lacking long setae and appressed to the labrum. This is apparently a unique development in Empidoidea and hence autapomorphic for this clinocerine genus.

5. R₂₊₃ branched

Vein R₂₊₃ is simple in Asiloidea and in all empidoids except Asymphyloptera;

hence a forked R_{2+3} is considered autapomorphic for this clinocerine genus.

6. R_{4+5} unbranched

In the ground plan of the Empidoidea including Protempis, R_{4+5} is branched. In Clinocerinae, an unbranched R_{4+5} is believed to have evolved independently in the genera Asymphyloptera and Oreothalia. Refer to character 21 above (Sec. 5.1.1) for discussion of distribution of this character state.

7. Tarsomeres 2-4 of foreleg equal in length

Tarsomeres 2-4 of the foreleg of most clinocerines are of unequal length. In Asymphyloptera, Hypenella, Clinocerella, and Roederiodes, tarsomeres 2-4 of fore leg are subequal in length. This condition is considered to have evolved independently in Asymphyloptera and Hypenella + Clinocerella + Roederiodes.

Asymphyloptera is the sister genus to the remaining Clinocerinae and is tentatively included in this subfamily primarily on the basis of a tubular spermatheca and stout costal setae. The larva is currently unknown and the structure of its mandible would certainly be informative in testing whether it should be classified with the Clinocerinae.

Clinocerinae, exclusive of Asymphyloptera

The Clinocerinae, exclusive of Asymphyloptera, form a very distinctive, readily recognized monophyletic group, defined on the basis of characters 8-15.

8. Mandible of final instar larva comprising six components

In the ground plan of the Empidoidea, the larval mandible comprises 4 components (Figs. 1,2): distal hook, two connecting sclerites and a ventral sclerite (Sinclair 1992). In genera of the Clinocerinae where details of the head capsule are known (Clinocera, Kowarzia, Dolichocephala, Wiedemannia, Trichoclinocera), the larval mandible consists of six components (Figs. 79,80): distal hook, 3 connecting sclerites and 2 ventral sclerites (Vaillant 1951, 1952a, 1952b; Dyte 1967). Although the larvae are known for only a few derived genera, I tentatively propose this character state as apomorphic for the Clinocerinae, exclusive of Asymphyloptera. The discovery and examination of the larval mandible of Proclinopyga and the former genus would effectively test the validity of this proposal.

A six-component mandible is known for the hemerodromiine genera Hemerodromia (Vaillant 1953) and Chelifera (pers. obs.). Since a plesiomorphic, four-component mandible was observed in larvae of Phyllodromia (Trehen 1969), the further subdivision and complexity in Hemerodromia and Chelifera is considered to have been derived independently from the Clinocerinae (Sinclair 1992).

9. Pupal caudal hooks present

In the Empidinae, Ocydromiinae, Tachydromiinae, Dolichopodidae and primitive genera of the Hemerodromiinae, caudal hooks are absent in the pupae. In all clinocerine genera where the pupa is known (Clinocera, Dolichocephala, Kowarzia, Trichoclinocera, Roederiodes, and Wiedemannia), caudal hooks are present. The derived condition is

proposed as an apomorphy of the Clinocerinae, exclusive of Asymphyloptera. However, since the pupae of Asymphyloptera and Proclinopyga are unknown, this character state must be considered tentative until they are associated with adults.

Caudal hooks are also known in Oreogeton (Sommerman 1962) and several genera of the Hemerodromiinae, but are lacking in basal genera of the Hemerodromiinae (Trehen 1969).

An additional pupal character that may prove useful as more immature stages are associated with adults is the presence of a long, filamentous prothoracic respiratory horn in the pupa. A pair of long filaments are known in Tachydromiinae and Dolichopodidae (Malloch 1917, Dyte 1967, Cumming and Cooper 1993). The prothoracic spiracle lacks a filament in Oreogeton, Empidinae, Clinocerinae and the ground plan of the Hemerodromiinae (Hobby and Smith 1962, Sommerman 1962, Smith 1968, Trehen 1969).

10. Unpaired anterior ventrocervical sclerite present

In the cervical region of adult empidoids there are a pair of ventrocervical sclerites (= cornicula of Ulrich 1984) and paired laterocervical sclerites (Marina 1985). In addition to these sclerites, Clinocerinae (except Asymphyloptera and Proagomyia), are characterized by an unpaired, thinly sclerotized, anterior ventrocervical sclerite (Marina 1985; Ulrich 1984, 1988). A ventrocervical sclerite is also present in Microphorinae and Dolichopodidae, but its presence is probably due to convergence (Ulrich 1984) (see

character 47, Sec 5.1.1).

11. Inner margin of labrum with slender apodeme

In all Clinocerinae, except Asymphyloptera and Proagomyia, there is a long, slender apodeme arising from the inner margin of the labrum, although it is often overlooked (Vaillant 1960a, figs. a,c). This character state appears to be unique to the Clinocerinae and hence autapomorphic for the subfamily, except the above two genera.

12. Base of hypopharynx greatly expanded, approximately three times width of salivary pump

In the basal lineages of the Empidoidea, the base of the hypopharynx is approximately equal to the width of the salivary pump (Krystoph 1961, figs. 8,9). In the Clinocerinae, exclusive of Asymphyloptera and Proagomyia, the base of the hypopharynx is greatly expanded, approximately 3 times the width of the salivary pump (Fig. 104). This character state is believed to be apomorphic for the remaining genera of the subfamily, except Asymphyloptera and Proagomyia. A similar development, considered here to be convergent, is found in Dolichopodidae.

In the elongate, piercing mouthparts of Roederiodes, the hypopharynx is greatly lengthened and the base is narrow. This condition is considered a reversal.

13. Labellum held horizontally, sucker-like

In the basal lineages of the Empidoidea, the labellum is held obliquely to the

premental plate and is not sucker-like (Krystoph 1961). In Clinocerinae exclusive of Asymphyloptera, the labellum is held at right angles to the premental plate, appearing sucker-like. This character state is apomorphic for the remaining genera of the subfamily. It is considered to have been secondarily lost in Roederiodes. A similar development, considered here to be convergent, is found in Dolichopodidae.

This condition is also found in the genus Proagomyia. It may have arisen independently in this genus or a sucker-like labellum may actually be part of the ground plan of the Clinocerinae and it has been secondarily lost in Asymphyloptera.

14. Hyandrium cone-shaped, with phallus arising apically

In the basal lineages of the Empidoidea, the hypandrium encircles the base of the phallus, which arises subapically. In Clinocerinae (except Asymphyloptera), the hypandrium is cone-shaped, does not surround the phallus, and the phallus arises apically. This character state is unique in the Empidoidea, thus autapomorphic for the Clinocerinae, exclusive of Asymphyloptera and Proagomyia.

15. Cercus of male subdivided and modified for clasping

In the empidoid ground plan, the male cercus is setose and cylindrical. In the Clinocerinae, exclusive of Asymphyloptera, the male cercus is subdivided into a cercal plate (surrounding the anus) and an erect lobe or clasping cercus, bearing modified setae on its inner surface (refer to Sec. 3.3.4.1). This peculiar modification of the cercus is unique among the Empidoidea and thus autapomorphic for Clinocerinae (except

Asymphyloptera and Proagomyia).

The male cercus in the ground plan of the Empidinae + Hemerodromiinae lineage is also modified for clasping (see character 11, Sec. 5.1.1). However, it is not considered homologous to the clasping cercus of clinocerines because the cercus in that lineage is not subdivided into two components.

Proclinopyga + Rhyacodromia + Trichoclinocera

These three genera form a monophyletic group on the basis of characters 16-18.

16. Posterior margin of tergite 8 of female with fringe of setae

In female empidoid terminalia, setae are evenly distributed on tergite 8. A posterior fringe of long setae on tergite 8 (Fig. 29) is proposed as a synapomorphy for Proclinopyga + Rhyacodromia + Trichoclinocera. This fringe is quite sparse in T. lapponica and related species.

17. Tergite 10 of female with deep U-shaped cleft, bearing modified setae

Tergite 10 of the female terminalia in the empidoid ground plan is subrectangular. Tergite 10 is divided by a deep U-shaped notch, bearing stout setae (Fig. 111) in Proclinopyga, Rhyacodromia, and Trichoclinocera, and is considered a synapomorphy of these three genera. Tergite 10 in Hypenella spumarius is similar; however, the sclerite is narrow and not deeply cleft, with stout setae confined to a posterior membranous region (Fig. 42). Thus the overall similarity between the female terminalia of Hypenella

and those of the Trichoclinocera-group are believed to be the result of convergent evolution.

18. Cercus of female with lateral ridge, setulae confined to ventral surface of cercus

In the ground plan of the Empidoidea, the female cercus is a narrow, cylindrical lobe, bearing setulae. In Proclinopyga, Rhyacodromia and Trichoclinocera, the cercus is characterized by a lateral ridge, with setulae confined to the ventral surface (Fig. 29). The derived condition is considered apomorphic for these three genera. Bergenstammia nudipes has similarly modified female terminalia; however, the cercus lacks a lateral ridge. Thus the similarity of the terminalia in this species is thought to be the result of convergent evolution.

Proclinopyga

Characters 19 and 20 support the monophyly of the genus Proclinopyga.

19. Dorsal margin of epandrium expanded, bearing setae

In Clinocerinae, the epandrium, as seen in profile, is usually evenly arched dorsally. In all species of Proclinopyga, the dorsal margin of the epandrium is expanded, sculptured and bearing long setae and setulae (Fig. 26). This character state is considered apomorphic for Proclinopyga.

20. Spermatheca loosely coiled

In the ground plan of Clinocerinae, the spermatheca is an elongate, tapering tube. The spermatheca of species of Proclinopyga is a long, well sclerotized, loosely coiled tube (Fig. 27). The configuration of the spermatheca is considered apomorphic for this genus, and evolved independently from Clinocera.

Rhyacodromia + Trichoclinocera

Characters 21 and 22 support the sister group relationship between Rhyacodromia and Trichoclinocera.

21. Labrum convex

In the ground plan of the Clinocerinae the labrum is flat as illustrated for a species of Kowarzia by Vaillant (1960a, figs. a,b,d). A convex labrum (Fig. 105) is apparently unique among the Clinocerinae and apomorphic for the clade Rhyacodromia + Trichoclinocera.

22. Male fore femur with stout, ventral setae or spine-like setae

In the basal lineages of the Empidoidea, the legs are clothed in fine setae. Stout, ventral setae on the fore femur of Rhyacodromia and Trichoclinocera are considered apomorphic for this lineage. In many other empidoids, stout ventral setae are usually associated with swollen, raptorial legs (see Oreothalia).

Rhyacodromia

Characters 23 and 24 support the monophyly of the genus Rhyacodromia.

23. Tergites 6 and/or 7 of male with pair of setose tubercles

In male Rhyacodromia, tergites 6 and/or 7 are modified into a pair of setose tubercles (Saigusa 1986, fig. 9). This character state is unique among the Clinocerinae. Similar modifications of tergites 6 and 7 have evolved independently in Ephydrempis (Trichopezinae).

24. Tergite 8 of male subdivided into pair of cercus-like lobes

The modification of the tergite 8 of the male abdomen into a pair of cercus-like lobes (Fig. 28) is unique among the Empidoidea and hence autapomorphic for Rhyacodromia.

Trichoclinocera

Characters 25-27 support the monophyly of the genus Trichoclinocera.

25. Vein R₁ with setae above

In the clinocerine genus Trichoclinocera, R₁ bears short, dark setae on the upper surface. The wing veins of all other clinocerine genera are bare and thus the presence of setae is apomorphic for Trichoclinocera. Setae on vein R₁ are also present in three other empidoid genera, Heterophlebus (Trichopezinae), Oreogeton (Oreogetoninae) and

Deuteronista Philippi (Empidinae).

26. R₄ nearly parallel to R₅

In the ground plan of the Empidoidea and Clinocerinae, R₄ is strongly divergent from R₅ (Fig. 68). In Trichoclinocera, R₄ runs nearly parallel to R₅ (Fig. 69); this condition is considered autapomorphic for this genus.

27. Ejaculatory apodeme sickle-shaped

In the ground plan of Clinocerinae, the ejaculatory apodeme is a wide, oval-shaped sclerite. In Trichoclinocera, the ejaculatory apodeme is sickle-shaped with a posterior projection. The shape of this apodeme is apparently unique among the Clinocerinae and thus autapomorphic for Trichoclinocera.

Clinocera + Oreothalia + Roederiodes + Hypenella + Clinocerella + Kowarzia +
Dolichocephala + Phacobalia + Bergenstammia + Wiedemannia

Character 28 supports the monophyly of the remaining genera of the Clinocerinae.

28. Lacinia fused to labial paraphysis

In the ground plan of Empidoidea, the maxilla comprises a slender stipes, which is found within the head capsule and extends to the base of the palpus where it is weakly fused to a thin stylet-like lacinia. In the ground plan of Clinocerinae, the lacinia is short, blade-like, tightly appressed to the labial paraphysis (a strengthening rod on the inner

wall of the labium). Upon maceration (in lactic acid), the lacinia becomes partially separated from the paraphysis.

The complete fusion of the lacinia to the labial paraphysis is considered apomorphic for all Clinocerinae, except Asymphyloptera, Proagomyia, Proclinopyga, Rhyacodromia, and Trichoclinocera (see character 15, Sec. 5.1.1 for discussion).

Clinocera + Oreothalia

The genera Oreothalia and Clinocera form a monophyletic group on the basis of characters 29 and 30.

29. Lower margin of face entire

Throughout the Empidoidea and Clinocerinae, the lower margin of the face is marked by a shallow to deep, membranous cleft (Krystoph 1961, fig. 25; Vaillant 1960a, fig. d). The lower margin of the face is entire, lacking a median cleft in Oreothalia + Clinocera and thus considered synapomorphic for these two genera. Bergenstammia nudipes has the lower margin of the face entire; because no other species of this genus apparently has this condition, I consider it to have evolved independently.

30. Surstylus greatly expanded and lengthened

In the ground plan of the Clinocerinae, the surstylus is short and narrow. A wide, greatly lengthened surstylus (Figs. 31, 129) is considered apomorphic for Oreothalia + Clinocera.

Clinocera

Characters 20 and 31 support the monophyly of the genus Clinocera as recognized here.

20. Spermatheca loosely coiled

In Clinocera, the spermatheca is lightly sclerotized and loosely coiled (Fig. 137) and this configuration is considered apomorphic for this genus. In Oreothalia, the spermatheca is twisted and often ends in a coiled ball (Fig. 33). A similar yet non-homologous spermathecal shape is believed to have evolved independently in Proclinopyga (Fig. 27).

31. Phallus with apical filament

In the clinocerine genera Proclinopyga and Rhyacodromia, the phallus is a solid tube, lacking apical modifications. In Clinocera, the apex of the phallus is differentiated into an apical whip-like filament, unique among this subfamily. The apical filament has become secondarily lost in several Nearctic species (e.g. species #11, 12A, 12B).

This restricted concept of Clinocera excludes the former subgenera Kowarzia, Phacobalia, and Bergenstammia. The removal of these taxa is justified because Clinocera was apparently paraphyletic as illustrated in this phylogenetic analysis.

Oreothalia

Characters 6 and 22 support the monophyly of the genus Oreothalia.

6. R₄₊₅ unbranched

In Oreothalia, R₄₊₅ is unbranched (Fig. 70). This condition is considered to be apomorphic for this genus. Refer to discussion under Asymphyloptera.

22. Male fore femur with stout, ventral setae or spine-like setae

An anteroventral row of spine-like setae on the apical half of the fore femur of Oreothalia is considered to be apomorphic for this genus. Similar spine-like setae are also found in Trichoclinocera dolicheretma, but are considered to have evolved independently. Refer to discussion under Rhyacodromia + Trichoclinocera.

Roederiodes + Hypenella + Clinocerella + Kowarzia + Dolichocephala + Phaeobalia + Bergenstammia + Wiedemannia

Character 32 supports the monophyly of the remaining genera of the Clinocerinae.

32. Cercal plate of male with setae confined to dorsolateral region

In the clinocerine ground plan, setae of the male cercal plate are evenly distributed (Fig. 136). In the apomorphic condition, setae of the cercal plate are confined to a small dorsolateral region (Fig. 34). This character state is considered apomorphic for Hypenella + Roederiodes + Clinocerella + Dolichocephala + Kowarzia +

Phaeobalia + Bergenstammia + Wiedemannia.

Roederiodes + Hypenella + Clinocerella

Characters 1,7 and 33 support the monophyly of this clade.

1. Gena wide, undivided

In Hypenella, Clinocerella and Roederiodes, the gena is wide and not divided by the frontoclypeal suture (Figs. 62,63). This condition is considered to be apomorphic for this clade. Refer to Asymphyloptera for further discussion of this character state.

7. Tarsomeres 2-4 of foreleg equal in length

In Hypenella, Clinocerella, and Roederiodes, tarsomeres 2-4 of foreleg are subequal in length. This condition is considered to be apomorphic for this clade. Refer to Asymphyloptera for further discussion of this character state.

33. Palpus short, broad and flattened

In the ground plan of Clinocerinae, the palpus is long and cylindrical (Fig. 60). A short, broad, flattened palpus is considered apomorphic for Hypenella + Clinocerella + Roederiodes (Figs. 62,63).

Roederiodes

Characters 34 and 35 support the monophyly of the genus Roederiodes.

34. Labrum long and slender

In the ground plan of the Clinocerinae, the labrum is short, nearly triangular in shape (Krystoph 1961, fig. 5B). In the long piercing mouthparts of Roederiodes, the labrum is greatly lengthened and slender (Fig. 62). Although a reversal to the condition found in the ground plan of the Empidoidea (Chvála 1983), this character state is considered apomorphic for the genus. The lengthened labrum of Asymphyloptera is probably convergent. In Clinocerella and Hypenella, which have a long proboscis, the labrum is short and triangular.

35. Labium rigid with well sclerotized labellum.

In the ground plan of the Empidoidea and Clinocerinae, the labium is flexible, with large, lightly sclerotized, fleshy labellum. A rigid, well sclerotized labellum (Fig. 62) is considered apomorphic for Roederiodes.

Hypenella + Clinocerella

Character 36 supports the monophyly of this clade.

36. Pulvilliform empodium wide, laterally compressed

In the ground plan of the Clinocerinae, the pulvilliform empodium is long and slender. In Hypenella and Clinocerella, the pulvilliform empodium is laterally compressed and wider than the fourth tarsomere. This character state is apparently unique among the Empidoidea and thus autapomorphic for these two genera.

Hypenella

Character 2 supports the monophyly of the genus Hypenella.

2. Clypeus convex, separated as a distinct sclerite

In Hypenella, the clypeus is a convex sclerite, partially separated from the face (Fig. 63). This character state is considered to have evolved independently in Hypenella and Asymphyloptera (see above).

Clinocerella

Character 37 tentatively supports the monophyly of the genus Clinocerella.

37. Phallus biarticulated

In the clinocerine genera Proclinopyga and Rhyacodromia the phallus is a solid tube, lacking apical modifications. Clinocerella is characterized by a biarticulated phallus (Fig. 38). The articulated condition has probably evolved independently in the genera Phaeobalia, Bergenstammia, and Wiedemannia (see below).

Clinocerella has traditionally been considered a subgenus of Wiedemannia on the basis of a wide gena and similar male terminalia. However as a result of this cladistic analysis, these similarities are likely due to homoplasy and elevation to generic status appears justified.

Kowarzia

Character 38 supports the monophyly of the genus Kowarzia.

38. Face with setulae

The presence of pale facial setulae is considered apomorphic for the clinocerine genus Kowarzia. This character state is unique among the Clinocerinae, except for a few species of Clinocera from the eastern Palearctic and Oriental regions.

Kowarzia has traditionally been viewed as a subgenus of Clinocera on the basis of similar plesiomorphic head structures (e.g. narrow gena). Based on differences in male terminalia shared with several other genera (character 32), this genus is distantly related to Clinocera and elevation to generic status appears justified.

Dolichocephala

Characters 39-41 support the monophyly of the genus Dolichocephala.

39. Neck high on occiput

In the clinocerine genus, Dolichocephala, the attachment of the neck high on the occiput (Fig. 64) is apparently unique among the Empidoidea and hence autapomorphic for this genus. Only in Trichoclinocera dolicheretma is the head attached in a similar manner (Fig. 83).

40. Spermatheca convoluted

In the clinocerine ground plan, the spermatheca is a fairly stright tube (Fig. 36). The spermatheca in Dolichocephala is a long, wide, convoluted, twisted tube (Fig. 47). This character state is considered apomorphic for this genus.

41. Subepandrial sclerite extended distal to base of clasping cercus

In the ground plan of the Clinocerinae, the subepandrial sclerite extends from the base of the hypandrium to the base of the clasping cercus. In Dolichocephala, a lobe of the subepandrial sclerite extends beyond the base of the clasping cercus. This character state is considered apomorphic for this genus, but not present in D. argus. A similar condition occurs in Wiedemannia hughesi, but the subepandrial sclerite, not a lobe, extends directly beyond the cercus.

Phacobalia + Bergenstammia + Wiedemannia

Characters 37 and 42 support the monophyly of this clade.

37. Phallus biarticulated

The clinocerine genera Phacobalia, Bergenstammia and Wiedemannia are characterized by a biarticulated phallus. This character state is proposed as a synapomorphy for these three genera. The biarticulated condition has become secondarily lost in W. hughesi. A biarticulated phallus is believed to have evolved independently in Clinocerella and in some species of Kowarzia (e.g. Vaillant and Vincon 1986, fig. 6) and

Dolichocephala (e.g. Vaillant 1968, fig. 3).

42. Subepandrial sclerite separated from base of clasping cercus

In the ground plan of the Clinocerinae, the subepandrial sclerite is positioned near the anterior margin of the epandrium and extends to the base of the clasping cercus. This sclerite has become reduced, shifted posteriorly and no longer extends to the base of the cercus in the genera Phaeobalia, Bergenstammia, and Wiedemannia. This character state appears to be unique to these three genera.

Phaeobalia + Bergenstammia

Characters 43 and 44 support the monophyly of this clade.

43. Ejaculatory apodeme with large keel

The clinocerine genera Phaeobalia and Bergenstammia are characterized by the presence of a large keel-like plate arising from the ventral margin of the ejaculatory apodeme. The shape of the ejaculatory apodeme is considered apomorphic for these two genera.

44. Clasping cercus divided into pair of lobes

In the ground plan of the Clinocerinae, the clasping cercus consists of a single lobe (Fig. 19). The clasping cercus is subdivided into a pair of lobes (Figs. 53,57) and is considered apomorphic for Phaeobalia + Bergenstammia. A similar condition occurs

independently in some species of Wiedemannia (e.g. W. hughesi and W. tricuspidata).

Both of these taxa have traditionally been viewed as subgenera of Clinocera, although Bergenstammia was recently elevated to full generic rank by Vaillant and Vinçon (1986) and Vaillant and Wagner (1989). On the basis of similarities of the male terminalia with those of Wiedemannia (e.g. characters 32 and 42), elevation of both to full generic status appears warranted.

Phaeobalia

Character 45 supports the monophyly of the genus Phaeobalia.

45. Wings spotted

In the clinocerine ground plan, the wings are infuscate, lacking distinct spots, other than the stigma. The wings of Phaeobalia are distinctly spotted, (except P. pokornyi); this condition is tentatively proposed as an apomorphy of this genus. Although similar spotted wings are found in several species of Clinocera (e.g. C. lecta), they are here considered to be due to convergent evolution. In Dolichocephala, the spotted wings are due to irrorations, or clear punctations on a fumose wing and thus is not homologous to the dark spots in Phaeobalia.

Bergenstammia

Character 46 supports the monophyly of the genus Bergenstammia.

46. Pulvilli vestigial and empodia reduced

In the clirocerine ground plan, the pulvilli are elongate pads and the empodia are pulvilliform, extending beyond the tarsal claws (Fig. 95). Bergenstammia is characterized by having vestigial pulvilli and the empodia reduced to half the length of the claws. This character state is considered apomorphic for this genus and a similar reduction is found only in Trichoclinocera dolicheretma.

Wiedemannia

Character 1 supports the monophyly of the genus Wiedemannia.

1. Gena wide, undivided

In Wiedemannia, the gena is wide and not divided by the frontoclypeal suture (Figs. 65,66). This condition is considered to be apomorphic for this genus. Refer to Asymphyloptera for discussion of this character state.

Phylogenetic Conclusions.

As a result of the above cladistic analysis, the genus Asymphyloptera is considered the sister group of the remaining Clinocerinae (Fig. 206). The retention of this genus within the Clinocerinae will be strongly influenced by the discovery, in the larva, of a four or six-component mandible. The Clinocerinae, exclusive of Asymphyloptera, is a well supported lineage of morphologically similar genera. Proagomyia is retained in Clinocerinae as incertae sedis, primarily since it appears not

independently in some species of Wiedemannia (e.g. W. hughesi and W. tricuspidata).

Both of these taxa have traditionally been viewed as subgenera of Clinocera, although Bergenstammia was recently elevated to full generic rank by Vaillant and Vinçon (1986) and Vaillant and Wagner (1989). On the basis of similarities of the male terminalia with those of Wiedemannia (e.g. characters 32 and 42), elevation of both to full generic status appears warranted.

Phaeobalia

Character 45 supports the monophyly of the genus Phaeobalia.

45. Wings spotted

In the clinocerine ground plan, the wings are infusate, lacking distinct spots, other than the stigma. The wings of Phaeobalia are distinctly spotted, (except P. pokorny); this condition is tentatively proposed as an apomorphy of this genus. Although similar spotted wings are found in several species of Clinocera (e.g. C. lecta), they are here considered to be due to convergent evolution. In Dolichocephala, the spotted wings are due to irrorations, or clear punctations on a fumose wing and thus is not homologous to the dark spots in Phaeobalia.

Bergenstammia

Character 46 supports the monophyly of the genus Bergenstammia.

46. Pulvilli vestigial and empodia reduced

In the clinocerine ground plan, the pulvilli are elongate pads and the empodia are pulvilliform, extending beyond the tarsal claws (Fig. 95). Bergenstammia is characterized by having vestigial pulvilli and the empodia reduced to half the length of the claws. This character state is considered apomorphic for this genus and a similar reduction is found only in Trichoclinocera dolicheretma.

Wiedemannia

Character 1 supports the monophyly of the genus Wiedemannia.

1. Gena wide, undivided

In Wiedemannia, the gena is wide and not divided by the frontoclypeal suture (Figs. 65,66). This condition is considered to be apomorphic for this genus. Refer to Asymphyloptera for discussion of this character state.

Phylogenetic Conclusions.

As a result of the above cladistic analysis, the genus Asymphyloptera is considered the sister group of the remaining Clinocerinae (Fig. 206). The retention of this genus within the Clinocerinae will be strongly influenced by the discovery, in the larva, of a four or six-component mandible. The Clinocerinae, exclusive of Asymphyloptera, is a well supported lineage of morphologically similar genera. Proagomyia is retained in Clinocerinae as incertae sedis, primarily since it appears not

to fit into any other empidoid lineage. This genus lacks several diagnostic character states such as a tubular spermatheca and a labral apodeme. Proagomyia is retained in this subfamily on the basis of highly homoplastic characters (pubescent eyes, pseudotrachea absent).

Kowarzia, Bergenstammia, and Phaeobalia, formerly subgenera of Clinocera, are elevated to generic status. Characters supporting placement within Clinocera were found to be based on symplesiomorphies and general morphological similarities. Clinocerella, formerly a subgenus of Wiedemannia is elevated to generic status. This genus is probably most closely related to Hypenella.

The relationships of Roederiodes + Clinocerella + Hypenella, Kowarzia, Dolichocephala, and Phaeobalia + Bergenstammia + Wiedemannia remain unresolved. The genera Phaeobalia, Bergenstammia, and Wiedemannia form a monophyletic group, supported on the basis of characters of the male terminalia.

5.1.3 RECONSTRUCTED PHYLOGENY OF THE SPECIES GROUPS OF TRICHOCLINOCERA

As stated in Sec. 5.1.2, Trichoclinocera is characterized by the following synapomorphies: vein R_1 with setae above; R_4 nearly parallel to R_5 ; ejaculatory apodeme sickle-shaped. The sister group of this genus is Rhyacodromia and together they share several distinguishing features (see Sec. 5.1.2).

Thirteen morphological characters are used in the phylogenetic analysis of Trichoclinocera. These characters are used in establishing the relationships between the

species and species groups of Trichoclinocera. The characters are numbered consecutively 1-13 throughout the text and numbers correspond to those used in the cladogram (Fig. 207).

T. dasyscutellum + T. comata group

Character 1 supports the monophyly of this clade.

1. Scutellar disc with setulae

Setulae are lacking on the scutellar disc in Proclinopyga, Rhyacodromia and most species of Trichoclinocera, although setulae are often present along the margin of the scutellum. The presence of setulae on the scutellar disc is considered apomorphic for T. dasyscutellum + T. comata group.

T. comata group

Characters 2 and 3 support the monophyly of the T. comata species group.

2. Notopleuron with 5-6 stout setae

In Clinocerinae, there are usually 2-3 slender, notopleural setae. The T. comata group is characterized by the presence of 5-6 stout notopleural setae that are considered apomorphic for this species group.

3. Vertex of head with tessellated pruinescence

The T. comata group is also characterized by distinctive black and white tessellated pruinescence on the vertex of the head. This unique colour pattern is considered autapomorphic for this species group.

T. cyanescens group + T. stackelbergi group + T. gracilis (ms) + T. fuscipennis + T. longipes group

Character 4 supports the monophyly of this clade.

4. Gena wide, not divided by frontoclypeal suture

In the ground plan of the Clinocerinae, the gena is narrow and divided by the frontoclypeal suture, which runs from the base of the palpus and anterior tentorial pit along the lower margin of the eye toward the antenna. In T. dolicheretma, the gena is completely divided by the suture (Fig. 83). In Proclinopyga, Rhyacodromia and T. dasyscutellum + T. comata group, the frontoclypeal suture divides the gena and runs along the lower margin of the eye. The remaining species of Trichoclinocera are characterized by an undivided gena and the frontoclypeal suture is removed from the lower margin of the face (Figs. 85,86). The derived state is considered apomorphic for all remaining species of Trichoclinocera. A similar gena has evolved independently in Wiedemannia.

T. cyanescens group

Characters 5-8 support the monophyly of the T. cyanescens species group.

5. Face convex

In the outgroup of Trichoclinocera, the face is flat. The T. cyanescens group is characterized by the apomorphic development of a convex face (Fig. 84, Vaillant 1960c, fig. 3j).

6. Fifth tarsomere dorsoventrally flattened

In the Clinocerinae, the fifth tarsomere is narrow, often appearing slightly laterally compressed (e.g. Roederiodes). A dorsoventrally compressed fifth tarsomere is considered apomorphic for the T. cyanescens group.

7. Tergite 10 of female with short, straight setae

In Proclinopyga, Rhyacodromia and most species of Trichoclinocera, the setae of tergite 10 are long and apically arched (Fig. 116). In the T. cyanescens group, the setae of tergite 10 are short and straight (Figs. 110-112). The derived condition is considered apomorphic for this species group.

8. Epandrium with expanded membranous region

The posteroventral margin of the epandrium in the outgroup of Trichoclinocera lacks an expanded membranous region. In the T. cyanescens group, the epandrium is

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uniquely characterized by an expanded membranous region at the posteroventral margin of the epandrium (Fig. 113, Vaillant 1960c, figs. 3g,l,q). This character is considered autapomorphic for the T. cyanescens group.

T. stackelbergi group + T. fuscipennis + T. longipes group

Character 9 supports the monophyly of this clade.

9. Face with median carina and lateral ridge

The face of Proclinopyga, Rhyacodromia and the ground plan of Trichoclinocera is divided medially by a shallow membranous cleft. In many species of Trichoclinocera, the face is characterized by a median carina and lateral ridge (Steyskal and Knutson 1981, fig. 47.26). This condition is considered apomorphic for T. stackelbergi group + T. fuscipennis + T. longipes group. This distinctive face superficially resembles the facial modifications of species of Wiedemannia, but is not considered homologous.

T. stackelbergi group

Characters 10 and 11 support the monophyly of the T. stackelbergi species group.

10. Face with wide, prominent, median carina

From the derived condition described in character 9, the facial carina has increased in prominence and is divided medially by a wide membranous cleft. This further modification of the face is considered apomorphic for T. stackelbergi group.

11. Mid and hind femora with posterodorsal setae

In the ground plan of Trichoclinocera, the mid and hind femora have sparse rows of stout, anterodorsal setae. In addition to stout, anterodorsal setae, the mid and hind femora of the T. stackelbergi group are characterized by stout posterodorsal setae. These additional setae of the mid and hind femora are considered to be apomorphic for the T. stackelbergi group.

T. longipes group

Characters 12 and 13 support the monophyly of the T. longipes species group.

12. Apex of phallus with slender folded sclerite

In the ground plan of Trichoclinocera, the apex of the phallus is primarily membranous (Figs. 106, 113). The T. longipes group is characterized by a slender, folded sclerite at the apex of the phallus, which expands open upon maceration (Fig. 117). The derived state is considered apomorphic for the T. longipes group.

13. Clasping cercus with slender setae on inner face

In the ground plan of Trichoclinocera, the inner face of the clasping cercus possesses numerous stout setae (Figs. 115). The lack of stout setae on the clasping cercus is considered apomorphic for the T. longipes group (Fig. 127).

Phylogenetic Conclusions.

The phylogenetic relationships outlined here must remain tentative until undescribed species from the eastern Palearctic and Oriental regions are documented. These undescribed species should be used to test the validity of the proposed species groups.

With present knowledge, there are approximately seven recognized species groups of Trichoclinocera (Fig. 207). Trichoclinocera dolicheretma and T. dasyscutellum + T. comata group represent the most basal clades of this genus and together represent the sister group to the remaining species of Trichoclinocera.

The T. longipes group is primarily confined to eastern North America. This species group appears to be most closely related to the T. stackelbergi group and T. fuscipennis, which are confined to east Asia.

5.1.4 RECONSTRUCTED PHYLOGENY OF THE SPECIES GROUPS OF CLINOCERA

As stated in Sec. 5.1.2, Clinocera is characterized by the following synapomorphies: phallus with apical filament; spermatheca a loosely, coiled tube. The sister group of this genus is Oreothalia and together they share several distinguishing features (see Sec. 5.1.2).

Fourteen morphological characters are used in this phylogenetic analysis of the relationships between the species groups of Clinocera. The characters are numbered consecutively 1-14 throughout the text and numbers correspond to those used in the

cladogram (Fig. 208).

C. gubernans group

Characters 1 and 2 support the monophyly of the C. gubernans species group.

1. Lower third of face with tubercle

In the genus Oreothalia, the sister group of Clinocera, the face is flat. The C. gubernans group is characterized by a large facial tubercle on the lower third. This distinctive feature is considered apomorphic for this species group.

2. Phallic filament equal to length of phallus

The phallic filament in all other species of Clinocera is at most equal to approximately one-half the length of the phallus. In the C. gubernans group, the phallic filament is greatly lengthened, nearly as long as the phallus (Fig. 129). This character state is considered apomorphic for this species group.

C. fuscipennis group

At present there are no apomorphies for this group. It may be found later that the distinct facial tubercle defining the C. gubernans group may actually evolve within the C. fuscipennis group. This requires further analysis and clarification (see Sec. 4.2.4.2).

Clinocera, exclusive of C. gubernans and C. fuscipennis groups

Character 3 supports the monophyly of this clade.

3. One postsutural supra-alar seta

There are two postsutural supra-alar setae in Oreothalia, and the C. gubernans and C. fuscipennis species groups. A single postsutural supra-alar seta is considered apomorphic for all remaining species groups of Clinocera.

C. conjuncta group

Characters 4 and 5 support the monophyly of the C. conjuncta species group.

4. Clasping cercus with truncate apex

The clasping cercus in other species groups of Clinocera and elsewhere in the Clinocerinae gradually tapers to a round, slender apex. In the C. conjuncta group, the clasping cercus is truncate (Fig. 131). This condition is considered apomorphic for this species group.

5. Apex of surstylus with deep notch

The apex of the surstylus of Oreothalia and most species of Clinocera is smoothly rounded. The C. conjuncta group is characterized by a deep notch on the apex of the surstylus. The derived state is considered apomorphic for this species group.

Clinocera sp.#22 group

Characters 6 and 7 support the monophyly of the Clinocera sp.#22 species group.

6. Apex of surstylus truncate

The surstylus of the C. sp.#22 group is apically truncate, rarely projecting freely beyond the epandrium (Fig. 133). This configuration of the surstylus appears unique among the species of Clinocera and hence autapomorphic for the C. sp.#22 group.

7. Base of phallic filament strongly arched and heavily sclerotized

The phallus in the Clinocera ground plan is believed to be similar to the phallus of the C. gubernans and C. fuscipennis groups. The uniquely shaped phallus of the C. sp.#22 group (Fig. 133) is considered autapomorphic for this group.

C. lineata + C. nigra + C. stagnalis groups

Character 8 supports the monophyly of this clade.

8. Apex of spermatheca with lightly sclerotized glandular material

In the ground plan of Clinocerinae, the long tapering spermatheca terminates in a poorly sclerotized sphere of glandular tissue (Fig. 87). In many species of Clinocera, this terminal glandular material has become lightly sclerotized (Fig. 137) and is considered apomorphic for the C. lineata + C. nigra + C. stagnalis groups.

C. lineata group

Characters 9 and 10 support the monophyly of the C. lineata species group.

9. Apex of surstylus with "nipple-like" projection

The apex of the surstylus in the C. lineata group is uniquely shaped (Fig. 134) and a very distinctive apomorphy of this species group.

10. Phallic filament strongly angled at base

The phallus in the ground plan of Clinocera is hypothesized to be similar to the phallus of the C. gubernans and C. fuscipennis groups. As in the C. sp.#22 group, the phallus is uniquely shaped (Fig. 134) and this configuration is considered apomorphic for this species group.

C. nigra + C. stagnalis groups

Character 11 supports the monophyly of this clade.

11. Phallic filament broadly flattened

In the ground plan of Clinocera, the phallic filament is slender and whip-like. In the C. nigra and C. stagnalis groups, the phallic filament is broadly flattened and is considered synapomorphic for these two species groups.

C. nigra group

Character 12 supports the monophyly of the C. nigra species group.

12. Outer surface of clasping cercus with dense setae

The outer surface of the clasping cercus in the C. nigra species group (except C. nigra) is characterized by fine, dense setae (Fig. 135). This arrangement of setae appears unique to this species group and hence is autapomorphic. Further analysis is required to test the validity of retaining the aberrant species, C. nigra in this group.

C. stagnalis group

Characters 13 and 14 support the monophyly of the C. stagnalis species group.

13. Wing with spots

This species group is characterized by round, dark spots on the wings, usually at the base of R_4 , apex of cell dm, r-m cross-vein and apex of cell bm. Although spotted wings occur in other species of Clinocera, they differ from the C. stagnalis group in their pattern and thus I do not consider them to be homologous.

14. Face convex with blue pruinescence

In Oreothalia and most species of Clinocera, the face is flat and not covered with a bright blue pruinescence. In this species group, the face is convex and covered with a bright blue pruinescence. This character state is believed to be apomorphic for the C.

stagnalis group.

Phylogenetic Conclusions.

The phylogenetic relationships outlined here must remain tentative until undescribed species from the Nearctic, Neotropical and Oriental regions have been documented. These undescribed species will be used to test the validity of the proposed species groups.

There are currently seven recognized species groups of Clinocera (Fig. 208). The C. gubernans and C. fuscipennis groups are believed to be the most basal species groups of Clinocera. The C. lineata + nigra + stagnalis groups are believed to form a well supported monophyletic group. The C. lineata group includes two species formerly described under Kowarzia. The C. stagnalis group is equivalent to the subgenus Hydrodromia.

5.1.5 RECONSTRUCTED PHYLOGENY OF THE SPECIES GROUPS OF WIEDEMANNIA

As stated in Sec. 5.1.2, Wiedemannia is characterized by the following synapomorphy: gena wide, undivided. The sister group of this genus is Phacobalia + Bergenstammia and together they share several distinguishing features (see Sec. 5.1.2).

Eleven morphological characters are used in this phylogenetic analysis of the relationships between the species groups of Wiedemannia. The characters are numbered consecutively 1-11 throughout the text and numbers correspond to those used in the

cladogram (Fig. 209).

Wiedemannia, exclusive of W. lepida group

Character 1 supports the monophyly of this clade.

1. Lower margin of face with deep cleft separated by chitinous ridges

In the ground plan of the Clinocerinae, the lower margin of the face is medially divided by a small region of membrane. In Wiedemannia, except the W. lepida group, the lower margin of the face is divided by a deep membranous cleft and separated by convergent ridges (Collin 1961, fig. 315). This modification of the face is considered apomorphic for this clade.

Roederella czernyi + Eucelidia pirata + E. zetterstedti

Character 2 supports the monophyly of this clade.

2. Fore coxa with 2-3 long, erect setae

The fore coxa of clinocerines is covered with short setae. In these three species of Wiedemannia, there are 2-3 long, erect setae on the inner anterior margin of the fore coxa. This arrangement of setae appears unique in Wiedemannia and thus apomorphic for Roederella czernyi + Eucelidia pirata + E. zetterstedti.

Chamaedipsia + Philolutra + Pseudowiedemania + W. rhynchops group + Wiedemania (s.s.)

Character 3 supports the monophyly of this clade.

3. Acrostichals extend to scutellum

In most genera of Clinocerinae, except Proclinopyga and Clinocerella sorex, acrostichal setae are weakly developed. Well developed acrostichal setae, extending around the prescutellar depression and onto the scutellum, occur in many species of Wiedemania. The presence of well developed acrostichal setae is considered apomorphic for Chamaedipsia + Philolutra + Pseudowiedemania + W. rhynchops group + Wiedemania (s.s.). Acrostichal setae extending to the scutellum are considered to occur independently in W. (Eucelidia) pirata.

Philolutra + Pseudowiedemania + W. rhynchops group + Wiedemania (s.s.)

Characters 4 and 5 support the monophyly of this clade.

4. Distiphallus with median, setose swelling

In the basal taxa of Wiedemania, the membranous margin of the distiphallus (articulated apical component of phallus) is smooth, lacking a central swelling. A central, setose swelling on the distiphallus (Fig. 150) is considered apomorphic for Philolutra + Pseudowiedemania + W. rhynchops group + Wiedemania (s.s.).

5. Segment eight of female longer than segment seven

In the ground plan of Wiedemannia, segment 8 of the female terminalia is equal in length to segment 7. An elongate segment 8 (Fig. 152) is considered apomorphic for Philolutra + Pseudowiedemannia + W. rhynchops group + Wiedemannia (s.s.).

Pseudowiedemannia + W. rhynchops group + Wiedemannia (s.s.)

Character 6 supports the monophyly of this clade.

6. Stigma round

A round stigma is a distinct, unique apomorphy among the Clinocerinae and characterizes Pseudowiedemannia, W. rhynchops group and Wiedemannia (s.s.). The stigma is often darker in males and vein R_{2+3} arches conspicuously beneath (Collin 1961, fig. 315).

W. rhynchops group + Wiedemannia (s.s.)

Characters 7 and 8 support the monophyly of this clade.

7. Double row of acrostichals surround prescutellar depression

In Chamaedipsia and Philolutra (except some W. simplex) there is a single row of acrostichals extending around either side of the prescutellar depression. Two rows of acrostichal setae extending around the prescutellar depression are considered apomorphic for W. rhynchops group + Wiedemannia (s.s.).

8. Postpronotal lobe with 2-4 short, stout setae

In the basal lineages of Wiedemannia there is a single postpronotal seta. In W. rhynchops group and Wiedemannia (s.s.), there are 2-4 short, stout postpronotal setae and this character state is considered apomorphic for these two lineages.

W. rhynchops group

Characters 9 and 10 support the monophyly of the W. rhynchops species group.

9. Clasping cercus slender and elongate

The shape of the clasping cercus is unique in the W. rhynchops group (see Wagner 1990, figs. 1-9). This character state is considered apomorphic for this species group.

10. Stigma at base of R₄

In Clinocerinae the stigma is positioned proximal to the base of vein R₄. In the W. rhynchops group the stigma is positioned at the base of R₄, closer to the tip of the wing. This character state is tentatively proposed as a synapomorphy of this species group, pending examination of additional species of this group.

Wiedemannia (s.s.)

Character 11 tentatively supports the monophyly of Wiedemannia (s.s.).

11. Antep pronotum with row of stout, dark setae

In Clinocerinae the antep pronotal setae are normally slender, pale, and inconspicuous. In Wiedemannia (s.s.), there are more than 3 pairs of dark, stout antep pronotal setae. Since only two of 9 species of this species group have been examined (W. bistigma and W. stylifera), this character state is only tentatively proposed as an apomorphy of this lineage.

Phylogenetic Conclusions.

The phylogenetic relationships of the species groups or subgenera outlined here must remain tentative until all Palearctic species have been examined. My knowledge of the Palearctic fauna is currently insufficient to question the validity of continued recognition of subgenera in Wiedemannia. In addition, there are many described species that I have have not been able to place in any of the current subgenera or species groups (see Sec. 4.2.5.2).

The W. lepida group is tentatively proposed as the most basal lineage of this genus (Fig. 209). The subgenera Roederella and Eucelidia appear to form a well supported monophyletic group. Consequently, the continued recognition of both subgenera does not appear to be warranted and maybe only Eucelidia (the oldest name) should be used. Philolutra + Pseudowiedemannia + Wiedemannia (s.s.) form a well supported monophyletic group.

Currently, I am not aware of any apomorphies defining the subgenera Chamaedipsia, Philolutra and Pseudowiedemannia. In the analysis, the W. koeppeni

group discussed in Sec. 4.2.5.2, is included in Chamaedipsia.

Although included with Wiedemannia (s.s) in the Palearctic Catalogue (Chvála and Wagner 1989), the W. rhynchops group was removed and treated separately for the purposes of this analysis. In future studies, the remaining species of Wiedemannia (s.s.) may be found to be paraphyletic with respect to the W. rhynchops group.

5.2 ZOOGEOGRAPHIC CONSIDERATIONS

5.2.1 TIME OF ORIGIN OF THE CLINOCERINAE

Estimates of the time of origin of the Clinocerinae are impeded by the lack of fossil evidence for this subfamily. Chvála (1983, fig. 140) believes that this subfamily was well established by least the Early Paleocene, based on superimposing the numerous fossils identified from many other lineages onto his cladogram of the Empidoidea. The Empidinae and Hybotinae were believed to have been well established by the Early Paleocene or upper Late Cretaceous (Chvála 1983). On the basis of fossil Empidinae and Hybotinae, Waters (1989) has recently suggested that these two lineages may actually have been well established in the early Late Cretaceous (93 mya), which is much earlier than that suggested by Chvála (1983). Based on this evidence and on present distribution patterns, it is likely that the Clinocerinae were also well established as early the Cenomanian Age (97-91 mya) of the Late Cretaceous.

5.2.2 TRICHOCLINOCERA

Tertiary Distributions. - Given the inadequate descriptions and revisionary work on the eastern Palearctic and Oriental species of Trichoclinocera, the phylogenetic relationships of the species groups presented in Sec. 5.1.3 should be considered preliminary. Consequently, the following zoogeographic discussion should be viewed as somewhat speculative.

Proclinopyga and Rhyacodromia, form the outgroup of Trichoclinocera, and are confined primarily to eastern Asia and western North America. Since the most basal lineages of Trichoclinocera (T. dolicheretma, T. dasyscutellum, and the T. comata group), are also restricted to this region, I believe that the ancestor of this genus probably originated within Asiamerica (Asia + western North America). Asia and western North America formed a large landmass, connected via Beringia, when epicontinental seaways bisected North America in the Cenomanian Age of the Late Cretaceous (91-97.5 mya), until 70 mya and the Turgai Straits divided Asia from Europe throughout the Cretaceous until approximately 30 mya (Cox 1974, Noonan 1986).

The ancestral Asiamerica distribution of Trichoclinocera was possibly fragmented due to disruptions of the Beringian land bridge. Based on the distributions of late Cretaceous mammals, there is evidence of a barrier between Asia and western North America at this time (Cox 1974). This barrier to mammals may also have briefly divided the ancestral range of Trichoclinocera into two allopatric populations, which subsequently evolved into the ancestors of the T. comata group, T. dolicheretma, and T. dasyscutellum.

I believe that the *T. cyanescens* group likely arose first in eastern Asia and may have extended into western North America, since the Beringian land bridge existed from the Cretaceous to at least the Oligocene and possibly until the Pliocene (Matthews 1979). The widespread distribution of *T. lapponica* is the result of more recent dispersal. This species may have arisen as global climates continued to cool during the Oligocene, and was able to disperse westward into Scandinavia with the disappearance of the Turgai Straits. During the Pleistocene, *T. lapponica* possibly survived in Beringia and dispersed eastward into the Canadian Arctic following the retreat of the ice sheets.

The *T. longipes* and *T. stackelbergi* species groups are found in warm to cool temperate regions, primarily associated with broadleaved deciduous forests. The eastern North American and eastern Asian distributions of these closely related species groups demonstrate an ancient disjunction also known in many plant taxa (e.g. Axelrod 1983). Given the apparent association with deciduous forests, it would appear that the historical zoogeographic pattern of these species groups (and probably many other clinocerines) likely reflects the paleobiogeographic relationships of the deciduous flora during the Tertiary.

Based on plant fossils (macrofossils) found in southern Alaska, Wolfe (1985) believed that a circumpolar broadleaved evergreen forest extended from 60-65°N, during the Late Paleocene-Early Eocene (50-55 mya). However, fossils from this region that are used for climatic reconstruction should be interpreted with caution (Taylor 1990). The north Pacific region consists of a series of microplates or terranes and the geographic location of these plates during the Tertiary remains unclear. The floras from the

formation that Wolfe examined could be allochthonous and may have been displaced northwards from possibly as far south as Washington (Axelrod 1983, Taylor 1990). It is now assumed that most of Alaska during the Early Tertiary was inhabited by a broadleaved deciduous forest, with a narrow band of megathermal (mean annual temperature $>20^{\circ}\text{C}$) flora along the southern border (Taylor 1990). But there is also no evidence of a homogeneous high latitude flora, that is similar to the existing temperate flora, occurred during the Eocene; ie. the Arcto-Tertiary Geoflora (Tiffney 1985, Taylor 1990). Nevertheless, the climate of the high latitudes during the Eocene appeared to be warm to cool temperate, which would probably be ideal for the ancestral populations of the *T. longipes* and *T. stackelbergi* groups. Temperate forest trees are also known from early Eocene deposits along the western Cordillera (Axelrod and Raven 1985, Wolfe 1987). Thus, the ancestral population of *Trichoclinocera* probably followed the southward migration of temperate flora and fauna during cooler periods of the Eocene.

By Late Eocene, global temperatures were dramatically cooling and large areas of the northern hemisphere (circumpolar) were occupied by microthermal ($<13^{\circ}\text{C}$) broadleaved deciduous forests (mixed Mesophytic forests) (Wolfe 1985). By the Early Miocene (20 mya), the mixed mesophytic forest was quite widespread and diverse. During the late Middle Miocene (13 mya), the climate again began cooling (result of uplift of the western Cordillera, see below), which resulted in the fragmentation of the broadleaved forests into temperate parts of Eurasia and eastern North America (Axelrod 1985). At this time, taxa associated with these forests were largely eliminated from the western Cordillera and Beringia (Wolfe 1987). Despite the similarities of the eastern

Asian and eastern North American floras, the sister group relationships of the constituents have rarely been analysed (Taylor 1990). Some Asian floras have been found to be most closely related to other Asian taxa, while North American and European species are more closely related.

I believe the disjunct distribution of the *T. longipes* and *T. stackelbergi* groups reflect the fragmentation of these ancient broadleaved forests. This scenario could be tested by assessing into which species group the many undescribed species of this genus in east Asia should be placed.

Species Radiation in North America. *T. comata* group. - The radiation of this species group may have occurred during the Late Miocene and Early Pliocene (9 Mya) as the Tertiary floral relicts were nearly extirpated and essentially replaced by modern flora (Barnosky 1984).

The changes in flora and fauna in western North America were the result of changes in rainfall patterns and climate. During the Middle Miocene, the Coast Range uplift commenced, while the Cascade Orogeny and the formation of the famous volcanic peaks began at the close of the Pliocene (Kummel 1970). The Sierra Nevada Mountains remained low during the Late Miocene and Early Pliocene, because evidence from fossil floras indicate little development of a rainshadow (Axelrod 1962; Kummel 1970). However at the close of the Pliocene, the Sierra Nevada range was high enough to form a major barrier (Axelrod 1962). During the Late Miocene to the Pliocene, the climate in the Rocky Mountains was probably becoming increasingly continental, due to the uplift

commencing further to the west (Barnosky 1984).

In addition, the arid flora of the intermontane regions developed and expanded, while the coniferous forest withdrew to higher elevations in western North America (Lafontaine 1982). Thus, the widespread, ancestral western species of Trichoclinocera followed the retreating coniferous forest up into the cooler, moist uplands. The populations were isolated into the eastern and western mountain ranges, and subsequently speciated.

T. longipes group. - Diversity of the T. longipes group may be due to events during the Miocene, when the distributions of eastern North American species were reduced due to cooler temperatures and changes in rainfall pattern. This population was further constricted and isolated into subpopulations during the Pleistocene. On the basis of plant macrofossils, the diversity of the Mixed Mesophytic forest increased greatly during the Miocene (Wolfe 1985). Thus it may be inferred that the diversity of Trichoclinocera, especially in eastern North America, also increased significantly at this time.

The differentiation of the Ozark Plateau species probably occurred during the Miocene. This species, T. ozarkensis, appears to be most closely related to T. agilis (west of the Appalachians) and T. falcata + fumosa (Appalachians). This interpretation agrees with that of Allen (1990), who suggested Cretaceous and Miocene vicariance events for the isolation and subsequent speciation in these two regions. In contrast, Ross (1965) postulated that Ozark and Appalachian populations of winter stoneflies and caddisflies became disjunct during the Pleistocene and subsequently speciated.

6. CONCLUDING REMARKS

The monophyly of the Clinocerinae has been established and this subfamily now contains 14 genera and approximately 240 valid described species, distributed worldwide. The remaining genera have been reclassified within other empidoid lineages. Two former clinocerine genera, Dipsomyia and Zanclostus have been transferred to the Oreogetoninae. Six former clinocerine genera (Boreodromia, Ceratempis, Ephydrempis, Niphogenia, Sabroskyella, and Trichopeza) have been transferred to the Trichopezinae, a newly recognized empidoid lineage. This lineage was first coined by Vaillant (1981), which included the single genus Trichopeza in his broad concept of the Hemerodromiinae. This subfamily also included all the remaining clinocerine genera placed in the tribe Clinocerini. There is no justification for this classification and I accept the traditional concept of the Clinocerinae, exclusive of the Trichopezini. Based on a phylogenetic analysis, the elevation of Trichopezini to subfamily ranking appears justified. In addition to the above six former clinocerine genera, six genera (Apalocnemis, Gloma, Heleodromia, Heterophlebus, Hyperperacera, Rubistella) previously placed in three different subfamilies are included in the Trichopezinae.

A cladistic analysis suggests that the Trichopezinae, Ceratomerinae and Brachystomatinae form an unresolved trichotomy. These three lineages, together with the Microphorinae + Dolichopodidae form a new lineage, supported on the basis of characters of the female terminalia. Unfortunately this analysis, was not able to establish the sister group to the Clinocerinae. Resolution of the basal lineages of the Empidoidea, especially the Oreogetoninae, will ultimately test the hypothesis presented in this thesis.

Much work remains to be done in the Clinocerinae, especially in the Nearctic region and this reclassification should help stimulate further research into this fascinating group of aquatic empidids. Revisions of the Nearctic species of Proclinopyga, Dolichocephala, and Clinocera are urgently needed and continued collections, especially in the western mountains of North America, are encouraged.

Clinocerines are poorly known from the Australasian, Oriental, and Neotropical regions and I suspect there are many undescribed species scattered throughout the mountain ranges in these biotic regions. Collection methods focused specifically on Diptera of small streams and cascades should result in many new discoveries. In addition, collections of immature stages should continue. Information concerning the configuration of the larval mandible (four or six components) and presence of pupal caudal hooks is urgently required, especially in the genera Asymphyloptera and Proclinopyga.

This revision of the Clinocerinae should be viewed by empidoid workers as a warning to not blindly accept the monophyly of higher taxa. Questions should be asked as to how a higher taxon is defined (e.g. what is a clinocerine?). Is the clade simply a collection of similarly looking genera or is the lineage defined by distinct synapomorphies.

I hope this revision will also encourage researchers to seek a knowledge of their taxon from a worldwide perspective. In addition, I hope taxonomists will attempt to include detailed figures and descriptions of female terminalia in generic revisions. I feel this is an untapped source of potential apomorphies for genera and possibly for higher

level classification.

TABLE 1. Larvae examined in this study.

NEMATOCERA

Tipulomorpha (sensu Wood & Borkent, 1989)

Tipulidae: Antocha sp.; Limonia spp.; Pedicia sp.; Pilaria recondita (O.S.); Tipula spp.; Ula sylvatica Meig.

Blephariceromorpha (sensu Wood & Borkent, 1989)

Nymphomyiidae: Palaeodipteron walkeri Ide

Blephariceridae: Blepharicera sp.

Deuterophlebiidae: Deuterophlebia sp.

Bibionomorpha (sensu Wood & Borkent, 1989)

Bibionidae: Bibio sp.

Psychodomorpha (sensu Wood & Borkent, 1989)

Psychodidae: Pericoma sp.

Anisopodidae: Sylvicola sp.

Trichoceridae: Trichocera sp.

BRACHYCERA

Xylophagomorpha (sensu Woodley, 1989)

Xylophagidae: Coenomyia ferruginea (Scopoli); Xylophagus reflectans Walker

Tabanomorpha (sensu Woodley, 1989)

Rhagionidae: Chrysopilus sp.; Symphoromyia sp.

Pelecorhynchidae: Glutops rossi Pechuman; Pelecorhynchus sp.

Athericidae: Atherix sp.

Tabanidae: Hybomitra epistates (O.S.)

Vermileonidae (incertae sedis): Vermileo comstocki Wheeler; V. opacus (Coquillett)

Stratiomyomorpha (sensu Griffiths, 1989)

Pantophthalmidae: Pantophthalmus tabaninus Thunb.

Xylomyidae: Xylomya sp.

Stratiomyidae: Sargus (s.s.) sp.

Nemestrinoidea (sensu Woodley, 1989)

Acroceridae: Exetasis eickstedtae Schlinger

Nemestrinidae: Trichopsidea clausa (O.S.)

TABLE 1. (continued)

Asiloidea (*sensu* Woodley, 1989)

Bombyliidae: Undetermined genus

Therevidae: Thereva candidata LoewMydidae: Mydas clavatus (Drury)Asilidae: Promachus sp.**Empidoidea**Oreogetoninae: Oreogeton sp.

Empidinae: Undetermined genus

Hemerodromiinae: Chelifera sp.; Hemerodromia sp.Clinocerinae: Clinocera sp.; Trichoclinocera sp.Ocydromiinae: Ocydromia sp. (first instar)Tachydromiinae: Chersodromia arenaria (Haliday)Dolichopodidae: Liancalus spp.; Thrypticus sp.; Undetermined genus**Cyclorrhapha - "Aschiza"**Platypezidae: Agathomyia wankowiczi Schnabl; A. unicolor Oldenb.;
Bertamyia notata (Loew); Melanderomyia kahli Kessel; Platypeza
sp.Lonchopteridae: Lonchoptera sp.Phoridae: Megaselia spp.; Spiniphora bergenstammi (Mik)**Cyclorrhapha - Schizophora**Sarcophagidae: Ravinia querula (Walker)

TABLE 2. Adult females examined in this study.

LOWER BRACHYCERA

- Rhagionidae: Symphoromyia hirta Johnson
 Bombyliidae: Comptosia lateralis (Newman); Eclimys harrisi (O.S.); Lepidophora sp.; Mythenteles (Galápagos sp.); Systropus sp.
 Therevidae: Pherocera albihalteralis Cole; Thereva frontalis Say
 Asilidae: Diogmites sp.; Proctacanthus sp.

EMPIDOIDEA

- Empidinae: Empis borealis L.
 Oreogetoninae: Anthepiscopus sp.; Apalocnemis sp.; Gloma luctosa Melander;
Hormopeza spp.; Oreogeton spp.
 Hemerodromiinae: Heleodromia sp.
 Brachystomatinae: Anomalempis sp.; Brachystoma nigrimanum Loew;
Brachystoma (S. Afr.) sp.
 Ceratomerinae: Ceratomerus mediocris Collin; C. paradoxus Philippi
 Clinocerinae: Niphogenia sp.; Trichopeza longicornis (Meig.)
 Ocydromiinae: Bicellaria sp.; Trichina sp.; Trichinomyia flavipes Meig.
 Tachydromiinae: Chersodromia spp.; Platypalpus holosericus Melander;
Symballophthalmus sp;
 Atelestinae: Atelestus pulicarius Fln.
 Microphorinae: Microphor sp.; Microphorella sp.; Parathalassius sp.;
Schistostoma armipes (Mel.);
 Dolichopodidae: Sciapus platyperus (Fab.)

CYCLORRHAPHA

- Platyezidae: Microsania sp.; Agathomyia sp.
-

TABLE 3. Adult males examined in this study (sequence is broadly phylogenetic based in part on Chvála (1983), Griffiths (1972) and Woodley (1989)). Note: all species illustrated by Wood (1991) were also examined.

NEMATOCERA

- Tipulidae: Dolichopeza obscura (Johnson); Liogma nodicornis (O.S.)
 Bibionidae: Hesperinus brevifrons Walker
 Blephariceridae: Paltostoma sp.
 Psychodidae: Bruchomyia sp.; Trichomyia capitanea Duckhouse
 Scatopsidae: Apistes sp.

LOWER BRACHYCERA

- Xylophagidae: Arthropeas sp.; Coenomyia ferruginea (Scopoli); Xylophagus decorus Williston
 Heterostomidae: Heterostomus curvipalpis Bigot
 Exeretoneuridae: Exeretonevra maculipennis Macquart
 Vermileonidae: Lampromyia canariensis Macquart; Vermileo comstocki Wheeler; V. vermileo (L.)
 Rhagionidae: Arthroceras pollinosum Williston; Atherimorpha nemoralis Philippi; Austroleptis sp.; Bolbomyia sp.; Chrysopilus sp.; Rhagio scolopacea L.; Symphoromyia sp.
 Pelecorhynchidae: Glutops sp.; Pelecorhynchus sp.
 Athericidae: Atherix pachypus Bigot
 Tabanidae: Hybomitra aurilimba (Stone)
 Pantophthalmidae: Pantophthalmus tabaninus Thunb.
 Stratiomyidae: Actina sp.; Chiromyza sp.; Stratiomys sp.
 Xylomyidae: Xylomya tenthredinoides (Wulp)
 Nemestrinidae: Atriadops javana (Wiedemann); Hirmoneura maculipennis (Macquart); Neorhynchocephalus sackenii (Williston); Trichophthalma barbarosa (Bigot)
 Acroceridae: Ogcodes pallidipennis Loew; Turbopsebius sulphuripes (Loew)
 Bombyliidae: Comptosia lateralis (Newman); Geron spp.; Heterostylum sp.; Mythicomyia sp.; Mythenteles (Galápagos sp.); Pantarbes sp.; Paraconsors sp.; Phthiria spp.; Systropus sp.; Toxophora sp.
 Therevidae: Apsilocephala longistyla Kröber; Apystomyia sp.; Bonjeania sp.; Henicomysia hubbardi Coq.; Nebritus pellucidus Coq., Penniverpa festina (Coquillett); Pherocera flavipes Cole; Spiriverpa candidata (Loew); Thereva sp.
-

TABLE 3.(continued)

Hilarimorphidae: Hilarimorpha sp
 Scenopinidae: Belosta albipilosa Hardy; Caenotus sp.; Prorates sp.; Scenopinus fenestralis (L.)
 Apioceridae: Apiocera haruspex O.S.; Neorhaphiomidas sp.
 Mydidae: Heteromydas bicolor Hardy; Mydas clavatus (Drury)
 Asilidae: Diogmites sp; Efferia sp.; Eudioctria sp.; Laphria sp; Machimus sadyates ?(Walker); Proctacanthus sp.; Philonicus sp.

EMPIDOIDEA

Oreogetoninae: Gloma luctuosa Mel.; Hesperempis mabelae (Mel.); Hormopeza bullata Mel.; H. copulifera Mel.; Itaphila nitidula Zett.; Oreogeton nigricornis (Philippi); Q. obscura Loew
 Empidinae: Empis borealis L.; E. pennipes L.; E. tessellata Fab.; Hilara interstincta (Fln.); Rhamphomyia fumosa Loew; R. longicauda Loew; Rhamphomyia spp.
 Hemerodromiinae: Chelifera precatoria (Fall.); Chelipoda albiseta (Zett.); Heleodromia sp.; Hemerodromia unilineata Zett.; Metachela albipes (Walker); Neoplasta sp.
 Ceratomerinae: Ceratomerus mediocris Collin; C. nr. paradoxus Philippi
 Brachystomatinae: Anomalempis archon Mel.; Brachystoma sp.; Homalocnemis adelensis (Miller)
 Clinocerinae: (all genera and species listed in thesis)
 Atelestinae: Atelestus pulicarius Fln.; Meghyperus ?nitidus Mel.
 Ocydromiinae: Bicellaria sp.; Trichina clavipes L.; Trichinomyia flavipes (Meig.)
 Hybotinae: Euhybus sp.; Syneches sp.
 Tachydromiinae: Austrodromia spp.; Chersodromia spp; Crossopalpus armata (Mel.); Drapetis exilis Meig.; Elaphropeza ephippiata (Fln.); Micrempis bomboxynon Chillcott; Platypalpus spp.; Stilpon spp.; Symballophthalmus masoni Chillcott; Tachydromia maculipennis Walker; Tachyempis nigra Mel.; Tachypeza spp.
 Microphorinae: Microphor pilimanus Str.; Microphor holosericus (Meig.); Microphorella sp.; Schistostoma armipes (Mel.)
 Dolichopodidae: Condylostylus nigrofemoratus (Walker); Dolichopus ?brevipennis Meig.; Sciapus platypterus (Fab.)

TABLE 3. (continued)

CYCLORRHAPHA

Opetidae: Opetia nigra Meig.

Platypozidae: Agathomyia spp.; Callomyia sp.; Melanderomyia kahli Kessel;
Microsania spp.; Platypeza sp.; Platypezina diversa (Johnson)

Lonchopteridae: Lonchoptera lutea Panzer; L. tristis Meig.; L. uniseta Curran

Ironomyiidae: Ironomyia nigromaculata White

Sciadoceridae: Sciadocera rufomaculata White

Phoridae: Aneurina sp.; Borophaga sp.; Dohrinophora sp.; Spiniphora sp.

Syrphidae: Cheilosa sp.; Syrphus ribesii (L.)

Pipunculidae: Pipunculus sp.; Verrallia sp.

Piophilidae: Neopiophila setaluna McAlpine

Coelopidae: Coelopa frigida (Fab.)

Sphaeroceridae: Opacifrons wheeleri Spuler

Tachinidae: sp.

Table 4. Character state matrix for the major lineages of the Empidoidea. Character numbers correspond to character numbers in text. See text for description of characters. 0 - plesiomorphic state; 1 - apomorphic state; 8 - either 0 or 1; ? - missing data.

	1	111111112	222222223	333333334	444444445	55555
	1234567890	1234567890	1234567890	1234567890	1234567890	12345
Cyclorha.	1111100001	0000000000	0000000000	0000000000	0000000000	00000
Oreogeton.	??100?1111	0000000000	0000000000	0000000000	0000000000	00000
Empidinae	1110011111	1000000000	0000000000	0000000000	0000000000	00000
Hemerodro.	1110011111	1110000000	0000000000	0000000000	0000000000	00000
Atelestin.	??100?1111	0100000001	1111100000	0000000000	0000000000	00000
Trichinini	??100?1111	0100000001	1000011111	0000000000	0000000000	00000
Oedaleini	??100?1111	0100000001	1000011111	0100000000	0000000000	00000
Ocydromii.	1110011111	0100000001	1000011111	1000000000	0000000000	00000
Hybotinae	??100?1111	0100010001	1000011111	0010000000	0000000000	00000
Tachydrom.	1110011111	0100010001	1000011111	0011100000	0000000000	00000
Trichopezi.	??100?1110	0000000000	0000000000	0000011110	0010000000	00000
Brachystom.	??100?1110	0000000000	0000000000	0000011110	0001110000	00000
Ceratomer.	??100?1110	0000010100	0000000000	0000011111	1100000000	00000
Microphor.	??100?1110	0001000000	1000001000	0000011000	0000001111	10000
Parathala.	??100?1110	0001000000	1000011000	0000011000	0000001111	01100
Dolichopo.	1110011110	0001000001	1000011000	0011011000	0000001111	01011
Clinocer.	1110011111	0001111110	0000000000	0000000000	0000000000	00000

Table 5. Character state matrix for the genera of the Clinocerinae.

Character numbers correspond to character numbers in text, except character 47, which is presence of tubular spermatheca (see Appendix 2). See text for description of characters. 0 - plesiomorphic state; 1 - apomorphic state; ? - missing data.

	1	111111112	222222223	333333334	4444444
	1234567890	1234567890	1234567890	1234567890	1234567
Proagomyia	0000000??0	0010000000	0000000000	0000000000	0000000
Asymphylo.	1111111??0	0000000000	0000000000	0000000000	0000001
Proclinop.	0000000??1	1111111111	0000000000	0000000000	0000001
Rhyacodro.	0000000??1	1111111100	1111000000	0000000000	0000001
Trichocli.	0000000111	1111111100	1100111000	0000000000	0000001
Clinocera	0000000111	1111100001	0000000111	1000000000	0000001
Oreothalia	0000010??1	1111100000	0100000111	0000000000	0000001
Roederiod.	1000001??1	1001100000	0000000100	0111100000	0000001
Hypenella	1100001??1	1111100100	0000000100	0110010000	0000001
Clinocere.	1000001??1	1111100000	0000000?00	0110011000	0000001
Kowarzia	0000000111	1111100000	0000000100	0100000100	0000001
Dolichoce.	0000000111	1111100000	0000000100	0100000111	1000001
Phaeobalia	0000000??1	1111100000	0000000100	0100001000	0111101
Bergensta.	0000000??1	1111100000	0000000100	0100001000	0111011
Wiedemann.	1000000111	1111100000	0000000100	0100001000	0100001

Figs. 1-4. Mouthparts of final instar larvae of Empidoidea (scale bars = 20 μ m, except Fig. 3 where scale bar = 100 μ m). 1, *Liancalus* sp., left mandible, aboral view; 2, *Liancalus* sp., left mandible, adoral view; 3, *Liancalus* sp., cephalopharyngeal skeleton (dorsal view), right mandible removed, left mandible outlined in cross hatchings; 4, *Oreogeton* sp., left mandible, aboral view.

Figs. 5-9. Left mandible of final instar larvae of Empidoidea (scale bars = 20 μm). 5, *Oreogeton* sp., adoral view; 6, *Chersodromia arenaria*, aboral view; 7, *C. arenaria*, adoral view; 8, *Chelifera* sp., aboral view; 9, *Chelifera* sp., adoral view.

Figs. 10-13. Female terminalia (scale bars = 100 μ m). 10, *Ceratomerus medioeris*, lateral view; 11, *Schistostoma* sp., lateral view; 12, *Microphor* sp., dorsal view; 13, *Sciapus platypterus*, dorsal view.

Figs. 14-19. Male terminalia. 14, Rhagio scolopacea, lateral view; 15, R. scolopacea, posterior view; 16, R. scolopacea, ventral view; 17, R. scolopacea, parameral sheath and aedeagus, ventral view; 18, Hornopeza copulifera, left epandrium cut away, lateral view; 19, Clinocera conjuncta, left epandrium, cerci and surstylus removed, lateral view.

Figs. 20-24. Male and female terminalia of species of *Asymphyloptera*, lateral view (scale bar = 100 μ m, except Fig. 23 where scale bar = 50 μ m). 20, *A. quadriseta*, female; 21, *A. quadriseta*, male; 22, *A. chiricahua*, male; 23, *A. lutea*, male; 24, *A. chiricahua*, female.

Figs. 25-27. Male and female terminalia of *Proclinopyga flavicoxa*, lateral view (scale bars = 100 μ m). 25, female, one accessory gland removed; 26, male; 27, spermatheca.

Figs. 28-30. Male and female terminalia of *Rhyacodromia evae*, lateral view (scale bars - 100 μ m). 28, male; 29, female; 30, spermatheca.

Figs. 31-33. Male and female terminalia of species of *Oreothalia*, lateral view (scale bars = 100 μ m). 31, *O. pelops*, male; 32, *O. spinitarsis*, female; 32, *O. spinitarsis*, spermatheca.

Figs. 34-37. Male and female terminalia of species of *Roederiodes* and *Clinocerella*, lateral view (scale bars = 100 μ m). 34, *R. junctus*, male; 35, *R. recurvatus*, female; 36, *R. recurvatus*, spermatheca; 37, *C. oldenbergi*, female.

Figs. 38-42. Male and female terminalia of species of *Clinocerella* and *Hypenella*, lateral view (scale bars = 100 μ m). 38, *C. sorex*, male; 39, *H. empodiata*, inner view of male clasper; 40, *H. empodiata*, male; 41, *H. spumaria*, spermatheca; 42, *H. spumaria*, female.

Figs. 43-45. Male and female terminalia of *Kowarzia bipunctata*, lateral view (scale bars = 100 μ m). 43, male; 44, female; 45, spermatheca.

Figs. 46-48. Male terminalia and spermatheca of species of *Dolichocephala* and *Kowarzia*, lateral view (scale bars = 100 μ m). 46, *D. fugitivus*, male; 47, *Dolichocephala* sp., spermatheca; 48, *K. sexmaculata*, male.

Figs. 49-52. Male and female terminalia of species of *Dolichocephala*, lateral view (scale bars = 100μm). 49, *D. argus*, sclerite of floor of genital chamber, female; 50, *D. argus*, female and spermatheca; 51, *D. cavaticum*, male; 52, *D. argus*, male.

Figs. 53-55. Male and female terminalia of species of *Bergenstammia*, lateral view (scale bars = 100 μ m). 53, *B. nudipes*, male; 54, *B. multiseta*, spermatheca; 55, *B. multiseta*, female.

Figs. 56-58. Male and female terminalia of *Phaeobalia trinotata*, lateral view (scale bars = 100 μ m). 56, spermatheca; 57, male; 58, female.

Figs. 59-66. Heads of species of Clinocerinae, lateral view (scale bars = 0.1mm). 59, Asymphyloptera chiricahua; 60, Proclinopyga sp.; 61, Clinocera lineata; 62, Røederiodes recurvatus; 63, Hypenella empodiata; 64, Dolichocephala sp.; 65, Wiedemannia lepida; 66, Wiedemannia simplex.

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Figs. 67-74. Wings of species of Clinocerinae (scale bars = 0.3mm). 67, Asymphyloptera chiricahua; 68, Proclinopyga monogramma; 69, Trichoclinocera minor; 70, Oreothalia rupestris, arrows identify stout, erect setae.; 71, Clinocera maculata; 72, Roederiodes recurvatus; 73, Dolichocephala argus; 74, Wiedemannia uncinata.

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Figs. 75-82. Larvae and pupae of Trichoclinocera. 75, T. fumosa, pupa, lateral view (scale bar = 0.5mm); 76, T. fumosa, pupa, dorsal view (scale bar = 0.5mm); 77, T. fumosa, pupa, ventral view (scale bar = 0.5mm); 78, Trichoclinocera sp., larva, terminal segment, dorsal view (scale bar = 0.5mm); 79, Trichoclinocera sp., larval mandible, adoral view (scale bar = 20 μ m); 80, Trichoclinocera sp., larval mandible, aboral view (scale bar = 20 μ m); 81, Trichoclinocera sp., larval antenna (scale bars = 20 μ m); 82, Trichoclinocera sp., cephalopharyngeal skeleton, dorsal view (scale bar = 50 μ m).

Figs. 83-87. Heads and spermatheca of species of *Trichoclinocera*, lateral view (scale bars = 0.1mm, except Fig. 87 where scale bar = 0.3mm). 83, *T. dolicheretma*; 84, *T. comata*; 85, *T. lapponica*; 86, *T. minor*, 87, *T. pectinifemur*, spermatheca and accessory gland.

Figs. 88-95. Male left fore femur and tibia of species of Trichoclinocera, inner view (scale bars = 0.1mm). 88, T. dolicheretma; 89, T. cascadiensis; 90, T. comata; 91, T. rupestris; 92, T. lapponica; 93, T. agilis; 94, T. ctenistes; 95, T. rupestris, tarsal claws, pulvilli and empodium, ventrolateral view.

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Figs. 96-103. Male left fore femur and tibia of species of Trichoclinocera, inner view (scale bars = 0.1mm). 96, T. dasycoxa; 97, T. hamifera; 98, T. falcata; 99, T. fumosa; 100, T. longipes; 101, T. minor; 102, T. ozarkensis; 103, T. pectinifemur.

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Figs. 104-106. Adult mouthparts and male terminalia of species of *Trichoclinocera* (scale bars = 100 μ m). 104, *T. longipes*, hypopharynx and right maxilla, anterior view (left maxilla and labellum removed); 105, *T. longipes* labrum, hypopharynx, fulcrum (torma + cibarium), lateral view; 106, *T. dolicheretma*, male, lateral view.

Figs. 107-109. Male terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μ m). 107, *T. cascadiensis*; 108, *T. comata*; 109, *T. rupestris*.

Figs. 110-112. Female terminalia of species of *Trichoclinocera* (scale bars = 100 μ m). 110, *T. lapponica*, lateral view; 111, *T. lapponica*, dorsal view; 112, *T. tadjikistana*, lateral view.

Figs. 113-116. Male and female terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μ m). 113, *T. lapponica*, male; 114, *T. stackelbergi*, male; 115, *T. stackelbergi*, inner view of male clasper; 116, *T. stackelbergi*, female.

Figs. 117-119. Male terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μm). 117, *T. agilis*; 118, *T. ctenistes*; 119, *T. dasycoxa*.

Figs. 120-122. Male terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μ m). 120, *T. fumosa*; 121, *T. falcata*; 122, *T. hamifera*.

Figs. 123-125. Male and female terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μ m). 123, *T. longipes*, male; 124, *T. minor*, male; 125, *T. minor*, female.

Figs. 126-128. Male terminalia of species of *Trichoclinocera*, lateral view (scale bars = 100 μ m). 126, *T. ozarkensis*; 127, *T. ozarkensis*, inner view of clasper; 128, *T. pectinifemur*.

Figs. 129-130. Male terminalia of species of *Clinocera*, lateral view (scale bars = 100 μ m). 129, *C. gubernans*; 130, *C. fuscipennis*.

Figs. 131-133. Male terminalia of species of *Clinocera*, lateral view (scale bars = 100 μ m). 131, *C. conjuncta*; 132, *C. sp. #22*, inner view of clasper; 133, *C. sp. #22*.

Figs. 134-135. Male terminalia of species of *Clinocera*, lateral view (scale bars 100 μ m). 134, *C. lineata*; 135, *C. bivittata*.

Figs. 136-138. Male and female terminalia of *Clinocera binotata*, lateral view (scale bars = 100 μ m). 136, male; 137, spermatheca; 138, female.

Figs. 139-140. Male and female terminalia of species of *Wiedemannia hughesi*, lateral view (scale bars = 100 μ m). 139, female; 140, male.

Figs. 141-144. Male terminalia of species of *Wiedemannia*, lateral view (scale bars = 100 μ m). 141, *W. uncinata*, clasper cercus; 142, *W. uncinata*, male; 143, *W. apicalis*, male; 144, *W. apicalis*, clasper cercus.

Figs. 145-148. Male terminalia of *Wiedemannia lepida*, lateral view (scale bars = 100 μ m). 145, male; 146-148, clasper cerci.

Fig. 149. Male terminalia of Wiedemannia vexillum, lateral view (scale bars = 100 μ m).

Figs. 150-152. Male and female terminalia of species of *Wiedemannia*, lateral view (scale bars = 100 μ m). 150, *W. simplex*, male; 151, *W. undulata*, male; 152, *W. simplex*, female and spermatheca.

Figs. 153-155. Male terminalia of *Proagomyia torrentium* (scale bars = 100 μ m). 153, lateral view; 154, tergite and sternite 8, anterior view; 155, anterior view, epandrium + surstyli removed.

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Figs. 156-158. Male and female terminalia of *Proagomyia tridentata* (scale bars = 200 μ m, except Fig. 158 where scale bar = 100 μ m). 156, male, lateral view, tergite 8 and left epandrial lobe removed; 157, female, dorsal view; 158, spermatheca.

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Figs. 159-160. Tergite 8 and male terminalia of *Boreodromia bicolor*, lateral view. 159, terminalia with sperm pump and anterior portion of phallus (scale bars = 200 μ m); 160, terminalia, sperm pump and anterior portion of phallus removed (scale bars = 100 μ m).

Figs. 161-163. Male and female terminalia of species of *Boreodromia*, *Apalocnemis* and an undescribed genus nr. *Apalocnemis*, lateral view (scale bars = 100 μ m, except Fig. 163 where scale bar = 200 μ m). 161, *B. bicolor*, female; 162, *A. oreas*(?), male; 163, nr. *Apalocnemis* sp., male.

Figs. 164-166. Male and female terminalia of *Ephydrepis setiventris*, lateral view (scale bars = 100 μ m, except Fig. 165 where scale bar = 200 μ m). 164, female, segment 7 removed; 165, male; 166, spermatheca.

Figs. 167-169. Male and female terminalia of species of *Sabroskyella* and *Trichopeza*, lateral view (scale bars = 100 μ m). 167, *S. rancheria*, female; 168, *T. albocincta*, male; 169, *S. rancheria*, spermatheca.

Figs. 170-173. Male and female terminalia of species of *Trichopeza* and *Ceratempis* (scale bars = 100 μm, except Fig. 170 where scale bar = 200 μm). 170, *T. longicornis*, female, lateral view; 171, *T. longicornis*, spermatheca; 172, *C. longicornis*, male, lateral view; 173, *C. longicornis*, male, dorsal view of hypandrium.

Figs. 174-176. Male and female terminalia of *Niphogenia curea* (scale bars = 100 μm).
 174, male, lateral view; 175, female, dorsal view; 176, female, lateral view.

Figs. 177-182. Male and female terminalia of species of Dipsomyia (scale bars = $100\mu\text{m}$, except Fig. 178 where scale bar = $50\mu\text{m}$). 177, D. mutabilis, female, lateral view; 178, D. mutabilis, spermatheca; 179, D. stigmosa, spermatheca; 180, D. stigmosa, male epandrium, dorsal view; 181, D. stigmosa, male hypandrium and phallus, lateral view; 182, D. stigmosa, female, lateral view.

Figs. 183-186. Male and female terminalia of *Dryodromia testacea* (scale bars = 100 μm). 183, male hypandrium and phallus, lateral view; 184, male epandrium and cerci, posterior view; 185, male epandrium and cercus, lateral view; 186, female and spermatheca, lateral view.

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Figs. 187-191. Male and female terminalia of species of *Zanclostus* (scale bars = 100 μ m). 187, *Z. dioktes*, male, lateral view; 188, *Zanclostus* n.sp., male, lateral view; 189, *D. dioktes*, male, dorsal view, epandrium and cerci removed; 190, *Z. dioktes*, female, lateral view; 191, *Z. dioktes*, spermatheca.

Figs. 192-193. Known distribution of *Trichoclinocera comata* - species group. 192, *T. cascadensis* sp. nov. (★), *T. rupestris* n.sp. (●); 193, *T. comata* (Melander).

Figs. 194-196. Known distribution of species of *Trichoclinocera*. 194, *T. lapponica* (Ringdahl); 195, *T. ctenistes* (Melander); 196, *T. minor* (Melander) (●), *T. ozarkensis* sp.nov. (★).

Figs. 197-199. Known distribution of species of *Trichoclinocera*. 197, *T. dasycoxa* sp.nov.; 198, *T. dolicheretma* (Melander); 199, *T. pectinifemur* sp.nov.

Figs. 200-201. Known distribution of species of *Trichoclinocera*. 200, *T. falcata* sp. nov. (●), *T. fumosa* (Vaillant) (★); 201, *T. hamifera* (Melander) (●), *T. longipes* (Walker) (★).

Figs. 202-203. Known distribution of species of *Wiedemannia*. 202, *W. apicalis* sp. nov. (★), *W. uncinata* sp. nov. (●); 203, *W. lepida* (Melander).

Fig. 204. Known distribution of W. simplex (Loew) (★) in North America, W. undulata sp. nov. (●) and W. vexillum sp. nov. (■).

Fig. 205. Hypothesized cladistic relationships of the major lineages of the Empidoidea. Numbers refer to characters listed in Table 4 and discussed in "Phylogenetic Interpretations" (Sec. 5.1.1). Shading denotes uncertainty regarding monophyly and "*" indicates homoplasy.

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Fig. 206. Hypothesized cladistic relationships of the genera of Clinocerinae. Numbers refer to characters listed in Table 4 and discussed in "Phylogenetic Interpretations" (Sec. 5.1.2). "*" indicates homoplasy.

Figs. 207-208. Hypothesized cladistic relationships of the species groups of Trichoclinocera and Clinocera. Numbers refer to characters discussed in "Phylogenetic Interpretations" (Sec. 5.1.3 and Sec. 5.1.4 respectively). Shading denotes uncertainty regarding monophyly. 207, Trichoclinocera; 208, Clinocera.

Fig. 209. Hypothesized cladistic relationships of the species groups of Wiedemannia. Numbers refer to characters discussed in "Phylogenetic Interpretations" (Sec. 5.1.5). Shading denotes uncertainty regarding monophyly and "*" indicates homoplasy.

Fig. 210. Cladistic relationships of the major lineages of the Empidoidea as presented by Cumming and Sinclair (1990). Shading denotes uncertainty regarding monophyly. Numbers refer to characters presented in their paper.

Eremoneura

Empidoidea

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8. APPENDIX I

LIST OF ABBREVIATIONS USED IN FIGURES

ab apod	abductor apodeme
acc gl	accessory gland
ad apod	adductor apodeme
ant	antenna
antprn	antepnotum setae
apod	apodeme
a s	anterior setae
av s	anteroventral setae
b md scl	basal mandibular sclerite
bm	cell basal medial
br	cell basal radial
c hk	caudal hook
cib	cibarium
clw	claw
cmp s	campaniform sensillum
con scl	connecting sclerite
cerc	cercus
cerc pl	cercal plate
cl cerc	clasping cercus
clyp	clypeus
CuA ₁	anterior branch of cubitus
cup	cell posterior cubital
dm	cell discal medial
d md hk	distal mandibular hook
ej apod	ejaculatory apodeme
emp	empodium
epand	epandrium
epand lb	epandrial lobe
epicon	epicondyle
frclyp sut	frontoclypeal suture
gen fk	genital fork
goncx	gonocoxite
goncx apod	gonocoxal apodeme
gonst	gonostylus
hypcon	hypocondyle
hypd	hypandrium
hyphar	hypopharynx
hypret	hypoproct
int aed proc	internal aedeagal process
lab scl	labial sclerite

lac	lacinia
lat ej proc	lateral ejaculatory process
lbl	labellum
lbr	labrum
lhr apodeme	labral apodeme
M ₂	posterior branch of media
mtceph rd	metacephalic rod
mx plp	maxillary palpus
npl	notopleural setae
ph	phallus
plp	palpus
pm sh	parameral sheath
pprn	postpronotal seta
preap s	preapical setae
presut spal	presutural supraalar setae
pulv	pulvilli
pv s	posteroventral setae
R ₁	anterior branch of radius
R ₂ , R ₃ , R ₄ , R ₅	posterior branches of radius
resp org	respiratory organ
sal p	salivary pump
Sc	subcosta
sp ch	sperm chamber
spnth	spermatheca
sbepand scl	subepandrial sclerite
sp	spiracle
st	sternite
stp	stipes
sur	surstylus
syntgst	syntergosternite
tg	tergite
tnt phgm	tentorial phragma
v md scl	ventral mandibular sclerite

9. APPENDIX II

PHYLOGENETIC RELATIONSHIPS OF THE EMPIDOIDEA AND CLINOCERINAE AS SUGGESTED BY USING THE COMPUTER PARSIMONY PROGRAM PAUP

The cladistic analysis was executed with PAUP (Phylogenetic Analysis Using Parsimony) (Swafford 1991), using a Heuristic search, stepwise addition (closest), and holding 5 trees at each step. The character matrix was generated on MacClade (Maddison and Maddison 1992). The following statistics were recorded: tree length, Consistency Index (CI), CI excluding uninformative characters, Retention Index (RI) and Rescaled Consistency Index (RC). The Consistency Index is a measure of the amount of homoplasy. A high CI indicates that the data fits the tree well and that there is little homoplasy (Wiley *et al.* 1991). The Retention Index measures the fraction of apparent synapomorphy to actual synapomorphy and Rescaled Consistency Index excludes characters that do not contribute to the fit of the tree (ie. autapomorphies and totally homoplastic characters), which prevents inflation of the CI (Wiley *et al.* 1991).

Classification of the Empidoidea

The character matrix (Table 4) consisted of 18 taxa and 55 binary characters. See Sec. 5.1.1 for discussion of character states. Polarization of character states was accomplished through outgroup analysis. The Asiloidea (*sensu* Woodley 1989) and Cyclorrhapha were chosen as the outgroup.

This analysis produced 10 equal-length trees, with a tree length of 63, CI =

0.825, CI (excluding uninformative characters) = 0.686, RI = 0.867, and RC = 0.716.

Using strict consensus, a tree with a large basal polychotomy was produced. The placement of Oreogetoninae, Empidinae, Hemerodromiinae, Clinocerinae, Atelestinae + Ocydromiinae + Tachydromiinae + Hybotinae, and Trichopezinae + Brachystomatinae + Ceratomerinae + Microphorinae + Dolichopodidae was unresolved.

Acanthophorites may also have developed independently in the Empidoidea (character 10) as opposed to being homologous to acanthophorites of Asiloidea. The effect of this interpretation on the classification of the Empidoidea is the creation of a large basal polychotomy identical to the above tree derived using strict consensus. Acanthophorites could have evolved independently in the Trichopezinae + Brachystomatinae + Ceratomerinae and Microphorinae + Dolichopodidae or may be a synapomorphy of both groups.

Classification of the Clinocerinae

The character matrix (Table 5) consisted of 15 taxa and 47 binary characters. See Sec. 5.1.2 for discussion of character states. Polarization of character states was accomplished through outgroup analysis. The remaining major lineages of the Empidoidea were chosen as the outgroup.

This analysis produced 2 equal-length trees, with a tree length of 56, CI = 0.804, CI (excluding uninformative characters) = 0.703, RI = 0.776, and RC = 0.623.

The two trees varied at two nodes: Proagomyia or Asymphyloptera alternated as

the sister group to the remaining Clinocerinae; and the Roederoides + Hypenella + Clinocerella and Phaeobalia + Bergenstammia + Wiedemannia clades were either sister groups and placed as an unresolved polychotomy with Kowarzia and Dolichocephala or all four taxa placed as part of an unresolved polychotomy, as illustrated in the hand-generated tree (Fig. 206). Character 47 from Sec. 5.1.1, (tubular spermatheca), was included in the character matrix, because the configuration of the spermatheca is a synapomorphy of the Clinocerinae and Asymphyloptera, exclusive of Proagomyia. If this character state is not included, Proagomyia is the sister group to the remaining Clinocerinae, exclusive of Asymphyloptera in all four trees.

Using strict consensus, a tree identical to the hand-generated cladogram (Fig. 206) is produced. The consensus tree is identical to one of the two equal-length trees.

10. APPENDIX III
THE PARASITIC ASSOCIATIONS OF LARVAL WATER MITES
(ACARI: PARASITENGONA: HYDRACHNIDA)
WITH IMAGINAL AQUATIC EMPIDIDAE (DIPTERA)

During the collection of material for a revision of the Clinocerinae (Diptera: Empididae), red water mites were observed on adult clinocerines and other flying insects associated with creeks, streams, springs and seepages. Mites, along with their hosts, are listed in Tables 1 and 2. Often 2 or 3 mites were observed per host. All mites were identified by Dr. Ian M. Smith (CNC). From the data listed in Tables 1 and 2, species of the water mite genus, Hydrovolzia were observed parasitizing clinocerine empidids almost exclusively and appear to be attached primarily to the legs of their hosts. The only non-clinocerine host record for Hydrovolzia is an apparently aberrant record on the ichneumonid Ceratophygadeuon, a parasitoid of stratiomyids confined to seepage habitats (Sinclair 1989).

The genus Hydrovolzia is widespread in the Holarctic and Oriental regions (Cook 1974). There are 5 described Nearctic species and a number of undescribed species (Smith 1991). The only described larval stage is that of H. gerhardi Mitchell, which parasitizes mesoveliid bugs (Mitchell 1954). This species was collected in warm (18-24°C) seepage habitats from Illinois. The only other published host association was a passing mention of H. placophora (Monti), found attached to the legs of Empididae (Efford 1966).

The numerous records of Hydrovolzia parasitizing almost exclusively empidids of the subfamily Clinocerinae (c.f. Tables 1 and 2) are the first confirmed records of this mite genus parasitizing Empididae, which may represent the primary host of Hydrovolzia. Although the larvae have not been reared, it is believed that they represent two or three species based on distribution records (Smith pers. comm.). Hydrovolzia marshallae Cook is known from northwestern U.S., B.C. and Alberta, H. montana Habeeb from southern Oregon and California and H. mitchelli Habeeb from Ontario to Nova Scotia (Smith 1991, Smith unpubl. data).

Hydrovolzia is believed to inhabit cold (0-9°C), stenothermous springs, seepages and small streams (Smith and Oliver 1986, Smith 1991). Larval mites were often collected on Trichoclinocera, a group that normally inhabits streams with elevated summer water temperatures (Table 1). Consequently, Hydrovolzia may have a much greater temperature tolerance than has been stated in the literature. For example, specimens from Anna Ruby Falls (Code 90.7) and Elkmont (Code 90.2) are both from large cool creeks (Table 1).

Upon hatching, larval mites crawl to the surface and leave the water, seeking hosts that frequent the water's surface or that are on vegetation (Smith and Oliver 1986). Water mites are usually opportunistic generalists and only a few genera are limited primarily to a specific host. It would appear that most species of Hydrovolzia, except H. gerhardi, prefer clinocerines. The parasitic larval stage is the primary mode of dispersal for water mites (Smith and Oliver 1986), but the impact of parasitism on their hosts is unknown.

Adult Clinocerinae are also heavily parasitized by several genera of Hydryphantidae. This mite group appears to be very opportunistic and is also known to parasitize Chironomidae, Tipulidae, Simuliidae, etc. (Smith and Oliver 1986). The hydryphantid parasites of clinocerines require further identification.

Table 1. Parasitic associations of larval water mites (Acari: Parasitengona: Hydrachnida) with imaginal Clinocerinae.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
34.1.1	WA: Mt. Rainier N.P., Mt. Burroughs, 21.VIII.1934	<u>C. prasinata</u>	<u>Hydrovolzia</u>	Tibiae 1,2,3
90.7.11	GA: White Co., Smith Ck., Anna Ruby Falls, 21.VI.90	<u>Clinocera</u> sp.#14	Hydryphantidae	genitalia
89.1.1	OR: Benton Co., Mary's Peak, 14.VII.1989	<u>C. trunca</u>	<u>Hydrovolzia</u>	hind tibia
89.2.1	OR: Lincoln Co., Cape Perpetua, 14.VII.1989	<u>C. trunca</u>	Hydryphantidae	7 specimens: legs, thorax, abd
89.10.1	OR: Marion Co., Silver Falls S.P., 12.VII.1989	<u>C. trunca</u>	Hydryphantidae	tergite 6
89.17.1	OR: Curry Co., 17.6 kmE Elk River Rd. 17.VII.89	<u>C. trunca</u>	<u>Hydrovolzia</u>	fore tibia, mid femur, hind femur
89.3.1	OR: Mt. Hood N.P., 12kmE Gov't Camp, 11.VII.1989	<u>Clinocera</u> sp.#17	Hydryphantidae	pleurites 7-9 sternites 7-9
89.4.1	WA: Mt. Rainier N.P., seep nr. Christine Falls, 8.VII.1989	<u>Clinocera</u> sp.#12A	<u>Hydrovolzia</u>	mid tibia hind tibia, tarsi
89.5.1	"	<u>C. brevitibia</u>	<u>Hydrovolzia</u> and <u>Hydryphantidae</u>	
89.20.1	BC: 30kmN Penticton, Hardy Falls S.P. 3.VII.89	<u>C. brevitibia</u>	Hydryphantidae	fore coxa, pleurites 1-3

Table 1. Continued.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
89.6.1	"	<u>C. lecta</u>	<u>Hydrovolzia</u>	tarsi of all legs, mouthparts
89.6.2	"	"	<u>Hydrovolzia</u>	wing, hind tarsi
89.7.1	BC: 4kmW Glacier N.P. 1.VII.1989	<u>C. olivacea</u>	<u>Hydryphantidae</u>	thoracic pleurae
89.8.1	BC: 30kmW Penticton, Hardy Falls Pk., 3.VII.89	<u>C. olivacea</u>	<u>Hydryphantidae</u>	between thorax - abdomen
89.25.1	WA: Mt. Rainier N.P., Paradise River, 8.VII.89	<u>C. olivacea</u>	<u>Hydrovolzia</u>	fore tibia
89.26.1	"	"	"	mid tibia
89.12.1	OR: Starvation Ck. S.P. 10.VII.1989	<u>Clinocera</u> sp.#12A	<u>Hydryphantidae</u>	tergite 1
89.13.1	OR: Benton Co., Mary's Peak, 14.VII.1989	<u>Clinocera</u> sp.#22	<u>Hydryphantidae</u>	hind coxa
89.14.1	WA: Mt. Rainier N.P., seep nr. Christine Falls, 8.VII.1989	<u>Clinocera</u> sp.#23	<u>Hydrovolzia</u> <u>Hydryphantidae</u>	hind tarsi, base of wing. fore coxa
89.24.1	WA: Mt. Rainier N.P., Paradise River, 8.VII.89	<u>Clinocera</u> sp.#3	<u>Hydrovolzia</u>	hind tibia

Table 1. Continued.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
41.1.1	TN: Smoky Mtns., Chimneys, 29.VI.1941	<u>T. fumosa</u>	<u>Hydrovolzia</u>	Tibia 3
90.1.1	NC: GSMNP, Cataloochee River, 12.VI.1990	<u>T. fumosa</u>	? <u>Piersigia</u>	thoracic pleurae
90.1.2	"	"	<u>Hydrovolzia</u>	mid tibia
90.2.2	TN: Sevier Co., GSMNP, Elkmont, 14.VI.1990	<u>T. fumosa</u>	<u>Hydrovolzia</u>	fore femur
90.2.3	"	"	<u>Hydryphantidae</u>	Tergite 1
90.7.1	GA: White Co., Smith Ck., Anna Ruby Falls, 21.VI.90	<u>T. fumosa</u>	<u>Hydrovolzia</u>	fore femur
90.7.3	"	"	"	fore femur
90.7.4	"	"	"	mid femur
90.7.5	"	"	"	hind femur
90.7.6	"	"	"	"
90.7.7	"	"	"	"
90.7.8	"	"	"	"
90.7.9	"	"	"	mid femur
90.7.11	"	"	"	fore femur
90.10.1	TN: Sevier Co., GSMNP, Elkmont, 14.VI.1990	<u>T. fumosa</u>	<u>Hydrovolzia</u>	hind femur
90.10.2	"	"	"	fore femur
90.8.1	SC: Sumter N.F., Brasstown Falls, 22.VI.90	<u>T. fumosa</u>	<u>Hydryphantidae</u>	tergite 4,5
90.6.1	GA: Lumpkin Co., Desoto Falls, 20.VI.1990	<u>T. fumosa</u>	<u>Hydrovolzia</u>	mid tibia

Table 1. Continued.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
90.2.4	TN: Sevier Co., GSMNP, Elkmont, 14.VI.1990	<u>T. hamifera</u>	<u>Hydrovolzia</u>	fore femur
91.3.1	ONT: Nipissing Co., Algonquin P.P., 19.VII.91	<u>T. hamifera</u>	<u>Parathrombium</u>	fore tarsus
89.11.1	OR: Starvation Ck. S.P. 10.VII.1989	<u>T. cascadenis</u>	Hydryphantidae	between thorax and abdomen
89.15.1	WA: Jefferson Co., Olympic N.P., 6.VII.1989	<u>T. comata</u>	Hydryphantidae	abd. pleurite 2
91.4.1	NM: Grant Co., Gila N.F., 29.V.1991	<u>T. dolicheretma</u>	Hydryphantidae	mid coxa
75.	NWT: Victoria Is., 23- 28.VII.1975	<u>T. lapponica</u>	?	
67.1.1	UT: Cache Co., Blacksmith Fork Cany. 26.VI.1967	<u>W. uncinata</u>	Hydryphantidae	sternite 6
67.1.2	"	<u>W. uncinata</u>	Hydryphantidae	tergite 1,
67.1.3	"	<u>W. uncinata</u>	Hydryphantidae	between pl. 5-6
89.19.1	OR: Starvation Ck. S.P., 10.VII.1989	<u>W. uncinata</u>	Hydryphantidae	tergites 1-3
75.1.1	CA: Monterey Co., E. Rogers, 9.V.1975	<u>W. lepida</u>	Hydryphantidae	between T5-T6
78.1.1	WA: Grays Harbour Co. Olympic N.F. 20.VII.1978	<u>W. lepida</u>	Hydryphantidae	hind coxa and trochanter
78.1.2	" 21.VII.1978	<u>W. lepida</u>	Hydryphantidae	between T6-T7
89.11.1	OR: Starvation Ck. S.P. 10.VII.1989	<u>W. uncinata</u>	Hydryphantidae	hind coxa tergites 1-3

Table 1. Continued.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
89.28.1	BC: Glacier N.P., 3.3kmW Rogers Pass, 1.VII.1989	<u>Oreothalia</u> (<u>spinitarsis</u> ?)	Hydryphantidae	Stenites 4-6 pleurites 1-3
89.28.2	"	"	Hydryphantidae	base of wing
90.2.1	TN: Sevier Co., GSMNP, Elkmont, 14.VI.1990	<u>Proclinopyga</u> sp.#4	Hydryphantidae	between thorax and abd.
89.9.1	OR: Lane Co., 10miS Yachats, 15.VII.1989	<u>Proclinopyga</u> sp.	Hydryphantidae	abd. pleura 4
89.22.1	WA: Jefferson Co., Olympic N.P., 6.VII.1989	<u>Proclinopyga</u> sp.	Hydryphantidae	base of wing
90.7.2	GA: White Co., Smith Ck., Anna Ruby Falls, 21.VI.90	<u>Roederiodes</u> <u>recurvatus</u>	<u>Hydrovolzia</u>	fore+mid femur hind femur
90.6.2	GA: Lumpkin Co., Desoto Falls, 20.VI.1990	<u>R. recurvatus</u> (?)	<u>Hydrovolzia</u>	fore+mid tibiae
91.2.1	AR: Stone Co., Ozark N.F., 21.V.1991	<u>R. recurvatus</u>	<u>Hydrovolzia</u>	mid femur

Table 2. Parasitic associations of larval water mites (Acari: Parasitengona: Hydrachnida) with imaginal aquatic insects.

CODE	LOCALITY	HOST	MITES	ATTACHMENT SITE
89.16.1	OR: Malheur Co., 73kmW Vale, roadcut seep, 19.VII.1989	<u>Hydrophorus</u> (?) or <u>Scellus</u> (?) (Dolichopodidae)	Hydryphantidae	base of wing
89.27.1	BC: 4kmW Glacier N.P. stream, 1.VII.1989	<u>Liancalus</u> (Dolichopodidae)	Hydryphantidae	between thorax and abdomen
90.3.1	NC: Swain Co., GSMNP, Cligmans Dome Rd, 15.VI.1990	<u>Dolichopeza</u> (<u>Oropeza</u>) <u>venosa</u> (Johnson) (Tipulidae)	<u>Calyptostoma</u>	detached
90.4.1	KY: Whitley Co., Cumberland S.P., seep. 18.VI.1990	<u>L. (Geranomysia)</u> <u>diversa</u> (O.S.) (Tipulidae)	Hydryphantidae	between tergites 1+2
90.4.2	KY: Whitley Co., Cumberland S.P., seep. 18.VI.1990	<u>Limonia simulans</u> (Walker) (Tipulidae)	Hydryphantidae and <u>Calyptostoma</u> (detached)	mouthparts; fore coxae; between thorax/abd.; tergites 1, 7+8; pleurites 6, 7+8
90.5.2	"	<u>L. (Geranomysia)</u> <u>diversa</u> (Tipulidae)	<u>Tyrellia</u>	tergite 7
90.5.3	"	<u>L. (Geranomysia)</u> sp. (Tipulidae)	<u>Tyrellia</u>	tergite 5, 7 and sternite 7
90.5.4	"	<u>L. (Dicranomyia)</u> <u>humidicola</u> (O.S.) (Tipulidae)	<u>Calyptostoma</u>	unknown (loose)

Table 2. Continued.

CODE	LOCALITY	HOST	MITE	ATTACHMENT SITE
90.9.1	KY: Whitley Co., Cumberland S.P., roadcut seep., 17-18.VI.1990	<u>L. (Dicranomyia)</u> sp. (Tipulidae)	<u>Calypstostoma</u> and <u>Ascidae</u>	unknown; pleurites 4+5
90.9.2	KY: Whitley Co., Cumberland S.P., roadcut seep., 17-18.VI.1990	<u>L. simulans</u> (Tipulidae)	Hydryphantidae	between tergites 3+4; between tergites 7+8
89.29.1	BC: 13km Revelstoke-Hwy 23, stream, 2.VII.1989	<u>Thaumalea</u> sp. (Thaumaleidae)	?	?
90.5.1	TN: Van Buren Co., Fall Ck. Falls S.P., seepage 19.VI.1990	<u>Thaumalea</u> <u>americana</u> (Thaumaleidae)	Hydryphantidae	genitalia
89.18.1	OR: Curry Co. 17.6kmE Pt. Orford, 17.VII.1989	Dixidae	<u>Johnstonianid</u> and <u>Utaxatag</u>	tergites 1-3; unknown
89.23.1	OR: Mt. Hood N.F., Trillium Lake Cpgd, Still Creek, 11.VII.1989	<u>Yoraperla</u> (?) (Peltoperlidae) (Plecoptera)	Hydryphantidae	thorax -lateral
91.1.1	AR: Stone Co., Ozark N.F., roadcut seep, 21.V.1991	<u>Ceratophygadeuon</u> <u>pechumani</u> Townes (Ichneumonidae)	<u>Hydrovolzia</u>	mid femur

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