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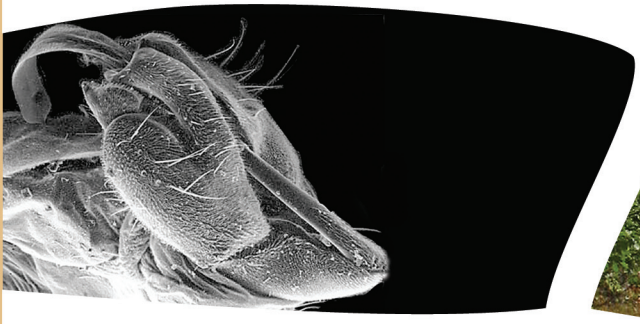
The Systematics of New World *Clinocera* Meigen (Diptera: Empididae: Clinocerinae)



BRADLEY J. SINCLAIR

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The Systematics of New World *Clinocera* Meigen (Diptera: Empididae: Clinocerinae)

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Abstract

The New World species of *Clinocera* Meigen (Diptera: Empididae: Clinocerinae) are revised and include 67 species, of which 44 and 23 occur in the Nearctic Region and Neotropical Region, respectively. The following 49 new species of *Clinocera* are described from the New World: *C. amarilla* **sp. nov.**, *C. appalachia* **sp. nov.**, *C. arizonica* **sp. nov.**, *C. arnaudi* **sp. nov.**, *C. attenuata* **sp. nov.**, *C. borkenti* **sp. nov.**, *C. brevicauda* **sp. nov.**, *C. brunnea* **sp. nov.**, *C. bulbosa* **sp. nov.**, *C. caerulea* **sp. nov.**, *C. chilensis* **sp. nov.**, *C. collini* **sp. nov.**, *C. colombiana* **sp. nov.**, *C. coloradensis* **sp. nov.**, *C. cordillerana* **sp. nov.**, *C. cummingi* **sp. nov.**, *C. daniellae* **sp. nov.**, *C. disjuncta* **sp. nov.**, *C. femorata* **sp. nov.**, *C. guttipennis* **sp. nov.**, *C. insularis* **sp. nov.**, *C. isabellina* **sp. nov.**, *C. lapazensis* **sp. nov.**, *C. longicauda* **sp. nov.**, *C. macdonaldi* **sp. nov.**, *C. madera* **sp. nov.**, *C. marshalli* **sp. nov.**, *C. melanderi* **sp. nov.**, *C. meridana* **sp. nov.**, *C. mexicana* **sp. nov.**, *C. miradorana* **sp. nov.**, *C. naomina* **sp. nov.**, *C. nigriscutata* **sp. nov.**, *C. notialis* **sp. nov.**, *C. obunca* **sp. nov.**, *C. pacifica* **sp. nov.**, *C. parana* **sp. nov.**, *C. penai* **sp. nov.**, *C. rainiericola* **sp. nov.**, *C. robinsoni* **sp. nov.**, *C. sabroskyi* **sp. nov.**, *C. schlinkerti* **sp. nov.**, *C. setitibia* **sp. nov.**, *C. stigma* **sp. nov.**, *C. sublineata* **sp. nov.**, *C. substagnalis* **sp. nov.**, *C. subtrunca* **sp. nov.**, *C. wallowa* **sp. nov.**, and *C. woodi* **sp. nov.**

The following new synonyms are proposed: *C. taos* Melander and *C. undulata* Melander = *C. conjuncta* Loew, *C. brevitibia* Melander = *C. fuscipennis* Loew, and *C. genualis* Coquillett = *C. stagnalis* (Haliday). *Aclinocera* Yang & Yang **syn. nov.** is newly synonymized with *Clinocera* and its type species is also transferred as *C. sinica* (Yang & Yang) **comb. nov.** Lectotypes are designated for *C. brevitibia, C. lecta, C. lineata*, and *C. oriunda*. Identification keys to genera of Clinocerinae of North and South America are included and keys are provided to species-groups and all known New World species of *Clinocera*. The distribution of each species is illustrated and a species-group phylogeny given. Distributions are used to support the hypothesis that southward dispersals into South America through Mesoamerica occurred once during the Late Cretaceous and again during the Pliocene.

Résumé

Les espèces du genre *Clinocera* Meigen (Diptera: Empididae: Clinocerinae) du Nouveau Monde sont révisées. *Clinocera* renferme maintenant 67 espèces, dont 44 et 23 se trouvent respectivement dans les régions néarctique et néotropicale. Parmi les espèces répertoriées, les 49 espèces suivantes sont nouvelles et issues du Nouveau Monde : *C. amarilla* **sp. nov.**, *C. appalachia* **sp. nov.**, *C. arizonica* **sp. nov.**, *C. arnaudi* **sp. nov.**, *C. attenuata* **sp. nov.**, *C. borkenti* **sp. nov.**, *C. brevicauda* **sp. nov.**, *C. brunnea* **sp. nov.**, *C. bulbosa* **sp. nov.**, *C. caerulea* **sp. nov.**, *C. chilensis* **sp. nov.**, *C. collini* **sp. nov.**, *C. colombiana* **sp. nov.**, *C. coloradensis* **sp. nov.**, *C. cordillerana* **sp. nov.**, *C. cummingi* **sp. nov.**, *C. daniellae* **sp. nov.**, *C. disjuncta* **sp. nov.**, *C. femorata* **sp. nov.**, *C. guttipennis* **sp. nov.**, *C. insularis* **sp. nov.**, *C. isabellina* **sp. nov.**, *C. lapazensis* **sp. nov.**, *C. longicauda* **sp. nov.**, *C. macdonaldi* **sp. nov.**, *C. madera* **sp. nov.**, *C. marshalli* **sp. nov.**, *C. melanderi* **sp. nov.**, *C. meridana* **sp. nov.**, *C. mexicana* **sp. nov.**, *C. miradorana* **sp. nov.**, *C. naomina* **sp. nov.**, *C. nigriscutata* **sp. nov.**, *C. notialis* **sp. nov.**, *C. obunca* **sp. nov.**, *C. pacifica* **sp. nov.**, *C. parana* **sp. nov.**, *C. penai* **sp. nov.**, *C. rainiericola* **sp. nov.**, *C. robinsoni* **sp. nov.**, *C. sabroskyi* **sp. nov.**, *C. schlinkerti* **sp. nov.**, *C. setitibia* **sp. nov.**, *C. stigma* **sp. nov.**, *C. sublineata* **sp. nov.**, *C. substagnalis* **sp. nov.**, *C. subtrunca* **sp. nov.**, *C. wallowa* **sp. nov.** et *C. woodi* **sp. nov.**

Voici une liste des nouveaux synonymes proposés : *C. taos* Melander et *C. undulata* Melander = *C. conjuncta* Loew, *C. brevitibia* Melander = *C. fuscipennis* Loew et *C. genualis* Coquillett = *C. stagnalis* (Haliday). *Aclinocera* Yang & Yang **syn. nov.** est nouvellement mise en synonymie avec *Clinocera* et son espèce type devient *C. sinica* (Yang & Yang) **comb. nov.** Des lectotypes sont offerts pour *C. brevitibia, C. lecta, C. lineata* et *C. oriunda*. L'article renferme des clés d'identification pour les genres de la sous-famille Clinocerinae de l'Amérique du Nord et de l'Amérique du Sud, de même que des clés pour divers groupes d'espèces et toutes les espèces connues du genre *Clinocera* du Nouveau Monde. On y présente également des illustrations de la répartition de chaque espèce et une description phylogénique du groupe. Les répartitions sont utilisées pour corroborer l'hypothèse voulant que la dispersion vers le sud pour atteindre l'Amérique du Sud par la Méso-Amérique se soit produite à deux reprises — une fois au Crétacé tardif et l'autre au cours du Pliocène.

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My family, especially my wife, helped immeasurably and were of great support throughout the various stages of this project.

Introduction

General biology of Clinocerinae

The aquatic dance fly subfamily Clinocerinae (Empididae) is one of the major groups of predacious Diptera in running water or lotic habitats. Adults are frequently encountered sitting on emergent rocks in springs, seepages, streams, and rivers (Figs. 1*a*, *d*). The subfamily is most common in the Nearctic and Palearctic regions and becomes significantly less common at lower latitudes and south of the equator. In Australia and New Zealand the dominance of this microhabitat is taken over by the subfamily Ceratomerinae (Sinclair 2003*b*).

Among adult flies, those of the genus *Clinocera* Meigen are among the most

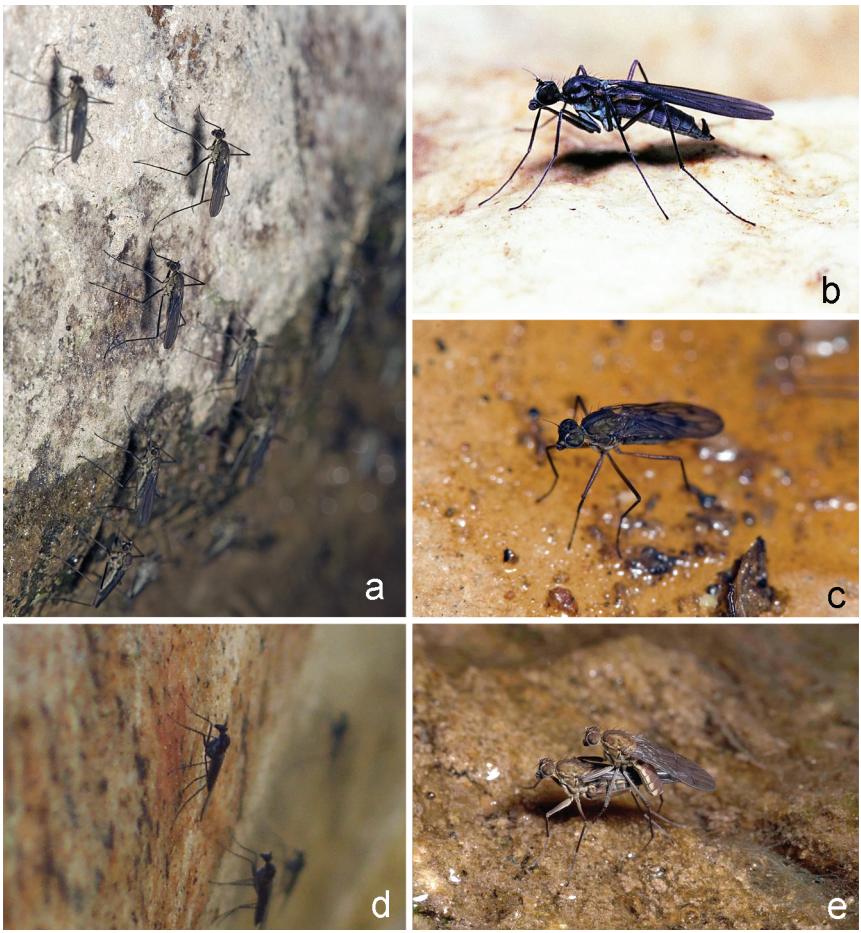

Fig. 1. Photographs of living individuals of species of Clinocerinae: *a*, *Trichoclinocera* sp. gathered on a rock in a creek; *b*, *Clinocera fuscipennis*; *c*, *Clinocera* sp. from Chile; *d*, *C. wallowa* gathered on rocks in a river; *e*, *C. binotata*, mating pair. (Photographs *a–c* and *e* by S.A. Marshall, reproduced with permission.)

commonly encountered in seepage habitats and are also encountered resting on rocks and moss in headwater streams. In the southern Appalachians and the western Cordillera, *Oreothalia* Melander is also found in seepages and small first-order streams. *Clinocera* is normally rare in large, open-canopy streams, creeks, and rivers, where *Trichoclinocera* Collin and *Wiedemannia* Zetterstedt predominate. The genus *Dolichocephala* Macquart occurs in wet seepage soil and moss and wet depressions near streams and very rarely in running-water habitats.

Overall, species of Clinocerinae are confined to relatively clean, cool running water with reduced silt content. Consequently the potential for the use of clinocerines as indicator species for water-quality studies is high, but this has not been well investigated. Only a few widespread clinocerine species (e.g., *C. fuscipennis* Loew, *C. stagnalis* (Haliday), *C. nigra* Meigen) inhabit organically enriched streams or streams where the percentage of silt is significant.

In North America the Clinocerinae range from beyond treeline in northern Canada to the southern humid canyons of New Mexico and Arizona. Few records are known from the central region (prairies) of North America, but this region has not been surveyed for clinocerines and present records are for widespread species, e.g., *C. lineata* Loew. This was the case for the isolated population of *C. lineata* from the Cypress Hills in southeastern Alberta, an isolated forested region surrounded by arid prairie.

Both larval and adult clinocerines are predacious, apparently feeding primarily on other flies. Both flying insects and larval prey have been reported (Table 1). Some are known to also feed on insect carrion trapped in algal mats on water surfaces. Larvae and adults occupy the same habitats.

During the collection of material for a revision of the Clinocerinae, red water mites were observed attached to adult clinocerines and other flying insects associated with creeks, streams, springs, and seepages. Twelve species of *Clinocera* were found to be hosts of larval water mites in this survey. The water mite genus *Hydrovolzia* Thor was observed parasitizing clinocerine empidids almost exclusively, and often 2 or 3 mites were found attached to their hosts, primarily to the legs.

Hydrovolzia is widespread in the Holarctic and Oriental regions and there are five described Nearctic species and a number of undescribed species (Smith 1991). These numerous records of *Hydrovolzia* parasitizing almost exclusively empidids of the subfamily Clinocerinae are the first confirmed records of this mite genus parasitizing Empididae, which may be the primary host of *Hydrovolzia*. 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* 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 clinocerines were also heavily parasitized by several genera of Hydryphantidae. This mite group appears to be very opportunistic and is also

Table 1. Partial summary of feeding records of adult and larval Clinocerinae.

Predator	Prey	Source
Clinocera fuscipennis Loew (A)	Chironomidae (A)	This study
C. olivacea Melander (A)	Chironomidae (L)	This study
C. stagnalis (Haliday) (A)	Flies trapped on surface	Lindroth 1931, cited in Downes and Smith 1969
Clinocera sp. (A)	Thaumaleidae (L)	Sinclair and Marshall 1987
Clinocera sp. (A)	Chironomidae (L and A)	Sinclair 1995
Clinocera sp. (A)	Simuliidae (L)	Peterson 1960
Roederiodes junctus Coquillett (A)	Simuliidae (dead and emerging P and A)	Peterson and Davies 1960
R. wirthi Chillcott (L and A)	Simuliidae (L; 1st instars)	Sinclair and Harkrider 2004
R. wirthi (L)	*Rheotanytarsus* sp. (Chironomidae) (L)	Sinclair and Harkrider 2004
Trichoclinocera hamifera (Melander) (A)	Chironomidae (A)	B.J. Sinclair, unpubl. data
T. ozarkensis Sinclair (A)	Chironomidae and Ceratopogonidae (A)	B.J. Sinclair, unpubl. data
T. rupestris Sinclair (A)	Chironomidae (A)	B.J. Sinclair, unpubl. data
Wiedemannia bistigma (Curtis) and *W. lota* Walker (A)	Dead insects (flies, caddisflies) on water film	Laurence 1953
Wiedemannia ouedorum Vaillant (L and A)	Simuliidae (L and P)	Vaillant 1952*a*
Wiedemannia sp. (A)	Simuliidae (L)	Wirth and Stone 1956
Wiedemannia (*s. s.*) sp. (A)	Simuliidae (L)	D. Werner, pers. comm., 2006

Note: A, adults; P, pupae; L, larvae.

known to parasitize Chironomidae, Tipulidae, Simuliidae, and other aquatic orders of insects (Smith and Oliver 1986).

Introduction to Clinocera

The genus *Clinocera* is generally confined to cool headwater streams, springs, and seepages and is occasionally found in larger, sunny, exposed streams and rivers (Figs. 2, 3). Adults are very numerous in such habitats, standing on the seepage or madicolous (= hygropetric) zone of springs and remaining very close to rock faces. The genus is most diverse in the Cordillera of western North America (see Biogeography section). There are some 60 species worldwide in addition to 49 new species described in this study. Species diversity of *Clinocera* is much greater in North America (44 species) than in Europe (13 species). In addition, two species-groups are restricted to North America.

Fig. 2. Photographs of *Clinocera* habitats: *a*, falls, Columbia River Gorge, Oregon; *b*, mountain stream crossing the Illecillewaet trail, Glacier National Park, British Columbia; *c*, Evan Thomas Creek, Kananaskis Country, Alberta; *d*, above Paradise River in early July, Mount Rainier National Park, Oregon; *e*, Halfway River, British Columbia; *f*, creek at Anna Ruby Falls, Georgia.

Adults range in wing length from about 3 mm to slightly more than 5 mm. They are often dark to yellowish brown with distinct patterns of bluish pruinescence (Figs. 1*b, c*). The pruinescence, together with narrow wings, long legs, pubescent eyes, and pulvilliform empodia, are important adaptations to living in the spray zone and on wet rocks associated with streams and waterfalls. The adults sit on emergent rocks in streams and seepages, where they have been observed feeding on larvae of seepage midges (Thaumaleidae) and larval and adult chironomid midges (Sinclair and Marshall 1987; Sinclair 1995). Vaillant (1956) listed seven species of *Clinocera* that were predacious (both adult and larval stages) on various larvae living in madicolous (or hygropetric) habitats. Adults of *C. stagnalis* have been observed feeding on flies trapped in the surface film (Lindroth 1931, cited in Downes and Smith 1969). Adults of *Clinocera* have also been observed feeding on black fly larvae and adults (see Table 1; Peterson 1960; Werner and Pont 2003).

Mating also occurs directly on the wet rock faces and is similar to that described for *Trichoclinocera* (Sinclair 1994) and *Wiedemannia* (Rogers 1981). No premating behaviour was noted; the male simply jumps on top of the female. In the "false male above position" (Huber et al. 2007), the male's abdomen and

Fig. 3. Photographs of *Clinocera* habitats: *a*, roadside spring and seepage, Inglis Falls Conservation Area, Ontario (photograph by S.A. Marshall, reproduced with permission); *b*, Mae Cotira River, Brazil, type locality for *C. parana* and *C. cummingi* (photograph by J.E. O'Hara, reproduced with permission); *c*, roadcut seepage, Jolly Cut, Ontario.

genitalia pass over the left side of the female's abdomen (Fig. 1*e*). The forelegs of male *C. binotata* close about the base of the female's wing, clamping down over the costal margin. The detailed position and coupling of the genitalia in *Clinocera* have not been observed, but are presumably somewhat similar to the description for *Empis borealis* L. (Ulrich 1972).

A number of surveys of the empidid fauna of streams are available and *Clinocera* is normally reported (Caspers and Wagner 1982; Harper 1980; Joost 1982; Landry and Harper 1985; Wagner 1980, 1982). In a 11-year survey of a stream in Germany, Wagner and Gathmann (1996) discussed phenological data, abundance and distribution patterns, annual variations, and effects of environmental conditions on the dominant species.

The adults are present throughout the spring and summer and often occur in much colder months also. For example, in rocky springs of southern Ontario (Canada), adults may be found throughout the winter months on the underside of emergent rocks (Sinclair and Marshall 1987). In Europe, *C. wesmaeli* also has been observed to overwinter as an adult (Chvála 1983; Niesiołowski 1992). In the present study, many species of the *C. fuscipennis* group were observed most frequently during autumn and winter.

Larvae and pupae of *Clinocera* occur in the same habitat, often being found in saturated mats of filamentous algae or submerged clumps of moss. Larvae prey on other aquatic larvae, especially chironomids. References and additional information concerning immature stages of *Clinocera* were summarized in Sinclair (1995, p. 692) and Wagner (1997).

Species of *Clinocera* are readily recognized by external colour patterns, but unequivocal determination usually requires examination of the male terminalia. Often the terminalia are exposed and visible above the abdomen, but it is usually best to dissect and clear the genitalia for species determination. The male terminalia of all described species have been illustrated in the literature and few taxonomic problems remain concerning these taxa.

Many species in eastern Asia remain undescribed, and the phylogenetic relationships among the species or species-groups of *Clinocera* have never been analyzed. This, combined with the poor knowledge of New World species, makes a revision of this group a priority among aquatic empidids.

Taxonomic history of Clinocera

The first Nearctic species of *Clinocera* were described by Loew (1860, 1862, 1876). Species were added by Melander (1902) with the first key to species of *Clinocera* (11 species). This key includes many species no longer assigned to *Clinocera*. An additional six species were later described by Melander (1928) in his monumental monograph on Nearctic Empididae, which remains the primary source for identification of many groups. He also provided a key to 27 species of

Clinocera s. lat., which included species of *Wiedemannia* and the then unrecognized genus *Trichoclinocera*. No additional taxonomic work on Nearctic *Clinocera* has appeared since, except for an unpublished thesis (Farr 1958) that included one additional new manuscript name. Consequently there are no reliable and up-to-date keys to North American species of *Clinocera*. The species definitions are not reliable, especially for western species, which handicaps identification in the west with its tremendous diversity of species.

The descriptions of the five known Neotropical species are scattered in the literature and no keys to their identification are available. The first description of a Neotropical species of *Clinocera* was by Bezzi (1909). Collin (1933) and Smith (1962) described the other four known species.

Prior to this study there were 17 Nearctic (Melander 1965) and 5 Neotropical (Smith 1967; *C. oriunda* was omitted from the list) described species. This is the first study to attempt to compile data for all available specimens and continues a series of revisions of the New World fauna of the Clinocerinae, which includes reviews of *Trichoclinocera* and *Wiedemannia* (Sinclair 1994, 1998).

Materials and methods

Source of material

This study is based on the examination of approximately 13 500 adult specimens of *Clinocera* and other clinocerines borrowed from or deposited in 50 institutions or individual collections. These collections are listed below, with the names of the curators and (or) assistants in parentheses. Collection codens in the text indicate the location of specimens and are based mostly on the list provided in the Website "The Insect and Spider Collections of the World" (http://hbs.bishopmuseum.org/codens/).

AMNH American Museum of Natural History, New York, USA (D. Grimaldi)
ANSP Department of Entomology, The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA (D. Azuma)
BARC M. Barták collection [private], Prague, Czech Republic (M. Barták)
BLKU Biosystematics Laboratory, Kyushu University, Fukuoka, Japan (T. Saigusa)
BMNH The Natural History Museum, London, England (J. Chainey and D. Notton).
BPBM Bernice P. Bishop Museum, Honolulu, Hawai′i, USA (N.L. Evenhuis)
BYU Monte L. Bean Life Sciences Museum, Brigham Young University, Provo, Utah, USA (R.W. Baumann)
CAS California Academy of Sciences, San Francisco, California, USA (P.H. Arnaud)
CMNH Section of Invertebrate Zoology, The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (C.W. Young)

CNC Canadian National Collection of Insects, Ottawa, Ontario, Canada (J.M. Cumming)
CSU Colorado State University, Fort Collins, Colorado, USA (S. Fitzgerald and B. Kondratieff)
CUIC Department of Entomology, Cornell University, Ithaca, New York, USA (E.R. Hoebeke and J.K. Liebherr)
DEBU University of Guelph, Guelph, Ontario, Canada (S.A. Marshall)
FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA (G.J. Steck)
HMOU Hope Entomological Collections, Oxford University, Oxford, England (A.C. Pont)
JBWM J.B. Wallis Museum, University of Manitoba, Winnipeg, Manitoba, Canada (R.E. Roughley)
KMNH Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (K. Ueda)
LACM Natural History Museum of Los Angeles County, Los Angeles, California, USA (C.L. Hogue and B.V. Brown)
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (D. Furth and P. Perkins)
MNHN Muséum national d'Histoire naturelle, Paris, France (C. Daugeron)
MNHNS Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta)
MSU Entomology Museum, Michigan State University, East Lansing, Michigan, USA (F.W. Stehr)
MSUB Department of Entomology, Montana State University, Bozeman, Montana, USA (R.L. Hurley)
MTD Museum für Tierkunde, Dresden, Germany (U. Kallweit)
MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (C.J.E. Lamas)
NYSM Biological Survey, New York State Museum, Albany, New York, USA (J.K. Barnes)
OSUC Department of Entomology, Oregon State University, Corvallis, Oregon, USA (N.H. Anderson)
PERC Purdue Entomological Research Collection, Purdue University, West Lafayette, Indiana, USA (J.F. MacDonald)
PSBC Behrend College, Pennsylvania State University at Erie, Erie, Pennsylvania, USA (now housed in ZFMK) (E. Masteller)
ROGC E.J. Rogers collection [private], Villa Grande, California, USA (E. Rogers)
ROM Royal Ontario Museum, Toronto, Ontario, Canada (G.E. Wiggins and D.C. Currie)
SEMC Snow Entomological Collections, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA (J.S. Ashe)

UBC Spencer Entomological Museum, University of British Columbia, Vancouver, B.C., Canada (S. Cannings)
UCB Essig Museum of Entomology, University of California, Berkeley, California, USA (J.A. Chemsak)
UCD R.M. Bohart Museum of Entomology, University of California, Davis, California, USA (S. Heyden)
UCR Department of Entomology, University of California, Riverside, California, USA (S.I. Frommer)
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UNH Department of Entomology, University of New Hampshire, Durban, New Hampshire, USA (J.F. Burger)
USNM United States National Museum of Natural History, Washington, D.C., USA (N.E. Woodley)
USUL Department of Biology, Utah State University, Logan, Utah, USA (W.J. Hanson)
UWL University of Wyoming, Laramie, Wyoming, USA (S.R. Shaw)
UZIL Museum of Zoology, Lund University, Lund, Sweden (R. Danielsson)
WSU Department of Entomology, Washington State University, Pullman, Washington, USA (W.J. Turner and R.S. Zack)
WOOC N.E. Woodley collection [private], Washington, D.C., USA (N.E. Woodley)
ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMH Zoological Museum, University of Helsinki, Helsinki, Finland (P. Vilkamaa)
ZMUC Zoological Museum, University of Copenhagen, Denmark (T. Pape)
ZSM Zoologische Staatssammlung München, Munich, Germany (M. Kotrba)

Abbreviations

The following abbreviations are used in the descriptions and material examined sections:

alc. – alcohol
Br. – Branch
Ck/ck – creek
Co. – county
Cons. – Conservation
Cpgd/cpgd – campground
CR – county road
Cyn/cyn – canyon
dc – dorsocentral bristle
EF – Experimental Forest
emerg. tp – emergence trap
Exp. – Experiment
Fk/fk – Fork
For./for. – forest
Gov't – Government
GSMNP – Great Smoky Mountains National Park
Hwy – highway

Is. – Island/Islands
jct. – junction
Lk./lk. – Lake/lake
Mt/Mtn(s) – Mount/Mountain(s)
MT – Malaise trap
N – north
NF – National Forest
NM – National Monument
NP – National Park
npl – notopleural bristle
nr – near
pal – postalar bristle
Pk – Park
Pkwy – Parkway
PP – Provincial Park
pprn – postpronotal bristle
presut spal – presutural supra-alar bristle
Prov. – Provincial
psut spal – postsutural supra-alar bristle
Pt – Point
PT – pan trap
R. – River/Rivière
Rd/rd – road
Rec.– Recreation
Res. – Reserve
Rt. – Route
sctl – scutellar bristle
SF – State Forest
SP – State Park
Spr./spr. – spring
Stn – station
Str./str. – stream
Tr. – trail
trib. – tributary
Twp – Township
ypans – yellow pan trap

The following abbreviations for the most frequent collectors are used in the "Material examined" sections: AB – A. Borkent; AF – A. Foley; ALM – A.L. Melander; BH – B. Heming; BJS – B.J. Sinclair; BVB – B.V. Brown; BVP – B.V. Peterson; CBDG – C.B.D. Garrett; CHC – C.H. Curran; CHM – C.H. Mann; CPA – C.P. Alexander; CRN – C.W. Nelson; CWJ – C.W. Johnson; CS – C.W. Sabrosky; DDW – D.D. Wilder, DEH – D.E. Hardy; DMW – D.M. Wood; DSC – D.S. Chandler; ECM – E.C. Masteller; EJR – E.J. Rogers; EMF – E.M. Fisher; EST – E.S. Tucker; ETC – E.T. Cresson; FCH – F.C. Harmston; FME – F. and M. Edwards; GCS – G.C. Steyskal; GEB – G.E. Bohart; GES – G.E. Shewell; GFK – G.F. Knowlton; GJS – G.J. Spencer; HBL – H.B. Leech; HER – H.E. Robinson; HJT – H.J. Teskey; HRF – H.R. Foxlee; JES – J.E. Swann; JFM – J.F. MacDonald; JFMC – J.F. McAlpine; JGC – J.G. Chillcott; JMA – J.M. Aldrich; JMC – J.M. Cumming; JRV – J.R. Vockeroth; LEP – L.E. Pena; LM – L. Masner; MCVD – M.C. Van Duzee; MTJ – M.T. James; NEW – N.E. Woodley; OB – O. Bryant; OSF – O.S. Flint; OY – O. Yata; PHA – P.H. Arnaud, Jr.; PPH – P.P. Harper; RAC – R.A. Cannings; REL – R.E. Leach; REO – R.E. Orth; RER – R.E. Roughley; RES – R. and E. Shannon; RLH – R.L. Hurley; RP – R. Pilfrey; RSZ – R.S. Zack; RWB – R.W. Baumann; SAM – S.A. Marshall; SF – S. Fitzgerald; SGC – S.G. Cannings; TS – T. Saigusa; TWF – T.W. Fisher; WJB – W.J. Brown; WJH – W.J. Hanson; WJT – W.J. Turner; WMW – W.M. Wheeler; WRMM – W.R.M. Mason; WRR – W.R. Richards; WWM – W.W. Moss; WWW – W.W. Wirth.

Collecting methods and specimen preservation and preparation

Adults were most readily collected by aspirating specimens directly from emergent rocks in riffle zones and rocky seepages or by skimming a sweep net

slightly above the water surface. Generally the adults remain very close to the substrate and consequently aspirating them directly is much more efficient than sweep-netting. Malaise traps set next to or across streams have been found to be effective in collecting some aquatic empidids, including clinocerines (J.F. MacDonald, pers. comm., 2007). Yellow pans rarely attract clinocerines and consequently were found to be not as effective as hand-collecting.

Freshly collected specimens were killed in tubes containing potassium cyanide or directly added into 70%–75% ethanol. Specimens from the killing tubes were either mounted the same day and stored at below 0 ˚C for a period of 2 months or laid out flat and dried in paper triangles. Specimens collected into alcohol were later critical-point-dried or dried in ethyl acetate following the methods of Vockeroth (1966). Abdomens and larval head capsules were macerated in crucibles of hot 85% lactic acid to examine terminalia and mouthparts. A strong base used as a clearing agent (e.g., KOH) was found to destroy the delicate membranous tip of the phallus.

Wings were mounted on microscope slides for photography. A wing was detached from the body and run through 2-propanol and then equal parts 2-propanol and cedarwood oil before being mounted directly from the last mixture into Canada balsam (or euparal). Light pressure with fine forceps on the cover slip eliminated bubbles and helped orientate the wing.

Drawings and wing measurements

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. Figures were drawn using a drawing device attached to a compound microscope. Before being inked on Mylar, line drawings were checked for accuracy under a dissecting microscope. Specimens were later removed from the shellac and stored in plastic microvials pinned under the adult specimen.

Measurements were made through a dissecting microscope at a low magnification. Body size is extremely variable in *Clinocera*, and among individuals it can vary depending on the age of the specimen when collected and whether it was air-dried, critical-point-dried, or dried directly from ethyl acetate. Consequently, to estimate the size of a species, the length of a wing was measured from the extreme base in a straight line along the costal margin to a line perpendicular to the tip of the wing.

Descriptive format

References to the original publication and junior synonyms are listed in order of date of description. Label data for primary types are cited in full, following the

style used in previous revisions (e.g., Sinclair 1994). Labels are listed from the top downward, with data from each label in quotation marks. Labels are cited in full, with original spelling, punctuation, and date, and lines are delimited by a slash (/). Additional information is included in [square] brackets. The repository of each type is given in parentheses. Secondary type data are abridged and listed alphabetically.

Additional material examined for previously described species is also listed, but the number of individual specimens per locality is omitted. All known previously described species are included in a list under each species-group. Types of many non-New World species examined are indicated. All valid species are preceded by one or more of the following letters indicating their biogeographic region of distribution:

AF Afrotropical, *sensu* Crosskey and White (1977)
NE Nearctic, *sensu* Griffiths (1980)
OR Oriental, *sensu* Delfinado and Hardy (1973)
PA Palearctic, *sensu* Soós and Papp (1984)
NT Neotropical, *sensu* Griffiths (1980)
AU Australasian, *sensu* Evenhuis (1989)

Cladistic methods

A preliminary cladistic analysis of the species-group relationships of *Clinocera* was performed using the parsimony program PAUP* version 4.0b10 (Swofford 2002) with the following settings: branch-and-bound search, all characters unordered and of equal weight, Multrees option in effect. Character evolution, character-state distributions, and alternative tree topologies were examined using the program MacClade version 4 (Maddison and Maddison 2003). The data matrix (Table 3) consists of 14 morphological characters (Table 2) compiled for 12 species of *Clinocera*. Ten binary and 4 multistate characters are treated. Exemplars from the genera *Trichoclinocera* and *Oreothalia* were used as outgroup taxa, as they are assumed to be closely related to *Clinocera* (see Sinclair 1995).

Morphology of *Clinocera*

Terms used for adult structures primarily follow those of McAlpine (1981). The term bristle is used for differentiated large setae on the head, mesonotum, and legs bearing a particular name or for one of a series with a particular name, e.g., notopleural bristle, dorsocentral bristle, anteroventral bristle.

Head and mouthparts

The head is attached slightly above the middle of the eye as seen in lateral view. The eye is slightly oval, strongly convex, and completely clothed with dense hairs or ommatrichia (Fig. 8*b*). The eye facets are subequal in size, not

Table 2. Characters used in the analysis of the species-groups of *Clinocera.*

1. *Face*: (0) flat; (1) with ventral tubercle; (2) convex
2. *Lower margin of face*: (0) cleft; (1) straight, not cleft
3. *Postsutural supra-alar bristle*: (0) one; (1) two; (2) absent
4. *Fifth tarsomere*: (0) truncate; (1) with dorsoapical extension
5. *Stigma*: (0) present; (1) absent
6. *Wing*: (0) infuscate only; (1) with distinct spots
7. *Phallus*: (0) lacking whip-like distiphallus; (1) with whip-like distiphallus
8. *Distiphallus*: (0) whip-like, flexible; (1) stiff and strongly recurved apically
9. *Distiphallus*: (0) continuous with phallic shaft; (1) sharply arched at apex of phallic shaft
10. *Apex of phallic shaft*: (0) narrow; (1) with wide membranous expansion, twice width of shaft
11. *Apex of surstylus*: (0) rounded; (1) beak-like; (2) truncate; (3) with shallow notch
12. *Surstylus size*: (0) short and narrow; (1) greatly expanded and lengthened
13. *Clasping cercus*: (0) truncate apically; (1) digitiform; (2) expanded apically with small anteroventral nipple-like projection
14. *Spermatheca*: (0) straight or wavy tube; (1) loosely coiled tube

enlarged anteriorly or dorsally. Both sexes are dichoptic, with the eyes separated by approximately 3 times the width of the ocellar triangle. The ocellar triangle bears a pair of normally long ocellar bristles inserted anterior to the lateral ocelli. Postocular setae are well developed and rather stout on the upper half of the eye. A pair of setae on the vertex posteromedial to the postocular row of setae could be viewed as vertical bristles as observed in Cyclorrhapha. Slender and pale genal setae arise ventral to the postocular row of setae. The gena is narrow, separated

Table 3. Data matrix for *Clinocera* species-groups, listing 14 terminal taxa and 14 characters used in the analysis.

	Character	
	1	1111
	1234567890	1234
Trichoclinocera hamifera	0010100??0	0010
Oreothalia pelops	0110000??0	0100
Clinocera tripunctata	0120000??1	0111
Clinocera caerulea	0100001010	2111
Clinocera conjuncta	0100011000	3101
Clinocera olivacea	0100001000	3101
Clinocera fuscipennis	1110001000	0121
Clinocera gubernans	1110011000	0121
Clinocera lineata	0100101101	1111
Clinocera madera	0100101101	1111
Clinocera nigra	0100101000	1111
Clinocera aucta	0100101000	0111
Clinocera stagnalis	2101111000	0111
Clinocera oriunda	2101111000	0111

Note: For character descriptions see Table 2. Character states were scored 0–3; ? denotes inapplicable data.

from the face by the frontoclypeal suture, which extends from the base of the palpus to the margin of the eye.

The face is flat, or somewhat convex (in some species of the *C. stagnalis* group), or distinctly swollen above the lower facial margin (in many species of the *C. fuscipennis* group), and usually lacking setulae (except in some species of the *C. lineata* group). The face often bears species-specific pruinescent patterns that can be viewed laterally or anteriorly. The lower margin of the face is entire and not divided by a median membranous cleft or notch. The width of the face is the same in both sexes and the clypeus is not differentiated.

The terminology of the antenna is taken from Stuckenberg (1999). The antenna is very uniform in this genus, dark and lacking any distinctive coloration, inserted above the middle of the eye, and directed upward. The scape (segment 1) is short and cylindrical, bearing several setulae. The pedicel (segment 2) is oval, bearing a preapical fringe of setulae. The postpedicel (first flagellomere) is short and onion-shaped and produced apically, bearing a long bi-articled, arista-like stylus. The basal article is nearly square and the apical article is normally rather stout, only slightly tapered, and lacking an apical mechanoreceptor (Fig. 6*a*).

The proboscis is short and sucker-like, only the labellum and palpi projecting beyond the head (Figs. 6*d*, 8*b*). The palpus is short and straight, lying close to the mouthparts, not projecting free (Fig. 6*c*). The palpus bears many slender setae, but lacks stout or distinctive setation. The clypeal ridge is articulated with the labrum and cibarium at the labrofulcral articulation point (Fig. 6*e*). The labrum is broadly triangular with the apex sometimes rather blunt. A long slender apodeme extends from the inner dorsal margin of the labrum. The epipharyngeal blades are very pronounced and separated from the labrum, bearing a series of stout mechanoreceptors. The lacinia is not free but secondarily fused to the inner labial sclerite and labial paraphysis. The inner apex of the lacinia bears a rod-shaped stipes, which is greatly lengthened to more than twice the length of the lacinia. The hypopharynx is needle-like, with a broad base. The labellum is held in a horizontal position, is sucker-like, and lacking pseudotracheae. The prey is held mostly by the labrum and hypopharynx, in a similar fashion to that observed in Dolichopodidae.

Wing

The homology of wing veins and cells in Diptera (Figs. 29*a*, *b*) follows the interpretation of Wootton and Ennos (1989) and Saigusa (2006)[1]. The wings of *Clinocera* are infuscate, often with cloudy spots or darkened areas along crossveins. The stigma is elongate, faint, and rarely dark, but is absent in several species-groups. At the base of the wing is a long stout seta and in some species of the *C. conjuncta* group there are often several basal pairs, with additional long setae extending distally along the costal margin. All veins except the costa are bare,

[1]T. Saigusa. 2006. Homology of wing venation of Diptera. Unpublished handout distributed at the 6th International Congress of Dipterology, Fukuoka, Japan.

lacking macrosetae. The costa bears stout erect setae from the apex of vein R_1 to the apex of R_{4+5} (see Sinclair 2000*b*, figs. 5, 6). The subcosta (Sc) is complete and R_1 joins the costa near the midlength of the wing. Vein R_{2+3} is normally straight, occasionally gently arched beneath the stigma. An auxiliary crossvein is sometimes present between R_{2+3} and R_4 (Fig. 29*g*). R_4 is strongly or weakly divergent from R_5, straight or bell-shaped. Cell dm is variable in shape, either truncate or produced apically; the bases of M_1 and M_2 are broadly separated and three veins are emitted from cell dm (M_1, M_2, M_4). Cell cua (anal cell or cell cu*p*) is slightly narrower than cell bm and rounded apically. The faint anal vein arising subapically from this cell (CuP+CuA or A_1+CuA_2) is usually reduced in thickness, mostly appearing simply as a streak, and does not extend to the wing margin.

Thorax

The thorax is compact and densely clothed in pruinescence. The prosternum is fused laterally to the proepisternum, forming a complete precoxal bridge. The scutum is often patterned dorsally, with a pair of median vittae or a single vitta that vary in colour (Fig. 5*b*). The notopleuron and prescutellar depression may also be differentiated with bluish pruinescence. The chaetotaxy is reduced to rows of distinct bristles (Fig. 5*b*): several acrostichal setulae anterior to the first dorsocentral bristles; normally 5 dorsocentral bristles (occasionally as many as 10), usually stout and well developed, increasing in length posteriorly; 1 post-pronotal bristle; 1 presutural supra-alar bristle; 2 or 3 notopleural bristles; 1 or 2 postsutural supra-alar bristles; 1 postalar bristle; 2 slightly divergent scutellar bristles.

The laterotergite bears a patch of pale setae and generally there are few additional pleural setae. There are often some pale setulae along the posterior margin of the mesepisternum and on the proepisternum.

Legs

The legs are long and slender with mostly only evenly scattered setae. The legs vary from dark-coloured to yellowish brown, with the ventral face of the femora often distinctly paler in various views. In the *C. stagnalis* group the apex or "knee" of the femora is often pale, in contrast to the remaining portion.

The anterior face of the forecoxa bears long soft setae, while the mid and hind coxae possess long lateral setae. The male forefemur usually possesses a double row of spine-like setae beneath, and a preapical anterior comb (Fig. 8*d*) is also usually present in both sexes. In males the foretibia bears an anterior apical comb and a biserial row of setae beneath. The hind tibia bears a posterior apical comb and dorsal and ventral erect setae of various lengths and strengths on the apical half. The second tarsomere of the foreleg is much longer than the third and fourth tarsomeres and the dorsal apex of the fifth tarsomere bears a prolongation

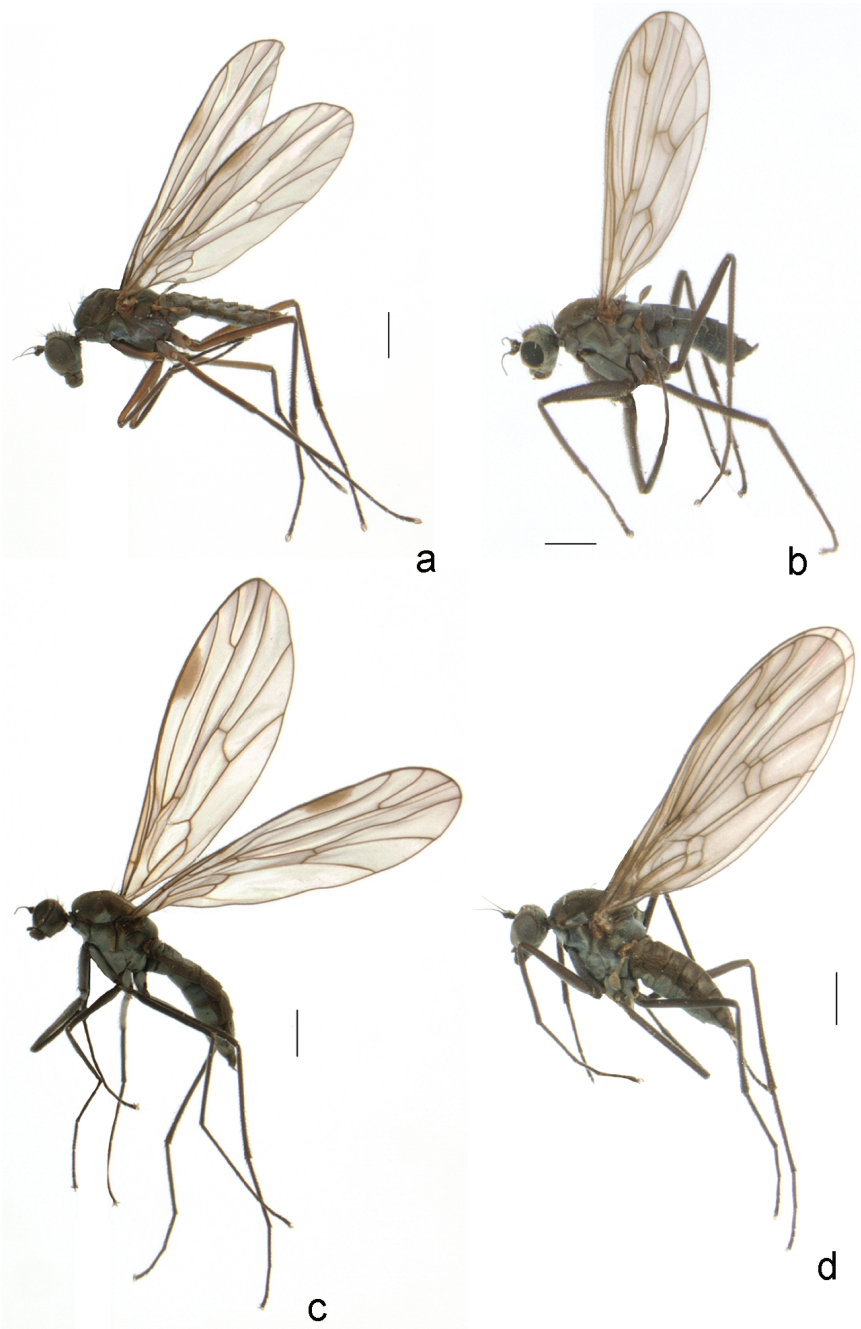

Fig. 4. Habitus photographs of dried mounted specimens of species of *Clinocera*: *a*, *C. caerulea*; *b*, *C. gubernans*; *c*, *C. stigma*; *d*, *C. fuscipennis*. Scale bars = 1.0 mm.

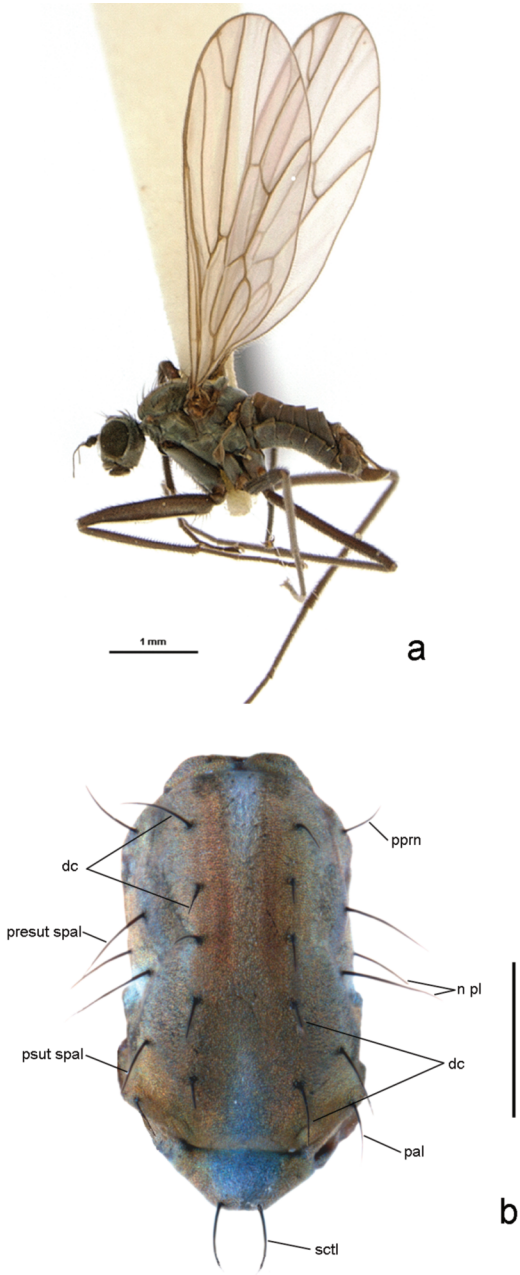

Fig. 5. Photographs of *Clinocera*: *a*, habitus of a dried mounted specimen of *C. schlinkerti*; *b*, *C. conjuncta*, thorax, dorsal view. Scale bar = 0.3 mm. (dc, dorsocentral bristle; n pl, notopleural bristle; pal, postalar bristle; pprn, postpronotal bristle; presut spal, presutural supra-alar bristle; psut spal, postsutural supra-alar bristle; sctl, scutellar bristle.)