

**Special Issue in Honor
of Ralph W. Holzenthal
for a Lifelong Contribution
to Trichoptera Systematics**

edited by

Steffen U. Pauls, Robin Thomson, Ernesto Rázuri-Gonzales

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SPECIAL ISSUE IN HONOR OF RALPH W. HOLZENTHAL FOR A
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Ralph W. Holzenthal – a mentor and friend retires

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A much too brief CV

Ralph Holzenthal began his studies in caddisfly diversity at the University of New Orleans, where he completed his Masters of Science degree in 1980 after exploring the caddisfly of southeastern Louisiana and southern Mississippi, which was in his own words, “as far as I could travel in a day with a non-existing budget”. Together with the research of Steve Harris and Paul Lago, Ralph’s MSc thesis significantly contributed to advancing our knowledge of caddisflies in the Southeastern United States (Harris et al. 1982; Holzenthal et al. 1982; Lago et al. 1982). After considering several topics and advisors, Ralph joined John Morse at Clemson University for his Ph.D. on Neotropical Leptoceridae. Specifically, he assessed and analyzed the diversity, evolution, and biogeography of Neotropical Leptoceridae and revised their systematics. At Clemson he also met Steve Hamilton. Ralph and ‘both Steves’ developed very productive professional relationships and personal friendships that last through today. Thus, Ralph became part of a line of Trichoptera workers that would significantly impact our knowledge of the Trichoptera fauna of North and South America. First and foremost, this line goes back to Herbert Ross, Fernand Schmid, Glenn Wiggins, Oliver Flint, and John Morse.

During his graduate studies, Ralph attended his first International Symposium of Trichoptera at Clemson in 1983 and presented and published the first paper of

his Ph.D. work in the symposium's proceedings: a description of the new genus *Achoropsyche* as the first contribution in the nine-part "Studies in Neotropical Leptoceridae" series (Holzenthal 1984). Perhaps more importantly he began many long-term relationships and friendships. He met Fernand Schmid of the Ministry of Agriculture Canada whose style and diligence in the preparation of Trichoptera he idolized and which Ralph has since passed on to generations of students. Through the Symposium he also intensified his interactions with Oliver Flint, an entomologist from the Smithsonian National Museum of Natural History, who became an important mentor for Ralph and whose collected material was the basis for a large part of Ralph's dissertation.

He completed his Ph.D. in Entomology at Clemson University in 1985. Ralph's Neotropical work then really took off when he received three National Science Foundation (NSF) grants to work on the caddisflies of Costa Rica. He began the first grant as a postdoctoral researcher at Clemson University in 1986 but was offered a faculty position as Faculty Director of the University of Minnesota Insect Collection (UMSP) at the University of Minnesota in spring of the same year. The grants and the work on Trichoptera of Costa Rica were instrumental to his tenure at UMSP. His six months sabbatical in 1997–1998 as visiting professor at the Universidade Federal do Paraná, Curitiba, Brazil was crucial to expanding his network in South America and broadening the taxonomic and regional scope of his work. The second influential grant to his career was a 2001 NSF "Partnerships for Enhancing Expertise in Taxonomy" (PEET) award. This grant, focused on formally training students in Trichoptera systematics and taxonomy, enabled Ralph to pursue one of his scientific career passions: training students from across the Americas in insect taxonomy, systematics, and biodiversity. He has since trained numerous younger colleagues through formal and informal avenues, thereby building a legacy of excellent Trichoptera taxonomists particularly known for their revisionary studies and excellent illustrations. Beyond teaching "standard" courses of an entomological curriculum, he also developed unique courses on scientific illustration of insects. These are sought after globally, and Ralph has been invited to give numerous workshops around the world to students and professionals. Ralph also excelled at communicating his knowledge with students. He was a cherished teacher and won multiple faculty teaching awards at the University of Minnesota. These included the FAME Award (Faculty Award for Mentorship in Entomology) presented through "Frenatae", the University of Minnesota's Entomology Graduate Student Organization in 2005 and 2010, which highlights how highly valued Ralph was as a teacher and mentor by his students. Many of his former mentees submitted articles to this volume, to show their gratitude and respect for Ralph's life work. The topics he thus influenced range from faunal surveys and checklists (Cavalcante-Silva et al. 2022; Chuluunbat et al. 2022; Houghton 2022; Luna-Luna et al. 2022) and ecological studies (Houghton et al. 2022; Ríos-Touma et al. 2022) to descriptive taxonomy (Bueno-Soria et al. 2022; Cavalcante-Silva et al. 2022; Martins et al. 2022; Pereira et al. 2022; Ramírez-

Table I. Students mentored by R.W. Holzenthal (in reverse chronological order).

M.Sc.	Ph.D.
Heather Cummins, 2014	Luis Ernesto Rázuri-Gonzales, 2020
Joel Gardner, 2013 (Co-Advisor with M. Spivak)	Lucas Marques de Carmagos, 2020
Anne M. Wasmund, 2006	Robin Thomson, 2014
Dianne M. Crane, 1994 (Co-Advisor with R.D. Moon)	Desiree R. Robertson, 2010
Margot P. Monson, 1994	Maria Lourdes Chamorro, 2009
Roger J. Blahnik, 1991	Henrique Paprocki, 2008
Roger M. Strand, 1991	Fernando Muñoz Quesada, 2003
	David Houghton, 2002
	Aysha Prather, 2002
	Roger J. Blahnik, 1996
	Atilano Contreras-Ramos, 1996
	Sonia M.N. Lazzari, 1990

Carmona et al. 2022; Rázuri-Gonzales et al. 2022) and systematic revisions (Blahnik and Andersen 2022; Sganga et al. 2022; Thomson et al. 2022a, b).

The impact of his scientific work on Neotropical and other Trichoptera is seen in the 708 species (Figs 1, 2) he has described in dozens of publications and compendia (e.g., Flint et al. 1999; Holzenthal and Calor 2017), the twelve new genera and subgenera described, the incredible collection he has built, and the many students he trained.

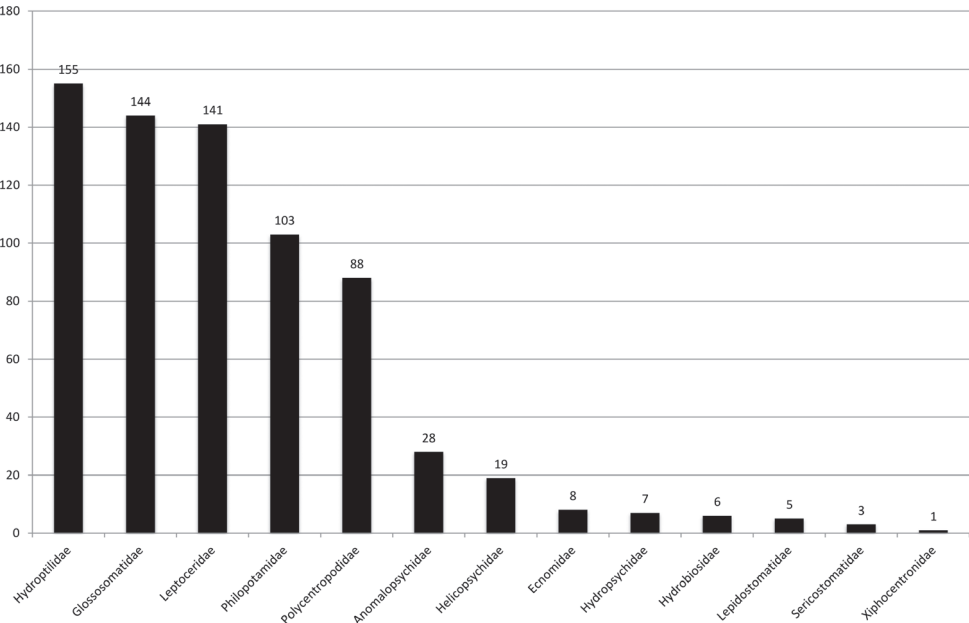


Figure 1. Number of new species described by R.W. Holzenthal by family (ordered by rank).

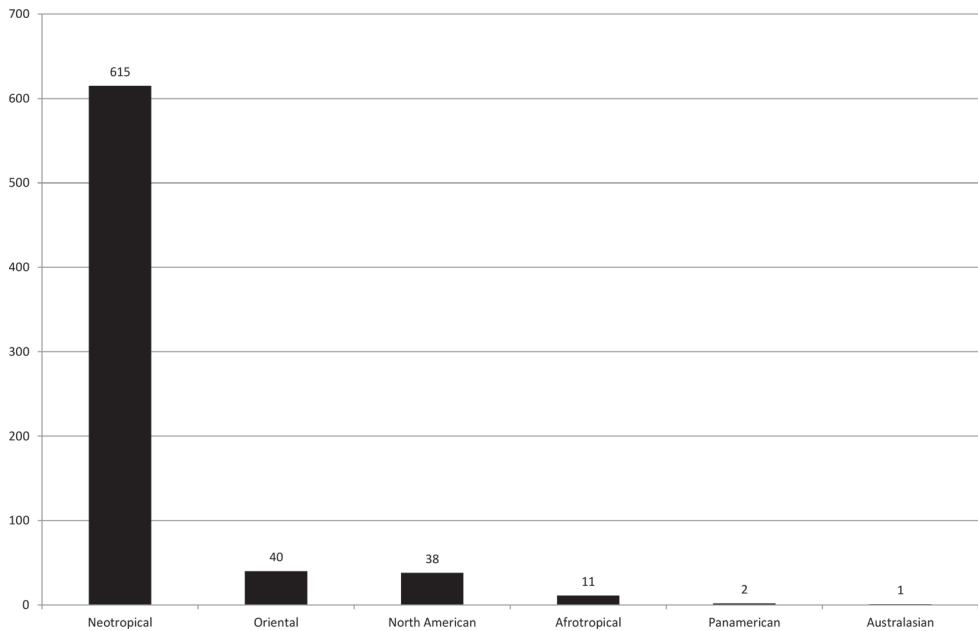


Figure 2. Number of species described by R.W. Holzenthal by biogeographical region (ordered by rank).

Our interpretation of the scientific legacy of Ralph W. Holzenthal

Ralph's impact goes beyond pure numbers; his taxonomic contributions are characterized by particularly comprehensive treatments of morphology and species descriptions, often representing extensive revisions of taxonomic groups (e.g., Holzenthal 1982; Holzenthal and Flint 1995) or regional faunas (e.g., Andersen and Holzenthal 2001, 2002) and authoritative catalogues (Flint et al. 1999; Holzenthal and Calor 2017). This resulted in a body of work of lasting value that is still relevant today, decades later, and is used not only as a basis for identifications but also for further systematic work.

In our opinion, and this was passed on to us by Ralph's mentoring, excellent taxonomic publications not only clarify the morphological characters that are central to the identification of the taxa in question but also allow interpretation of homology of characters relevant for evolutionary analysis. Excellent and clear illustrations are central for this purpose. Ralph has developed his own style for traditionally and digitally inked line drawings and illustrations that succeed in being both unambiguous, thereby allowing identification, but also being sufficiently detailed to allow initial assessments of homology and convergence. He has introduced these methods to many subsequent generations through formal classes and informal courses and workshops.

Another cornerstone in Ralph's career has been an openness to innovative methodologies. Ralph conducted phylogenetic analyses to clarify evolutionary questions early in his doctoral studies, initially following the principles established by Hennig (1969). Hennigian phylogenetics were a major innovation in taxonomy at the time of Ralph's first studies, influencing his decision to work with John Morse for his Ph.D., as John

Morse was already using these methods. Throughout his career Ralph applied many methodological innovations to his work. These included digital approaches to illustration (Holzenthal 2008), database systems for collections management, and computer-generated natural language descriptions and taxonomic keys (e.g., DELTA; Dallwitz 1974, 1980). He later adopted the use of molecular data in phylogenetic systematics and developed them further in cooperation with colleagues (Kjer et al. 2001), up to current applications of genomics in phylogenetics (Thomson et al. 2022b). As Faculty Director of the University of Minnesota Insect Collection (UMSP), he leaves behind one of the foremost Neotropical Trichoptera collections in the world, and a well-curated insect collection of more than 4 million specimens where species level identification lies at an astonishing ~ 70%. All Trichoptera specimens are databased and have machine-readable barcode labels (for a searchable database of these specimens, see <https://scan-bugs.org/portal/>). This approach to taxonomy and systematics, not only for its own sake but also as a service to other scientists, is what we believe sets Ralph's contributions apart.

Ralph also has a strong awareness of obstacles to taxonomic publication and the central role of identification keys in organismal biology. This awareness led Ralph to join ZooKeys as a Trichoptera subject editor, where for five years his editorial leadership influenced many authors of excellent taxonomic papers. This is a further example of his service-oriented mindset.

But to what end did Ralph make these contributions? By making the world's caddisfly fauna more available to systematists as well as evolutionary and conservation biologists, Ralph has helped advance the taxonomy of Trichoptera beyond the pioneering efforts of Dr. Oliver S. Flint to a new stage of knowledge for the Neotropics. In addition to descriptive and revisionary taxonomy, he has also advocated for the value of museums and collections in an ongoing and uphill endeavor. In the face of global climate change, this is an enterprise that now seems more important than ever because the secure refuges set aside to protect species no longer seem so permanent or secure. Natural habitats have been disappearing at alarming rates for the last few decades, which impacts our livelihoods and welfare. Biological inventories in turn raise awareness of the benefits of protecting these habitats and the biodiversity they hold. However, particularly in the tropics, these inventories usually focus on relatively well-known, easily identifiable, or charismatic groups such as birds, mammals, butterflies, and ants, while many other groups are scarcely known. By subsequently establishing protected areas known to be diverse, conservationists and biodiversity researchers aspire that these less well-known groups can also be protected and eventually described. At the rate natural habitats are being destroyed, however, it is unlikely the focus on few protected areas will suffice to preserve all the hitherto unknown diversity.

In a recent paper, Ralph and colleagues recorded 310 caddisfly species from Ecuador and estimated that only 54% of the Trichoptera fauna from this country is known to science (Ríos-Touma et al. 2017). Moreover, several Neotropical genera found in Ecuador are highly endemic at the species level (e.g., *Amphoropsycha*, *Atanatolica*, and *Contulma*), with new genera and species routinely discovered and described in these areas (Holzenthal et al. 2017, 2018). The same scenario applies in the forests of other tropical countries, and estimating how many additional species may have initially been present before these forests were deforested is impossible to accomplish.

Beyond diversity predictions and reserving natural habitats in the hope of protecting diversity, a fundamental concern for the loss of species should begin with a sense of urgency to know what might be lost. Because species are not really fathomable until they are more than theoretical numbers. How can one truly mourn the loss of species that were not even known to exist? How will one know that they were truly lost if there are no records that they existed in the first place? How do we still have such a poor knowledge of our planet's biodiversity after more than 250 years naming species? If the diversity of species on the planet is as great as scientists have estimated, why does the description of biodiversity of the planet receive such a low priority?

Ralph understands that providing empirical evidence and a comprehensible characterization of biological diversity is of utmost importance to supporting conservation efforts. After a stellar career in taxonomy, with the description of hitherto 708 species previously unknown to science (see Figs 1, 2), Ralph can join the ranks of the many thousands of taxonomists who have contributed to the description of the Earth's biological diversity. Many of his descriptions were conducted with students he trained, thereby ensuring a lasting legacy of his work and his ideas on high-quality approaches to taxonomy that will transcend through generations.

Over the years, Ralph's thinking and his approach to taxonomy have inspired many others, especially young scientists and students, as is evident in the articles in this issue. Perhaps more importantly, all his students maintain a love and appreciation of both taxonomy and the diversity of aquatic insects. Ralph's knowledge and enthusiasm for these topics has impressed his students to such a degree that they all maintained subject and mentor close to their hearts.

List of publications

1980

Poirrier MA, Holzenthal RW (1980) Records of spongilla-flies [Neuroptera: Sisyridae] from Mississippi. *Journal of the Mississippi Academy of Science* 25: 1–2.

1982

Harris SC, Lago PK, Holzenthal RW (1982) An annotated checklist of the caddisflies (Trichoptera) of Mississippi and Southeastern Louisiana. Part II: Rhyacophiloidea. *Proceedings of the Entomological Society of Washington* 84: 509–512.

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New genera and subgenera circumscribed by R.W. Holzenthal

Achoropsyche Holzenthal, 1984

Amazonatolica Holzenthal & Pes, 2004

Amphoropsyche Holzenthal, 1985

Aymaradella Holzenthal, Blahnik & Ríos-Touma, 2018

Fernandoschmidia Holzenthal & Andersen, 2007

Mejicanotrichia Harris & Holzenthal, 1997

Mortoniella (*Nanotrichia*) Blahnik & Holzenthal, 2017

Neoathripsodes Holzenthal, 1989

Notalina (*Neonotalina*) Holzenthal, 1986

Orinochotrichia Harris, Flint & Holzenthal, 2002

Osflintia Calor & Holzenthal, 2008

Tizatetrichia Harris, Flint & Holzenthal, 2002

New species described by R.W. Holzenthal (arranged alphabetically by family and species)

Anomalopsychidae

Contulma adamsae Holzenthal & Flint, 1995
Contulma bacula Holzenthal & Flint, 1995
Contulma boliviensis Holzenthal & Robertson, 2006
Contulma caldensis Holzenthal & Flint, 1995
Contulma cataracta Holzenthal & Flint, 1995
Contulma colombiensis Holzenthal & Flint, 1991
Contulma costaricensis Holzenthal & Flint, 1995
Contulma echinata Holzenthal & Flint, 1995
Contulma ecuadorensis Holzenthal & Flint, 1995
Contulma fluminensis Holzenthal & Robertson, 2006
Contulma inornata Holzenthal & Flint, 1995
Contulma lanceolata Holzenthal & Flint, 1995
Contulma lina Holzenthal, Ríos-Touma & Rázuri-Gonzales, 2017
Contulma meloi Holzenthal & Robertson, 2006
Contulma nevada Holzenthal & Flint, 1995
Contulma palaguillensis Holzenthal & Ríos-Touma, 2012
Contulma papallacta Holzenthal & Flint, 1995
Contulma penai Holzenthal & Flint, 1995
Contulma quito Holzenthal, Ríos-Touma & Rázuri-Gonzales, 2017
Contulma sancta Holzenthal & Flint, 1995
Contulma sangay Holzenthal, Ríos-Touma & Rázuri-Gonzales, 2017
Contulma spinosa Holzenthal & Flint, 1991
Contulma talamanca Holzenthal & Flint, 1995
Contulma tapanti Holzenthal & Flint, 1995
Contulma tica Holzenthal & Flint, 1995
Contulma tijuca Holzenthal & Flint, 1995
Contulma tripui Holzenthal & Robertson, 2006
Contulma valverdei Holzenthal & Flint, 1995

Ecnomidae

Austrotinodes abrachium Thomson & Holzenthal, 2010
Austrotinodes belchioris Thomson & Holzenthal, 2010
Austrotinodes boliviensis Thomson & Holzenthal, 2010
Austrotinodes cressae Thomson & Holzenthal, 2010
Austrotinodes doublesi Munioz-Quesada & Holzenthal, 1993
Austrotinodes inbio Munioz-Quesada & Holzenthal, 1993
Austrotinodes longispinum Thomson & Holzenthal, 2010
Austrotinodes taquaralis Thomson & Holzenthal, 2010

Glossosomatidae

- Canoptila williami* Robertson & Holzenthal, 2006
Culoptila bidentata Blahnik & Holzenthal, 2006
Culoptila buenoi Blahnik & Holzenthal, 2006
Culoptila cascada Blahnik & Holzenthal, 2006
Culoptila hamata Blahnik & Holzenthal, 2006
Culoptila pararusia Blahnik & Holzenthal, 2006
Culoptila plummerensis Blahnik & Holzenthal, 2006
Culoptila tapanti Blahnik & Holzenthal, 2006
Culoptila unispina Blahnik & Holzenthal, 2006
Culoptila vexillifera Blahnik & Holzenthal, 2006
Itauara alexanderi Robertson & Holzenthal, 2011
Itauara bidentata Robertson & Holzenthal, 2011
Itauara blahniki Robertson & Holzenthal, 2011
Itauara charlotta Robertson & Holzenthal, 2011
Itauara emilia Robertson & Holzenthal, 2011
Itauara flinti Robertson & Holzenthal, 2011
Itauara guyanensis Robertson & Holzenthal, 2011
Itauara jamesii Robertson & Holzenthal, 2011
Itauara julia Robertson & Holzenthal, 2011
Itauara lucinda Robertson & Holzenthal, 2011
Itauara ovis Robertson & Holzenthal, 2011
Itauara peruensis Robertson & Holzenthal, 2011
Itauara rodmani Robertson & Holzenthal, 2011
Itauara simplex Robertson & Holzenthal, 2011
Itauara spiralis Robertson & Holzenthal, 2011
Itauara stella Robertson & Holzenthal, 2011
Itauara tusci Robertson & Holzenthal, 2011
Itauara unidentata Robertson & Holzenthal, 2011
Mastigoptila complicornuta Holzenthal, 2004
Mastigoptila elae Holzenthal, 2004
Mortoniella acauda Blahnik & Holzenthal, 2011
Mortoniella acutiterga Blahnik & Holzenthal, 2017
Mortoniella adamsae Blahnik & Holzenthal, 2017
Mortoniella agosta Blahnik & Holzenthal, 2011
Mortoniella akantha Blahnik & Holzenthal, 2008
Mortoniella akrogeneios Blahnik & Holzenthal, 2017
Mortoniella anakantha Blahnik & Holzenthal, 2008
Mortoniella applanata Blahnik & Holzenthal, 2017
Mortoniella asymmetris Blahnik & Holzenthal, 2011
Mortoniella auricularis Blahnik & Holzenthal, 2017
Mortoniella aviceps Blahnik & Holzenthal, 2008

Mortoniella barinasi Blahnik & Holzenthal, 2017
Mortoniella biramosa Blahnik & Holzenthal, 2017
Mortoniella bocaina Blahnik & Holzenthal, 2011
Mortoniella bothrops Blahnik & Holzenthal, 2017
Mortoniella brachyrhachos Blahnik & Holzenthal, 2008
Mortoniella brevis Blahnik & Holzenthal, 2017
Mortoniella buenoi Blahnik & Holzenthal, 2008
Mortoniella bulbosa Blahnik & Holzenthal, 2017
Mortoniella carinula Blahnik & Holzenthal, 2008
Mortoniella catherinae Blahnik & Holzenthal, 2017
Mortoniella caudicula Blahnik & Holzenthal, 2008
Mortoniella chalalan Blahnik & Holzenthal, 2017
Mortoniella cognata Blahnik & Holzenthal, 2017
Mortoniella coheni Blahnik & Holzenthal, 2017
Mortoniella cornuta Blahnik & Holzenthal, 2017
Mortoniella crescentis Blahnik & Holzenthal, 2011
Mortoniella cressae Blahnik & Holzenthal, 2017
Mortoniella croca Blahnik & Holzenthal, 2017
Mortoniella curtispina Blahnik & Holzenthal, 2017
Mortoniella curvistylus Blahnik & Holzenthal, 2017
Mortoniella dentiterga Blahnik & Holzenthal, 2017
Mortoniella dinotes Blahnik & Holzenthal, 2017
Mortoniella dolonis Blahnik & Holzenthal, 2011
Mortoniella draconis Blahnik & Holzenthal, 2017
Mortoniella emarginata Blahnik & Holzenthal, 2017
Mortoniella esrossi Blahnik & Holzenthal, 2017
Mortoniella falcicula Blahnik & Holzenthal, 2008
Mortoniella flexuosa Blahnik & Holzenthal, 2017
Mortoniella froeblichii Blahnik & Holzenthal, 2011
Mortoniella furcula Blahnik & Holzenthal, 2017
Mortoniella gilli Blahnik & Holzenthal, 2017
Mortoniella gracilis Blahnik & Holzenthal, 2017
Mortoniella grandiloba Blahnik & Holzenthal, 2017
Mortoniella guahybae Blahnik & Holzenthal, 2011
Mortoniella guyanensis Blahnik & Holzenthal, 2017
Mortoniella hamata Blahnik & Holzenthal, 2017
Mortoniella hystricosa Blahnik & Holzenthal, 2011
Mortoniella intervalles Blahnik & Holzenthal, 2011
Mortoniella langleyae Blahnik & Holzenthal, 2017
Mortoniella latispina Blahnik & Holzenthal, 2011
Mortoniella licina Blahnik & Holzenthal, 2017
Mortoniella longispina Blahnik & Holzenthal, 2011
Mortoniella longiterga Blahnik & Holzenthal, 2017

Mortoniella meloi Blahnik & Holzenthal, 2011
Mortoniella membranacea Blahnik & Holzenthal, 2017
Mortoniella mexicana Blahnik & Holzenthal, 2008
Mortoniella monopodis Blahnik & Holzenthal, 2017
Mortoniella munozi Blahnik & Holzenthal, 2008
Mortoniella opinionis Blahnik & Holzenthal, 2008
Mortoniella panamensis Blahnik & Holzenthal, 2008
Mortoniella papillata Blahnik & Holzenthal, 2008
Mortoniella paraguayensis Blahnik & Holzenthal, 2011
Mortoniella parameralda Blahnik & Holzenthal, 2017
Mortoniella parauna Blahnik & Holzenthal, 2011
Mortoniella paraunota Blahnik & Holzenthal, 2011
Mortoniella paucispina Blahnik & Holzenthal, 2017
Mortoniella pectinella Blahnik & Holzenthal, 2008
Mortoniella pica Blahnik & Holzenthal, 2017
Mortoniella proakantha Blahnik & Holzenthal, 2017
Mortoniella prolata Blahnik & Holzenthal, 2017
Mortoniella propinqua Blahnik & Holzenthal, 2008
Mortoniella pumila Blahnik & Holzenthal, 2011
Mortoniella pusilla Blahnik & Holzenthal, 2011
Mortoniella quadridactyla Blahnik & Holzenthal, 2017
Mortoniella quadrispina Blahnik & Holzenthal, 2017
Mortoniella rectiflexa Blahnik & Holzenthal, 2017
Mortoniella redunca Blahnik & Holzenthal, 2008
Mortoniella rodmani Blahnik & Holzenthal, 2008
Mortoniella ruedae Blahnik & Holzenthal, 2017
Mortoniella schlingeri Blahnik & Holzenthal, 2017
Mortoniella sricula Blahnik & Holzenthal, 2008
Mortoniella silacea Blahnik & Holzenthal, 2017
Mortoniella simplicis Blahnik & Holzenthal, 2017
Mortoniella sinuosa Blahnik & Holzenthal, 2017
Mortoniella spangleri Blahnik & Holzenthal, 2017
Mortoniella spatulata Blahnik & Holzenthal, 2017
Mortoniella stilula Blahnik & Holzenthal, 2008
Mortoniella tanyrhabdos Blahnik & Holzenthal, 2017
Mortoniella tapanti Blahnik & Holzenthal, 2008
Mortoniella taurina Blahnik & Holzenthal, 2008
Mortoniella triangularis Blahnik & Holzenthal, 2017
Mortoniella tridens Blahnik & Holzenthal, 2017
Mortoniella tripuiensis Blahnik & Holzenthal, 2011
Mortoniella triramosa Blahnik & Holzenthal, 2017
Mortoniella truncata Blahnik & Holzenthal, 2011
Mortoniella tusci Blahnik & Holzenthal, 2017

Mortoniella umbonata Blahnik & Holzenthal, 2008
Mortoniella uruguayensis Blahnik & Holzenthal, 2011
Mortoniella variabilis Blahnik & Holzenthal, 2017
Mortoniella venezuelensis Blahnik & Holzenthal, 2017
Mortoniella zamora Blahnik & Holzenthal, 2017
Protoptila altura Holzenthal & Blahnik, 2006
Protoptila bribri Holzenthal & Blahnik, 2006
Protoptila chitaria Holzenthal & Blahnik, 2006
Protoptila cristula Holzenthal & Blahnik, 2006
Protoptila diablita Robertson & Holzenthal, 2008
Protoptila jolandae Holzenthal & Blahnik, 2006
Protoptila julieta Robertson & Holzenthal, 2008
Protoptila kjeri Holzenthal & Blahnik, 2006
Protoptila strepsicera Holzenthal & Blahnik, 2006
Protoptila trichoglossa Holzenthal & Blahnik, 2006
Tolhuaca brasiliensis Robertson & Holzenthal, 2005

Helicopsychidae

Helicopsyche alajuela Johanson & Holzenthal, 2010
Helicopsyche angeloi Holzenthal, Blahnik & Calor, 2016
Helicopsyche auroa Johanson & Holzenthal, 2004
Helicopsyche camuriensis Johanson & Holzenthal, 2004
Helicopsyche circulata Johanson & Holzenthal, 2004
Helicopsyche disjuncta Johanson & Holzenthal, 2004
Helicopsyche dorsocurvata Johanson & Holzenthal, 2010
Helicopsyche golfitoensis Johanson & Holzenthal, 2010
Helicopsyche guara Holzenthal, Blahnik & Calor, 2016
Helicopsyche laneblina Johanson & Holzenthal, 2004
Helicopsyche lara Johanson & Holzenthal, 2004
Helicopsyche lazzariae Holzenthal, Blahnik & Calor, 2016
Helicopsyche linabena Johanson & Holzenthal, 2004
Helicopsyche neblinensis Johanson & Holzenthal, 2004
Helicopsyche perija Johanson & Holzenthal, 2004
Helicopsyche succincta Johanson & Holzenthal, 2004
Helicopsyche sucrensis Johanson & Holzenthal, 2004
Helicopsyche tachira Johanson & Holzenthal, 2004
Helicopsyche venezuelensis Johanson & Holzenthal, 2004

Hydrobiosidae

Atopsyche allani Holzenthal & Cressa, 2002
Atopsyche blahniki Santos & Holzenthal, 2012

Atopsyche galharada Santos & Holzenthal, 2012

Atopsyche parauna Santos & Holzenthal, 2012

Atopsyche rinconi Holzenthal & Cressa, 2002

Atopsyche segninii Holzenthal & Cressa, 2002

Hydropsychidae

Smicridea figueroai Holzenthal, 2004

Smicridea lourditae Pauls, Blahnik, Zhou, Wardwell & Holzenthal, 2010

Smicridea nemorosa Holzenthal & Blahnik, 1995

Smicridea patinae Pauls, Blahnik & Holzenthal, 2010

Smicridea singri Holzenthal & Blahnik, 1995

Smicridea tapanti Holzenthal & Blahnik, 1995

Smicridea travertinera Paprocki, Holzenthal & Cressa, 2003

Hydroptilidae

Alisotrichia tiza Harris & Holzenthal, 1993

Angrisanoia otarosa Wasmund & Holzenthal, 2007

Angrisanoia shorti Thomson & Holzenthal, 2012

Bredinia alza Harris, Holzenthal & Flint, 2002

Bredinia davenporti Harris, Holzenthal & Flint, 2002

Bredinia emarginata Harris, Holzenthal & Flint, 2002

Bredinia espinosa Harris, Holzenthal & Flint, 2002

Bredinia guanacasteca Harris, Holzenthal & Flint, 2002

Bredinia manabiensis Harris, Holzenthal & Flint, 2002

Bredinia mexicana Harris, Holzenthal & Flint, 2002

Bredinia pilcopata Harris, Holzenthal & Flint, 2002

Bredinia selva Harris, Holzenthal & Flint, 2002

Bredinia spangleri Harris, Holzenthal & Flint, 2002

Bredinia sucrensis Harris, Holzenthal & Flint, 2002

Bredinia venezuelensis Harris, Holzenthal & Flint, 2002

Bredinia zulia Harris, Holzenthal & Flint, 2002

Byrsopteryx abrelata Harris & Holzenthal, 1994

Byrsopteryx chaconi Harris & Holzenthal, 1994

Byrsopteryx cuchilla Harris & Holzenthal, 1994

Byrsopteryx esparta Harris & Holzenthal, 1994

Byrsopteryx espinhosa Harris & Holzenthal, 1994

Byrsopteryx gomezi Harris & Holzenthal, 1994

Byrsopteryx loja Harris & Holzenthal, 1994

Byrsopteryx rayada Harris & Holzenthal, 1994

Byrsopteryx solisi Harris & Holzenthal, 1994

Byrsopteryx tapanti Harris & Holzenthal, 1994

Byrsopteryx tica Harris & Holzenthal, 1994
Costatrichia carara Holzenthal & Harris, 1999
Costatrichia cressae Holzenthal & Harris, 1999
Costatrichia flinti Holzenthal & Harris, 1999
Flintiella alajuela Harris, Flint & Holzenthal, 2002
Flintiella astilla Harris, Flint & Holzenthal, 2002
Flintiella boraceia Harris, Flint & Holzenthal, 2002
Flintiella heredia Harris, Flint & Holzenthal, 2002
Flintiella panamensis Harris, Flint & Holzenthal, 2002
Flintiella pizotensis Harris, Flint & Holzenthal, 2002
Flintiella tamaulipasa Harris, Flint & Holzenthal, 2002
Flintiella yanamona Harris, Flint & Holzenthal, 2002
Hydroptila carara Harris & Holzenthal, 1999
Hydroptila carolae Holzenthal & Kelley, 1983
Hydroptila cressae Thomson & Holzenthal, 2012
Hydroptila disgalera Holzenthal & Kelley, 1983
Hydroptila maritza Harris & Holzenthal, 1999
Hydroptila maza Harris & Holzenthal, 1999
Hydroptila nusagandia Harris & Holzenthal, 1999
Hydroptila osa Harris & Holzenthal, 1999
Hydroptila ouachita Holzenthal & Kelley, 1983
Hydroptila paradenza Harris & Holzenthal, 1999
Hydroptila poirrieri Holzenthal & Kelley, 1983
Hydroptila rastrilla Harris & Holzenthal, 1999
Hydroptila roberta Hamilton & Holzenthal, 1984
Hydroptila singri Harris & Holzenthal, 1999
Hydroptila tridentata Holzenthal & Kelley, 1983
Leucotrichia angelinae Thomson & Holzenthal, 2015
Leucotrichia denticulata Thomson & Holzenthal, 2015
Leucotrichia dianeae Thomson & Holzenthal, 2015
Leucotrichia fulminea Thomson & Holzenthal, 2015
Leucotrichia hispida Thomson & Holzenthal, 2015
Leucotrichia kateae Thomson & Holzenthal, 2015
Leucotrichia pectinata Thomson & Holzenthal, 2015
Leucotrichia repanda Thomson & Holzenthal, 2015
Leucotrichia rhomba Thomson & Holzenthal, 2015
Leucotrichia rioustoumae Thomson & Holzenthal, 2015
Leucotrichia sidneyi Thomson & Holzenthal, 2015
Leucotrichia tapantia Thomson & Holzenthal, 2015
Leucotrichia zopilote Holzenthal & Harris, 1999
Mayatrichia illobia Harris & Holzenthal, 1990
Mejicanotrichia estaquilloa Harris & Holzenthal, 1997
Metrichia acicula Bueno-Soria & Holzenthal, 2003

Metrichia alajuela Bueno-Soria & Holzenthal, 2003
Metrichia amplitudinis Bueno-Soria & Holzenthal, 2003
Metrichia ancora Bueno-Soria & Holzenthal, 2003
Metrichia angulosa Bueno-Soria & Holzenthal, 2003
Metrichia bostrychion Thomson & Holzenthal, 2012
Metrichia decora Bueno-Soria & Holzenthal, 2003
Metrichia gordita Bueno-Soria & Holzenthal, 2003
Metrichia luna Bueno-Soria & Holzenthal, 2003
Metrichia magna Bueno-Soria & Holzenthal, 2003
Metrichia mechuda Bueno-Soria & Holzenthal, 2003
Metrichia meta Bueno-Soria & Holzenthal, 2003
Metrichia picuda Bueno-Soria & Holzenthal, 2003
Metrichia prolata Bueno-Soria & Holzenthal, 2003
Metrichia pseudopatagonica Bueno-Soria & Holzenthal, 2003
Metrichia savegra Bueno-Soria & Holzenthal, 2003
Metrichia separata Bueno-Soria & Holzenthal, 2003
Metrichia sesquipedalis Bueno-Soria & Holzenthal, 2003
Metrichia spica Bueno-Soria & Holzenthal, 2003
Metrichia triquetra Bueno-Soria & Holzenthal, 2003
Metrichia truncata Bueno-Soria & Holzenthal, 2003
Nothotrichia munozii Holzenthal & Harris, 2002
Nothotrichia tupi Holzenthal & Harris, 2022
Ochrotrichia affinis Bueno-Soria & Holzenthal, 2004
Ochrotrichia alargada Bueno-Soria & Holzenthal, 2004
Ochrotrichia amorfa Bueno-Soria & Holzenthal, 2004
Ochrotrichia assita Bueno-Soria & Holzenthal, 2004
Ochrotrichia avicula Bueno-Soria & Holzenthal, 2008
Ochrotrichia avis Bueno-Soria & Holzenthal, 1998
Ochrotrichia bractea Bueno-Soria & Holzenthal, 2004
Ochrotrichia catarina Bueno-Soria & Holzenthal, 2004
Ochrotrichia citra Bueno-Soria & Holzenthal, 2004
Ochrotrichia compacta Bueno-Soria & Holzenthal, 2004
Ochrotrichia conformalis Bueno-Soria & Holzenthal, 2008
Ochrotrichia curvata Bueno-Soria & Holzenthal, 2004
Ochrotrichia cuspidata Bueno-Soria & Holzenthal, 2004
Ochrotrichia delgada Bueno-Soria & Holzenthal, 2004
Ochrotrichia dulcea Bueno-Soria & Holzenthal, 1998
Ochrotrichia indefinida Bueno-Soria & Holzenthal, 2004
Ochrotrichia involuta Bueno-Soria & Holzenthal, 2004
Ochrotrichia ixtlahuaca Bueno-Soria & Holzenthal, 2004
Ochrotrichia jolandae Bueno-Soria & Holzenthal, 2008
Ochrotrichia leona Bueno-Soria & Holzenthal, 2004
Ochrotrichia longispina Bueno-Soria & Holzenthal, 2004

Ochrotrichia membrana Bueno-Soria & Holzenthal, 1998
Ochrotrichia patulosa Wasmund & Holzenthal, 2007
Ochrotrichia quasi Bueno-Soria & Holzenthal, 2008
Ochrotrichia quebrada Bueno-Soria & Holzenthal, 1998
Ochrotrichia quinealensis Bueno-Soria & Holzenthal, 1998
Ochrotrichia ramona Bueno-Soria & Holzenthal, 1998
Ochrotrichia regiomontana Bueno-Soria & Holzenthal, 2004
Ochrotrichia silva Bueno-Soria & Holzenthal, 1998
Ochrotrichia spina Bueno-Soria & Holzenthal, 2004
Ochrotrichia spinula Bueno-Soria & Holzenthal, 2004
Ochrotrichia spira Thomson & Holzenthal, 2012
Ochrotrichia unicornia Bueno-Soria & Holzenthal, 2004
Ochrotrichia vieja Bueno-Soria & Holzenthal, 1998
Ochrotrichia yavesia Bueno-Soria & Holzenthal, 2004
Orinocotrichia calcariga Harris, Flint & Holzenthal, 2002
Oxyethira apinolada Holzenthal & Harris, 1992
Oxyethira bettyae Thomson & Holzenthal, 2012
Oxyethira cuernuda Holzenthal & Harris, 1992
Oxyethira culebra Holzenthal & Harris, 1992
Oxyethira espinada Holzenthal & Harris, 1992
Oxyethira hilosa Holzenthal & Harris, 1992
Oxyethira itascaae Monson & Holzenthal, 1993
Oxyethira kingi Holzenthal & Kelley, 1983
Oxyethira quiramae Thomson & Holzenthal, 2012
Oxyethira rareza Holzenthal & Harris, 1992
Oxyethira redunca Thomson & Holzenthal, 2012
Oxyethira sencilla Holzenthal & Harris, 1992
Oxyethira sierruca Holzenthal & Harris, 1992
Oxyethira tica Holzenthal & Harris, 1992
Rhyacopsyche benwa Wasmund & Holzenthal, 2007
Rhyacopsyche bulbosa Wasmund & Holzenthal, 2007
Rhyacopsyche colei Wasmund & Holzenthal, 2007
Rhyacopsyche colombiana Wasmund & Holzenthal, 2007
Rhyacopsyche colubrinosa Wasmund & Holzenthal, 2007
Rhyacopsyche dikrosa Wasmund & Holzenthal, 2007
Rhyacopsyche flinti Wasmund & Holzenthal, 2007
Rhyacopsyche hasta Wasmund & Holzenthal, 2007
Rhyacopsyche intraspina Wasmund & Holzenthal, 2007
Rhyacopsyche rhamphisa Wasmund & Holzenthal, 2007
Rhyacopsyche tanylobosa Wasmund & Holzenthal, 2007
Tizatetrichia costaricensis Harris, Flint & Holzenthal, 2002
Tupiniquintrichia procera Thomson & Holzenthal, 2015

Lepidostomatidae

Lepidostoma chiriquiense Holzenthal & Strand, 1992

Lepidostoma ectopium Holzenthal & Strand, 1992

Lepidostoma polylepidum Holzenthal & Strand, 1992

Lepidostoma tapanti Holzenthal & Strand, 1992

Lepidostoma xolotl Holzenthal & Strand, 1992

Leptoceridae

Adicella uwuensis Andersen & Holzenthal, 2002

Amazonatolica hamadae Holzenthal & Oliveira Pes, 2004

Amphoropsyche aragua Holzenthal, 1985

Amphoropsyche ayura Holzenthal, 1985

Amphoropsyche carchi Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2017

Amphoropsyche cauca Holzenthal, 1985

Amphoropsyche choco Holzenthal, 1985

Amphoropsyche flinti Holzenthal, 1985

Amphoropsyche matsigenka Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2017

Amphoropsyche napo Holzenthal, 1985

Amphoropsyche quebrada Holzenthal, 1985

Amphoropsyche real Holzenthal, 2016

Amphoropsyche refugia Holzenthal, 1985

Amphoropsyche spinifera Holzenthal, 1986

Amphoropsyche stellata Holzenthal, 1985

Amphoropsyche tandayapa Holzenthal & Rázuri-Gonzales, 2011

Atanatolica acuminata Holzenthal, 1988

Atanatolica andina Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2018

Atanatolica angulata Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2018

Atanatolica aurea Holzenthal, 1988

Atanatolica caldas Holzenthal, 1988

Atanatolica choco Holzenthal, 1988

Atanatolica cotopaxi Holzenthal, 1988

Atanatolica curvata Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2018

Atanatolica decouxi Rázuri-Gonzales, Holzenthal & Ríos-Touma, 2018

Atanatolica flinti Holzenthal, 2018

Atanatolica manabi Holzenthal, 2018

Atanatolica moselyi Denning & Holzenthal, 1988

Atanatolica muyupampa Holzenthal, 2018

Atanatolica nigra Holzenthal, 2018

Atanatolica nivea Holzenthal, 2018

Atanatolica panamensis Holzenthal, 2018

Atanatolica penai Holzenthal, 2018

- Atanatolica zongo* Holzenthal, 2018
Fernandoschmidia amudita Holzenthal & Andersen, 2007
Fernandoschmidia aramaniya Holzenthal & Andersen, 2007
Grumichella blahniki Calor & Holzenthal, 2016
Grumichella boraceia Calor & Holzenthal, 2016
Grumichella cressae Calor & Holzenthal, 2016
Grumichella jureia Calor & Holzenthal, 2016
Grumichella leccii Calor & Holzenthal, 2016
Grumichella muelleri Calor & Holzenthal, 2016
Grumichella paprockii Calor & Holzenthal, 2016
Grumichella parati Calor & Holzenthal, 2016
Grumichella trujilloi Calor & Holzenthal, 2016
Nectopsyche exophthalma Holzenthal, 1995
Nectopsyche monticola Holzenthal, 1995
Nectopsyche navasi Holzenthal, 2000
Nectopsyche onyx Holzenthal, 1995
Nectopsyche ortizi Holzenthal, 1995
Nectopsyche padrenavasi Holzenthal, 2000
Nectopsyche tapanti Holzenthal, 1995
Nectopsyche tuanis Holzenthal, 1995
Nectopsyche utleyorum Holzenthal, 1995
Neothripsodes anomalus Holzenthal, 1989
Neotriplectides froehlichii Holzenthal, 1997
Notalina brasiliiana Holzenthal, 1986
Notalina cipo Holzenthal, 1986
Notalina froehlichii Calor & Holzenthal, 2006
Notalina hamiltoni Holzenthal, 1986
Notalina matthiasi Holzenthal, 1986
Notalina morsei Holzenthal, 1986
Notalina nanay Holzenthal, 1986
Notalina paulista Calor & Holzenthal, 2006
Notalina roraima Holzenthal, 1986
Oecetis acciptrina Blahnik & Holzenthal, 2014
Oecetis acuticlasper Quinteiro & Holzenthal, 2017
Oecetis agosta Blahnik & Holzenthal, 2014
Oecetis angularis Blahnik & Holzenthal, 2014
Oecetis apache Blahnik & Holzenthal, 2014
Oecetis bidigitata Quinteiro & Holzenthal, 2017
Oecetis blahniki Quinteiro & Holzenthal, 2017
Oecetis calori Quinteiro & Holzenthal, 2017
Oecetis campana Blahnik & Holzenthal, 2014
Oecetis carinata Quinteiro & Holzenthal, 2017
Oecetis cassicoleata Quinteiro & Holzenthal, 2017

Oecetis constricta Blahnik & Holzenthal, 2014
Oecetis flinti Quinteiro & Holzenthal, 2017
Oecetis gibbosa Quinteiro & Holzenthal, 2017
Oecetis hastapulla Quinteiro & Holzenthal, 2017
Oecetis houghtoni Blahnik & Holzenthal, 2014
Oecetis licina Quinteiro & Holzenthal, 2017
Oecetis machaera Quinteiro & Holzenthal, 2017
Oecetis maritza Blahnik & Holzenthal, 2014
Oecetis mexicana Blahnik & Holzenthal, 2014
Oecetis patula Blahnik & Holzenthal, 2014
Oecetis pertica Quinteiro & Holzenthal, 2017
Oecetis plenuspinosa Quinteiro & Holzenthal, 2017
Oecetis protrusa Blahnik & Holzenthal, 2014
Oecetis quasipunctata Quinteiro & Holzenthal, 2017
Oecetis sordida Blahnik & Holzenthal, 2014
Oecetis tumida Blahnik & Holzenthal, 2014
Oecetis uncata Blahnik & Holzenthal, 2014
Oecetis verrucula Blahnik & Holzenthal, 2014
Osflintia manu Calor & Holzenthal, 2008
Setodes arenatus Holzenthal, 1982
Setodes dixiensis Holzenthal, 1982
Tagalopsyche apratita Holzenthal & Andersen, 2007
Tagalopsyche jolandae Holzenthal & Andersen, 2007
Tagalopsyche kjaerandseni Holzenthal & Andersen, 2007
Tagalopsyche udagama Holzenthal & Andersen, 2007
Triaenodes acanthus Holzenthal & Andersen, 2004
Triaenodes akosua Andersen & Holzenthal, 2001
Triaenodes akua Andersen & Holzenthal, 2002
Triaenodes amma Andersen & Holzenthal, 2001
Triaenodes bulupendek Andersen & Holzenthal, 1999
Triaenodes chirripo Holzenthal & Andersen, 2004
Triaenodes clauseni Holzenthal & Andersen, 2004
Triaenodes cuyotenango Holzenthal & Andersen, 2004
Triaenodes flintorum Holzenthal & Andersen, 2004
Triaenodes guadaloupe Holzenthal & Andersen, 2004
Triaenodes hansii Pauls, Holzenthal & Ngera, 2010
Triaenodes hodgesi Holzenthal & Andersen, 2004
Triaenodes hornitos Holzenthal & Andersen, 2004
Triaenodes kilambe Holzenthal & Andersen, 2004
Triaenodes kofi Andersen & Holzenthal, 2002
Triaenodes kwabena Andersen & Holzenthal, 2002
Triaenodes kwadwo Andersen & Holzenthal, 2001
Triaenodes kwaku Andersen & Holzenthal, 2002
Triaenodes kwame Andersen & Holzenthal, 2002

Triaenodes kwasi Andersen & Holzenthal, 2002
Triaenodes malickyi Pauls, Holzenthal & Ngera, 2010
Triaenodes mexicanus Holzenthal & Andersen, 2004
Triaenodes moncho Holzenthal & Andersen, 2004
Triaenodes morai Holzenthal & Andersen, 2004
Triaenodes nicaraguensis Holzenthal & Andersen, 2004
Triaenodes oaxacensis Holzenthal & Andersen, 2004
Triaenodes tajo Holzenthal & Andersen, 2004
Triaenodes talamanca Holzenthal & Andersen, 2004
Triaenodes tapanti Holzenthal & Andersen, 2004
Triaenodes tico Holzenthal & Andersen, 2004
Triaenodes tuxtlenensis Holzenthal & Andersen, 2004
Triaenodes woldai Holzenthal & Andersen, 2004
Triplectides chilensis Holzenthal, 1988
Triplectides flintorum Holzenthal, 1988
Triplectides misionensis Holzenthal, 1988
Triplectides neblinus Holzenthal, 1988
Triplectides neotropicus Holzenthal, 1988
Triplectides nevadus Holzenthal, 1988
Triplectides tepui Holzenthal, 1988
Triplectides ultimus Holzenthal, 1988

Philopotamidae

Chimarra amica Blahnik & Holzenthal, 1992
Chimarra antheae Blahnik, Holzenthal & Huisman, 2009
Chimarra caduca Blahnik, Holzenthal & Huisman, 2009
Chimarra calori Blahnik & Holzenthal, 2012
Chimarra cauca Blahnik & Holzenthal, 2012
Chimarra chanchuluni Blahnik, Holzenthal & Huisman, 2009
Chimarra colmillo Blahnik & Holzenthal, 1992
Chimarra curvipenis Blahnik & Holzenthal, 2012
Chimarra cuspidata Blahnik, Holzenthal & Huisman, 2009
Chimarra cygnus Blahnik, Holzenthal & Huisman, 2009
Chimarra danumensis Blahnik, Holzenthal & Huisman, 2009
Chimarra dejongi Blahnik, Holzenthal & Huisman, 2009
Chimarra denticula Blahnik, Holzenthal & Huisman, 2009
Chimarra desirae Blahnik & Holzenthal, 2012
Chimarra devogeli Blahnik, Holzenthal & Huisman, 2009
Chimarra drepane Blahnik, Holzenthal & Huisman, 2009
Chimarra fuilianae Blahnik, Holzenthal & Huisman, 2009
Chimarra guanacasteca Blahnik & Holzenthal, 1992
Chimarra gyrospina Blahnik, Holzenthal & Huisman, 2009
Chimarra inchoata Blahnik & Holzenthal, 2012

- Chimarra jannekae* Blahnik, Holzenthal & Huisman, 2009
Chimarra janzeni Blahnik & Holzenthal, 1992
Chimarra jemima Blahnik & Holzenthal, 1992
Chimarra karlijnae Blahnik, Holzenthal & Huisman, 2009
Chimarra kinabaluensis Blahnik, Holzenthal & Huisman, 2009
Chimarra lambi Blahnik, Holzenthal & Huisman, 2009
Chimarra lata Blahnik & Holzenthal, 1992
Chimarra latiforceps Blahnik & Holzenthal, 2012
Chimarra liwaguensis Blahnik, Holzenthal & Huisman, 2009
Chimarra longiterga Blahnik & Holzenthal, 1992
Chimarra munozi Blahnik & Holzenthal, 1992
Chimarra nicehuh Blahnik & Holzenthal, 2012
Chimarra noloyan Blahnik, Holzenthal & Huisman, 2009
Chimarra noohi Blahnik, Holzenthal & Huisman, 2009
Chimarra onchyrrhina Blahnik & Holzenthal, 2012
Chimarra paraortiziana Blahnik & Holzenthal, 1992
Chimarra peineta Blahnik & Holzenthal, 1992
Chimarra phillipsae Blahnik, Holzenthal & Huisman, 2009
Chimarra physanoton Blahnik, Holzenthal & Huisman, 2009
Chimarra pollex Blahnik & Holzenthal, 1992
Chimarra preapicalis Blahnik, Holzenthal & Huisman, 2009
Chimarra scolops Blahnik, Holzenthal & Huisman, 2009
Chimarra silausilau Blahnik, Holzenthal & Huisman, 2009
Chimarra sinitorum Blahnik, Holzenthal & Huisman, 2009
Chimarra solisi Blahnik & Holzenthal, 1992
Chimarra soroa Blahnik & Holzenthal, 2012
Chimarra stenodactylus Blahnik, Holzenthal & Huisman, 2009
Chimarra sunima Blahnik & Holzenthal, 2012
Chimarra vantoli Blahnik, Holzenthal & Huisman, 2009
Chimarra vanwelzeni Blahnik, Holzenthal & Huisman, 2009
Chimarra ventritropis Blahnik, Holzenthal & Huisman, 2009
Chimarra virgencita Blahnik & Holzenthal, 1992
Chimarra xiphosella Blahnik, Holzenthal & Huisman, 2009
Chimarra yanura Blahnik & Holzenthal, 1992
Chimarrhodella choco Holzenthal, Blahnik & Ríos-Touma, 2018
Chimarrhodella costaricensis Blahnik & Holzenthal, 1992
Chimarrhodella flinti Blahnik & Holzenthal, 1992
Chimarrhodella pilcopata Blahnik & Holzenthal, 1992
Chimarrhodella tapanti Blahnik & Holzenthal, 1992
Chimarrhodella tobagoensis Blahnik & Holzenthal, 1992
Hydrobiosella andina Holzenthal, Blahnik & Ríos-Touma, 2018
Wormaldia andrea Munoz-Quesada & Holzenthal, 2015
Wormaldia anhelitus Munoz-Quesada & Holzenthal, 2015
Wormaldia araujoi Munoz-Quesada & Holzenthal, 2015

Wormaldia aymara Munoz-Quesada & Holzenthal, 2015
Wormaldia barbai Munoz-Quesada & Holzenthal, 2015
Wormaldia birneyi Munoz-Quesada & Holzenthal, 2008
Wormaldia bolivari Munoz-Quesada & Holzenthal, 2015
Wormaldia boteroi Munoz-Quesada & Holzenthal, 2015
Wormaldia buenorum Munoz-Quesada & Holzenthal, 2015
Wormaldia calderonae Munoz-Quesada & Holzenthal, 2015
Wormaldia chrismark Munoz-Quesada & Holzenthal, 2015
Wormaldia clauseni Munoz-Quesada & Holzenthal, 2008
Wormaldia contrerasi Munoz-Quesada & Holzenthal, 2015
Wormaldia cornuta Bueno-Soria & Holzenthal, 1986
Wormaldia dachiardiorum Munoz-Quesada & Holzenthal, 2015
Wormaldia eberhardi Munoz-Quesada & Holzenthal, 2015
Wormaldia flinti Munoz-Quesada & Holzenthal, 2015
Wormaldia francovilla Munoz-Quesada & Holzenthal, 2015
Wormaldia fredycarol Munoz-Quesada & Holzenthal, 2015
Wormaldia gallardoi Munoz-Quesada & Holzenthal, 2015
Wormaldia gonzalezae Munoz-Quesada & Holzenthal, 2015
Wormaldia hedamafera Munoz-Quesada & Holzenthal, 2015
Wormaldia imberti Munoz-Quesada & Holzenthal, 2015
Wormaldia imbrialis Holzenthal, Blahnik & Ríos-Touma, 2018
Wormaldia inca Munoz-Quesada & Holzenthal, 2015
Wormaldia isela Munoz-Quesada & Holzenthal, 2015
Wormaldia juarox Munoz-Quesada & Holzenthal, 2015
Wormaldia lauglo Munoz-Quesada & Holzenthal, 2015
Wormaldia luma Bueno-Soria & Holzenthal, 1986
Wormaldia machadorum Munoz-Quesada & Holzenthal, 2015
Wormaldia maesi Munoz-Quesada & Holzenthal, 2015
Wormaldia menchuae Munoz-Quesada & Holzenthal, 2015
Wormaldia monsonorum Munoz-Quesada & Holzenthal, 2015
Wormaldia navarroae Munoz-Quesada & Holzenthal, 2015
Wormaldia paprockevi Munoz-Quesada & Holzenthal, 2015
Wormaldia savoriorum Munoz-Quesada & Holzenthal, 2015
Wormaldia tarasca Bueno-Soria & Holzenthal, 1986
Wormaldia tocajoma Munoz-Quesada & Holzenthal, 2015
Wormaldia trondi Munoz-Quesada & Holzenthal, 2015
Wormaldia tupacamara Munoz-Quesada & Holzenthal, 2015
Wormaldia zunigae Munoz-Quesada & Holzenthal, 2015
Wormaldia zunigarceorum Munoz-Quesada & Holzenthal, 2015

Polycentropodidae

Cernotina antonina Holzenthal & de Almeida, 2003
Cernotina lazzarii Holzenthal & de Almeida, 2003

Cernotina tiputini Camargos, Ríos-Touma & Holzenthal, 2017
Cernotina waorani Camargos, Ríos-Touma & Holzenthal, 2017
Polycentropus acinaciformis Hamilton & Holzenthal, 2011
Polycentropus amphirhamphus Hamilton & Holzenthal, 2011
Polycentropus ancistrus Hamilton & Holzenthal, 2011
Polycentropus boraceia Hamilton & Holzenthal, 2011
Polycentropus caaete Hamilton & Holzenthal, 2011
Polycentropus cachoeira Hamilton & Holzenthal, 2011
Polycentropus carioca Hamilton & Holzenthal, 2011
Polycentropus carolae Hamilton & Holzenthal, 2011
Polycentropus cheliceratus Hamilton & Holzenthal, 2011
Polycentropus cipoensis Hamilton & Holzenthal, 2011
Polycentropus cressae Hamilton & Holzenthal, 2005
Polycentropus fasthi Holzenthal & Hamilton, 1988
Polycentropus fluminensis Hamilton & Holzenthal, 2011
Polycentropus fortispinus Holzenthal & Hamilton, 1988
Polycentropus froehlichi Hamilton & Holzenthal, 2011
Polycentropus galharada Hamilton & Holzenthal, 2011
Polycentropus graciosa Hamilton & Holzenthal, 2011
Polycentropus inusitatus Hamilton & Holzenthal, 2011
Polycentropus itatiaia Hamilton & Holzenthal, 2011
Polycentropus minero Hamilton & Holzenthal, 2011
Polycentropus neblinensis Hamilton & Holzenthal, 2005
Polycentropus nebulosus Holzenthal & Hamilton, 1988
Polycentropus paprockii Hamilton & Holzenthal, 2011
Polycentropus quadricuspidis Hamilton & Holzenthal, 2005
Polycentropus rosalsae Hamilton & Holzenthal, 2011
Polycentropus santateresae Hamilton & Holzenthal, 2011
Polycentropus silex Hamilton & Holzenthal, 2005
Polycentropus soniae Hamilton & Holzenthal, 2011
Polycentropus thaxtoni Hamilton & Holzenthal, 1986
Polycentropus tripui Hamilton & Holzenthal, 2011
Polycentropus urubici Holzenthal & De Almeida, 2003
Polycentropus verruculus Hamilton & Holzenthal, 2011
Polycentropus virginiae Hamilton & Holzenthal, 2011
Polycentropus volcanus Holzenthal & Hamilton, 1988
Polycentropus zurqui Holzenthal & Hamilton, 1988
Polyplectropus adamsae Chamorro & Holzenthal, 2010
Polyplectropus alatespinus Chamorro & Holzenthal, 2010
Polyplectropus amazonicus Chamorro & Holzenthal, 2010
Polyplectropus andinensis Chamorro & Holzenthal, 2010
Polyplectropus beccus Hamilton & Holzenthal, 2005
Polyplectropus blahniki Chamorro & Holzenthal, 2010

Polyplectropus bolivianus Chamorro & Holzenthal, 2010
Polyplectropus brasiliensis Chamorro & Holzenthal, 2010
Polyplectropus brborichorum Chamorro & Holzenthal, 2010
Polyplectropus clauseni Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus colombianus Chamorro & Holzenthal, 2010
Polyplectropus corniculatus Chamorro & Holzenthal, 2010
Polyplectropus cressae Chamorro & Holzenthal, 2010
Polyplectropus cuzcoensis Chamorro & Holzenthal, 2010
Polyplectropus ecuadoriensis Chamorro & Holzenthal, 2010
Polyplectropus exilis Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus flintorum Chamorro & Holzenthal, 2010
Polyplectropus gaesum Chamorro & Holzenthal, 2010
Polyplectropus guyanae Chamorro & Holzenthal, 2010
Polyplectropus hollyae Chamorro & Holzenthal, 2010
Polyplectropus hymenochilus Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus hystricosus Chamorro & Holzenthal, 2010
Polyplectropus insularis Chamorro & Holzenthal, 2010
Polyplectropus juliae Chamorro & Holzenthal, 2010
Polyplectropus kanukarum Chamorro & Holzenthal, 2010
Polyplectropus kylistos Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus maculatus Chamorro & Holzenthal, 2010
Polyplectropus manuensis Chamorro & Holzenthal, 2010
Polyplectropus matatlanticus Chamorro & Holzenthal, 2010
Polyplectropus minensium Chamorro & Holzenthal, 2010
Polyplectropus novafriburgensis Chamorro & Holzenthal, 2010
Polyplectropus paradelphae Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus perpendicularis Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus peruvianus Chamorro & Holzenthal, 2010
Polyplectropus petrae Chamorro & Holzenthal, 2010
Polyplectropus pratherae Chamorro & Holzenthal, 2010
Polyplectropus profaupar Holzenthal & De Almeida, 2003
Polyplectropus puyoensis Chamorro & Holzenthal, 2010
Polyplectropus robertsonae Chamorro & Holzenthal, 2010
Polyplectropus rodmani Chamorro & Holzenthal, 2010
Polyplectropus rondoniensis Chamorro & Holzenthal, 2010
Polyplectropus tragularius Chamorro & Holzenthal, 2010
Polyplectropus tripunctatum Chamorro & Holzenthal, 2010
Polyplectropus venezolanus Chamorro & Holzenthal, 2010
Polyplectropus woldai Chamorro & Holzenthal, 2010
Polyplectropus yolandae Chamorro-Lacayo & Holzenthal, 2004
Polyplectropus zamoranoensis Chamorro & Holzenthal, 2010
Polyplectropus zuliae Chamorro & Holzenthal, 2010

Sericostomatidae

Notidobiella amazoniana Holzenthal & Blahnik, 2011

Notidobiella brasiliiana Holzenthal & Blahnik, 2011

Notidobiella ecuadorensis Holzenthal & Blahnik, 2011

Xiphocentronidae

Machairocentron chorotegae Vilarino & Holzenthal, 2020

Machairocentron eugeniarguedasae Vilarino & Holzenthal, 2020

Machairocentron kalinae Vilarino & Holzenthal, 2020

Xiphocentron moncho Munoz-Quesada & Holzenthal, 1997

Species named after R.W. Holzenthal

Alisotrichia holzenthali Santos, 2011

Alterosa holzenthali Blahnik, 2005

Anchitrichia holzenthali Oláh & Flint, 2012

Chimarra holzenthali Lago & Harris, 1987

Corydalus ralphi Martins, Azevêdo, Hamada & Contreras, 2022

Helicopsyche holzenthali Johanson, 2003

Helicopsyche ralphi Cavalcante-Silva, Pereira & Calor, 2022

Hydroptila holzenthali Sykora & Harris, 1994

Kisaura holzenthali Phander & Saini, 2014

Leucotrichia holzenthali Thomson, Armitage & Harris, 2022

Marilia holzenthali Bueno-Soria & Rojas-Ascencio, 2004

Metalype holzenthali (Schmid, 1997)

Neoathripsodes holzenthali Dias, Quinteiro & Calor, 2015

Notalina (*Neonotalina*) *ralphi* Silva Pereira, Oliveira, Robson Desidério, Calor & Hamada, 2022

Phylloicus holzenthali Prather, 2003

Polycentropus holzenthali Bueno-Soria & Hamilton, 1986

Silvatares holzenthali Rázuri-Gonzales, Ngera & Pauls, 2022

Smicridea holzenthali Flint & Denning, 1989

Smicridea ralphi Almeida & Flint, 2002

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New species of the genus *Chimarra* Stephens from Africa (Trichoptera, Philopotamidae) and characterization of the African groups and subgroups of the genus

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Abstract

This paper is primarily based on collections in Tanzania and Ghana in 1990–1991 and 1991–1994, respectively. In all, 46 species of *Chimarra* were collected, 31 of them new species. All these species are illustrated or re-illustrated and described in the paper. Additionally, five species from Africa from collections in Illinois and Minnesota, four of them new, are included. This provided the incentive to review the species of *Chimarra* from the African subregion and assign the majority of them to species groups and subgroups. In the process, several species were synonymized. In all 147 valid species are recognized, of which 51 are treated in this paper. Two major species groups are recognized for Africa, the *marginata* Group and the *georgensis* Group. The former is based on the type species for the genus; this is the first formal characterization of this group, as distinct from other species groups in the subgenus. Mainland African species in the *marginata* Group mostly fall into four large species-diverse subgroups, but a number of smaller subgroups are also recognized. Membership in these subgroups is specified for the majority of African species and characters defining the subgroups informally discussed. The *georgensis* Group includes a single Asian species and nine previously described African species. They are assigned to two subgroups, one newly recognized in this paper. Several additional species were considered unassigned to subgroup within the *georgensis* Group. The majority of the new species described in this paper belong to the *georgensis* Group.

Keywords

Democratic Republic of the Congo, Ghana, new synonyms, South Africa, species groups, species subgroups, Tanzania

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Introduction

Chimarra is currently the largest genus in the order Trichoptera, with approximately 950 species, or just under 6% of the diversity for the entire order. It is distributed on all major continents, except Antarctica, and divided into four subgenera, three of them endemic to the New World. New World subgenera were comprehensively treated in several relatively recent revisions (Blahnik 1997, 2002; Flint 1998). The fourth and

nominate subgenus is found throughout the Old World, including Africa, Asia, and the Australian Region, including many of the Pacific islands, and also has a substantial radiation in the New World in both North and South America, except for the Chilean subregion. The type species, *Chimarra marginata* (Linnaeus), is the only species of the genus widely distributed in Europe, and also occurs in northern Africa. New World members of the subgenus were treated in a revision by Blahnik (1998). Old World species have not been comprehensively revised, but several valuable resources are available for identification of species in various regional faunas [southeast Asia: Malicky (2010); Australia and New Guinea: Cartwright (2002, 2020); the Pacific islands: Johanson and Espeland (2010), Johanson et al. (2011), Johanson and Oláh (2012)]. Also of inestimable value is a searchable online catalogue of described species for the entire order Trichoptera (Morse 2021). Confirmation for the general monophyly of the subgenera, including the nominate subgenus, was provided by two independent molecular analyses (Kjer et al. 2014; Wahlberg and Johanson 2014).

Currently, 115 species of *Chimarra* are described from Africa and Madagascar. Of these, three are brought into synonymization in the current work and an additional 35 new species are described. Undoubtedly, many additional species remain to be described. Most of the known species were described one or a few at a time, in a number of papers, some obscure and difficult to obtain. The general quality of the descriptions and illustrations for many of the species is not high; many species lack comparative diagnoses and identification may be difficult or uncertain. The most useful compilation of the literature, not only for *Chimarra*, but for the entire African fauna of Trichoptera, was provided by Tobias and Tobias (2008), as an online resource that is no longer updated, but is archived at (<http://trichoptera.senckenberg.de/Trichoptera%20africana/introduction.htm>). This mostly contains species illustrations without the accompanying descriptions, but literature references are included, as well as comments on possible synonyms. Several recent papers treating the African fauna have begun revisionary work on selected groups within the genus *Chimarra*, or enumeration of related taxa (Gibon 2015, 2017, 2018), but the majority of African and Madagascan taxa have not been so treated. A more comprehensive, but still preliminary, contribution to this endeavor can be found in Table 1. However, some species are only known from females or have illustrations or descriptions too incomplete to be useful in making assessments; they are included at the end of Table 1.

Background

Most of the material on which this paper is based was collected during two projects by the Department of Natural History, University Museum of Bergen, Norway (former Museum of Zoology, University of Bergen). The field work during the first project targeted the fauna in the mountain rainforests in the West Usambara Mountains in northeastern Tanzania. The study area was located near the Mazumbai Forest Reserve, where caddisflies were collected in 1990 and 1991 along the Kaputu Stream (Andersen and Johanson 1993) (Fig. 1). The stream originates at 1860 m above sea level and runs

down to a marshy area at ~ 1400 m altitude. Four relatively large waterfalls are located along the stream, but in most stretches the water current is moderate. The stream is surrounded by nearly undisturbed rain forest with trees that can reach a height of 50 m.

The West Usambara Mountains belong to the Eastern Arc, a chain of mountains that stretch from the Taita Hills in Kenya in the north, south to the Udzungwa and Mahenge Mountains in Tanzania. They were formed at least one hundred million years ago along a fault lying to the east of the East African Rift, which is a more recent structure. Approximately thirty million years ago, all this area was covered by extensive rainforest. During a period, some ten million years ago, when the climate was cooler and drier, the lowland forests were converted to savannah, leaving the mountain ranges as “islands” where the tropical forests continued to flourish, fed by moisture from the Indian Ocean. This isolation of each mountain range has led to a great deal of endemism, and a very diverse flora and fauna (Burgess et al. 2007; Mumbi et al. 2017).

Andersen and Johanson (1993) estimated that more than 50 species of Trichoptera were collected along the Kaputu Stream. Most unexpected was the first species of the family Beraeidae, *Notoernodes inornatus* Andersen & Kjærandsen, taken in the Afrotropical Region (Andersen and Kjærandsen 1997). The Hydroptilidae have been treated in several articles (Wells and Andersen 1995, 1996; Kjærandsen 2004) and the genus *Tangatrachia* Wells & Andersen was erected based on material from the project. Further some Lepidostomatidae (Weaver and Andersen 1995), Ecnomidae (Andersen and Kjærandsen 2005), and Helicopsychidae (Johanson 1993) have been treated.



Figure 1. Malaise trap across Kaputu Stream at 1535 m altitude in the Mazumbai Forest Reserve in the West Usambara Mountains, northeastern Tanzania (Photo: Trond Andersen).

During the second project, Trichoptera were collected in most provinces of Ghana from 1991 to 1998 (see Kjærandsen and Andersen 1997). In Ghana, three major vegetation zones are recognized, a belt of tropical rainforest along the southern coast, a transition zone in central Ghana, while northern Ghana is covered with savannah. The forest in southern Ghana belong to the Guinean forests of West Africa, a belt of tropical moist broadleaf forests stretching along the coast of West Africa from Sierra Leone and Guinea in the west to the Sanaga River in Cameroon in the east. The Dahomey Gap, a region of savannah and dry forest in Togo and Benin, divides the Guinean forests into the Upper Guinean forests and Lower Guinean forests. Hall and Swaine (1976) compiled a detailed vegetation map of the rainforest zone in Ghana, showing four main types of forest according to decreasing levels of precipitation from the coast moving inland.

Caddisflies were collected in several localities in the southern, forested part of Ghana. The Ankasa Conservation Area is situated in the Western Region in southwestern Ghana near the border to the Ivory Coast. The conservation area is ~ 500 square kilometers and incorporates the Nini Suhien National Park in the north and the Ankasa Forest Reserve in the south. The altitude varies from 35 m to 170 m and there are three larger rivers and many smaller streams in the area (Fig. 2). The forest is classified as wet evergreen forest (Hall and Swaine 1976) and is an ancient rainforest with the highest biodiversity in Ghana (UICN/PACO 2010).



Figure 2. Malaise trap across a small tributary to Ankasa River in the wet evergreen forest in Ankasa Forest Reserve, southwestern Ghana (Photo: Jostein Kjærandsen).

The Kakum National Park is situated in the Central Region in southern Ghana. It was established as a reserve in 1931 and received the status as a national park in 1992. The Park covers 375 square kilometers and is generally flat with only a few undulating hills ranging 150–250 m above sea level. The forest is classified as moist semi-deciduous forest (Hall and Swaine 1976).

Most of the material treated here is from a study of the caddisfly community along a headwater stream in the Agumatsa Wildlife Sanctuary in the Volta Region, situated in the transition zone in the eastern part of Ghana (Andersen and Kjærandsen 2001; Kjærandsen 2005). The sanctuary lies in the southwestern part of the Togo Mountains where it embraces a ravine-riverine forest valley with rather steep sides. The Agumatsa-Nubui headwater stream runs through the valley originating at ~ 750 m altitude on the top of a mountain ridge and falls 250 m, mainly in two large waterfalls, into the bottom of the valley at ~ 350 m altitude (Fig. 3).

Northern Ghana is covered with savannah and is crossed by several large rivers flowing southwards. Caddisflies were mainly collected at two of these rivers, the Black Volta and Oti rivers. The Black Volta originates in Burkina Faso and in Ghana it forms the border with Ivory Coast before it joins the White Volta. The Oti River has its headwaters in Benin and Burkina Faso and flows through Benin and Togo before it joins the Volta River in Ghana.

Kjærandsen and Andersen (1997) listed eight *Chimarra* species from Ghana, today 34 species are known from the country (Table 1). Other taxa have also been described based on the material collected in Ghana during the project, among them the tribe Blyzophilini (Leptoceridae) based on *Blyzophilus dorsohamatus* Andersen & Kjærandsen collected in the Ankasa Conservation Area (Andersen et al. 1999). Of other Leptoceridae genera *Triaenodes* (Andersen and Holzenthal 2001, 2002a), *Adicella* (Andersen and Holzenthal 2002b), and *Tagalopsyche* (Holzenthal and Andersen 2007) have been treated. Of Hydroptilidae two new genera, *Wlitrichia* Kjærandsen and *Cyclopsiella* Kjærandsen were erected based on material from the Ankasa Conservation Area (Kjærandsen 1997), and new species of *Dahtrichia* (Kjærandsen 2004) and *Jabitrichia* (Kjærandsen and Andersen 2002) have been added. Further, new species of Polycentropodidae (Kjærandsen and Netland 1997), Ecnomidae (Andersen and Kjærandsen 2005), and Lepidostomatidae (Weaver and Andersen 1995) have also been described.

Materials and methods

Because of the frequent use of species group names to refer to taxa in the subgenus *Chimarra*, in different regions where it occurs, we have adopted a more formal convention. Hopefully, it will not be found confusing. This includes the use of the species epithet of the first species described in a group or subgroup, followed by use of “Group” or “subgroup.” The difference in capitalization is used to diminish confusion between the two divisions, and because the same species name may be used to characterize both a species group and subgroup. Only formal “Group” names established in this paper are



Figure 3. The lower waterfall of Agumatsa-Nubui headwater stream in the Agumatsa Wildlife Sanctuary, eastern Ghana (Photo: Jostein Kjæranden).

capitalized. In this paper, four major species groups are recognized within the subgenus *Chimarra*: the *marginata* Group, the *georgensis* Group, the *tsudai* Group, and the *minuta* Group. The last two groups are restricted to Asia. The *georgensis* Group is predominantly found in Africa; a single Asian species is currently assigned to the group (Blahnik et al. 2012), and it is possible that others may occur. The *marginata* Group is found worldwide, throughout the distribution of the subgenus. It encompasses most of the species group names previously proposed for the subgenus, from various parts of the world. These names would be considered subgroups within the *marginata* Group, as the group name is used here. A few taxa, in various regions, may be difficult to place within this structure. They should be considered as unassigned to species group, until their relationships are better established. Subgroup names, for the most part, are regionally restricted.

The fieldwork during the project in Tanzania targeted the fauna in the mountain rainforests in the West Usambara Mountains in northeastern Tanzania. The study area is located near the Mazumbai Forest Reserve, where caddisflies were collected along the Kaputu Stream (Andersen and Johanson 1993). Malaise traps were situated for shorter or longer periods at 11 sites along the stream between late October 1990 and early February 1991. The material was preserved directly in a container with ethylene-glycol and later transferred to 80% ethanol. In addition, caddisflies were collected with sweep nets, both in the Mazumbai Forest Reserve, as well as along other streams and rivers in the West Usambara Mountains. One species was also taken on the campus of the Teachers college in Morogoro.

During the second project, Trichoptera were collected in most provinces of Ghana from 1991 to 1998 (see Kjærandsen and Andersen 1997); only the material collected between 1991 and 1994 is included in the present study. The Ankasa Conservation Area was visited repeatedly in 1993 and we collected at several sites in the southern part of the reserve. The Kakum National Park was visited in the autumn of 1994, and we collected mainly near the main entrance. In the Agumatsa Wildlife Sanctuary caddis flies were collected at 12 sites along a 5 km stretch of the Agumatsa-Nubui head-water stream in spring and autumn 1993 (Kjærandsen 2005). In northern Ghana we collected at the Black Volta and Oti rivers in 1991 to 1993.

During the project in Ghana, caddisflies were mainly collected in light traps, Malaise traps, and with sweep nets and preserved in 80% ethanol. The females were tentatively associated with the males based on their co-occurrence with males and relative similarity. Because of this uncertainty, and because multiple species were collected at many sites, females of most new species are not listed in the paratype series, but instead included as additional material.

Illustrations were made using an ocular grid and inked in Adobe Illustrator. All figures are drawn of the left side or appendage, unless otherwise noted. Setation is generally omitted from the right side. Terminology used follows Blahnik (1998).

Type material is deposited in the collections of the University of Minnesota, St. Paul, Minnesota (**UMSP**), Department of Natural History, University Museum of Bergen (**ZMBN**), and the collection of the Illinois Natural History Survey, Champaign, Illinois (**INHS**), as indicated in the species descriptions.

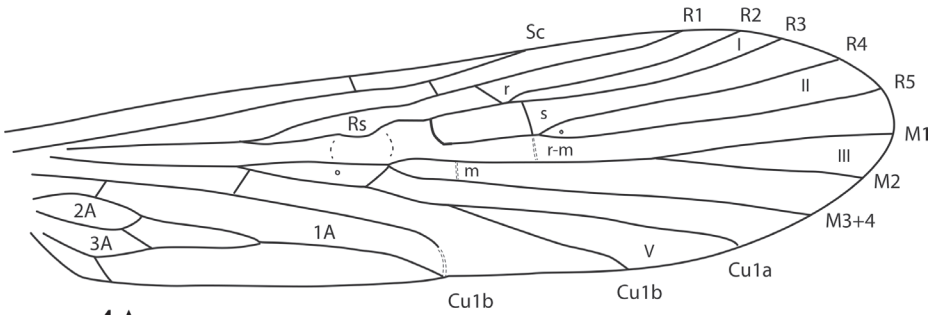
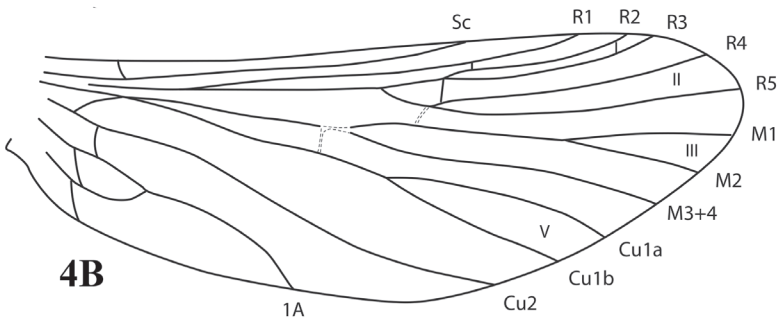
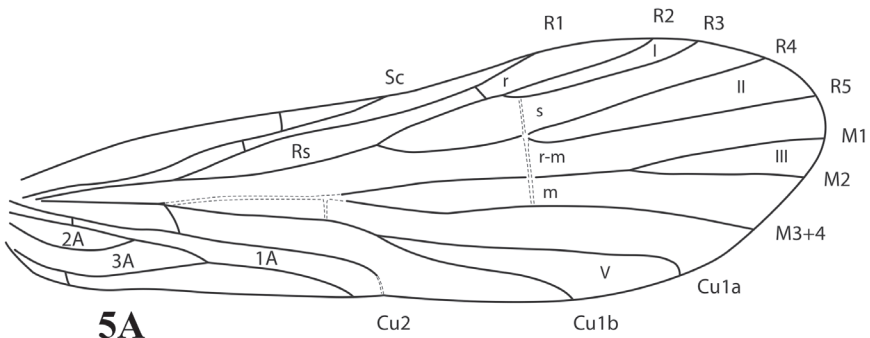
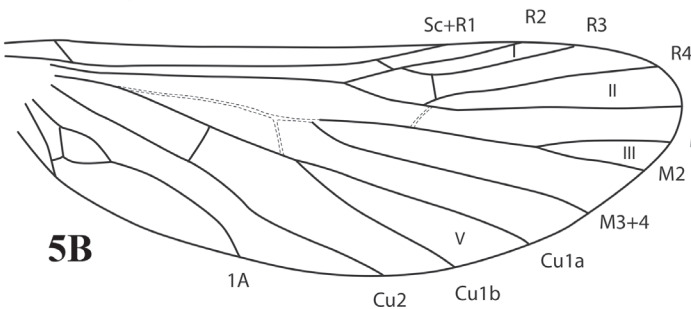
Results

Taxonomic overview

The species described here can be placed into two well-defined species groups, the *marginata* Group and the *georgensis* Group. The *marginata* Group includes species previously placed in the *digitata* group (Blahnik et al. 2009, 2012), but is more broadly defined to include *Chimarra marginata*, the type species for the genus *Chimarra*, and additional species and lineages basal to this group, specifically including species in which the anal loops of the forewing have a crossvein so that the 2A vein appears to be “forked” apically (Fig. 4). In the *georgensis* Group, but also in the *minuta* and *tsudai* Groups of Asia and the subgenera *Curgia* and *Otarrha* of the Americas, the usual configuration is for both the 2A and 3A veins of the forewing to be looped to the 1A vein, that of the 3A vein distal to the 2A; thus, no crossvein is apparent (Fig. 5). The character state is usually easy to ascertain (with the removal of some of the setae covering the wing), because the anal veins are found on the dorsal margin of the wing, just behind the head, when the wings are folded over the body. This character state appears to be unique to the genus *Chimarra*; in taxa in other families in which a crossvein is absent between the anal veins of the forewing, the 3A vein is looped to the 2A vein. In some genera of Trichoptera, a crossvein may also occur between the 1A and 2A veins. This is ostensibly also the situation in the *marginata* Group, in which a crossvein occurs between the 1A and 2A veins, near the terminus of the 2A vein, often giving the vein the appearance of being “forked” apically. The significance of this difference, and the probability that the character state in the *marginata* Group represents a character reversal, was discussed in a previous paper (Blahnik et al. 2012). Unfortunately, even for described species in which the forewing is illustrated, the character state is often misrepresented, so it is prudent to be cautious about assigning species to these species groups without actually examining specimens. A few taxa may also be homoplasious for one or another character state, but this appears to be uncommon.

Most of the mainland African species of the *marginata* Group can be placed into four species diverse subgroups, the *fallax*, *kenyana*, *minima*, and *ruficeps* subgroups. The *fallax* and *minima* subgroups were proposed and populated by Gibon (2018 and 2015, respectively). The *fallax* subgroup is more completely treated in the current work and the *kenyana* and *ruficeps* subgroups are newly proposed here. A number of additional small subgroups from Africa with only one to several species also belong in the *marginata* Group. Other subgroups of the *marginata* Group are broadly represented in the Asian, Australian (including New Guinea and the Pacific Islands), and American faunas. Most of the various species groups recognized from these regions would be considered subgroups of the *marginata* Group, under the usage employed here.

The *georgensis* Group was recognized by Blahnik et al. (2012) in the description of a new species from Vietnam, without circumscribing the African members of the

**4A****4B****5A****5B**

Figures 4, 5. 4 *Chimarra marginata* (Linnaeus), *marginata* Group, wings **A** forewing **B** hind wing
 5 *Chimarra ankylis* sp. nov., *georgensis* Group, wings **A** forewing **B** hind wing.

group beyond *Chimarra georgensis* itself. *Chimarra georgensis* Barnard is the designated type species for the genus *Chimarrhafa* Lestage (1936), which was synonymized under *Chimarra* by Ross (1956). The genus was specifically designated for species in which the R_1 vein of the hind wing is lost (or fused to the subcosta), the stem of the R_s in the forewing is straight, and the chord of the forewing (composed of the s , $r-m$, and m crossveins) is unpigmented and linear (Fig. 5). Except for the first character, which exhibits a good deal of homoplasy within the genus *Chimarra*, the character states are probably plesiomorphic. African species of the *georgensis* Group were more completely listed by Gibon (2018), when describing a new species of the group from Madagascar. The list is expanded here to include two subgroups, the *georgensis* subgroup, including the species listed by Gibon (2018), and the *evoluta* subgroup, including three previously described species. An additional described taxon is recognized as belonging to the *georgensis* Group, but not assigned to subgroup. The 20 new species of the *georgensis* Group described in this paper greatly expand the known diversity of the two subgroups; the number includes two additional new species that were not assigned to subgroup.

In addition to new species described in this paper, other species from Africa and Madagascar were also assessed for their relationships. A list of the species and their assignment to subgroups within the major species groups is found in Table 1. The list is followed by taxa that were left unassigned to subgroup. The subgroups recognized are considered preliminary and provisional. A discussion of the subgroups, for new species described in this paper, precedes the species descriptions. Species subgroups not treated in this paper: The *marginata* subgroup includes only *C. marginata* itself. The species is widespread in Europe, but also occurs in the northern part of Africa. A molecular assessment of its placement within the genus by Wahlberg and Johanson (2014) supported its relationship to a subset of Asian taxa, which, collectively, were related to New World species in the subgenus *Chimarra*. In the study by Kjer et al. (2014), *C. marginata* was closest to African taxa, but there was no convincing support for this relationship. The species seems to be relatively isolated from other species of the subgenus occurring in Africa. The *apiconigra* subgroup includes two species from Madagascar that were acknowledged to be closely related at the time of their original descriptions. This subgroup is recognized to establish a nuclear subgroup to which other taxa may belong. *Chimarra blahniki* may belong here, as noted at the time of its description, but is not included because of its somewhat different venational attributes (less curved R_s vein of the forewing). *Chimarra apiconigra* was also compared to *C. cognata* at the time of its description, which is in the *minima* subgroup. An overall similarity to this subgroup is acknowledged, but the phallic spines in members of the *apiconigra* subgroup are relatively short and simple, rather than elongate and modified, and the overall shape of the inferior appendages is different from species in the *minima* subgroup. The *lehibemavo* subgroup, from Madagascar, was established and treated comprehensively by Gibon (2017). The *pondoensis*

subgroup contains only two species from South Africa, both with elongate, narrow lateral lobes of tergum X and short curved phalli. Venational characters of the subgroup suggest its placement in the *marginata* Group, but possibly in a relatively basal position, since the curvature of the Rs vein of the forewing is minimal. Its relatively primitive characters may account for the original placement of *C. crocifera* within *Chimarrhafa*, considered by Morse (1974) a subgenus of *Chimarra*.

Table 1. African *Chimarra* species.

The *marginata* Group

The *apiconigra* subgroup

Chimarra apiconigra Johanson, 2010 [Madagascar]

Chimarra gassa Johanson, 2010 [Madagascar]

The *cara* subgroup

**Chimarra bispinosa* Gibbs, 1973 [Ghana, Ivory Coast]

Chimarra cara Mosely, 1936 (*Chimarrha*) [Cameroon]

The *fallax* subgroup

?*Chimarra bettinae* Marlier & Marlier, 1982 (proposed by Gibon 2018) [Réunion]

**Chimarra calundoensis* Marlier, 1965 [Angola, DR of the Congo, Ghana]

**Chimarra dybowskina* Navás, 1931 (*Chimarrha*) [Burkina Faso, Cape Verde, DR of the Congo, Ghana, Guinea, Ivory Coast, Madagascar, Mali, Togo]

Syn.: *C. caboverdensis* Nybom, 1960, syn. nov. [Cape Verde]

Syn.: *C. divergena* Gibbs, 1973, syn. nov. [Ghana]

**Chimarra elga* Mosely, 1939 (*Chimarrha*) [DR of the Congo, Kenya]

Chimarra falcifera Jacquemart, 1966 [DR of the Congo]

**Chimarra fallax* Ulmer, 1912 (*Chimarrha*) [Cameroon, DR of the Congo, Ghana, Madagascar, Sao Tomé]

Syn.: *C. lukawei* Jacquemart, 1961 (*Chimarrha*), syn. nov. [DR of the Congo]

**Chimarra jacquemarti* sp. nov. [Ghana]

**Chimarra lanceolata* sp. nov. [Ghana]

Chimarra lejea Mosely, 1948 (*Chimarrha*) [Ethiopia, Yemen]

Chimarra mauritania Jacquemart, 1960 (*Chimarrha*) [Mauritius]

**Chimarra robynsi* (Jacquemart, 1967), comb. nov. (*Chimarrhafa*) [DR of the Congo, Tanzania]

**Chimarra togoana* (Ulmer, 1907) (*Wormaldia*) [Ghana, Togo]

Chimarra travei Jacquemart, 1963 [Mauritius]

The *kenyana* subgroup

**Chimarra akana* Gibbs, 1973 [Ghana, Ivory Coast]

Chimarra ambulans Barnard, 1934 (*Chimarrha*) [South Africa]

Chimarra baculifera Marlier, 1965 [Angola]

Chimarra camerunensis Marlier, 1980 [Cameroon]

Chimarra chicapa Marlier, 1965 [Angola]

**Chimarra eshowensis* sp. nov. [South Africa]

Chimarra flaviseta Wahlberg, Espeland & Johanson, 2014 [Malawi]

Chimarra intermedia Jacquemart, 1961 [DR of the Congo]

Chimarra kenya Ulmer, 1931 (*Chimarrha*) [DR of the Congo, Kenya, South Africa, Zaire]

Syn.: *C. wittei* Jacquemart, 1961 (*Chimarrha*) (proposed by Marlier 1980) [Zaire]

**Chimarra krugeri* Jacquemart, 1963 [South Africa, Tanzania]

Chimarra longistylis Jacquemart & Statzner, 1981 [DR of the Congo]

- **Chimarra morogoroensis* sp. nov. [Tanzania]
Chimarra mulanjae Wahlberg, Espeland & Johanson, 2014 [Malawi]
Chimarra mushuvae Marlier, 1951 (*Chimarrha*) [DR of the Congo]
 **Chimarra pedaliotus* sp. nov. [Ghana]
Chimarra psittacus Wahlberg, Espeland & Johanson, 2014 [Malawi]
Chimarra quadrispinosa Jacquemart & Statzner, 1981 [DR of the Congo]
Chimarra rhodesi Kimmins, 1957 [DR of the Congo, Zimbabwe]
Chimarra saudia Malicky, 1986 [Yemen]
Chimarra somereni Marlier, 1951 (*Chimarrha*) [Kenya]
 **Chimarra szunyoghii* Oláh, 1986 [Tanzania]
 **Chimarra tanzaniensis* sp. nov. [Tanzania]
Chimarra triangularis Kimmins, 1963 [Ethiopia]
 **Chimarra triangularis occidentalis* Gibon, 1985 [Ghana, Ivory Coast]
Chimarra trispina Jacquemart, 1961 (*Chimarrha*) [DR of the Congo]
Chimarra uwirana Marlier, 1951 (*Chimarrha*) [DR of the Congo, Zambia]
 **Chimarra waensis* Gibon, 1985 [Ghana, Ivory Coast]
Chimarra zombaensis Wahlberg, Espeland & Johanson, 2014 [Malawi]

The *lehibemavo* subgroup

- Chimarra cebegepi* Gibon, 2017 [Madagascar]
Chimarra fenoovo Gibon, 2017 [Madagascar]
Chimarra fotobohitra Gibon, 2017 [Madagascar]
Chimarra forcellini Gibon, 2017 [Madagascar]
Chimarra gattolliati Gibon, 2017 [Madagascar]
Chimarra gensonae Gibon, 2017 [Madagascar]
Chimarra hamatra Gibon, 2017 [Madagascar]
Chimarra jejiyorum Gibon, 2017 [Madagascar]
Chimarra lehibemavo Gibon, 2017 [Madagascar]
Chimarra makiorum Gibon, 2017 [Madagascar]
Chimarra moramanga Gibon, 2017 [Madagascar]
Chimarra saha Gibon, 2017 [Madagascar]
Chimarra tamara Gibon, 2017 [Madagascar]

The *leta* subgroup

- **Chimarra amakyei* sp. nov. [Ghana]
Chimarra leta Mosely, 1936 (*Chimarrha*) [Cameroon]

The *marginata* subgroup

- Chimarra marginata* (Linnaeus, 1767) (*Phryganea*) [Algeria, Morocco, Tunisia]

The *mazumbai* subgroup

- **Chimarra mazumbai* sp. nov. [Tanzania]
 **Chimarra usambara* sp. nov. [Tanzania]
 **Chimarra wliensis* sp. nov. [Ghana]

The *minima* subgroup

- Chimarra ambaja* Mosely, 1939 (*Chimarrha*) [Cameroon, DR of the Congo]
Chimarra angolensis Marlier, 1965 [Angola]
Chimarra antsymeloka Gibon, 2015 [Madagascar]
Chimarra assambae Gibon, 2015 [Cameroon]
Chimarra bertrandi Scott, 1974 [Zimbabwe]
 **Chimarra callasae* Gibon, 1982 [Ghana, Guinea, Mali, Sierra-Leone]
Chimarra cereris Barnard, 1934 (*Chimarrha*) [Zimbabwe]
Chimarra cognata Kimmins, 1957 [Angola, Namibia, Zimbabwe]

- **Chimarra intexta* Mosely, 1931 (*Chimarrha*) [Ghana, Guinea, Ivory Coast, Sierra-Leone]
Chimarra koualeensis Johanson & Mary, 2009 [Mayotte Island]
Chimarra loffae Gibon, 2015 [Cameroon, Guinea]
Chimarra lufirae Jacquemart, 1961 (*Chimarrha*) [DR of the Congo, South Africa, Zimbabwe]
 **Chimarra minima* Ulmer, 1907 (*Chimarrha*) [Benin, Burkino Faso, Cameroon, Ghana, Guinea, Ivory Coast, Mali, Togo]
 Syn.: *C. petri* Gibbs, 1973 (proposed by Gibon 2015) [Ghana]
 Syn.: *C. voltae* Marlier, 1978 (proposed by Gibon 1985) [Burkino Faso]
Chimarra prodhoni Gibon, 1985 [Burkino Faso, Guinea, Ivory Coast]
Chimarra sanagae Gibon, 2015 [Cameroon]
 **Chimarra sassandrae* Gibon, 1982 [Cameroon, Ghana, Guinea, Ivory Coast Mali, Togo]
Chimarra toubensis Gibon, 1985 [Guinea, Ivory Coast]
Chimarra vulgaris Gibon, 2015 [Madagascar]

The *pondoensis* subgroup

- Chimarra crocifera* Morse, 1974 [South Africa]
Chimarra pondoensis Barnard, 1941 (*Chimarrha*) [South Africa]

The *ruficeps* subgroup

- Chimarra chechewa* Wahlberg, Espeland & Johanson, 2014 [Malawi]
Chimarra circumverta Wahlberg, Espeland & Johanson, 2014 [Malawi]
Chimarra clara Mosely, 1939 (*Chimarrha*) [Uganda]
Chimarra cornuta Jacquemart & Statzner, 1981 (hom. of *C. cornuta* Ross, 1959) [DR of the Congo]
 **Chimarra dulensis* sp. nov. [Tanzania]
Chimarra fuscipes Kimmins, 1958 [Mozambique, South Africa]
 **Chimarra kibiensis* sp. nov. [Ghana]
Chimarra lwirona Statzner, 1976 [DR of the Congo]
 **Chimarra minacis* sp. nov. [Ghana]
Chimarra ruficeps Ulmer, 1914 (*Chimarrha*) [South Africa]
 **Chimarra tangaensis* sp. nov. [Tanzania]
Chimarra uncata Morse, 1974 [South Africa]

The *georgensis* Group

The *georgensis* subgroup

- **Chimarra ankylis* sp. nov. [Tanzania]
 **Chimarra aurita* sp. nov. [Ghana]
 **Chimarra crescentis* sp. nov. [Tanzania]
Chimarra furcata Jacquemart, 1961 [DR of the Congo]
Chimarra georgensis Barnard, 1934 (*Chimarrha*) [South Africa]
Chimarra hoogstraali Ross, 1956 [Sudan]
 **Chimarra indicis* sp. nov. [Ghana]
Chimarra kabashana (Marlier, 1943) (*Chimarrhafa*) [DR of the Congo]
 **Chimarra latidentis* sp. nov. [Tanzania]
 **Chimarra leptodactylus* sp. nov. [Tanzania]
 **Chimarra obuncata* sp. nov. [Ghana]
 **Chimarra polycentropoides* sp. nov. [DR of the Congo]
 **Chimarra ralphi* sp. nov. [Ghana]
 **Chimarra serrella* sp. nov. [Ghana]
 **Chimarra triramosa* sp. nov. [Ghana]
 **Chimarra uncinata* sp. nov. [Ghana]
 **Chimarra vermitergata* sp. nov. [Tanzania]
Chimarra zombitsei Gibon, 2018 [Madagascar]

The *evoluta* subgroup*Chimarra aciculata* Morse, 1974 [South Africa]*Chimarra evoluta* Kimmins, 1957 [Zimbabwe]*Chimarra foliata* Kimmins, 1959 [Uganda]**Chimarra giboni* sp. nov. [Ghana]**Chimarra lobulata* sp. nov. [Ghana]**Chimarra mgwashi* sp. nov. [Tanzania]**Chimarra parafoliata* sp. nov. [Ghana]**Chimarra pectinella* sp. nov. [Ghana]**Not assigned to subgroup****Chimarra agumatsa* sp. nov. [Ghana]*Chimarra ino* Marlier, 1981 [Zambia]**Chimarra kjaerandseni* sp. nov. [Ghana]****Unassigned***Chimarra abyssinica* Banks, 1913 (*Chimarrha*) [Ethiopia]*Chimarra africana* Enderlein, 1929 (*Chimarrha*) [♀, Tanzania]*Chimarra armata* Jacquemart, 1961 (*Chimarrha*) (hom. of *C. armata* Navás) [DR of the Congo]*Chimarra auripilis* Navás, 1933 (*Chimarrha*) [Niger]*Chimarra berghei* Marlier, 1951 (*Chimarrha*) [DR of the Congo]*Chimarra beylaensis* Gibon, 1986 [Guinea]*Chimarra blahniki* Johanson, 2010 [Madagascar]*Chimarra calidopectoris* Wahlberg, Espeland & Johanson, 2014 [Malawi]*Chimarra deksamensis* Malicky, 1999 [Yemen]*Chimarra dioni* Gibon, 1986 [Guinea]*Chimarra goedefroita* Gibon, 2016 [Madagascar]*Chimarra isbal* Malicky, 2015b [Madagascar, Nosy Be]*Chimarra lacroixi* Navás, 1921 (*Chimarrha*) [♀, Madagascar]*Chimarra lomor* Malicky, 2015b [Madagascar, Nosy Be]*Chimarra lupialae* Jacquemart, 1961 (*Chimarrha*) (the *fallax* subgroup?) [DR of the Congo]*Chimarra mayottensis* Johanson & Mary, 2009 [Madagascar, Mayotte Island]**Chimarra multisensillata* sp. nov. [Tanzania]*Chimarra philipponi* Gibon, 1986 [Guinea]*Chimarra saganeitina* Navás, 1932 (*Chimarrha*) [Ethiopia]*Chimarra sylvestris* Gibon, 1985 (the *georgensis* subgroup?) [Ivory Coast]*Chimarra tamsi* Mosely, 1936 (*Chimarrha*) [Sao Tome]*Chimarra zoria* Mosely, 1939 (*Chimarrha*) [Uganda]

*Described or redescribed in this article.

**Species unassigned to subgroup are either based on females, inadequately illustrated, morphologically isolated from other species, known only from Madagascar or other islands, or some combination of above.

Species descriptions**The *marginata* Group**

The first characterization of evolutionary relationships in the genus *Chimarra* was provided by Ross (1956), who used exemplars at hand to characterize various lineages. One of the lineages characterized was the *digitata* type, based on a species collected from India. Characters of especial note were the reduction of the sensilla of the lateral lobes

of tergum X to exactly two and the development of a membranous mesal lobe of tergum X. Ross noted that some ancestral form with the same character set invaded the New World to give rise to the many species lineages found there. Usage of the name, as the *digitata* lineage, was continued by Blahnik (1998) in a revision of New World species of the subgenus *Chimarra*, partly because of an agreement that American species of the subgenus were closely related to Asian species. The *digitata* group was more formally characterized and discussed by Blahnik et al. (2009, 2012), in describing new species of *Chimarra* from Borneo and Vietnam. However, specific membership in the group was deferred, except for the taxa directly treated. It was already realized that *Chimarra marginata*, as the type species for the subgenus *Chimarra*, might be a more appropriate species around which to characterize this group, since it also possesses many of its defining characters. In contrast, some species assigned to the subgenus *Chimarra*, both in Asia and Africa, have more plesiomorphic characters. This is the first formal recognition of the *marginata* Group as a lineage within the subgenus *Chimarra*, as distinct from more plesiomorphic lineages in the same subgenus, which are assigned to other species groups. The group name more or less replaces the *digitata* group, as previously characterized (Blahnik et al. 2009, 2012), although somewhat more broadly defined and encompassing a wider number of taxa from throughout Asia, Australia, Africa, and the New World. A number of these have been referred to various species groups in previous regional literature, which are here recognized as subgroups within the *marginata* Group.

The first, and most useful, character defining the *marginata* Group is that the 2A vein of forewing has a crossvein to 1A (2A apparently forked apically). This character would appear to be a primitive character state; the probability that it is a secondary and rederived character state was discussed by Blahnik et al. (2012). Outside of the *marginata* Group, it only regularly occurs in the subgenus *Chimarrita* of the New World. Other taxa within *Chimarra*, including the subgenera *Curgia* and *Otarra*, but also the *tsudai*, *minuta*, and *georgensis* Groups of the subgenus *Chimarra*, have both the 2A and 3A veins looped to the 1A, that of the 3A distal to the 2A. Thus, no crossvein is apparent. Some homoplasy occurs, as might be expected for a character reversal, but appears to be very infrequent. An example of this may be the type species for the subgenus *Curgia*, the wings of which were illustrated by Flint (1998: fig. 5) and clearly have a crossvein present between the 1A and 2A veins of the forewing. However, an examination of species from all of the species groups of the subgenus recognized by Flint, including other species in the same species group as the type species for the subgenus, revealed no other examples of this.

A character usually used to define the subgenus *Chimarra*, and diagnostic when it occurs, is for the Rs vein of the forewing to be inflected or curved. The character state is found in *C. marginata*, in which it is particularly pronounced, and also commonly occurs in many other species of the group. However, it is generally acknowledged to be absent in species of the *georgensis* Group, which, partly on this basis, were assigned to the genus *Chimarrhafra* by Lestage (1936). The conclusion drawn from this is that an inflection of the Rs vein is not a synapomorphy for the entire subgenus but must have arisen within some lineages. Blahnik et al. (2009, 2012) used the presence of an

inflection or loop in the Rs vein of the forewing as one character defining the *digitata* group, here reassigned to the *marginata* Group. The difficulty of applying this character was commented on by Wahlberg and Johanson (2014), who found a loop or inflection of the Rs vein of the forewing to be frequently absent in many of the taxa assigned to the *marginata* Group, based on the primary character defining the group (a crossvein between the anal veins), as discussed above. The discussion below is meant to address this issue.

The presence of an inflected Rs vein is often accompanied by other character state changes and can be useful for assessing relationships within the subgenus when the characters are considered in combination. Characters frequently occurring in the *marginata* Group, in addition to a sinuously inflected Rs vein, include a distinct sclerotized node, either at the point of inflection or extending into the cell below. The R_1 and/or base of the M vein may also be sinuously inflected. Often, the basal fork of the discoidal cell also is thickened, and the fork loses its strict symmetry. Other character changes that are commonly associated with this character development include a change of the *s* crossvein to a character state in which it is pigmented and more evidently developed, rather than unpigmented or hyaline and weakly developed, and the movement of the *m* crossvein of the forewing to a position more proximal than the *s* and *r-m* crossveins, thus making the chord no longer linear. These associated character states are found in *C. marginata* (Fig. 4) and are also both common and widespread in other species of the *marginata* Group throughout its geographic distribution. However, in various taxa of the *marginata* Group, the Rs vein may be rather weakly inflected, or may even appear to be almost straight, either reflecting a more primitive state in those taxa, or a character reversal. Probably both explanations apply in different cases. Part of the difficulty, in this case, may be in the application or assignation of a character state, especially when the wing is mounted on a slide. At least a slight tendency for the Rs vein to be bowed outward from the plane of the wing seems to be inherent in the entirety of the subgenus *Chimarra*, including even species of the *georgensis* Group, in which the vein is generally characterized as being straight. The same is true of the *minuta* Group from Asia. In the *tsudai* Group of Asia, an inflection is generally noticeable, but is variable. Other associated characters states discussed above may sometimes occur, either within or among these groups. These are probably parallel developments.

Described species of the *marginata* Group have been placed into various subgroups, as listed below. A number of species from Africa are difficult to assign to subgroup, based on literature descriptions and illustrations. Most are probably members of the *marginata* Group. Some may represent additional subgroups not represented by species from Ghana and Tanzania.

The *cara* subgroup

Included species. *Chimarra bispinosa* Gibbs, 1973; and *C. cara* Mosely, 1936.

Members of this subgroup have the same generalized features that characterize the *marginata* Group, but the *m* crossvein of the forewing is more or less continuous with the *r-m* and *s* crossveins, although strongly angled; thus, it is not displaced proximally as in most described species in the *marginata* Group as a whole. A similar character state occurs in the *leta* subgroup, discussed below. Like members of the *kenyana* subgroup, the species have a tergum X with lateral lobes that are simple (neither divided, nor with ventral periphallallic processes) and have two sensilla at the apex of a digitate lobe that emerges either basally or midlaterally. Members of both of these groups also have a relatively short ventral process on sternum IX. The species of the *cara* subgroup are characterized by short rounded inferior appendages, with a pronounced cusp on the mesal surface, and also by an angular preapical projection on tergum X. The latter is a relatively common feature in various species of the subgenus *Chimarra*, also found in various Asian, American, and other African species, and may represent a primitive or plesiomorphic character for the *marginata* Group as a whole. If so, the character has been lost in many lineages. The species placed here have two small and more or less symmetrically placed endothecal spines, but the endotheca seems to lack a very distinctly textured region or tract with minute spines.

In the molecular analysis of species in the genus *Chimarra* by Wahlberg and Johanson (2014), *C. calidopetoris* Wahlberg, Espeland & Johanson was a close taxon to *C. bispinosa*, also included in their study. Although we do not question the relative placement of the taxa in their study, the characters presented in the description of the *C. calidopetoris* are not completely congruent with the definition of the *cara* subgroup, as defined here. We therefore prefer to defer placement of *C. calidopetoris*. Perhaps it would be better treated in a subgroup of its own.

***Chimarra bispinosa* Gibbs, 1973**

Fig. 6A–F

Chimarra bispinosa Gibbs, 1973: 367, figs 8–10.

Chimarra bispinosa Gibbs: Gibon 1985: 28 (distribution: Ivory Coast).

Material examined. GHANA – **Brong Ahafo Reg.** • 2♂♂1♀; Kintampo, Saunders Waterfall; 8°05'23"N, 1°41'50"W; 19 June 1993; JS Amakye & J Kjærandsen leg.; light trap; ZMBN • 1♂; same collection data as for preceding except 13 Feb. 1993; J Kjærandsen leg.; sweep net; ZMBN. – **Central Reg.** • 4♂♂9♀♀; Kakum Forest Reserve; 5°21'N 1°22'W; 8–15 June 1994; T Andersen leg.; Malaise trap; ZMBN • 1♂1♀; same collection data as for preceding except 8 Nov. 1994; light trap; ZMBN. – **Eastern Reg.** • 1♂; Boti Falls; 6°11'40"N, 0°13'05"W; 24 Feb. 1993; JS Amakye & J Kjærandsen leg.; light trap; ZMBN • 1♂; same collection data as for preceding; UMSP • 1♂; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjærandsen

leg.; light trap; ZMBN. – **Volta Reg.** • 2♀♀; Wli, Agumatsa waterfall, station # 1^A; 7°07'29"N, 0°35'31"E; 5–14 Mar. 1993; JS Amakye & J Kjærandsen leg.; Malaise trap; ZMBN • 1♂6♀♀; same collection data as for preceding except 12–21 Nov. 1993; J Kjærandsen leg.; ZMBN • 2♂♂; same collection data as for preceding except station # 1^B; 11–14 Mar. 1993; JS Amakye & J Kjærandsen leg.; ZMBN • 8♂♂; same collection data as for preceding except 12–21 Nov. 1993; J Kjærandsen leg.; ZMBN • 3♂♂3♀♀; same collection data as for preceding except station # 3^A; 4–13 Mar. 1993; JS Amakye & J Kjærandsen leg.; ZMBN • 1♀; same collection data as for preceding except 11–20 Nov. 1993; J Kjærandsen leg.; ZMBN • 1♂; same collection data as for preceding except station # 3^B; 4–7 Mar. 1993; JS Amakye & J Kjærandsen leg.; UMSP • 226♂♂95♀♀; same collection data as for preceding except station # 3; 10 Mar. 1993; JS Amakye & J Kjærandsen leg.; light trap; ZMBN • 1♀; same collection data as for preceding; UMSP • 113♂♂438♀♀; same collection data as for preceding except 17 Nov. 1993; J Kjærandsen leg.; ZMBN • 1♂1♀; same collection data as for preceding except station # 6; 11 Mar. 1993; JS Amakye & J Kjærandsen leg.; ZMBN • 2♀♀; same collection data as for preceding except 20 Nov. 1993; J Kjærandsen leg.; ZMBN.

Diagnosis. The two species included in this subgroup are very similar. The differences, as evident from the original illustrations, lie mostly in the shape and length of the lateral lobes of tergum X, the relative shape of the apices of these lobes, as well as in the more bulbous bases of the phallic spines in *C. bispinosa*. It is also possible that the overall shape of the inferior appendages in *C. cara* are slightly more rounded. The specimen illustrated here (Fig. 6A–F) most closely conforms to *C. bispinosa* and we have identified it as such. Any minor differences from the original illustration should not be accorded significance, at least until the variation within the two known species of the subgroup is better assessed.

Redescription. Adult. Overall color (in alcohol) light brown, appendages paler, head and prothorax slightly darker (anterior and posterior setal warts pale and contrasting). Head short and rounded (postocular parietal sclerite short). Palps relatively short; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short (slightly > 2× 1st), apex with cluster of ~ 12 stiff setae, 3rd segment moderately elongate, distinctly longer than 2nd, 4th segment short (shorter than 2nd), 5th segment slightly longer than 3rd. Forewing length: male, 5.5–7.0 mm; female, 6.5–7.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs inflected at past midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell distinctly enlarged, fork asymmetric, length of cell slightly > 2× width, fork I subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at fork I, chord nearly linear (*s* and *r-m*, crossveins linear, *m* crossvein diagonal, continuous with *r-m*), *s* pigmented (like wing), *r-m* and *m* hyaline, 2A with crossvein, (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II subsessile, fork III distal and relatively wide, anal loop small and incomplete (not joining 1A). Forelegs with apical tibial spur short; male with foretarsi unmodified, claws small and symmetrical.

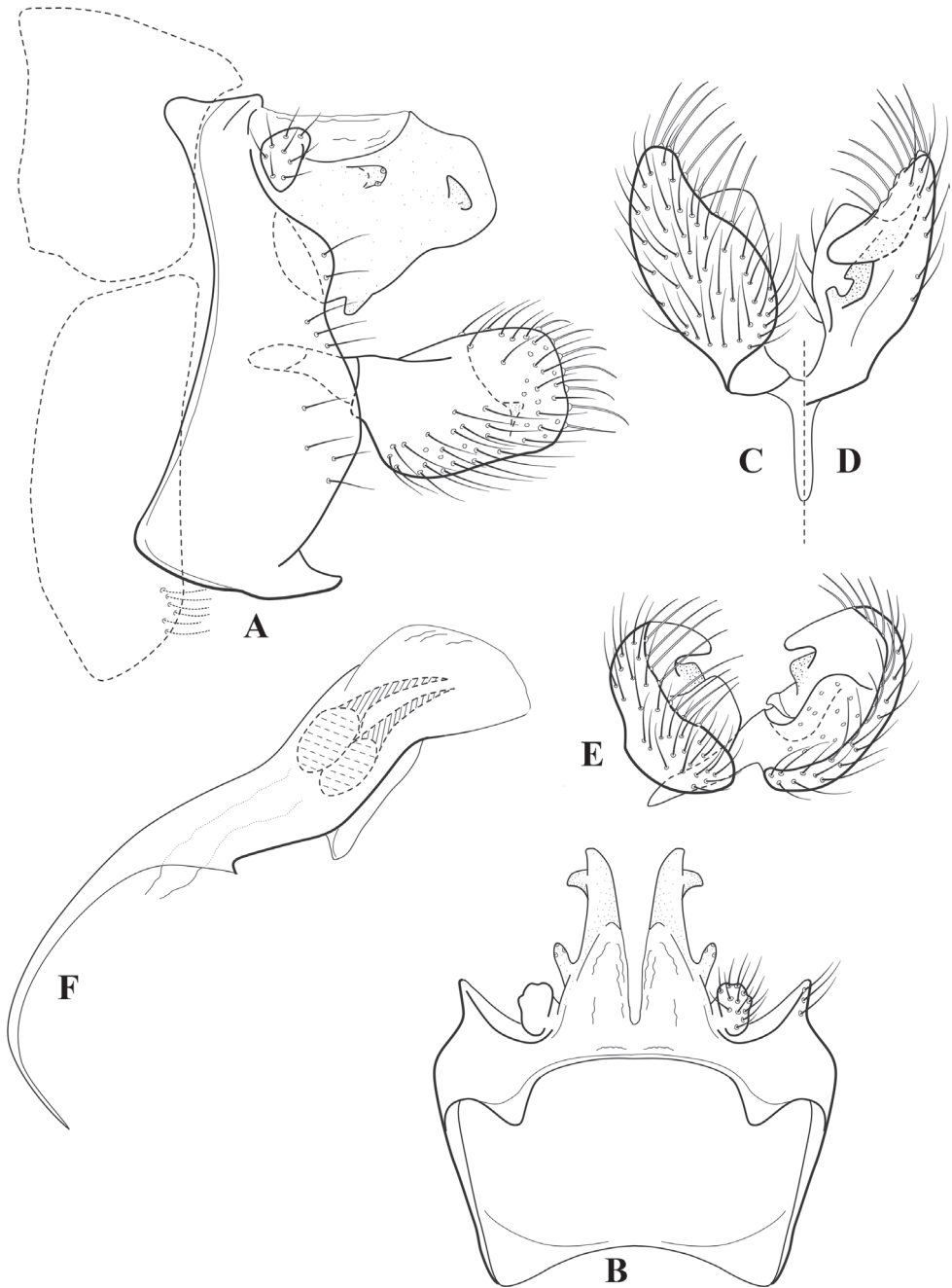


Figure 6. *Chimarra bispinosa* Gibbs, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** inferior appendage, oblique lateral **F** phallus, lateral.

Male genitalia. Segment VIII relatively short, tergum wider dorsally, sternum without posteroventral projection. Segment IX, in lateral view, short, with anteroventral margin weakly, angularly inflected in basal 1/4, concavely narrowing dorsally; tergum very short dorsally, with short anterior apodemes; dorsal margin very narrow, but continuous mesally between apodemes; posterior margin with inferior appendages mounted relatively high on segment, below mid-height, margin very weakly produced below preanal appendages, basally with short, subtriangular, posteriorly projecting, ventral process; anterior margin of sternum subtruncate as viewed dorsally or ventrally, slightly concave mesally. Lateral lobes of tergum X short and simple in form, without periphallalic processes, each lobe with short, acute, preapical lateral projection, basally with very short, digitate process with 2 apical sensilla; mesal lobe of tergum X membranous and divided mesally, continuous with sclerotized lateral lobes. Preanal appendages short and knob-like, slightly flattened, membranous basally. Inferior appendage very short and rounded apically, with weak basal inflection, marginally with elongate setae; as viewed ventrally or caudally, with distinct cusp on mesal surface and very short, mesally directed, basodorsal process. Phallic apparatus relatively short, phallobase tubular, with usual basodorsal expansion, ventral margin slightly bulging, with weakly sclerotized ventral projection; endotheca with two short and nearly symmetrically positioned spines, each with enlarged base, membrane not or only weakly textured, phallotremal sclerite complex not evident.

Distribution. Ghana, Ivory Coast.

The *fallax* subgroup

Included species. ?*Chimarra bettiniae* Marlier & Marlier, 1982; *C. calundoensis* Marlier, 1965; *C. dybowskina* Navás, 1931; *C. elga* Mosely, 1939; *C. falcifera* Jacquemart, 1966; *C. fallax* (Ulmer, 1912); *C. jacquemarti* sp. nov.; *C. lanceolata* sp. nov.; *C. lejea* Mosely, 1948; *C. mauritania* Jacquemart, 1967; *C. robynsi* (Jacquemart, 1967); *C. togoana* (Ulmer, 1907); and *C. travei* Jacquemart, 1963.

The *fallax* subgroup of *Chimarra* was first proposed by Gibon (2018), who also gave a preliminary list of species. The list of included species is somewhat enlarged here, and several species synonymized. A number of described species, particularly those with an upturned, acute, sclerotized tergum X and ventral periphallalic processes, are very similar to one another. Available illustrations and descriptions make it difficult to identify the species confidently, since the species were never treated comparatively, nor were the characters useful in diagnosing similar species discussed. This is complicated by what seems to be a certain degree of intraspecific variability. The subgroup is obviously in need of a revision, including examination of material from throughout Africa and also holotype specimens. Ideally, the two should be done in conjunction with one another, but this is outside the scope of the current paper. The following taxonomic treatment of species from Ghana and Tanzania, which includes many of the morphological forms represented in the literature, is offered in lieu of a formal revisionary treatment and to simplify the identification of known species. In the pro-

cess, we have synonymized some of the described species. It is possible that a future comprehensive revisionary study will reveal that one or more of these forms should be resurrected. As it stands, however, existing names serve little purpose in allowing taxonomists to identify species. The interim taxonomy presented here is meant to lead to a more stable and meaningful use of names.

Species of the *fallax* subgroup are characterized by an elongate ventral process on segment IX, which is distinctly flattened apically so that the apex appears more or less acute in lateral view and rounded in ventral view. The ventral surface of the apex is often roughened and more or less file-like or rasp-like. Most species have the dorsal margin of segment IX obsolete (membranous), as in the *minima* subgroup. Also, the posteroventral margin of sternum VIII is distinctly projecting, in at least the majority of species, and the length of this segment is quite short. The ventral projection of sternum VIII should probably not be interpreted as a ventral process. This character was used to assign some species to this subgroup, rather than to the *ruficeps* subgroup, which seems to be closely related. The lateral lobes of tergum X, in many of the species, are formed into curved, usually upright, spine-like, and distinctly sclerotized lobes. In at least some instances, it is obvious that these lobes bear the pair of sensilla usually found on the lateral lobes of species of the *marginata* Group of *Chimarra*. However, in addition to these spine-like lobes, there are paired ventral processes, referred to here as periphallalic processes, but whether they originated by a lateral division of the lateral lobes of tergum X, or represent de novo outgrowths from the periphallalic membrane is uncertain; in some species these are almost completely ventral to the phallic apparatus and fused basally, but usually with the apices separated, thus providing a ventral source of support for phallus. The prominent development of these processes in some species of the subgroup seems to have a correlation with the greatly projecting ventral apex of the phallobase, which also characterizes some species. In the species from Mauritius, *C. mauritania* Jacquemart and *C. travei* Jacquemart, the periphallalic processes are less developed, but distinct, and in *C. togoana* (Ulmer) and *C. lanceolata* sp. nov., and also in species of the *ruficeps* subgroup, inferred to be the sister taxon of the *fallax* subgroup, tergum X is divided from the posterior margin into dorsal and ventral lobes, possibly suggesting the origin of the periphallalic processes.

The subgroup is probably most closely related to the *C. ruficeps* subgroup and the placement of individual species in one group or the other may be equivocal in some cases. The *ruficeps* subgroup also has species with an elongate ventral process on segment IX, but the apex of the process is broadened, as viewed laterally, and usually has its ventral margin formed into a pad of short, stiff setae or spines. Most described members of the *ruficeps* subgroup have a similar coloration, with a yellowish or orangish colored head and thorax, contrasting with darker wings. However, color attributes are difficult to ascertain in specimens that have been in alcohol for some time and may not be consistent for all members of the group. Species of the *ruficeps* subgroup also lack a ventral projection from sternum VIII.

In the study by Wahlberg and Johanson (2014), species that we have assigned to the two subgroups placed among species of *Chimarra* from Australia and the Pacific

Islands, as separate clades in the parsimony analysis and as sister clades in the Bayesian analysis. Additional undetermined or undescribed species of the clades were also included in their study. The species from Australia and the Pacific Islands otherwise constituted a monophyletic group. Despite the overall support for this placement in their Bayesian analysis, the inclusion of these two African clades within the Australian lineage should probably be considered a hypothesis requiring further confirmation. Nevertheless, the relative proximity of the two clades in the analysis can probably be taken as an indication of their relationship to one another.

***Chimarra calundoensis* Marlier, 1965**

Fig. 7A–E

Chimarra calundoensis Marlier, 1965: 26, fig. 1.

Material examined. GHANA – **Central Reg.** • 1♂; Kakum Forest Reserve; 5°21'N 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; UMSP.

Diagnosis. Phallobase with ventral apex greatly produced and strongly bent, apex rounded; phallic spines both rather short; inferior appendage tapered, bent, acute apically, cusps of ventromesal margin not evident in lateral view.

Chimarra calundoensis is most similar to and most likely to be confused with either *C. dybowskina* or *C. falcifera*. However, diagnoses of other species in the subgroup should be considered to eliminate other possibilities. *Chimarra calundoensis* resembles *C. dybowskina* in having the apicoventral lobe of the phallobase strongly bent and in having the dorsal lobe of the inferior appendages at least somewhat bent. It differs in that the ventral apex of the phallobase is rounded, rather than subtruncate, and the dorsal lobes of the inferior appendages are more tapering and less distinctly bent. Additionally, the phallic spines are slightly shorter than in *C. dybowskina*. We considered synonymizing *C. falcifera* Jacquemart with *C. calundoensis*; it seems to differ primarily in having the ventral apex of the phallobase less distinctly bent. However, the illustration of the hind wing of *C. falcifera* provided by Jacquemart (1966b: fig. 7C) indicates an absence of fork III. This is not the case in *C. calundoensis*, or any other species of the *fallax* group investigated. Individual, sometimes unilateral, variations in venational forking are not particularly unusual. The matter should probably be investigated before a synonymy is made.

Redescription. Adult. Color of head, prothorax, and appendages (in alcohol) yellowish, mesothorax, body, and spurs yellowish brown. Head relatively short (postocular parietal sclerite < 1/2 diameter of eye). Palps relatively short; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (< 3 × 1st), apex with small cluster of stiff setae, 3rd segment only slightly longer than 2nd, 4th segment very short (shorter than 2nd), 5th segment subequal to 3rd. Forewing length: male, 5.4 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ sinuous, stem of Rs inflected at past midlength (with distinct small node at

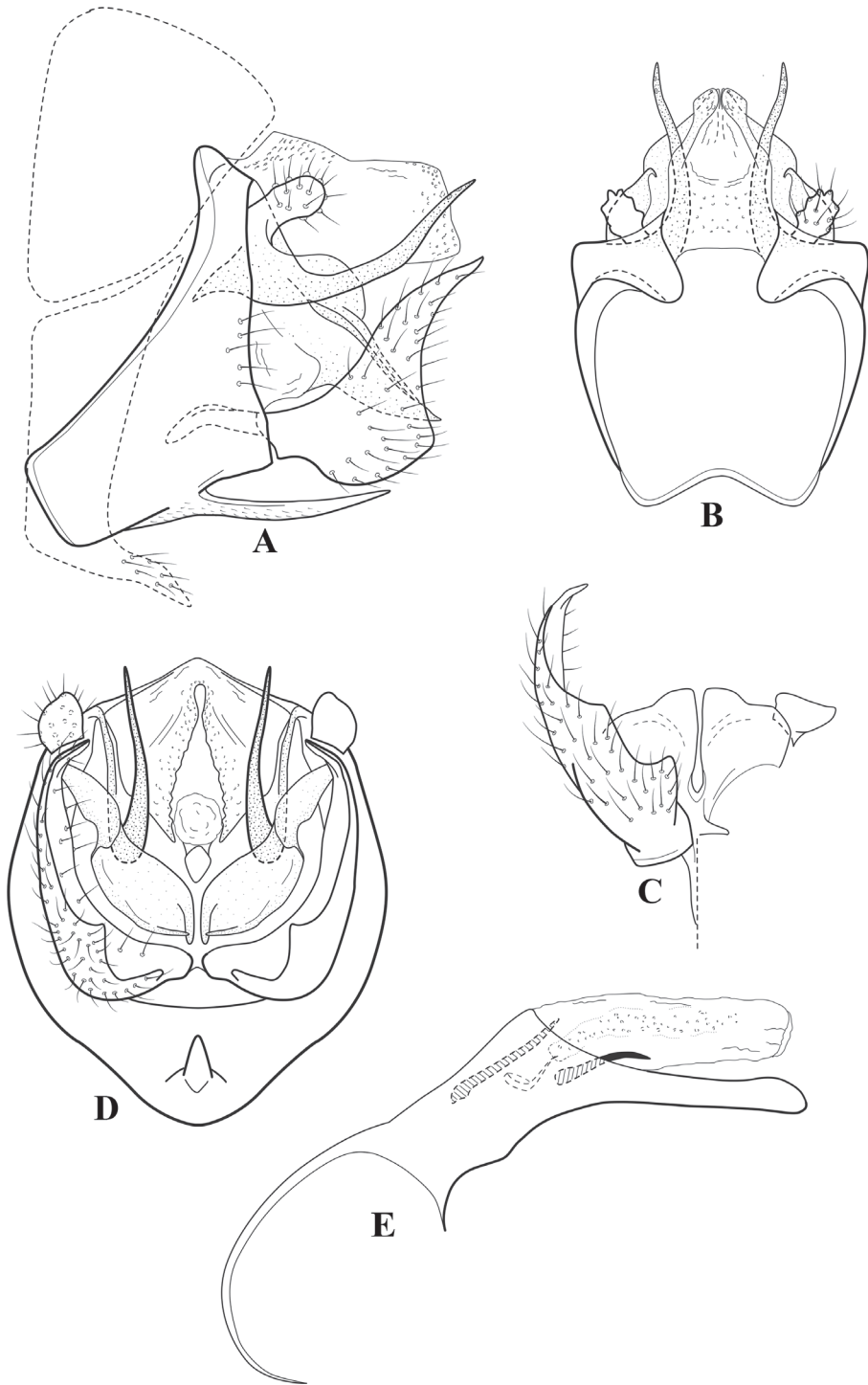


Figure 7. *Chimarra calundoensis* Marlier, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage and periphallal processes, caudal **D** caudal **E** phallus, lateral.

inflection), basal fork of discoidal cell distinctly enlarged, fork asymmetric, length of cell $\sim 2\times$ width, fork I strongly subsessile, fork II sessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, s and $r-m$, crossveins linear, m crossvein more proximal, s pigmented (like wing), $r-m$ and m crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and fork II subsessile, fork III distal and relatively wide, anal loop small. Forelegs with apical tibial spur short; male with tarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, ventrally with distinct projection from posterior margin, tergum wider, expanded dorsally ($\sim 2\times$ width of sternum at base). Segment IX, in lateral view, with anteroventral margin moderately produced, anterior margin with angular inflection in ventral $\frac{1}{4}$, weakly concave and narrowing dorsally; tergum very short dorsally, with short anterior apodemes, obsolete mesally between apodemes; posterior margin nearly linear; ventral margin sloping, more or less linear, with elongate, narrow ventral process at approximately midlength, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum, as viewed dorsally or ventrally, subtruncate, slightly concave mesally. Lateral lobes of tergum X formed into dorsally curved, sclerotized, spine-like processes, bearing two preapical sensilla; mesal lobe of tergum X membranous, moderately elongate; ventrally with strongly projecting, paired, sclerotized, periphallallic processes, subtending phallic apparatus. Preanal appendages short and knob-like, constricted basally, membranous basally, but fused laterally to periphallallic processes. Inferior appendage with pronounced basal inflection, apex dorsally inflected and strongly narrowing, somewhat posteriorly curved, apex acute; as viewed ventrally, with weakly sclerotized, angular projections or cusps near base and before midlength, projections not or scarcely evident in lateral view; mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin very strongly projecting, sclerotized, strongly ventrally deflected, apex of ventral projection more or less evenly rounded, as viewed laterally; endotheca with two relatively short and asymmetrically positioned spines, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure.

Distribution. Angola, Democratic Republic of the Congo, Ghana.

Chimarra dybowskina Navás, 1931

Fig. 8A–E

Chimarra dybowskina Navás, 1931: 123–124, fig. 61.

Chimarra dybowskina Navás: Fischer 1961: 59; Malicky 2015b: 41 (text), 44 (figure) (distribution: Madagascar); Gibon 2018: 121–122, figs 3A, 5, (distribution: Burkina Faso, Guinea, Ivory Coast, Madagascar, Mali, Togo).

Chimarra divergena Gibbs, 1973: 367–369, figs 5–7. Syn. nov.

Chimarra caboverdensis Nybom, 1960: 1–3, figs A–G. Syn. nov.

Material examined. CAPE VERDE • 1♂; Brava, Fajã d' Agua; 100 m a.s.l.; 17 Feb. 2007; E Aistleitner leg.; UMSP. GHANA – **Central Reg.** • 1♂; Kakum Forest Reserve; 5°21'N, 1°22'W; 8 Nov. 1994; T Andersen leg.; light trap; ZMBN. – **Eastern Reg.** • 1♂1♀; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjærandsen leg.; light trap; ZMBN. – **Volta Reg.** • 1♂; Hohoe, Matvin Hotel; 7°09'43"N, 0°28'31"E; 11 Nov. 1993; J Kjærandsen leg.; at light; ZMBN • 3♀♀; Wli, Agumatsa waterfall, station # 3; 7°07'29"N, 0°35'31"E; 11–20 Nov. 1993; J Kjærandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding except station # 6; ZMBN • 2♀♀; same collection data as for preceding except station # 7; ZMBN • 1♀; same collection data as for preceding except station # 8; ZMBN • 5♂♂15♀♀; same collection data as for preceding except station # 3; 17 Nov. 1993; light trap; ZMBN • 1♀; same collection data as for preceding except station # 6; 11 Mar. 1993; JS Amakye & J Kjærandsen leg.; ZMBN • 1♀; same collection data as for preceding except 20 Nov. 1993; J Kjærandsen leg.; ZMBN • 1♂; same collection data as for preceding; UMSP • 1♂3♀♀; same collection data as for preceding except station # 10; 19 Nov. 1993; ZMBN • 3♂♂4♀♀; same collection data as for preceding except station # 12; 16 Nov. 1993; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. Phallobase with ventral margin greatly produced and strongly bent, apex enlarged and subtruncate, dorsal margin slightly upturned; phallic spines both moderately elongate and narrow; inferior appendage with dorsal projection abruptly narrowed, nearly uniform in width and distinctly bent, apex acute, ventromesal cusps of inferior appendage often both evident in lateral view (character possibly variable or inconsistent).

Chimarra dybowskina is most similar to *C. calundoensis*, *C. falcifera*, and *C. jacquemarti* sp. nov. The species are best distinguished by differences in the shape and inflection of the dorsal lobe of the inferior appendages, and by the shape of the apex and inflection of the apicoventral projection of phallobase, as well as in the relative length of the phallic spines. Like both *C. calundoensis* and *C. jacquemarti*, the ventral apex of the phallobase is very strongly bent; the apex of the structure is more truncate than in *C. calundoensis*, but bent slightly upward, rather than downward, as in *C. jacquemarti*. The dorsal process of the inferior appendages is generally more uniform in width and more strongly bent in *C. dybowskina* than in the other species, and the cusps of the mesal surface are more likely to be evident in lateral view. The phallic spines are comparable in length to those of *C. jacquemarti*, but slightly longer than in either *C. calundoensis* or *C. falcifera*.

Our illustration closely matches that presented by Gibon (2018), which was based on the holotype of *C. dybowskina* Navás from the Democratic Republic of the Congo. We are less convinced that the illustration of *C. dybowskina* presented by Malicky (2015b) from Nosy Bé, Madagascar is the same species, although admittedly close. The inferior appendage in his illustration has the general shape and form of *C. dybowskina*, but the ventral projection of the phallobase is not as strongly deflexed and the apex is rounded, rather than truncate.

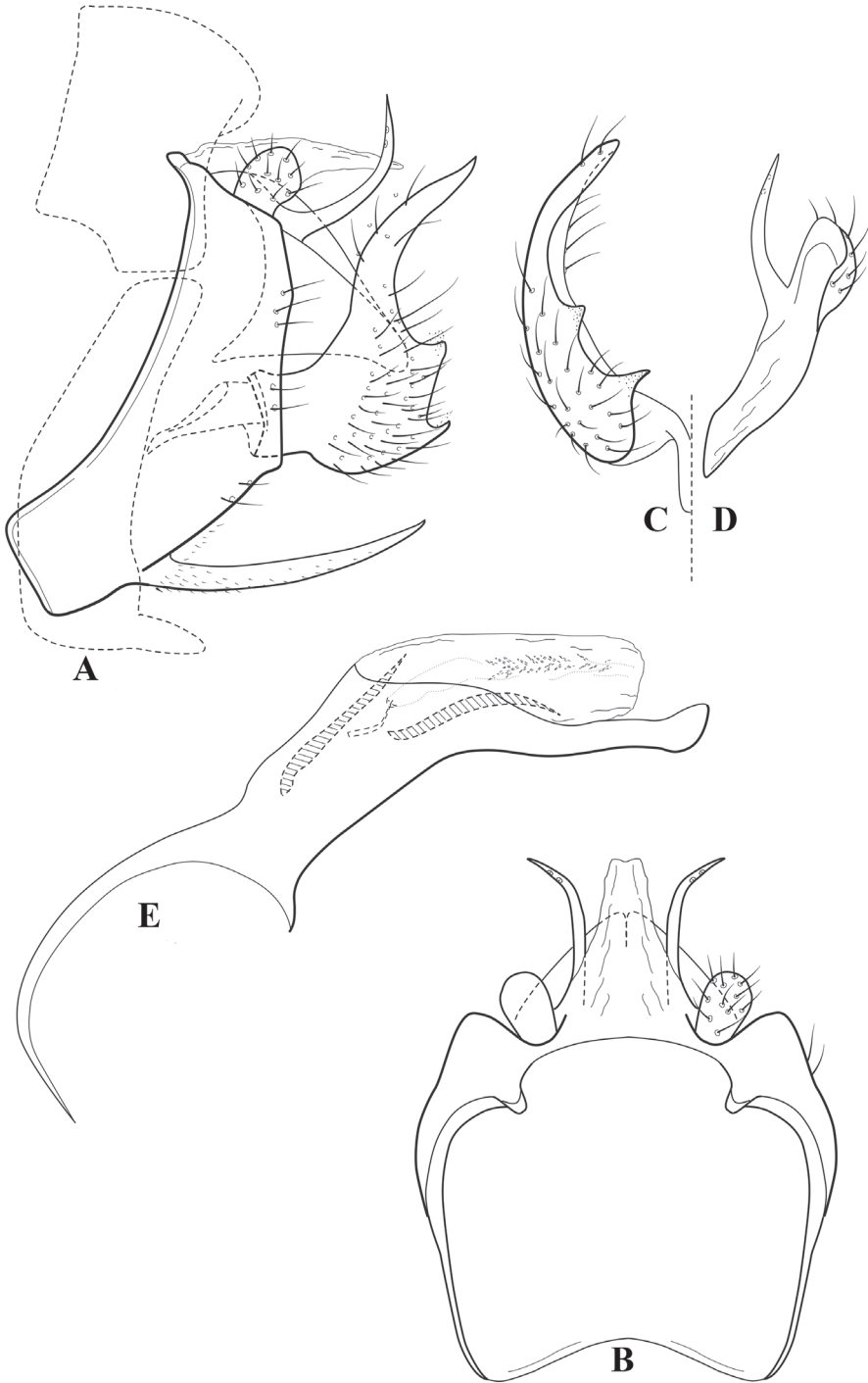


Figure 8. *Chimarra dybowskina* Navás, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** tergum X and periphallalic process, right caudal **E** phallus, lateral.

Chimarra divergena Gibbs, described from Ghana, has enough of the significant features of *C. dybowskina* to be considered a synonym, especially the strongly deflexed ventral projection of the phallobase, with its apex subtruncate and slightly upturned. There was no available illustration of *C. dybowskina* when it was published. The primary difference is that the mesal cusps of the inferior appendage are not apparent in lateral view in the illustration of *C. divergena*. The difference seems too minor to warrant species status. *Chimarra caboverdensis* is undoubtedly also a synonym, based on the structure of the ventral apex of the phallobase, which, in the illustration of the type, is clearly truncate apically, with the apex slightly upturned. Examination of a specimen collected from Cabo Verde revealed no distinctive differences from *C. dybowskina*. Pending further evidence of its species status, we prefer to consider *C. caboverdensis* Nybom to also be a synonym of *C. dybowskina* Navás.

Redescription. Adult. Overall color (in alcohol) yellowish brown, head and prothorax not lighter, spurs slightly darker. Head relatively short (postocular parietal sclerite $\sim 1/2$ diameter of eye). Palps relatively elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate ($\sim 4 \times 1^{\text{st}}$), apex with small cluster of stiff setae, 3rd segment slightly longer than 2nd, 4th segment short ($\sim 1/2$ length of 3rd), 5th segment elongate, slightly shorter than 3rd and 4th combined. Forewing length: male, 5.0–6.0 mm; female 5.5–6.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 very slightly sinuous, stem of Rs weakly inflected at past midlength (without distinct node at inflection), basal fork of discoidal cell slightly asymmetric, length of cell $\sim 2 \times$ width, fork I slightly subsessile, fork II sessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, s and $r-m$, crossveins linear, m crossvein more proximal, s pigmented (like wing), $r-m$ and m crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, fork I and fork II subsessile, fork III relatively distal, anal loop small. Forelegs with tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum short, ventrally with distinct ventral projection, tergum somewhat wider, expanded dorsally. Segment IX, in lateral view, with anteroventral margin moderately produced, anterior margin with angular inflection at approximately ventral $1/4$, concavely narrowing dorsally; tergum narrow dorsolaterally, with short anterior apodemes, obsolete mesally between apodemes; posterior margin nearly linear; ventral margin sloping, more or less linear, with elongate, narrow ventral process, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum subtruncate as viewed dorsally or ventrally, slightly concave mesally. Lateral lobes of tergum X formed into dorsally curved, sclerotized, spine-like processes, bearing two preapical sensilla; dorsum of tergum X moderately elongate, membranous; tergum ventrally with strongly projecting, paired, sclerotized, periphallic processes, subtending phallic apparatus. Preanal appendages short and knob-like, constricted basally, fused laterally to periphallic processes. Inferior appendage with pronounced basal inflection, apex dorsally inflected and strongly narrowed, distinctly posteriorly curved, apex acute; as viewed ventrally, with distinct

sclerotized projections near base and before midlength, generally evident in lateral view; mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin sclerotized, strongly deflexed and projecting, apex enlarged, subtruncate, with dorsal margin slightly upturned; endotheca with two relatively elongate, asymmetrically positioned spines, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure.

Distribution. Burkina Faso, Cape Verde, Democratic Republic of the Congo, Ghana, Guinea, Ivory Coast, Madagascar, Mali, Togo.

Chimarra elga Mosely, 1939

Fig. 9A–D

Chimarra elga Mosely, 1939: 300–301, figs 20–23.

Chimarra elga Mosely: Fischer 1971: 209.

Material examined. DEMOCRATIC REPUBLIC OF THE CONGO • 3♂♂; South Kivu, CRSN Lwiro, Kabindi, Guest House, Site 3; 2°14.270'S, 28°42.907'E; 1.668 m a.s.l.; 27 Sept. 2005; UMSP • 1♂; same collection data as for preceding except 19 Apr. 2006; UMSP.

Diagnosis. *Chimarra elga* is another species in the *fallax* subgroup belonging to the complex of species with spine-like dorsolateral lobes of tergum X and a phallobase with a projecting and deflexed ventral apex. Among these, *C. elga* is easily diagnosed by the relatively short, flexed dorsal process of its inferior appendage. It is included in the current paper mostly for comparative purposes.

Redescription. **Adult.** Overall color (in alcohol) yellowish brown, vertex of head darker than setal warts. Head relatively short (postocular parietal sclerite < 1/2 diameter of eye). Palps moderately elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (~ 3 × 1st), apex with small cluster of stiff setae, 3rd segment slightly longer than 2nd, 4th segment short (~ 1/2 length of 3rd), 5th segment subequal to 3rd. Forewing length: male, 5.7–6.6 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ slightly sinuous, stem of Rs inflected at past midlength (with distinct node at inflection, not extending into cell below), basal fork of discoidal cell enlarged, slightly asymmetric, length of cell ~ 2 1/2 × width, fork I distinctly subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II subsessile, fork III relatively distal, anal loop small. Forelegs with tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, ventrally with distinct ventral projection, tergum somewhat wider, expanded dorsally. Segment IX, in lateral view, with anteroventral margin moderately produced, anterior margin with rounded projection at approximately ventral 1/4, concavely narrowing dorsally; tergum short

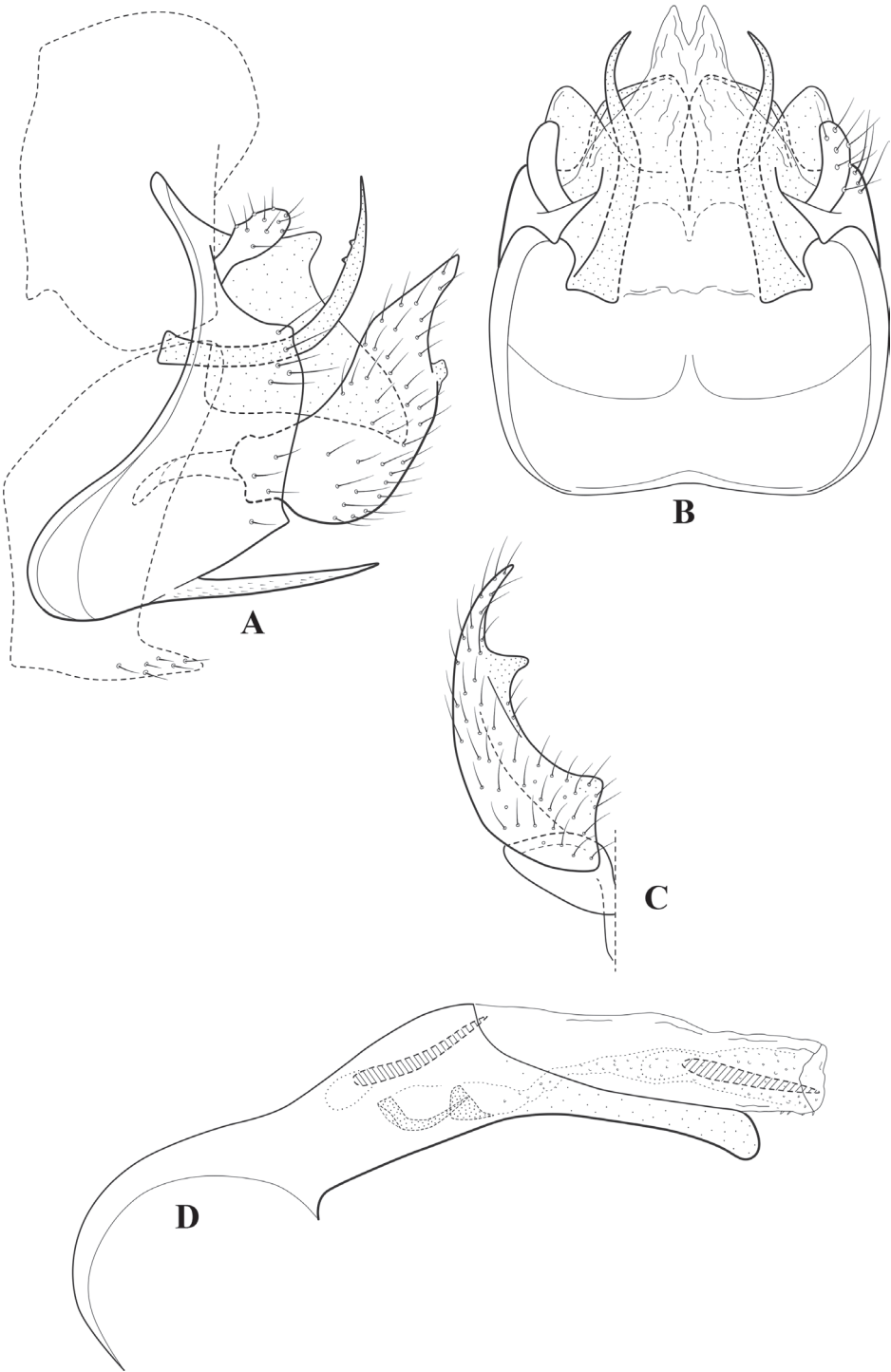


Figure 9. *Chimarra elga* Mosely, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral/caudal **D** phallus, lateral.

dorsolaterally, with prominent anterior apodemes, obsolete mesally between apodemes; posterior margin widening below preanal appendages, nearly linear to ventral margin; ventral margin, with elongate, narrow ventral process, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum subtruncate as viewed dorsally or ventrally, not or only slightly concave mesally. Lateral lobes of tergum X formed into dorsally curved, sclerotized, spine-like processes, bearing two preapical sensilla; dorsum of mesal lobe of tergum X moderately elongate, membranous; tergum ventrally with strongly projecting, paired, sclerotized, periphallallic processes, subtending phallic apparatus. Preanal appendages short and knob-like, constricted basally. Inferior appendage with pronounced basal inflection, apex dorsally inflected, apex of inflection relatively short and strongly narrowed, distinctly posteriorly curved, apex acute; as viewed ventrally, with distinct sclerotized projections near base and before midlength, evident in ventral view, basal projection not evident in lateral view; base very strongly rounded and relatively short; mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin sclerotized, strongly deflexed and projecting, apex slight enlarged and rounded; endotheca with two moderately elongate, asymmetrically positioned spines, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure and small apical sclerite.

Distribution. Democratic Republic of the Congo, Kenya.

Chimarra fallax (Ulmer, 1912)

Fig. 10A–E

Wormaldia fallax Ulmer, 1912: 84–85, figs 5–8a.

Chimarrha fallax (Ulmer): Marlier 1959 (distribution: Sao Tomé); Fischer 1961: 59; Fischer 1971: 210.

Chimarra lukawei Jacquemart, 1961a: 40, fig. 27a. Syn. nov.

Chimarra lukawei Jacquemart: Jacquemart, 1961b: 230; Jacquemart 1966a: 49, fig. 14A–B; Wahlberg and Johanson 2014: 437–439, figs 1–3; Gibon 2018: 123–124, figs 1B, 3B–D, 5 (distribution: Madagascar).

Chimarra lukawaei [sic] Jacquemart: Morse 2021 [also, many online taxonomic resources using the Trichoptera World Checklist as a source].

Chimarra sp. AK: Gibon & Elouard, 1996: 510.

Material examined. GHANA – **Central Reg.** • 28♂♂41♀♀; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN • 1♂1♀; same collection data as for preceding; UMSP. – **Western Reg.** • 5♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN • 1♂; same collection data as for preceding except 9 Dec. 1993; light trap; ZMBN.

Diagnosis. Inferior appendage short and rounded apically; phallobase with ventral apex short and only weakly projecting, not enlarged apically; phallic spines both relatively elongate and narrow, differing in length; periphallic processes fused mesally, comparatively narrow and weakly developed; posteroventral margin of sternum VIII distinctly projecting.

Within the *fallax* subgroup, the distinguishing feature of this species is the relatively short inferior appendages with apices that appear rounded in lateral view. The only evident difference in the illustrations provided for *C. fallax* and that of *C. lukawei* is the more prominent dorsal spine-like projections of tergum X in *C. fallax*. The difference is minor, and we do not consider it to be of species-level significance.

Within the group of taxa assigned to the *fallax* subgroup with a spine-like modification to the lateral lobes of tergum X, it is the only species in which the ventral apex of the phallobase is weakly or only moderately projecting; the periphallic processes are also much less developed than in the other species. Thus, it probably represents a basal species of this clade.

Redescription. Adult. Overall color (in alcohol) yellowish brown, appendages slightly paler. Head relatively short (postocular parietal sclerite $< 1/2$ diameter of eye). Palps relatively short; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate, apex with small cluster of stiff setae, 3rd segment subequal to segment 2, 4th segment short ($\sim 1/2$ length of segment 2), 5th segment subequal to 2nd or 3rd. Forewing length: male, 5.0–6.0 mm; female 5.5–6.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 very sinuous, stem of R_s inflected at past midlength (with distinct small node at inflection), basal fork of discoidal cell distinctly enlarged, fork asymmetric, length of cell $\sim 2\times$ width, forks I and II both subsessile, r crossvein diagonal, intersecting discoidal cell at past midlength, s and $r-m$, crossveins linear, m crossvein more proximal, s pigmented (like wing), $r-m$ and m crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 reduced, but evident, narrowly parallel to subcosta, forks I and II strongly subsessile, fork III distal and relatively wide, anal loop small. Forelegs with apical tibial spur short; male with tarsal claws unmodified, apical segments of tarsi narrow, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, ventrally with distinct projection from posterior margin, tergum slightly longer, expanded dorsally. Segment IX, in lateral view, with anteroventral margin weakly produced, anterior margin with angular inflection in ventral $1/4$, weakly concave and narrowing dorsally; tergum short dorsolaterally, with short, rounded apodemes, obsolete mesally between apodemes; posterior margin nearly linear; ventral margin sloping, more or less linear, with inferior appendages mounted high on segment (nearly midlaterally), basally with elongate, narrow ventral process near base, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum subtruncate as viewed dorsally or ventrally. Lateral lobes of tergum X formed into short, narrow, sclerotized, dorsolaterally curved spine-like processes; dorsum of

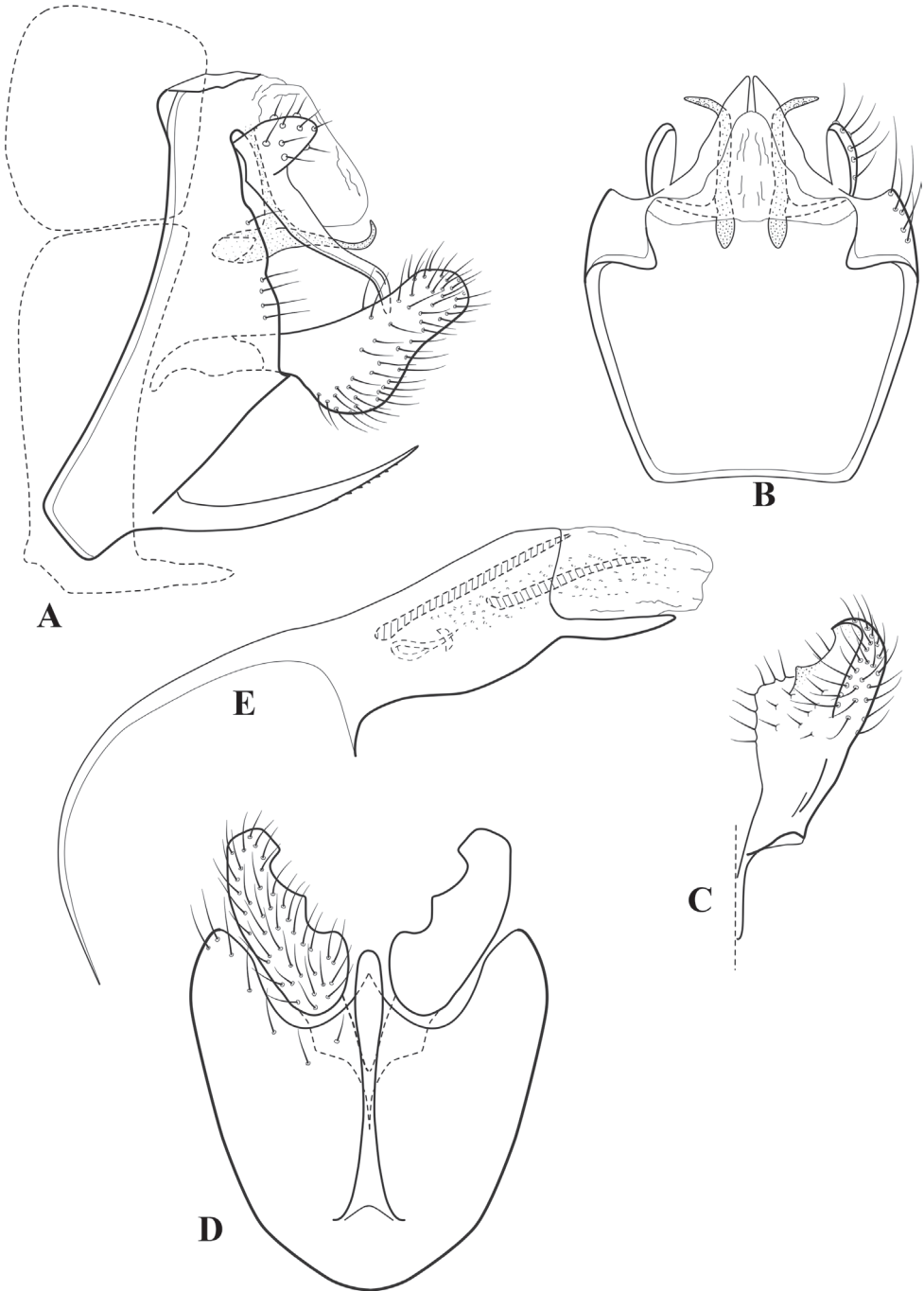


Figure 10. *Chimarra fallax* (Ulmer), ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, dorsal **D** segment IX and inferior appendages, ventral **E** phallus, lateral.

tergum X relatively short, membranous; tergum ventrally with relatively narrow, projecting, mesally fused, sclerotized, periphallallic process, subtending phallic apparatus. Preanal appendages short and knob-like, distinctly flattened, membranous basally, but fused laterally to periphallallic process. Inferior appendage relatively short, with pronounced basal inflection, apex dorsally inflected, broadly rounded, cupped (concave on mesal surface); as viewed ventrally, with weakly sclerotized projections near base and before midlength (projections not evident in lateral view); mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin not, or only weakly, projecting; endotheca with two asymmetrically positioned spines of moderate length, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure, with small preapical sclerite.

Distribution. Cameroon, Democratic Republic of the Congo, Ghana, Madagascar, Sao Tomé.

***Chimarra jacquemarti* sp. nov.**

<http://zoobank.org/3ADE8459-D153-46E2-B49B-33EA58E171EC>

Fig. 11A–D

Type material. Holotype. GHANA – **Central Reg.** • ♂ (in alcohol); Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; UMSP 000550005.

Diagnosis. Phallobase with ventral apex produced and strongly bent, extreme apex enlarged and bent downward; both phallic spines narrow and elongate; inferior appendage with apex strongly narrowed and only weakly bent, cusps of ventromesal margin not evident in lateral view.

Although similar in overall morphology to other species in the *fallax* subgroup with acute dorsal processes on tergum X, it is the only species in which the ventral projection of the phallobase has its apex truncate, extending straight on its dorsal margin, but distinctly hooked downward on its ventral margin. This species is most similar to *C. dybowskina*. Both species are characterized by an elongate and strongly bent ventral projection of the phallobase, which is slightly expanded and subtruncate apically. However, as noted above, *C. jacquemarti* sp. nov. differs in that the apex of the projection, in lateral view, is strongly compressed and bent down, with the dorsal margin projecting straight, whereas *C. dybowskina* has the apex truncate or subtruncate, with the dorsal margin bent upward. Although the phallic spines are relatively elongate in both species, those in *C. jacquemarti* seem to be narrower and slightly more elongate. The general shape of the inferior appendages is also somewhat different.

Description. Adult. Color of head, prothorax, and appendages (in alcohol) yellowish, body and spurs yellowish brown. Head relatively short (postocular parietal sclerite < 1/2 diameter of eye). Palps relatively short; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderate in length (distinctly shorter than segment 3), apex with small cluster of stiff setae, 3rd segment moderately elongate, 4th segment

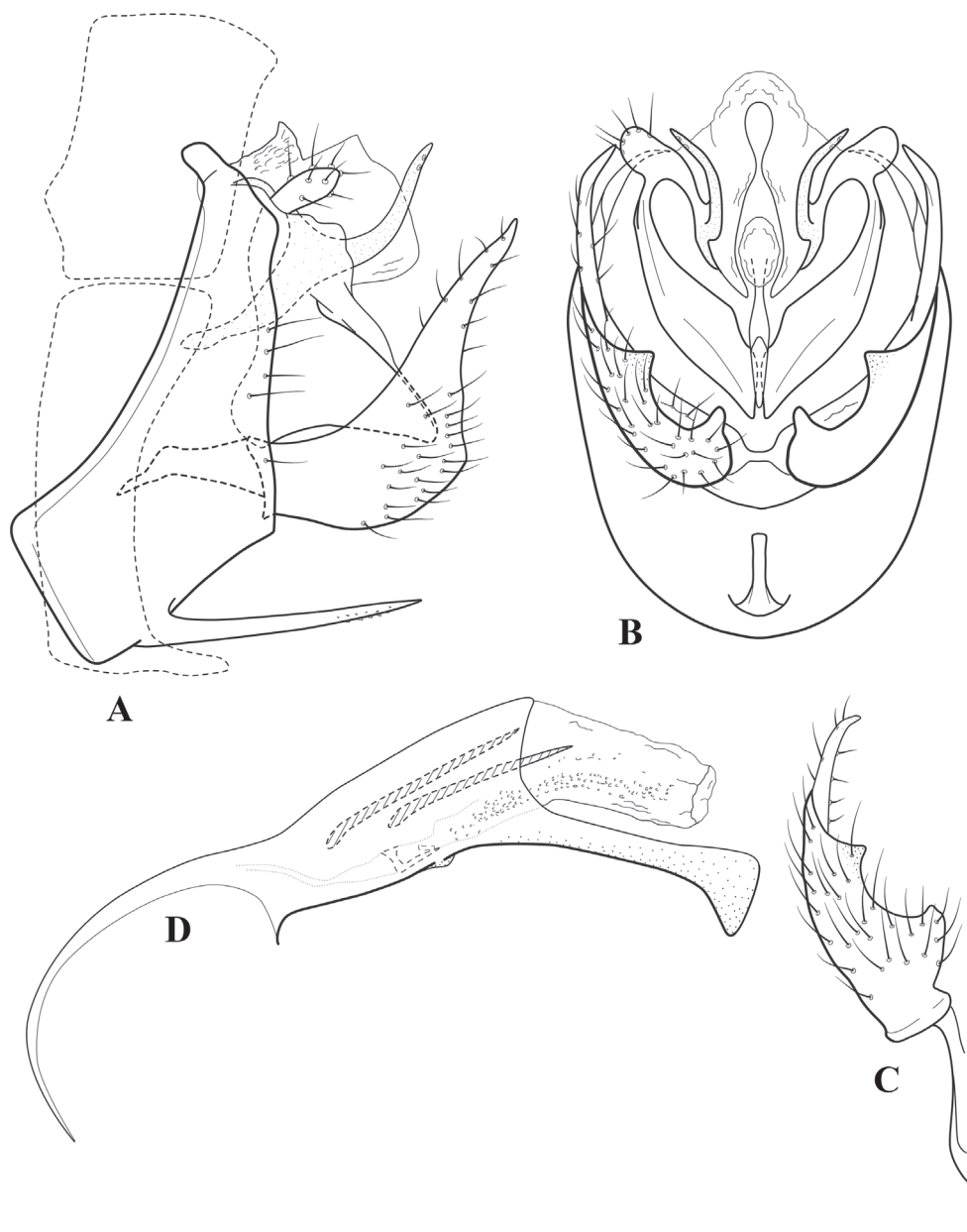


Figure 11. *Chimarra jacquemarti* sp. nov., ♂ genitalia **A** lateral **B** caudal **C** inferior appendage, ventral **D** phallus, lateral.

very short ($\sim \frac{1}{2}$ length of segment 2), 5th segment subequal to segment 3. Forewing length: male, 5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 very sinuous, stem of Rs inflected at past midlength (with distinct small node at inflection), basal fork of discoidal cell distinctly enlarged, fork asymmetric, length of cell $\sim 2\times$ width, fork I somewhat sessile, fork II approximately sessile, r crossvein diagonal,

intersecting discoidal cell at past midlength, just before fork I, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 reduced, but evident, narrowly parallel to subcosta, forks I and II sub sessile, fork III distal and relatively wide, anal loop moderate in size. Forelegs with apical tibial spur prominent; male with tarsal claws unmodified, apical segments of tarsi narrow, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, ventrally with distinct projection from posterior margin, tergum longer ($\sim 2\times$ length of sternum at base). Segment IX, in lateral view, with anteroventral margin moderately produced, anterior margin with angular inflection at approximately ventral $\frac{1}{4}$, slightly concave and narrowing dorsally; tergum short dorsolaterally, with distinct apodemes, obsolete mesally between apodemes; posterior margin nearly linear; ventral margin sloping, more or less linear, with elongate, narrow ventral process near base, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum subtruncate as viewed dorsally or ventrally, slightly concave mesally. Lateral lobes of tergum X formed into dorsally curved, sclerotized, spine-like processes, bearing two preapical sensilla; dorsum of tergum X relatively short, membranous; tergum ventrally with strongly projecting, paired, sclerotized, periphallic processes, subtending phallic apparatus. Preanal appendages short and knob-like, distinctly flattened, membranous basally, but fused laterally to periphallic processes. Inferior appendage with pronounced basal inflection, apex dorsally inflected and strongly narrowing, slightly posteriorly curved, apex acute; as viewed ventrally, with weakly sclerotized projection near base and more strongly sclerotized projection before midlength, projections not or scarcely evident in lateral view; mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, somewhat flared apically, apicoventral margin very strongly projecting, sclerotized, and ventrally deflected, apex of ventral projection, as viewed laterally, expanded, dorsal margin extending almost straight, apex truncate, ventral margin distinctly downturned and acute, apex strongly compressed and flattened as viewed ventrally or caudally; endotheca with two elongate, narrow, and asymmetrically positioned spines, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure.

Etymology. *Chimarra jacquemarti*, name used as a genitive, for S. Jacquemart, in recognition of his substantial contributions to the description of African caddisflies, including a number of species of *Chimarra*.

***Chimarra lanceolata* sp. nov.**

<http://zoobank.org/8FA0E7BC-98AE-4F16-98E4-57550C3CEA6E>

Fig. 12A–E

Type material. Holotype. GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 3; 7°07'29"N, 0°35'31"E; 17 Nov. 1993, J Kjørandsen leg.; light trap; UMSP 000550006. **Paratypes.** GHANA – Volta Reg. • 2♂♂; same data as for

holotype; ZMBN. – **Central Reg.** • 1♂; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T. Andersen leg.; Malaise trap; ZMBN.

Additional material. GHANA – **Central Reg.** • 2♀♀; Kakum Forest Reserve; 5°21'N 1°22'W; 8–15 Nov. 1994; T. Andersen leg.; Malaise trap, ZMBN • 1♀; same collection data as for preceding; UMSP. – **Volta Reg.** • 1♀; Wli, Agumatsa waterfall, station # 5^C; 7°07'29"N, 0°35'31"E; 12–15 Mar. 1993, JS Amakye & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding except station # 8^B; 4–7 Mar. 1993; ZMBN • 1♀; same collection data as for preceding except station # 3; 10 Mar. 1993; light trap; ZMBN • 4♀♀; same collection data as for preceding except 18 Nov. 1993; J Kjørandsen leg.; ZMBN. – **Western Reg.** • 1♀; Ankasa Game Production Reserve; 5°15'N 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN.

Diagnosis. Ventral process of segment IX incredibly elongate; tergum X without spine-like dorsal projection, ventral part completely divided laterally, but not strongly deflexed; inferior appendage mounted at approximately midheight on segment, far above ventral process, dorsal apex strongly narrowed, acute apically, and also very strongly posteriorly bent, ventral cusps visible in lateral view; phallobase with ventral apex extended and sclerotized, but not bent or excessively produced; phallic spines both moderately elongate and narrow; sternum VIII with posteroventral margin weakly produced.

Chimarra lanceolata is most readily identified by the very elongate ventral process of segment IX; the character is so unusual that it would almost appear to be an aberrant or mutation, but there is no evidence of this. Other characters, especially the overall shape of the inferior appendages, are also distinctive for this species and thus it is unlikely to be confused with any other species.

Description. Adult. Overall color (in alcohol) yellowish brown, appendages paler, tibial spurs slightly darker. Head relatively short (postocular parietal sclerite ~ 1/2 length of eye). Palps moderately elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short (~ 2× 1st), apex with small cluster of stiff setae, 3rd segment elongate, almost 2× 2nd, 4th segment short (shorter than 2nd), 5th relatively elongate (longer than 3rd). Forewing length: male, 6.0–6.5 mm; female, 5.5–6.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs weakly inflected at past midlength, basal fork of discoidal cell distinctly enlarged, fork slightly asymmetric, length of cell > 2× width, fork I sub sessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II sub sessile, anal loop moderate. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short ventrally, with very short, posteriorly-projecting ventromesal projection, tergum slightly longer than sternum. Segment IX, in lateral view, with anteroventral margin distinctly produced, anterior margin with very angular inflection in ventral ¼, almost linearly narrowing dorsally; tergum very short dorsolaterally, with prominent apodemes, obsolete mesally

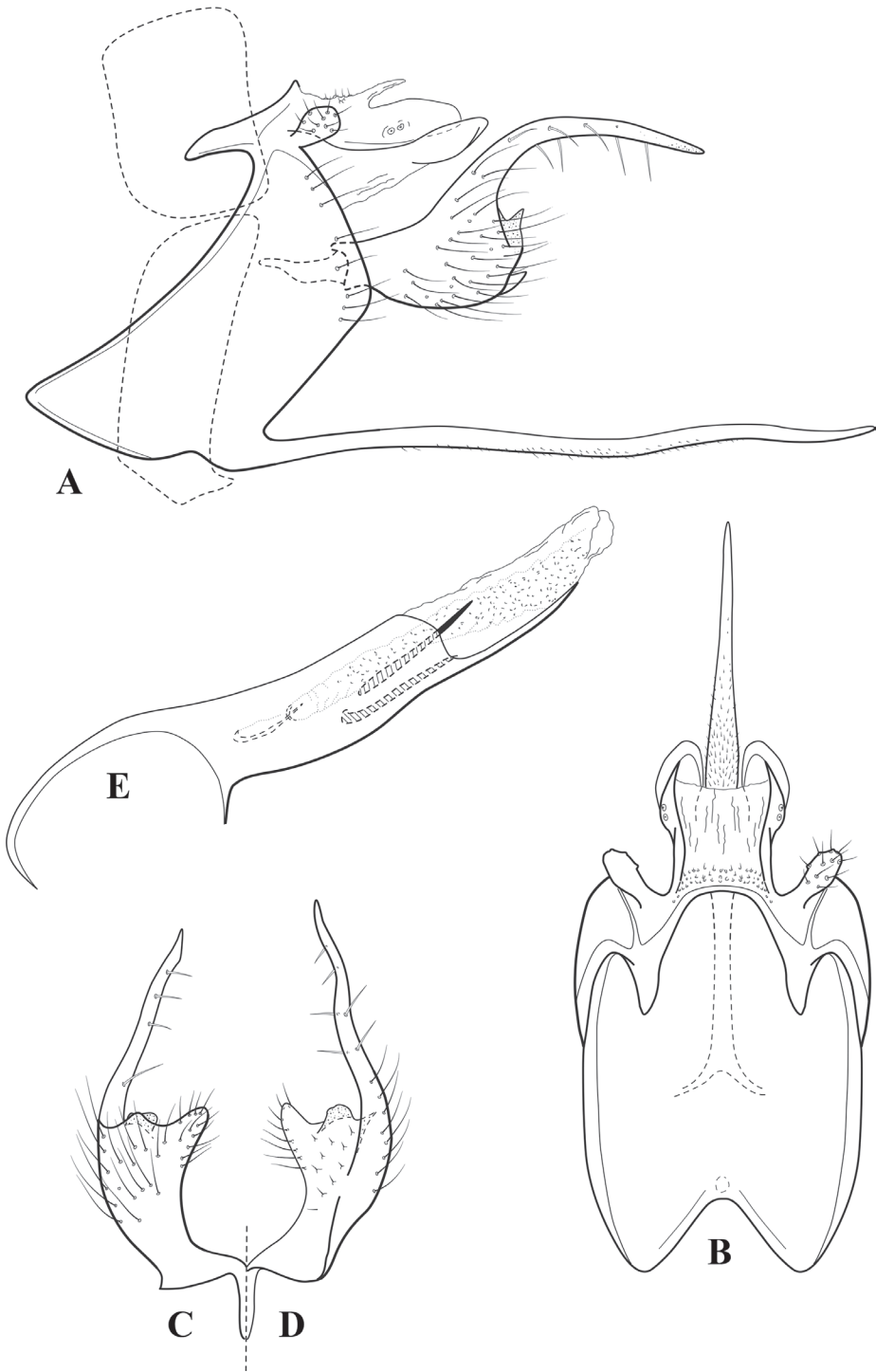


Figure 12. *Chimarra lanceolata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

between apodemes; posterior margin with obtuse angular projection at middle, at insertion of inferior appendages, ventral margin with extremely elongate, narrow, posteriorly-projecting, apically acute, ventral projection; anteroventral margin, as viewed dorsally or ventrally, with very distinct mesal invagination. Lateral lobes of tergum X relatively short, each divided midlaterally into short rounded dorsal lobe, with two sensilla at midlength, and somewhat longer ventral lobe; mesal lobe of tergum X short, membranous. Preanal appendages short and knob-like, constricted basally. Inferior appendage with basal inflection and dorsal process; ventral margin with apex acute, mesally curved, not strongly sclerotized; mesal margin below dorsal process with very strongly sclerotized cusp, at least partially visible in lateral view; dorsal projection elongated, narrow, apically acute, very strongly posteriorly bent. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin with acute, narrow, sclerotized projection, extending almost straight (not ventrally deflected). Endotheca with two asymmetrically positioned spines of moderate length, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure with short apical sclerite.

Etymology. *Chimarra lanceolata*, used as an adjective, from the Latin *lanceolatus*, meaning spear-like, and referring to lance-like ventral process of segment IX, reminiscent of the elongate lance used in medieval jousting tournaments.

Chimarra robynsi (Jacquemart, 1967)

Fig. 13A–E

Chimarrafra [sic] *robynsi* Jacquemart, 1967 (1966a): 49–51, fig. 15.

Chimarra robynsi (Jacquemart, 1967). Comb. nov.

Material examined. TANZANIA – **Tanga Reg.** • 1♂; West Usambara Mt., Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 17–20 Nov. 1990; T Andersen leg.; Malaise trap; UMSP.

Diagnosis. Phallobase with ventral apex greatly produced, but only weakly bent, apex slightly enlarged and more or less rounded apically; phallic spines both relatively short; inferior appendage relatively narrow overall, with dorsal projection narrow and tapering, not or only scarcely bent, cusps of ventromesal surface not evident in lateral view.

We are somewhat unsure of our attribution of the specimen illustrated (Fig. 13A–E) here to *C. robynsi*, especially considering their different provenance. However, among the species of the *fallax* complex, it has the most slender inferior appendage, with a very narrow dorsal process that is not, or scarcely, bent apically. The slightly narrower dorsal process of the inferior appendage in the illustration by Jacquemart can probably be attributed to a slight difference in the orientation of the specimen when illustrated, as suggested by slightly rotating the specimen. Among the species of the *fallax* subgroup with an elongate ventral apex to the phallobase, considered here, *C. robynsi* has the apex least ventrally flexed or bent, possibly similar in this respect

to *C. falcifera*, which was not available for comparison. As noted in the description of *C. calundoensis*, the hind wing of *C. falcifera* was illustrated as lacking fork III (Jacquemart 1966b: fig. 7C) which is not true of the specimen illustrated here, in which the fork is prominent, as in Fig. 4B.

Redescription. Adult. Head, prothorax, and appendages (in alcohol) yellowish; mesothorax and body yellowish brown, spurs slightly darker. Head relatively short (postocular parietal sclerite $\sim 1/2$ diameter of eye). Palps moderately elongate; maxillary palp with 1st segment slightly longer than wide, 2nd segment moderately elongate ($\sim 3 \times 1^{\text{st}}$), apex with small cluster of stiff setae, 3rd segment only slightly longer than 2nd, 4th segment short ($\sim 1/2$ length of 3rd), 5th segment subequal to 3rd. Forewing length: male, 7.1 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with stem of Rs rather weakly inflected at past midlength, basal fork of discoidal cell distinctly enlarged, length of cell $\sim 2 \times$ width, fork I slightly subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile, anal loop small. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, ventrally with distinct projection from posterior margin, tergum slightly longer. Segment IX, in lateral view, with anteroventral margin moderately produced, anterior margin with angular inflection in ventral $1/4$, weakly concave and narrowing dorsally; tergum short dorsally, with short anterior apodemes, obsolete mesally between apodemes; posterior margin nearly linear; ventral margin sloping, more or less linear, with elongate, narrow ventral process, apex of process acute as viewed laterally, rounded as viewed ventrally, apicoventral surface of ventral process roughened and file-like; anterior margin of sternum, as viewed dorsally or ventrally, subtruncate, slightly concave mesally. Lateral lobes of tergum X formed into dorsally curved, sclerotized, spine-like processes, with one or two sensilla apically; mesal lobe of tergum X membranous, moderately elongate; ventrally with strongly projecting, paired, sclerotized, periphallic processes, subtending phallic apparatus. Preanal appendages short and knob-like, constricted basally, fused laterally to periphallic processes. Inferior appendage relatively slender and narrow, with pronounced basal inflection, apex dorsally inflected and strongly narrowing, nearly straight, apex acute; as viewed ventrally, with weakly sclerotized, angular projections or cusps near base and before midlength, projections not evident in lateral view; mesal surface without projections or ridges. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin very strongly projecting, sclerotized, weakly ventrally deflected, apex of ventral projection more or less rounded, as viewed laterally; endotheca with two relatively short and asymmetrically positioned spines, membrane textured with small spines, phallotremal sclerite complex composed of short rod and ring structure and small apical sclerite.

Distribution. Democratic Republic of the Congo, Tanzania.

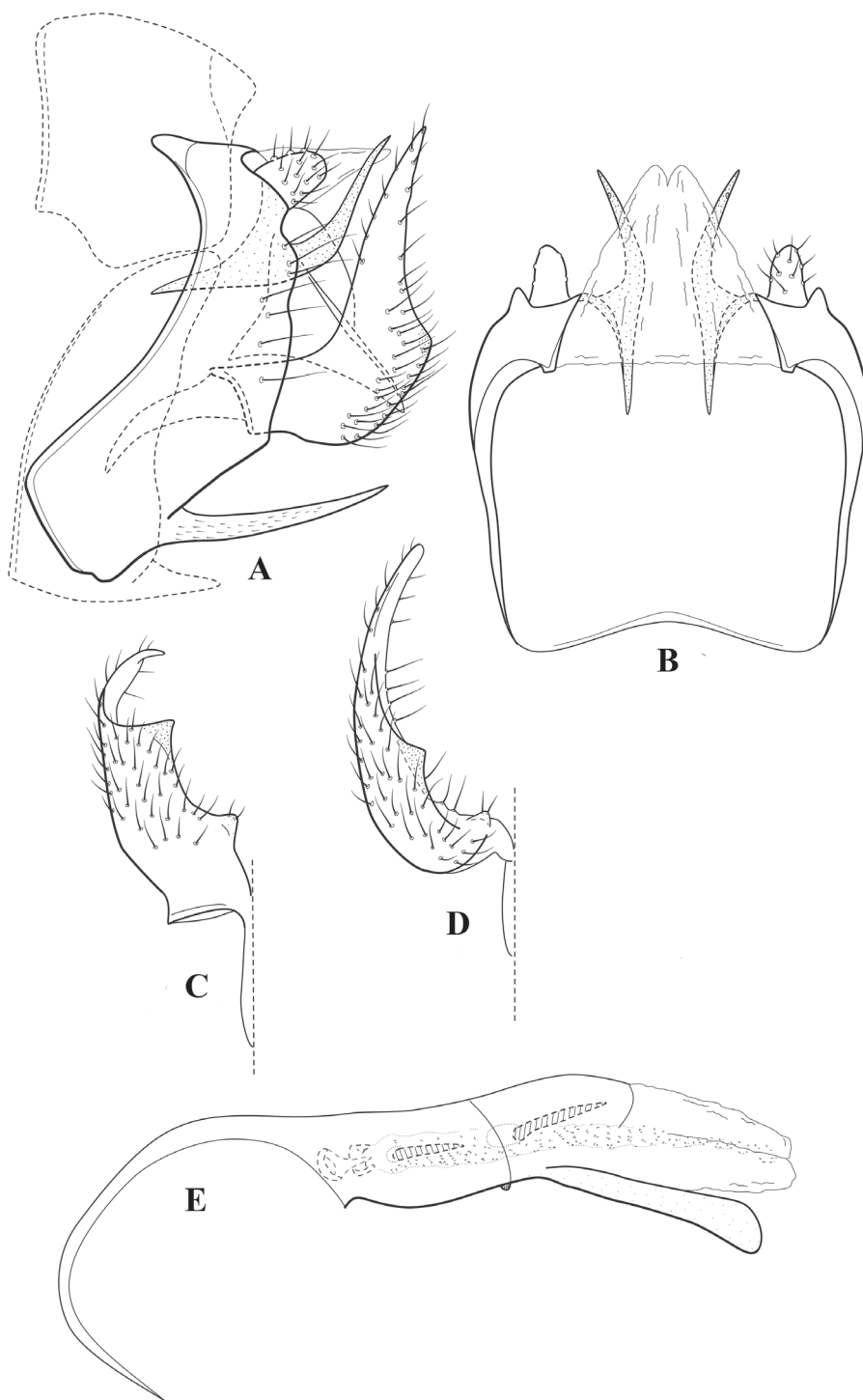


Figure 13. *Chimarra robynsi* (Jacquemart), ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, caudal **E** phallus, lateral.

***Chimarra togoana* (Ulmer, 1907)**

Fig. 14A–E

Wormaldia togoana Ulmer, 1907: 42–43, figs 61–63.*Chimarrha togoana* (Ulmer): Ulmer 1931: 3.*Chimarra togoana* (Ulmer): Fischer 1961: 71; Gibbs 1973: 67 (distribution: Ghana).

Material examined. GHANA – Volta Reg. • 1♂ 2♀♀; Wli, Agumatsa waterfall, station # 3; 7°07'29"N, 0°35'31"E; 17 Nov. 1993; J Kjærandsen leg.; light trap; ZMBN • 1♂; same collection data as for preceding; UMSP • 3♀♀; same collection data as for preceding except station # 10; 11 Nov. 1993; ZMBN • 1♀; same collection data as for preceding except 20 Nov. 1993; J Kjærandsen leg.; UMSP.

Diagnosis. *Chimarra togoana* is a very distinctive species, readily identified by the elongate, apically flared shape of its inferior appendages, with a distinctive mesal cusp at approximately midlength, and the elongate ventral process of segment IX, which is somewhat inflated apically, but apparently lacks the cluster of apicoventral spines characteristic of species in the *ruficeps* subgroup. It is only provisionally placed in the *fallax* subgroup since some of its characters could equally well be used to place it in the *ruficeps* subgroup. Characters supporting the latter interpretation include the overall shape of segment IX, which is strongly produced anteroventrally and has its ventromesal margin concave, and the distinctly formed and enlarged dorsolateral apodemes of the same segment. Characters supporting its placement in the *fallax* subgroup include the posteroventral projection of segment VIII. It is also possible that it belongs to a lineage basal to both of those subgroups. The rather simple tergum X, with an apicolateral cleft on each of its lateral lobes, is probably a primitive character; it may be ancestral to both subgroups, if the periphallallic processes of the *fallax* subgroup had their origin as a cleft in each of the lateral lobes of tergum X.

Redescription. Adult. Overall color (in alcohol) nearly uniformly yellowish brown. Head relatively short (postocular parietal sclerite ~ 1/2 diameter of eye). Palps relatively elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short (~ 3× 1st), apex with small cluster of stiff setae, 3rd segment relatively elongate (nearly 2× 2nd), 4th segment short (slightly shorter than 2nd), 5th segment elongate (nearly as long as 3rd and 4th combined). Forewing length: male, 6.2–7.0 mm; female, 6.5–7.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs weakly inflected at past midlength, without node at inflection, basal fork of discoidal cell not enlarged, fork nearly symmetric, length of cell ~ 2× width, fork I slightly subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *s* and *r-m* crossveins linear, *m* crossvein very distinctly more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline. 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II strongly subsessile, fork III distal and relatively wide, anal loop small. Foreleg with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

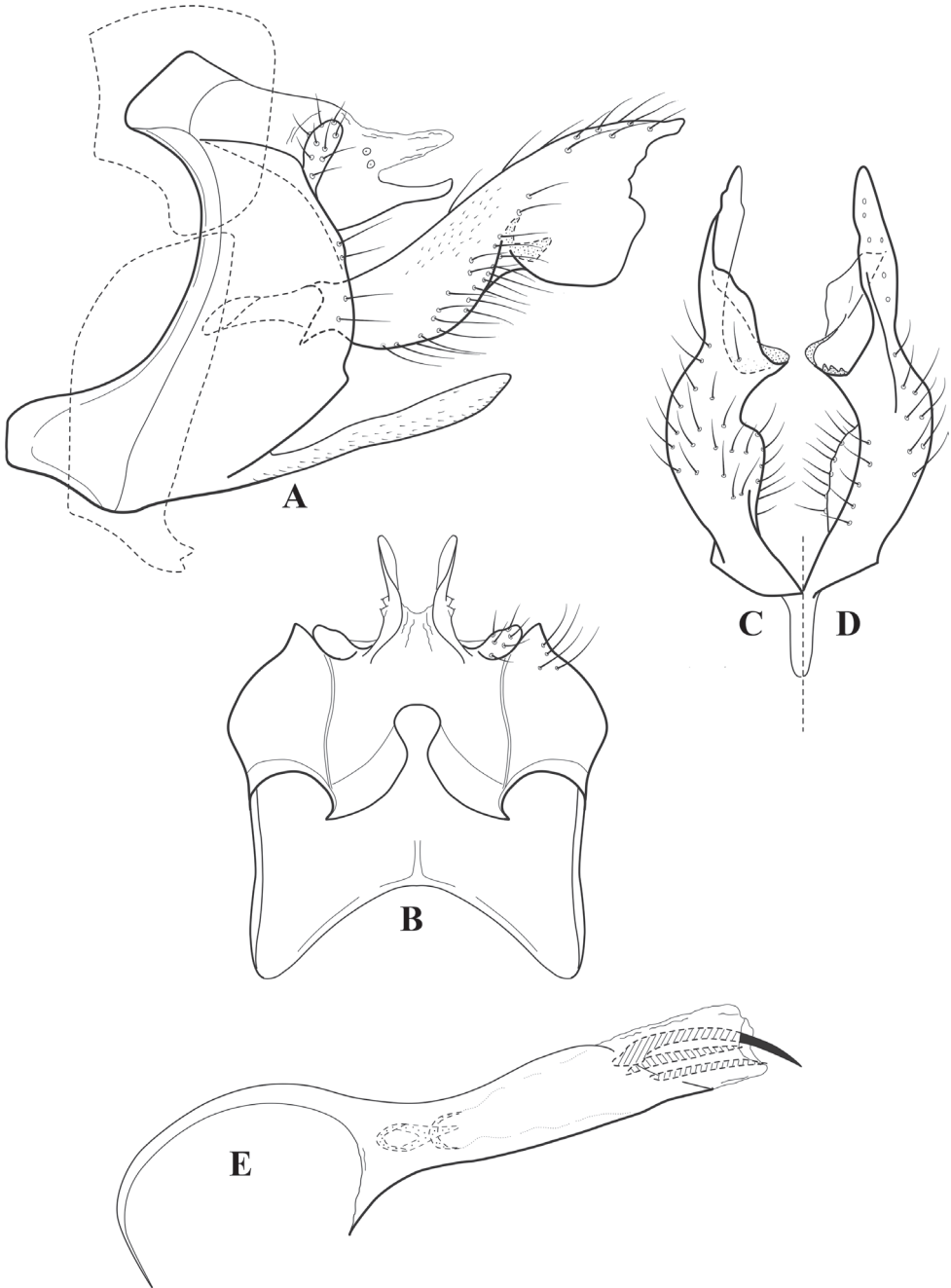


Figure 14. *Chimarra togoana* (Ulmer), ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

Male genitalia. Segment VIII relatively short, sternum with short, posteriorly projecting, ventromesal projection, tergum slightly longer than sternum. Segment IX, in lateral view, with anterior margin distinctly produced and rounded in ventral $\frac{1}{4}$, dorsolaterally with prominent rounded apodemes, margin strongly convex between apodemes; tergum continuous dorsally, forming deep, narrow emargination mesally between apodemes; posterior margin broadly convex; posteroventral margin with elongate, narrow, posteriorly-projecting, ventral process, apex of process slightly expanded. Segment IX, in dorsal or ventral views, with anteroventral margin strongly concave. Lateral lobes of tergum X short, each partially divided from posterior margin into dorsal and ventral lobes, dorsal lobe with two sensilla in basal half; mesal lobe of tergum X very short, membranous. Preanal appendages short and rounded, somewhat flattened, constricted basally. Inferior appendage, in lateral view, elongate, projecting, widened and flared apically, distal margin subtruncate; appendage with prominent, sclerotized mesal cusp at approximately midlength, visible in lateral view as notch on ventral margin. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin only weakly projecting, endotheca with three spines, one relatively elongate, curved, and strongly sclerotized, other two relatively short, asymmetrically positioned; phallotremal sclerite complex composed of short rod and ring structure with small apical sclerite.

Distribution. Ghana, Togo.

The *kenyana* subgroup

Included species. *Chimarra akana* Gibbs, 1973; *C. ambulans* Barnard, 1934; *C. baculifera* Marlier, 1965; *C. chicapa* Marlier, 1965; *C. flaviseta* Wahlberg, Espeland & Johanson, 2014; *C. intermedia* Jacquemart, 1961; *C. kenyana* Ulmer, 1931; *C. krugeri* Jacquemart, 1963; *C. longistylis* Jacquemart & Statzner, 1981; *C. morogoroensis* sp. nov.; *C. mulanjae* Wahlberg, Espeland & Johanson, 2014; *C. mushuvae* Marlier, 1951; *C. pedalotus* sp. nov.; *C. psittacus* Wahlberg, Espeland & Johanson, 2014; *C. quaridspinosus* Jacquemart & Statzner, 1981; *C. rhodesi* Kimmins, 1957; *C. saudia* Malicky, 1986; *C. somereni* Marlier, 1951; *C. szunyoghysi* Oláh, 1986; *C. tanzaniensis* sp. nov.; *C. triangularis* Kimmins, 1963; *C. triangularis occidentalis* Gibon, 1985; *C. trispina* Jacquemart, 1961; *C. uvirana* Marlier, 1951; and *C. zombaensis* Wahlberg, Espeland & Johanson, 2014.

General features of subgroup: tergum X with lateral lobes entire (or sometimes cleft apically), with digitate process near dorsal margin bearing two sensilla, process sometimes short. Inferior appendage with distinct basal inflection and mesal curvature, variable in length, but generally relatively narrow, with variably modified apex; mesal cusps absent. Ventral process of segment IX short, usually posteriorly projecting; the shape of the ventral process and genital capsule is variable among species and often usefully diagnostic. Phallus often with a pair of symmetrically positioned spines.

The number of known species assigned to this subgroup is large. Although there is considerable variation in the shape of the genital capsule, ventral process, phallic

armature, etc., most species have a general similarity that readily allows them to be placed in the subgroup. Distinguishing differences between some species are relatively minor. A revision of the subgroup would be a useful contribution.

Chimarra akana Gibbs, 1973

Fig. 15A–E

Chimarra akana Gibbs, 1973: 366–367, figs 14–16.

Chimarra akana Gibbs: Marlier 1980: 62 (as possible synonym of *C. kenyana* Ulmer); Gibon 1985: 25, figs 7, 12 (distribution: Ivory Coast).

Material examined. GHANA – **Eastern Reg.** • 4♂♂3♀♀; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjærandsen leg.; light trap; ZMBN. – **Volta Reg.** • 1♂; Kute, River Menu; 7°22'N, 0°36'E; 11 Dec. 1990; JS Amakye leg.; light trap; ZMBN • 1♂; Wli, Agumatsa waterfall, station # 2^A; 7°07'29"N, 0°35'31"E; 8–11 Mar. 1993; JS Amakye & J Kjærandsen leg.; Malaise trap; ZMBN • 15♂♂11♀♀; same collection data as for preceding except station # 3; 17 Nov. 1993; J Kjærandsen leg.; light trap; ZMBN • 1♂; same collection data as for preceding except station # 6; 11 Mar. 1993; JS Amakye & J Kjærandsen leg.; ZMBN • 1♂; same collection data as for preceding except station # 10; 19 Nov. 1993; J Kjærandsen leg.; UMSP • 10♂♂2♀♀; same collection data as for preceding except station # 15; 5 Dec. 1993; ZMBN • 1♀; same collection data as for preceding except station # 19; 9 Dec. 1993; ZMBN. – **Western Reg.** • 1♂1♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN • 1♂; same collection data as for preceding except 11 Mar. 1993; J Kjærandsen leg.; light trap; ZMBN • 10♂♂3♀♀; same collection data as for preceding except 5–9 Dec. 1993; T Andersen & J Kjærandsen leg.; ZMBN • 1♀; same collection data as for preceding except 19 Dec. 1993; UMSP.

Diagnosis. Characters, in combination, that confirm the identification and can be used to distinguish *C. akana* from other species in the subgroup include: the general shape and length of tergum X and position and length of digitate dorsal process; overall shape and length of inferior appendage and shape of apex in lateral view (orientation of appendage is slightly more bowed outward in specimen from Ghana); general shape of segment IX and length and shape of ventral process; details of phallus, especially the pair of curved ventral spines and upturned dorsal apex of phallobase.

The form illustrated here (Fig. 15A–E) closely matches the illustration provided by Gibon (1985: figs 7–8). As compared to the illustration of the species provided by Gibbs (1973: fig.16), the apex of the inferior appendage appears to be more sinuate. This is probably a matter of the orientation of the structure when illustrated (more or less caudal in the specimen illustrated by Gibon (1985: fig. 8), and more ventral in the specimen illustrated by Gibbs (1973: fig.16). For now, we accept Gibon's illustration as representing this species. Marlier (1980), who synonymized *C. wittei* Jacquemart with *C. kenyana* Ulmer, also suggested that *C. akana* may be synonym of this species. Both of these species would have name priority over *C. akana*. Unfortunately, the illustrations provided for the species

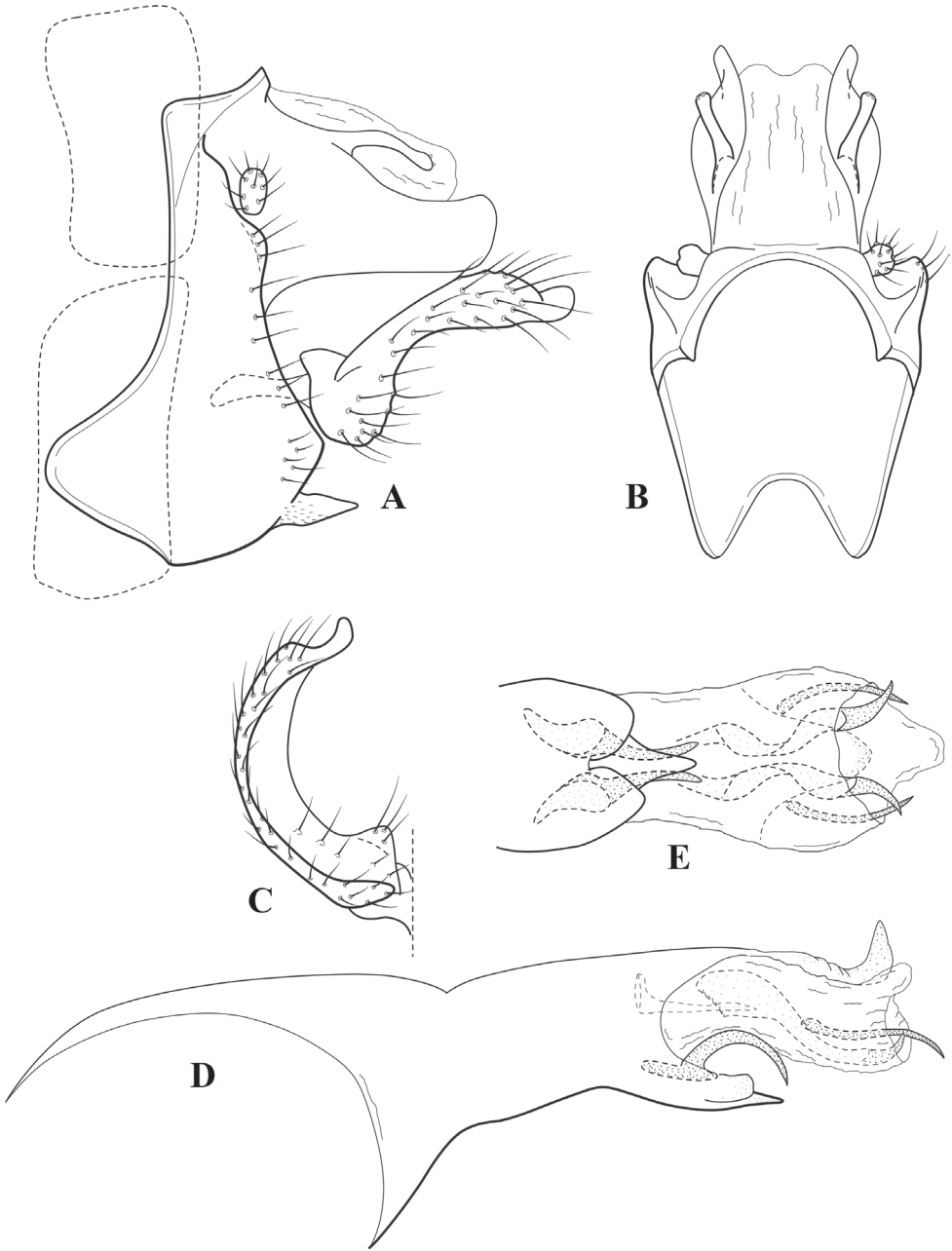


Figure 15. *Chimarra akana* Gibbs, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** phallus, lateral **E** phallus apex, ventral.

do not provide enough details to make an informed conclusion. The issue, including the synonymy made by Marlier, should be addressed in a future revision of the subgroup.

Diagnostic features of *C. akana* include, in particular, the shape of the inferior appendages which are relatively narrow and strongly bowed, with the apex somewhat

narrowed and upturned, as viewed caudally, with the relatively elongate dorsal sensilla-bearing lobes of tergum X and the phallic armature, which includes a pair of ventrally curved spines near the base of the endotheca and also a pair of very narrow spines apically, in addition to the phallotremal sclerite complex. The dorsal margin of the phallobase is also somewhat produced and upturned apically, but only weakly sclerotized, so the feature may not always be evident. As in all species of the *kenyana* subgroup, the shape of the genital capsule and ventral process of segment IX are also important considerations in making species determinations, even if these features are not absolutely consistent. Compared to other species in the subgroup, *C. akana* has a relatively short segment IX, with the anteroventral margin produced and a narrow, posteriorly projecting ventral process.

Redescription. Adult. Overall color (in alcohol) nearly uniformly yellowish brown. Head relatively short (postocular parietal sclerite $< 1/2$ diameter of eye). Palps moderately elongate; maxillary palp with 1st segment very short (slightly longer than wide), 2nd segment short ($\sim 2 \times 1^{\text{st}}$), apex with small cluster of stiff setae, 3rd segment elongate ($\sim 1\frac{1}{2} \times 2^{\text{nd}}$), 4th segment short (slightly shorter than 2nd), 5th segment elongate (subequal to 3rd). Forewing length: male, 4.5–5.2 mm; female, 4.8–5.8 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 somewhat sinuous, stem of R_s inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork asymmetric, length of cell $\sim 2 \times$ width, forks I and II slightly subsessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, m crossvein proximal to s and $r-m$ crossveins, s pigmented (like wing), $r-m$ and m crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile. Foreleg with apical tibial spur short; male with foretarsi modified, claws enlarged, outer claw twisted and asymmetrical.

Male genitalia. Segment VIII relatively short, sternum and tergum subequal in length. Segment IX, in lateral view, relatively short, anterior margin distinctly produced and rounded in ventral $\frac{1}{4}$, dorsolaterally with broad, weakly developed, apodeme; tergum continuous dorsally, forming concave excavation between lateral apodemes; posterior margin very weakly produced below preanal appendage, widening ventrally to level of inferior appendage; ventral margin rounded between anteroventral production and inferior appendage, ventral process midway between, short, narrow, acute apically. Segment IX, in dorsal or ventral views, with anteroventral margin deeply concave mesally. Lateral lobes of tergum X relatively elongate, subtruncately rounded apically, with moderately elongate, digitate, sensilla-bearing process from dorsal margin in basal half; mesal lobe of tergum X elongate, membranous, somewhat shorter than lateral lobes. Preanal appendages small, rounded, constricted basally. Inferior appendage, in lateral view, relatively elongate, narrow, strongly dorsally flexed near base, apex somewhat narrowed, rounded as viewed laterally, with sinuous dorsal inflection as viewed caudally; appendage, in caudal view, very strongly mesally curved. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, apicoventral margin weakly projecting, dorsal margin somewhat extended, weakly sclerotized, with apex slightly upturned; endotheca with pair of prominent, symmetrical, ventrally curved spines basoventrally, and pair of very narrow, needle-like spines apically; phallotremal sclerite

complex composed of moderately elongate rod and ring structure, with relatively elongate, paired apicolateral sclerites, each terminating in a distinct short spine.

Distribution. Ghana, Ivory Coast.

***Chimarra eshowensis* sp. nov.**

<http://zoobank.org/AB398DFA-9761-4F81-8D07-8CDD8D876EB8>

Fig. 16A–F

Type material. *Holotype*. SOUTH AFRICA • ♂ (pinned); KwaZulu-Natal, Eshowe, Mpushi ni Falls; 28°54.529'S, 31°26.858'E; 9 Jan. 2000; KM Kjer & RJ Blahnik leg.; UMSP 000172258. *Paratypes*. SOUTH AFRICA • 1♂3♀♀; same data as for holotype; UMSP.

Diagnosis. *Chimarra eshowensis* sp. nov. is very similar to *C. chicapa* Marlier, described from Angola. Both species are distinctive in having relatively short inferior appendages, with their apices little modified and also in having paired, curved, dorsal spines near the base of the endotheca; both were also collected near waterfalls. The differences in the shape of segment IX, forming the genital capsule, length of the dorsal sensilla-bearing processes of tergum X, and particularly the overall shape of the inferior appendages and degree to which their apices are inturned apically, all suggest the two are different species. The assessment is admittedly subjective. The collection of specimens with intermediate character states from intervening areas might warrant a reassessment of their species status.

Description. *Adult*. Overall color dark brown, including appendages, femurs paler. Head relatively short and rounded (postocular parietal sclerite ~ 1/2 diameter of eye). Palps relatively short; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (~ 3 × 1st), apex with small cluster of stiff setae, 3rd segment slightly longer than 2nd, 4th segment short (~ 1/2 length of 3rd), 5th segment subequal to 2nd. Forewing length: male, 4.5–4.8 mm; female, 4.5–5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs weakly inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork very asymmetric, length of cell ~ 2 × width, fork I subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *m* crossvein proximal to *s* and *r-m* crossveins, approximately midway between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, *m* very faint, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II subsessile. Foreleg with apical tibial spur distinct; male with foretarsi modified, claws enlarged, approximately symmetrical.

Male genitalia. Segment VIII relatively short, tergum slightly longer dorsally. Segment IX, in lateral view, relatively short, anterior margin distinctly, subangularly produced in ventral 1/4, dorsolaterally with broadly rounded, rather weakly developed, apodeme; tergum continuous dorsally, sclerotized region very short, nearly linear between lateral apodemes; posterior margin very weakly produced below preanal appendage, widening ventrally to level of inferior appendage; ventral margin with rather prominent,

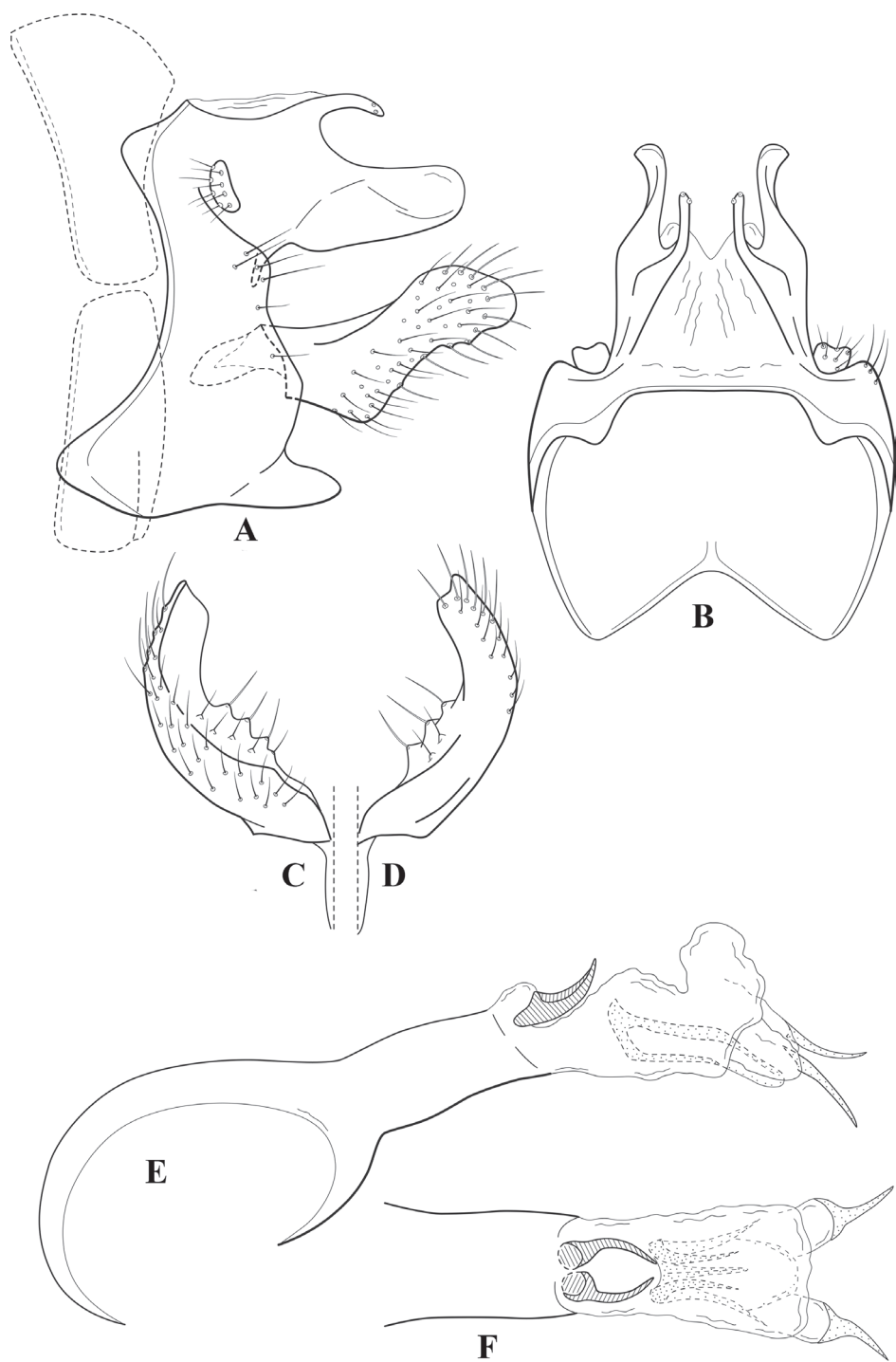


Figure 16. *Chimarra eshowensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus apex, dorsal.

posteriorly projecting, ventral process, length greater than width at base, apex subangular. Segment IX, in dorsal or ventral views, with anteroventral margin moderately, angularly, invaginated mesally. Lateral lobes of tergum X, in lateral view, moderately elongate, apices rounded, weakly sclerotized, dorsal margin with moderately elongate, posteriorly curved, digitate, sensilla-bearing process at approximately midlength; mesal lobe of tergum X membranous, extending $> 1/2$ length of lateral lobes. Preanal appendages small, rounded, and somewhat flattened, constricted basally. Inferior appendage, in lateral view, relatively short, dorsally flexed near base, posteriorly recurved near apex, apex not or very little narrowed, rounded as viewed laterally, subtruncate as viewed dorsally or ventrally; appendage, in dorsal or ventral views, only moderately bowed or curved, apices not more so, basomesally with distinct setae. Phallic apparatus with phallobase relatively short, tubular, with usual basodorsal expansion, apicoventral margin not projecting; endotheca, basodorsally, with pair of prominent, symmetrical, dorsally curved spines; endotheca apically with paired membranous lobes, each terminating in tapering, moderately sclerotized spine; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with elongate, paired, rather weakly sclerotized, dorsal sclerites.

Etymology. *Chimarra eshowensis*, used as an adjective and meaning “from Eshowe” in reference to the place of origin of the holotype specimen.

Chimarra krugeri Jacquemart, 1963

Fig. 17A–E

Chimarra krugeri Jacquemart, 1963: 395–397, figs 48, 49.

Chimarra krugeri Jacquemart: Scott 1974: 244–245, figs 22–24.

Material examined. TANZANIA – **Morogoro Reg.** • 1♂; Uluguru Mts, Kimboza Forest Reserve, Ruvu River; 7°2'S, 37°47'E; 20 Oct. 1990, T Andersen leg.; sweep net; UMSP.

Diagnosis. The most diagnostic aspects of *Chimarra krugeri*, in combination, include the very elongate lateral lobes of tergum X, with apices rounded and dorsal margin more strongly sclerotized, and with a very elongate, digitate, sensilla-bearing process basally; the single, very elongate phallic spine; the shape of segment IX, especially the subtriangular ventral process and prominent anterodorsal apodeme; and the general shape of the inferior appendages, whose apices are somewhat broadened or enlarged, as viewed laterally. The latter character will distinguish it from *C. waensis*, *C. baculifera*, and *C. camerunensis*, all of which also have a basally broad, subtriangular, ventral process on segment IX and elongate digitate processes on tergum X but have the inferior appendages more or less uniformly narrow. Among the species of the *kenyana* subgroup treated here, *C. krugeri* is unusual in having a very short discoidal cell in both the fore- and hind wings, with very elongate forks I and II. It is most similar, in this respect, to *C. waensis*, in which the characters are similar, but not quite as exaggerated.

Redescription. Adult. Overall color (in alcohol) nearly uniformly yellowish brown. Head elongate (postocular parietal sclerite subequal in length to diameter of eye). Palps

elongate; maxillary palp with 1st segment very short (slightly longer than wide), 2nd segment elongate (distinctly longer than 3rd), apex with cluster of stiff setae, 3rd segment moderately elongate (normal), 4th segment short ($\sim 2 \times 1^{\text{st}}$), 5th segment elongate (subequal to 3rd). Forewing length: male, 5.9 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 somewhat sinuous, stem of Rs short, inflected at approximately midlength, with small node extending into cell below, discoidal cell very short, width subequal to length, basal fork not enlarged, forks I and II (of both fore- and hind wings) very elongate, forks petiolate, r crossvein diagonal, intersecting discoidal cell at approximately midlength, $r-m$ crossvein of forewing slightly proximal to s , m crossvein proximal to $r-m$, very near basal fork of M, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, discoidal cell very small. Foreleg with apical tibial spur short; male with foretarsi modified, claws enlarged and symmetrical.

Male genitalia. Segment VIII relatively short. Segment IX, in lateral view, relatively short, anterior margin distinctly, subangularly, produced in ventral $\frac{1}{4}$, dorsolaterally with very prominent, broadly rounded apodeme, margin concave between; tergum very short and narrowly sclerotized, but continuous dorsally, in dorsal view, forming concave excavation between lateral apodemes; posterior margin obliquely and linearly widened from preanal appendage to ventral process; ventral margin extended apically to form very basally wide, weakly projecting, subtriangular ventral process. Segment IX, in dorsal or ventral views, with anteroventral margin moderately concave mesally. Lateral lobes of tergum X very elongate, subtruncately rounded apically, dorsal margin distinctly sclerotized, basodorsally with elongate, posteriorly oriented, digitate, sensilla-bearing process; lateral lobes, in dorsal view, narrowly parallel; mesal lobe of tergum X membranous, nearly as long as lateral lobes, inconspicuous because of closely apposed lateral lobes. Preanal appendages short, constricted basally, knob-like. Inferior appendage, in lateral view, relatively elongate, narrow, strongly dorsally flexed near base, apex distinctly widened, extreme apex weakly notched or bifid, noticeable in some orientations; appendage, in dorsal or ventral views, more or less uniformly mesally curved. Phallic apparatus with phallobase broadly tubular, with usual basodorsal expansion, apicoventral margin moderately projecting; endotheca with single, very elongate spine, nearly as long as ventral margin of phallobase; phallotremal sclerite complex composed of very short rod and ring structure, with small, paired apicolateral sclerites.

Distribution. Republic of South Africa, Tanzania.

***Chimarra morogoroensis* sp. nov.**

<http://zoobank.org/0B638A45-3548-4BFE-B932-00FEB3A6CA1C>

Fig. 18A–E

Type material. Holotype. TANZANIA – **Morogoro Reg.** • ♂ (in alcohol); Morogoro, Teachers College; 6°49'S, 37°42'E; 12 Dec. 1990; T Andersen leg.; sweep net; UMSP 000550015. **Paratype.** TANZANIA – **Morogoro Reg.** • 1♂; same data as for holotype; ZMBN.

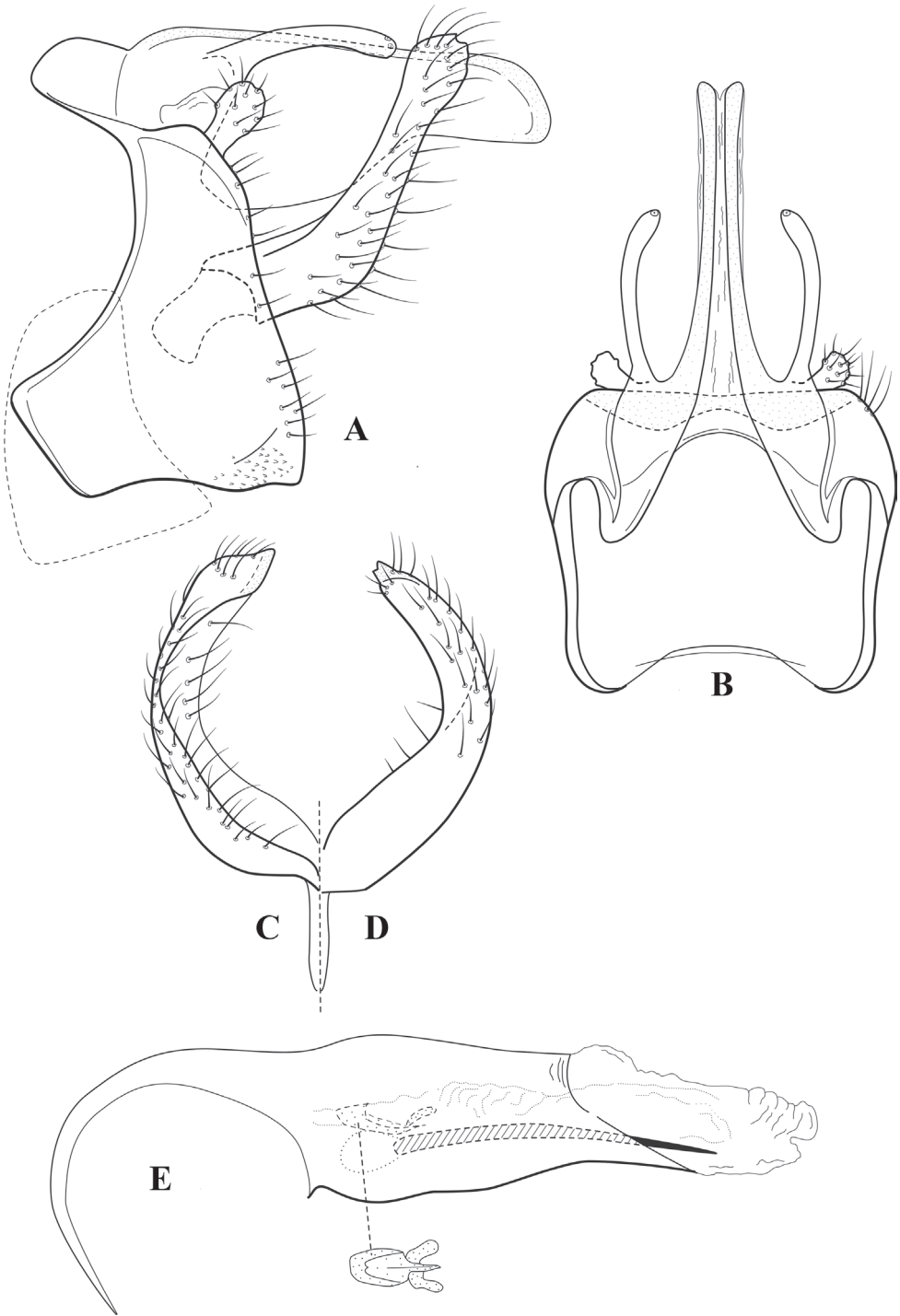


Figure 17. *Chimarra krugeri* Jacquemart, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

Diagnosis. *Chimarra morogoroensis* is very similar to *C. szunyoghyi* Oláh, and we are not completely sure that it is a distinct species. The inferior appendages, tergum X, and the general form of segment IX and its ventral process are more or less identical in the two species. Like *C. szunyoghyi* and *C. tanzaniensis* sp. nov., the apex of the inferior appendages is very distinctly developed and acute, more distinctly so in both *C. morogoroensis* and *C. szunyoghyi* than in *C. tanzaniensis*, which usefully distinguishes them. Differences between *C. morogoroensis* and *C. szunyoghyi* are found mostly in phallic structures. The differences, however, are qualitative and involve characters that could function in isolating the two species. The primary differences are the elongate, extensible dorsal lobe on the endotheca in *C. szunyoghyi*, with two small apical spines, and the very much extended and sharply downturned ventral apex of the phallobase in *C. morogoroensis*. In *C. morogoroensis*, the dorsal phallic lobe appears to be relatively simple and much shorter, without apical spines, and in *C. szunyoghyi*, the ventral apex of the phallobase is only very weakly developed and projecting. We consider the differences significant enough to warrant the recognition of two species.

Description. Adult. Overall color (in alcohol) medium brown, vertex of head darker than setal warts. Head elongate (postocular parietal sclerite nearly as long as diameter of eye). Palps relatively short, maxillary palp with 1st segment short (approximately as long as wide), 2nd segment short (~ 2× length of 1st), apex with small cluster of stiff setae, 3rd elongate (almost 2× length of 2nd), 4th segment short (shorter than 2nd), 5th segment elongate (subequal to 3rd). Forewing length: male, 5.9 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 somewhat sinuous, stem of R_s inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, very asymmetric, discoidal cell elongate, length greater than two × width, forks I and II sessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, $r-m$ crossvein nearly continuous with s , m crossvein proximal to s and $r-m$ crossveins, slightly closer to $r-m$ crossvein than basal fork of M , s pigmented (like wing), $r-m$ and m crossveins hyaline, very weakly developed, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II approximately sessile. Foreleg with apical tibial spur short; male with foretarsi not modified.

Male genitalia. Segment VIII relatively short, tergum slightly longer dorsally. Segment IX, in lateral view, moderate in length, anterior margin strongly, angularly produced ventrally, dorsolaterally with distinct rounded apodemes, margin strongly concave between; tergum, in dorsal view, continuous between apodemes, but very short, forming deeply concave excavation; posterior margin short dorsally, weakly, obtusely produced below preanal appendages, more or less linearly widening ventrally to ventral process; posteroventral margin with rather prominent, subtriangular, posteriorly projecting, ventral process, length greater than width at base, apex acute. Segment IX, in dorsal or ventral views, with anteroventral margin deeply concave mesally. Lateral lobes of tergum X moderate in length, rounded apically, with very short, rounded, sensilla-bearing process near dorsal margin at approximately midlength, ventrolaterally with compressed, rounded projection, hardly evident in lateral view, but forming distinct rounded projection, as viewed dorsally; mesal lobe of tergum X membranous, short, only at base of

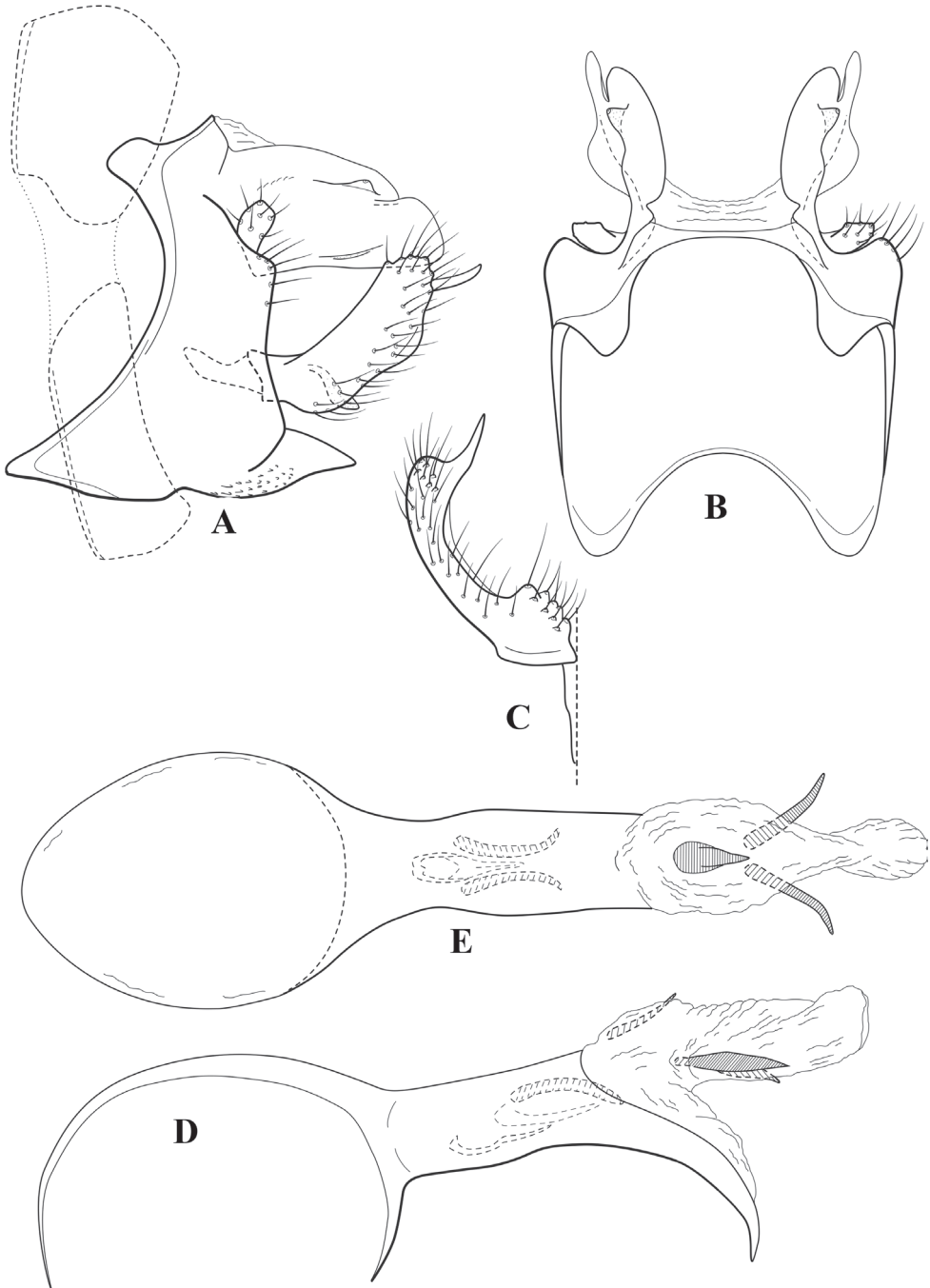


Figure 18. *Chimarra morogoroensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral **E** phallus, dorsal.

lateral lobes. Preanal appendages short, rounded, constricted basally. Inferior appendage, in lateral view, relatively narrow and short, dorsally flexed near base, with apex forming very distinct spine-like projection, readily visible in both lateral and ventral views; appendage, in dorsal or ventral views, moderately mesally curved, with short basomesal enlargement at basal inflection, apex very prominent and spine-like, somewhat mesally curved. Phallic apparatus with phallobase relatively short and tubular, with usual basodorsal expansion, apicoventral margin forming a very distinct and strongly ventrally curved projection, apex acute; endotheca membranous, without minute spines, but with three very distinct, moderate elongate spines, one dorsomesal and two lateral, symmetrically positioned; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with pair of distinct, narrow, curved, dorsolateral sclerites.

Etymology. *Chimarra morogoroensis*, used as an adjective and meaning “from Morogoro” in reference to the town in Tanzania where this species was collected.

***Chimarra pedaliotus* sp. nov.**

<http://zoobank.org/E741B076-E7DD-46D8-88DB-29BAD6D1020D>

Fig. 19A–G

Type material. Holotype. GHANA – **Volta Reg.** • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 12; 7°07'29"N, 0°35'31"E; 7 Mar. 1993; JS Amakye & J Kjørandsen leg.; light trap; UMSP 000550008. **Paratypes.** GHANA – **Volta Reg.** • 1♂; same data as for holotype except station # 10^A; 7–10 Mar. 1993; Malaise trap; ZMBN • 1♂; same data as for holotype except station # 3; 10 Mar. 1993; light trap; ZMBN • 4♂♂; same data as for holotype except 17 Nov. 1993; J Kjørandsen leg.; ZMBN • 2♂♂; same data as for holotype except station # 6; 11 Mar. 1993; ZMBN • 1♂; same data as for holotype except 20 Nov. 1993; J Kjørandsen leg.; ZMBN • 1♂; same data as for holotype except station # 10; 8 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 3; 12 Nov. 1993; J Kjørandsen leg.; sweep net; ZMBN. – **Eastern Reg.** • 1♂; Boti Falls; 6°11'40"N, 0°13'05"W; 19 Nov. 1991; J Amakye leg.; light trap; ZMBN • 1♂; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN. CAMEROON • 20♂♂1♀; Muguka, Victoria Division; 24–29 June 1949; B Malkin leg.; INHS • 2♂♂; same collection data as for preceding; UMSP • 1♂; Victoria, British Cameroons; May 1949; B Malkin leg.; INHS. NIGERIA • 1♂; Cross River State, Ikom, Igoja Prov.; 6 Jan. 1949; B Malkin leg.; INHS.

Additional material. GHANA – **Eastern Reg.** • 2♀♀; Boti Falls; 6°11'40"N, 0°13'05"W; 19 Nov. 1991; JS Amakye leg.; light trap; ZMBN • 1♀; same collection data as for preceding except 28 Oct.–4 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN • 8♀♀; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN. – **Volta Reg.** • 2♀♀; Hohoe, Matvin Hotel; 7°09'43"N, 0°28'31"E; 11 Nov. 1993; J Kjørandsen leg.; at light; ZMBN • 1♂; Fodoma, Nubui stream; 7 June 1995; T Andersen & J Kjørandsen leg.; light trap; UMSP • 1♀; Wli, Agumatsa waterfall, station # 3^B; 7°07'29"N, 0°35'31"E; 4–7 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding except station #

9^B; UMSP • 1♀; same collection data as for preceding except station # 4^B; 7–10 Mar. 1993; ZMBN • 5♀♀; same collection data as for preceding except station # 3; 10 Mar. 1993; light trap; ZMBN • 6♀♀; same collection data as for preceding except 17 Nov. 1993; J Kjørandsen leg.; ZMBN • 1♀; same collection data as for preceding except station # 6; 11 Mar. 1993; JS Amakye & J Kjørandsen leg.; ZMBN • 2 ♀♀; same collection data as for preceding except 20.xi.1993; J Kjørandsen leg.; ZMBN • 12♀♀; same collection data as for preceding except station # 10; 19 Nov. 1993; ZMBN • 30♀♀; same collection data as for preceding except station # 12; 16 Nov. 1993; ZMBN.

Diagnosis. Inferior appendage relatively short, uniform in width in lateral view, apex subacute in ventral view; ventral apex of phallobase expanded, laterally compressed, and ventrally deflexed; phallus with pair of small, curved, symmetrically placed spines; apex of lateral lobe of tergum X subacute.

Chimarra pedalotus is similar to *C. occidentalis* Gibon but is easily diagnosed by the very distinctive apex of the phallobase, which is enlarged and rounded, as viewed laterally, and also strongly compressed. Specimens from Cameroon differed slightly in the armature of the phallus, including phallic spines that tended to be bifid apically and were also somewhat larger, and a more elongate apical spine. The differences are rather minor and somewhat variable even in the material examined; on the other hand, the overall similarity is significant. We do not consider the differences significant enough to warrant varietal or species status. Future collecting may require a reassessment of this conclusion.

Description. Adult. Overall color (in alcohol) yellowish brown. Head short and rounded (length of postocular parietal sclerite ~ 1/2 diameter of eye). Palps relatively short, maxillary palp with 1st segment very short (length subequal to width), 2nd segment relatively short (~ 3 × 1st), apex with small cluster of stiff setae, 3rd segment slightly longer than 2nd, 4th segment short (~ 1/2 length of 3rd), 5th segment short (subequal to 2nd). Forewing length: male, 3.8–5.0 mm; female, 4.5–5.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs weakly inflected at approximately midlength, with node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork very asymmetric, length of cell ~ 2 × width, forks I and II slightly subsessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *m* crossvein proximal to *s* and *r-m* crossveins, approximately midway between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline and very faint, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II slightly subsessile. Foreleg with apical tibial spur short; male with foretarsi modified, claws enlarged, outer claw twisted and asymmetric.

Male genitalia. Segment VIII moderately elongate, sternum and tergum subequal in length. Segment IX, in lateral view, elongate, anterior margin strongly, subangularly produced in ventral 1/3, dorsolaterally with distinct rounded apodeme, margin strongly convex between; tergum, in dorsal view, continuous between apodemes, but very short, forming deeply concave excavation; posterior margin nearly linear, slightly widening ventrally; ventral margin with rather prominent, posteriorly projecting, ventral process, length greater than width at base, apex subacute. Segment IX, in dorsal or ventral views,

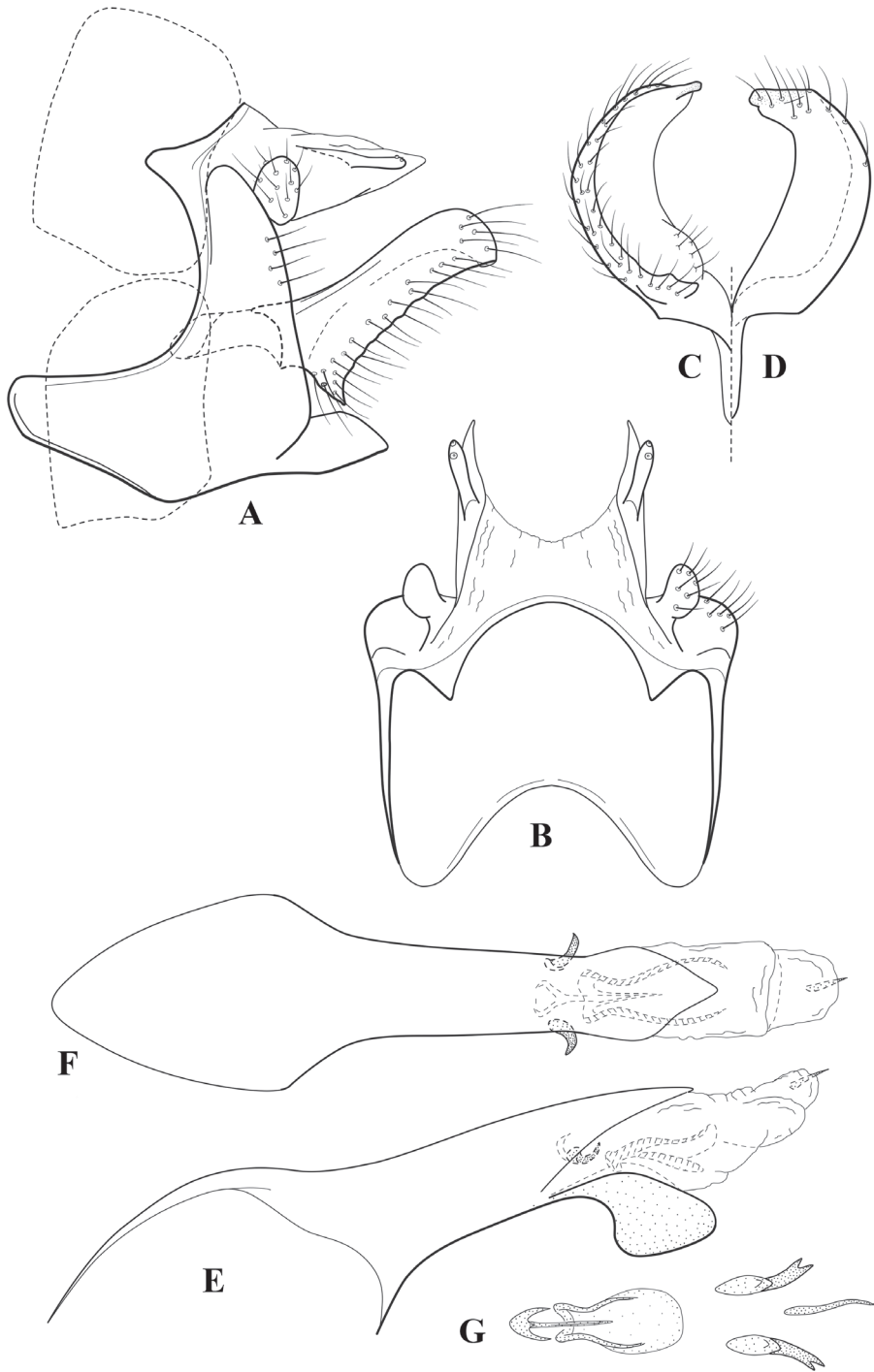


Figure 19. *Chimarra pedaliotus* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, dorsal **G** phallic armature, dorsal, variant from Cameroon.

with anteroventral margin deeply concave mesally. Lateral lobes of tergum X relatively short, subacute apically, with moderately elongate, posteriorly projecting, digitate, sensilla-bearing process near dorsal margin in basal half; mesal lobe of tergum X membranous, $\sim 1/2$ length of lateral lobes. Preanal appendages short, rounded, constricted basally. Inferior appendage, in lateral view, only moderately elongate, nearly uniform in width, dorsally flexed near base, with small angular ventral projection at point of inflection, apex incurved and forming short, rounded projection, not visible in lateral view; appendage, in dorsal or ventral views, uniformly and only moderately mesally curved. Phallic apparatus with phallobase tubular, with usual basodorsal expansion, dorsal margin tapering and acute apically, but only weakly sclerotized, apicoventral margin forming a broadly rounded and deflexed, laterally compressed and keel-like, sclerotized projection; endotheca relatively short and without minute spines, basally with pair of short, curved, symmetrical, laterally emergent spines; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with narrow, paired, dorsolateral sclerites.

Etymology. *Chimarra pedaliotus*, as an adjective from the Greek *pedaliotos*, meaning “with a rudder,” and referring to the keeled and somewhat rudder-like ventral apex of the phallobase in this species.

Chimarra szunyoghyi Oláh, 1986

Fig. 20A–E

Chimarra szunyoghyi Oláh, 1986: 141–143, fig. 1A–D.

Material examined. TANZANIA – Tanga Reg. • 1♂; West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 26 Nov. 1990; T Andersen leg.; Malaise trap; UMSP • 1♂; INHS.

Diagnosis. *Chimarra szunyoghyi* is very similar to *C. morogoroensis* sp. nov., as discussed in the diagnosis for that species. Both species have general features of the inferior appendages, tergum X, and the general shape of segment IX, including its ventral process, nearly identical. The elongate, acute apical projection on the inferior appendages is usefully diagnostic for both species, and differs from the similar, but shorter, projection found in *C. tanzaniensis* sp. nov. The primary differences separating *C. szunyoghyi* from *C. morogoroensis* are found in structures of the phallic apparatus and include, especially, the elongate, extensible dorsal lobe on the endotheca, found in *C. szunyoghyi*, which has a pair of small apical spines, and the very elongate and strongly downturned ventral apex of the phallobase found in *C. morogoroensis*. The dorsal lobe on the endotheca in *C. morogoroensis* is simpler, much shorter, and lacks apical spines, and the ventral apex of the phallobase in *C. szunyoghyi* is much shorter. The differences, while minor, are distinctive.

Redescription. Adult. Overall color (in alcohol) medium brown, vertex of head darker than setal warts. Head elongate (postocular parietal sclerite nearly as long as diameter of eye). Palps relatively short, maxillary palp with 1st segment short (approximately

as long as wide), 2nd segment short ($\sim 2\times$ length of 1st), apex with small cluster of stiff setae, 3rd elongate (almost $2\times$ length of 2nd), 4th segment short (shorter than 2nd), 5th segment elongate (slightly longer than 3rd). Forewing length: male, 5.1 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 somewhat sinuous, stem of R_s inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, very asymmetric, discoidal cell moderately elongate, length $\sim 2\times$ width, forks I and II slightly subsessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, $r-m$ crossvein nearly continuous with s , m crossvein proximal to s and $r-m$ crossveins, approximately midway between basal fork of M and $r-m$ crossvein, s pigmented (like wing), $r-m$ and m crossveins hyaline, very weakly developed, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile. Foreleg with apical tibial spur short; male with foretarsi apparently weakly modified, claws symmetric, slightly enlarged.

Male genitalia. Segment VIII relatively short, tergum slightly longer dorsally. Segment IX, in lateral view, moderate in length, anterior margin strongly, angularly produced ventrally, dorsolaterally with distinct rounded apodeme, margin strongly convex between; tergum, in dorsal view, continuous between apodemes, but very short, forming deeply concave excavation; posterior margin short dorsally, weakly, obtusely produced below preanal appendages, more or less linearly widening ventrally to ventral process; posteroventral margin with rather prominent, subtriangular, posteriorly projecting, ventral process, length greater than width at base, apex acute. Segment IX, in dorsal or ventral views, with anteroventral margin deeply concave mesally. Lateral lobes of tergum X moderate in length, rounded apically, with very short, rounded, sensilla-bearing process near dorsal margin in basal half, ventrolaterally with compressed, rounded projection, hardly evident in lateral view, but forming distinct rounded projection, as viewed dorsally; mesal lobe of tergum X membranous, short, and divided mesally, more extended laterally. Preanal appendages short, rounded, constricted basally. Inferior appendage, in lateral view, relatively narrow and short, dorsally flexed near base, with apex forming very distinct spine-like projection, readily visible in both lateral and ventral views; appendage, in dorsal or ventral views, moderately mesally curved, with short basomesal enlargement at basal inflection, apex very prominent and spine-like, somewhat mesally curved. Phallic apparatus with phallobase relatively short and tubular, with usual basodorsal expansion, apicoventral projection short, acute, only weakly projecting and deflexed; endotheca membranous, without minute spines, but with very elongate, pleated, extensible, membranous lobe with two short apical spines, endotheca also with three very distinct, moderately long spines, one dorsomesal and two lateral, symmetrically positioned, extensible lobe, when extended, as long or longer than ventral margin of phallobase; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with pair of distinct, narrow, curved, dorsolateral sclerites.

Distribution. Tanzania.

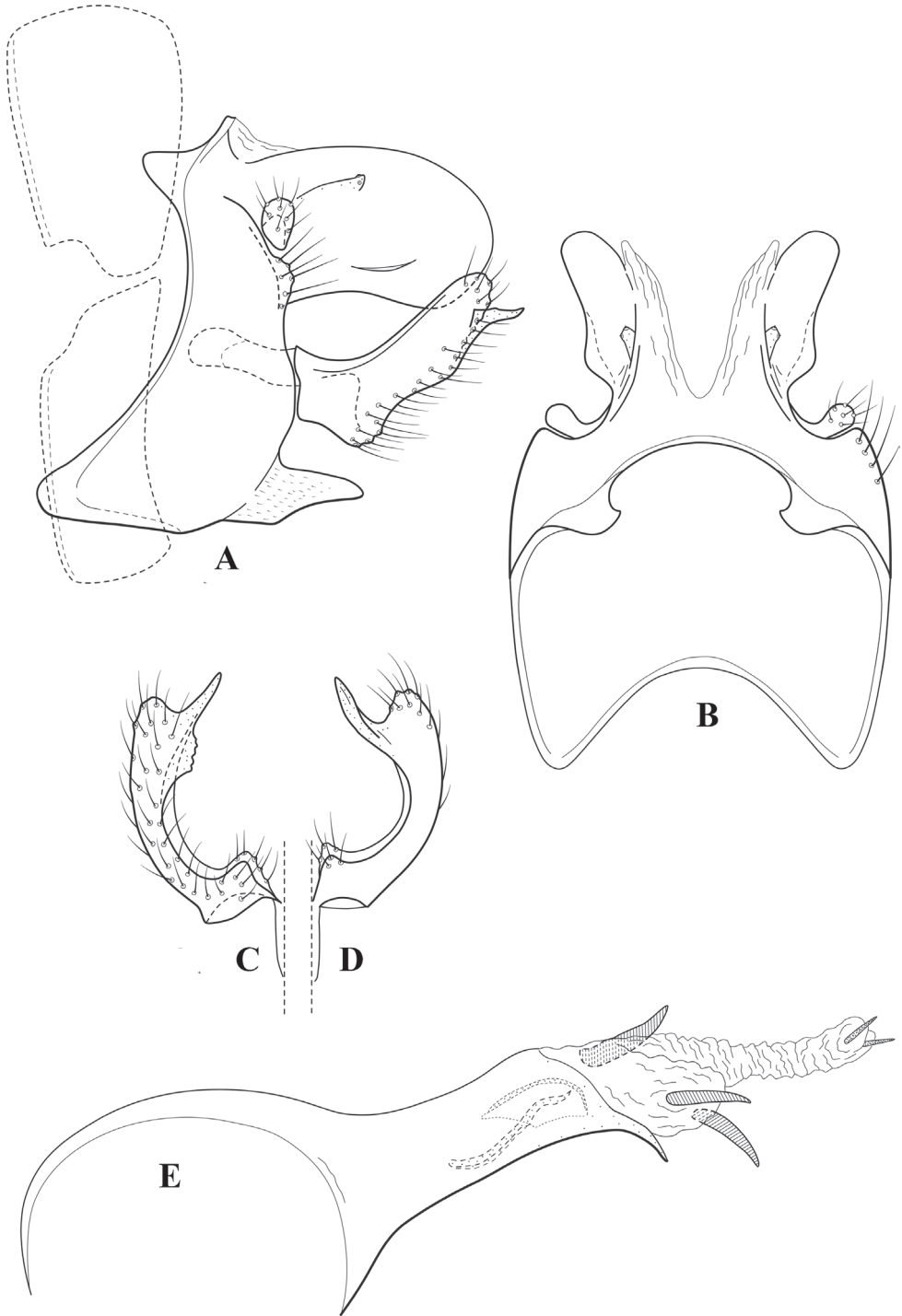


Figure 20. *Chimarra szunyoghyi* Oláh, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

***Chimarra tanzaniensis* sp. nov.**

<http://zoobank.org/C728A834-7039-47DE-AF50-D22EA22BCF22>

Fig. 21A–E

Type material. *Holotype*. TANZANIA – **Tanga Reg.** • ♂ (in alcohol); West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 30 Oct. 1990–12 Feb. 1991; T Andersen leg.; Malaise trap; UMSP 000550066. *Paratypes*. TANZANIA – **Tanga Reg.** • 11♂♂; same data as for holotype; ZMBN • 2♂♂; same data as for holotype except 4–12 Feb. 1991; UMSP • 2♂♂; same data as for holotype except 5 Nov. 1990; sweep net; ZMBN.

Diagnosis. *Chimarra tanzaniensis* probably has its overall closest similarity to *C. quadrispinosa* Jacquemart & Statzner, particularly in the overall shape of segment IX and inferior appendages, which have a very similar shape and acute, spine-like apices. The apices of the inferior appendages also resemble *C. szunyoghysi* Oláh, but are not quite so pronounced as in that species. Differences from *C. quadrispinosa* include a less produced posteroventral margin of segment IX, absence of distinct basomesal projections on the inferior appendages, and a different armature of the phallus. The four spines of *C. quadrispinosa*, based on its illustration, seem to include two prominent, symmetrically placed dorsal spines, which are common among various species of the *kenyana* group, and two apical spines, possibly elements of the phallotremal sclerite complex. The phallotremal sclerite complex of *C. tanzaniensis* also has elongate lateral sclerites, but the dorsal spines in this species are very small and occur at the end of a narrow membranous projection, much as that found in *C. szunyoghysi*. The overall differences are significant enough to warrant the recognition of a new species.

Description. *Adult*. Overall color (in alcohol) dark brown. Head relatively short (postocular parietal sclerite ~1/2 diameter of eye). Palps moderately elongate, maxillary palp with 1st segment short (length slightly greater than width), 2nd segment short (~ 2× length of 1st), apex with small cluster of stiff setae, 3rd elongate (~ 2× as long as 2nd), 4th segment short (shorter than 2nd), 5th segment elongate (subequal to 3rd). Forewing length: male, 6.0–7.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat sinuous, stem of Rs inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork asymmetric, discoidal cell elongate, length > 2× its width, forks I and II sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, *r-m* crossvein diagonal, continuous with *s*, *m* crossvein proximal to *s* and *r-m* crossveins, approximately midway between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II subsessile. Foreleg with apical tibial spur short; male with foretarsi unmodified, or nearly so, claws small and symmetrical.

Male genitalia. Segment VIII moderate in length, tergum slightly longer dorsally. Segment IX, in lateral view, relatively elongate, anterior margin very strongly produced ventrally, forming rounded lateral projection in ventral 1/3, dorsolaterally with distinct rounded apodeme, margin strongly concave between; tergum, in dorsal view,

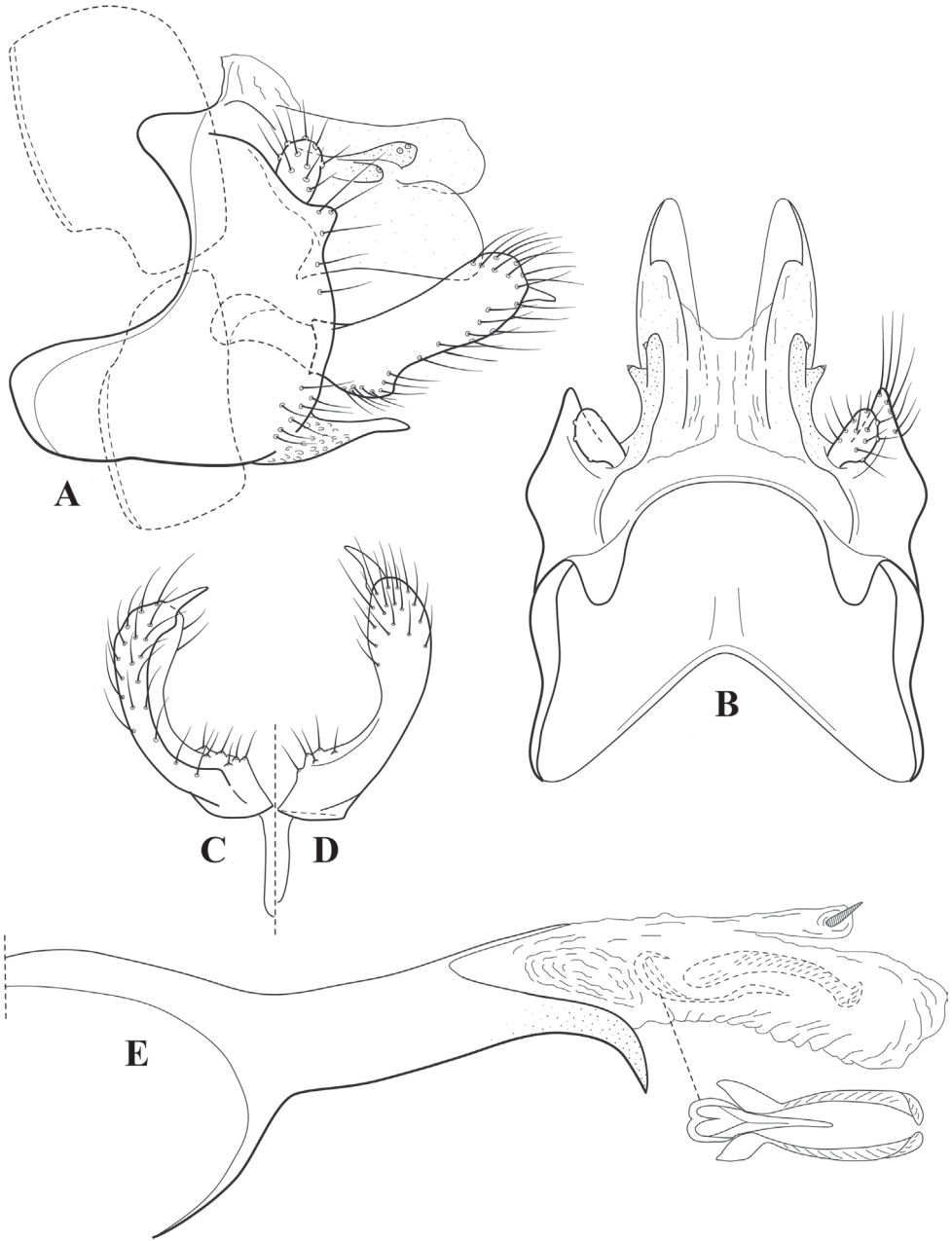


Figure 21. *Chimarra tanzaniensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral, with dorsal detail of phallotremal sclerite complex.

continuous between apodemes, but very short, forming deeply concave excavation; posterior margin short dorsally, weakly produced below preanal appendages, more or less linear to ventral process; posteroventral margin with prominent, moderately elongated

gate, posteriorly projecting, ventral process, length $> 2\times$ width at base, apex acute. Segment IX, in dorsal or ventral views, with anteroventral margin deeply, angularly, concave mesally. Lateral lobes of tergum X moderate in length, relatively wide, with apex partially divided into rounded dorsal and ventral lobes, dorsal lobe with very short, rounded, sensilla-bearing process in basal half; mesal lobe of tergum X membranous, extending $\sim 1/2$ length of lateral lobes. Preanal appendages short, rounded, constricted basally. Inferior appendage, in lateral view, relatively narrow and short, dorsally flexed near base, with apex forming distinct, short, spine-like projection, visible in both lateral and ventral views; appendage, in dorsal or ventral views, moderately mesally curved, with distinct basomesal enlargement at basal inflection, apex narrowed and spine-like, curvature more or less continuous with lateral margin of appendage. Phallic apparatus with phallobase moderate in length and tubular, with usual basodorsal expansion, apicoventral margin with distinct, ventrally curved projection, apex acute; endotheca membranous, without minute spines, but with narrow membranous dorsal lobe, with small apical spine; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with pair of distinct, narrow, curved, dorsolateral sclerites.

Etymology. *Chimarra tanzaniensis*, used as an adjective and meaning “from Tanzania,” in reference to the country of origin of the holotype specimen.

Chimarra triangularis occidentalis Gibon, 1985

Fig. 22A–G

Chimarra triangularis occidentalis Gibon, 1985: 27, figs 11–12.

Material examined. GHANA – **Western Reg.** • 1♂; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 11 Dec. 1993; T Andersen & J Kjærandsen leg.; light trap; UMSP • 12♂♂9♀♀; same collection data as for preceding except 5–9 Dec. 1993; ZMBN • 1♀; same collection data as for preceding; UMSP • 3♂♂; same collection data as for preceding except 31 Apr. 1993; J Kjærandsen leg.; ZMBN • 2♂♂; same collection data as for preceding except 6–12 Dec. 1993; Malaise trap; ZMBN.

Diagnosis. Characters, in combination, that confirm the identification and can be used to distinguish *C. triangularis occidentalis* from the nominate subspecies and other species in the subgroup include: the general shape of inferior appendages, shape of segment IX and ventral process, relatively short tergum X and length of sensilla-bearing process, and presence of large apical phallic spine.

Chimarra triangularis occidentalis was considered a subspecies of *C. triangularis* Kimmins when described by Gibon, probably because of the overall similarity between the two forms in the shape of the inferior appendages, length of tergum X, and similarity of its phallic armature. Kimmins described *C. triangularis* as having two sets of paired inclusions in the phallus and two single, unpaired inclusions. One of the sets of paired inclusions and one of the unpaired inclusions seem to be elements of the phallotremal sclerite complex, including a central rod and ring structure and paired

lateral sclerites. The other inclusions include a set of small, paired spines, common in members of the *kenyana* subgroup, and an unpaired apical spine-like sclerite. Gibon described the subspecies based mainly on differences in the phallic armature, including a larger unpaired spine than that found in the nominate form. We have used this as the basis for identifying the form illustrated here as *C. triangularis occidentalis* (Fig. 22A–G), in addition to its relatively proximate geographic location. The nominotypical form was described from Ethiopia, on the other side of the African continent. The apical spine is somewhat unusual, very lightly sclerotized, and appearing somewhat feathered or striated. Its apical part appears wider in lateral view than in dorsal view, suggesting that it is somewhat blade-like. We are uncertain about the species or varietal status of this form, as distinct from the form described by Kimmins.

Chimarra triangularis occidentalis is most diagnostically recognized by the overall shape of its inferior appendages, with its short tergum X and very short basal sensilla-bearing process. Among species treated here it is probably most similar in these regards to *C. pedalotus* sp. nov., which is easily diagnosed by the very enlarged and compressed ventral apex of its phallobase.

Description. Adult. Overall color (in alcohol) pale yellowish brown. Head relatively elongate (length of postocular parietal sclerite nearly diameter of eye). Palps relatively short, maxillary palp with 1st segment very short (length subequal to width), 2nd segment short ($\sim 3 \times 1^{\text{st}}$), apex with small cluster of stiff setae, 3rd segment relatively short (slightly longer than 2nd), 4th segment short (shorter than 2nd), 5th segment short (subequal to 2nd). Forewing length: male, 3.8–4.5 mm; female, 4.7–5.2 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 somewhat sinuous, stem of R_s inflected at approximately midlength, with distinct node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork asymmetric, length of cell $\sim 2 \times$ width, forks I and II slightly subsessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, m crossvein proximal to s and $r-m$ crossveins, s pigmented (like wing), $r-m$ and m crossveins hyaline and very faint, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile, fork III relatively terminal. Foreleg with apical tibial spur short; male with foretarsi modified, claws enlarged, outer claw twisted and asymmetric.

Male genitalia. Segment VIII moderately elongate, sternum and tergum subequal in length. Segment IX, in lateral view, elongate, anterior margin greatly, subangularly produced in ventral $\frac{1}{4}$, dorsolaterally with short rounded apodeme, margin strongly concave between; tergum, in dorsal view, continuous between apodemes, forming concave excavation; posterior margin weakly produced below preanal appendages, extending more or less linearly to ventral process; ventral process prominent, posteriorly projecting, length greater than width at base, apex rounded. Segment IX, in dorsal or ventral views, with anteroventral margin deeply concave mesally. Lateral lobes of tergum X moderate in length, rounded apically, each with moderately elongate, posteriorly projecting, digitate, sensilla-bearing process on dorsal margin at approximately midlength; mesal lobe of tergum X membranous,

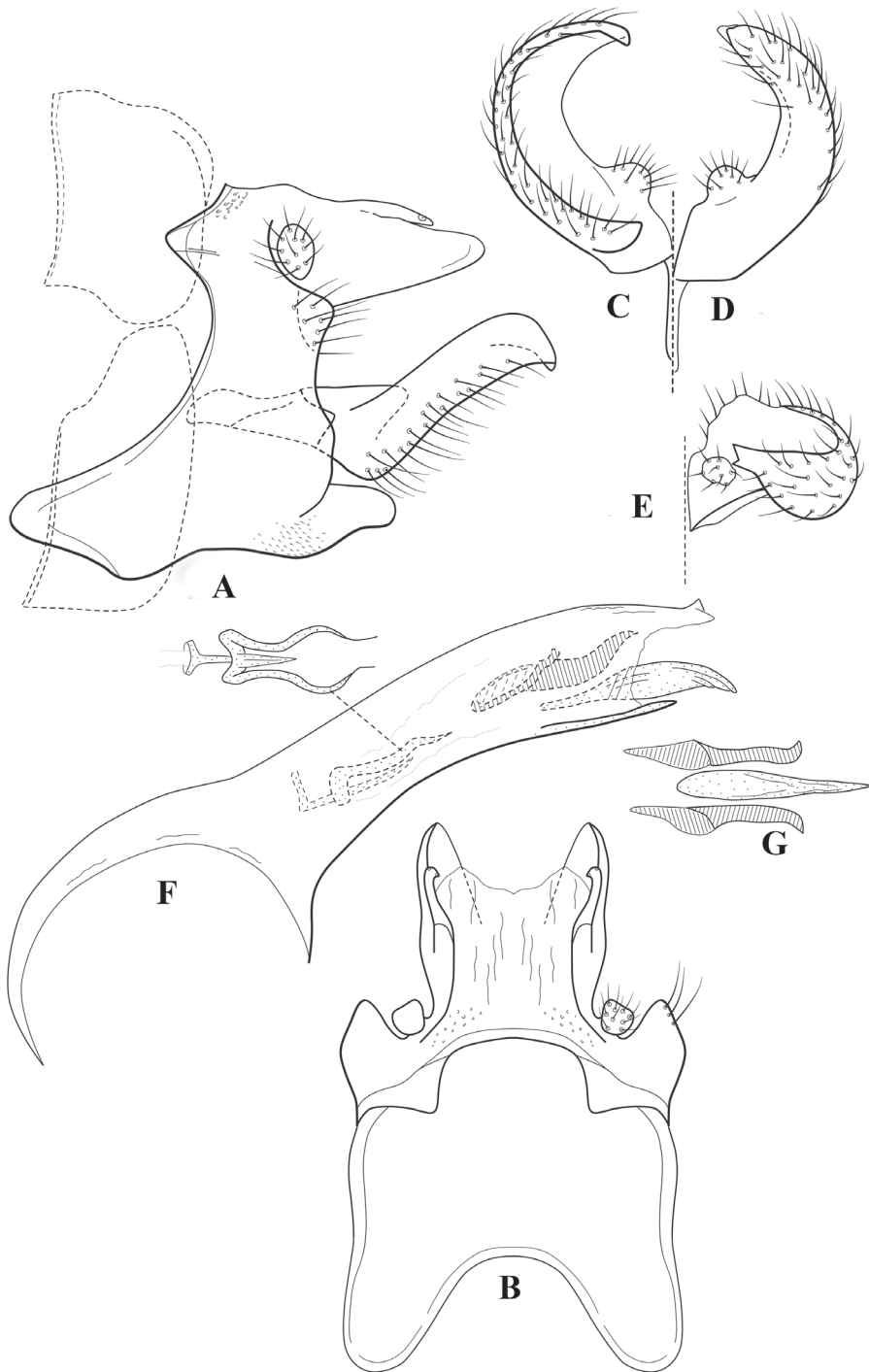


Figure 22. *Chimarra triangularis occidentalis* Gibon, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** inferior appendage, oblique dorsal **F** phallus, lateral, with dorsal detail of phallotremal sclerite complex **G** phallic spines, dorsal.

somewhat shorter than the lateral lobes. Preanal appendages small, rounded, constricted basally. Inferior appendage, in lateral view, moderately elongate, narrow, nearly uniform in width, dorsally flexed near base, apex incurved and narrowed, in dorsal/caudal views, forming short, subtruncate, weakly bifid, projection; appendage, in dorsal or ventral views, strongly and uniformly curved, with short, rounded, setose, basomesal projection. Phallic apparatus with phallobase moderately elongate, tubular, with usual basodorsal expansion, dorsal margin somewhat projecting, but only weakly sclerotized, apicoventral margin slightly projecting, extending nearly straight; endotheca apparently without minute spines, but with two symmetrically positioned spines and an additional large, unpaired, lightly sclerotized, mesal spine, which is somewhat irregular, wider in lateral than in dorsal view; phallotremal sclerite complex composed of moderately elongate rod and ring structure, with narrow, paired, dorsolateral sclerites.

Distribution. Ghana, Ivory Coast.

***Chimarra waensis* Gibon, 1985**

Fig. 23A–E

Chimarra waensis Gibon, 1985: 26, figs 9–10.

Material examined. GHANA – **Brong Ahafo Reg.** • 1♀; Asubende, River Pru; 8°01'18"N, 1°01'58"W; 24 Nov. 1990; JS Amakye leg.; light trap; ZMBN. – **North-ern Reg.** • 1♀; Sabari, Oti River; 9°17'41"N, 0°14'43"E; 22–24 Nov. 1991; JS Amakye leg.; Malaise trap; ZMBN. – **Upper East Reg.** • 1♀; Nangodi, Nangodi Bridge; 10°51'48"N, 0°39'36"W; 26 June 1993; JS Amakye leg.; light trap; ZMBN. – **Volta Reg.** • 1♀; Wli, Agumatsa waterfall, station # 12; 7°07'29"N, 0°35'31"E; 16 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN. – **Western Reg.** • 2♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding except 9 Dec. 1993; J Kjørandsen leg.; light trap; UMSP • 1♂; same collection data as for preceding except 31 Mar. 1993; J Kjørandsen leg.; light trap; UMSP • 1♀; same collection data as for preceding; ZMBN • 7♀♀; same collection data as for preceding except 8–10 Dec. 1993; T Andersen & J Kjørandsen leg.; ZMBN.

Diagnosis. Characters, in combination, that confirm the identification and can be used to distinguish *C. waensis* from other species in the subgroup include: length and position of digitate process of tergum X; general shape and length of inferior appendage; subtriangular shape of ventral process of tergum X; the single, moderately elongate phallic spine; and the curved, projecting apex of the phallobase. The anterior margin of segment IX, in the original illustration of *C. waensis* (Gibon 1985: fig. 10), is less sinuate than in our illustration. Particularly, the prominent dorsal apodeme is not featured. This is more likely a deficit in the illustration than a genuine difference, since the anterior contour of the segment, as illustrated in Fig. 23A, is not characteristic of

any species of the *kenyana* subgroup. We consider the matching features sufficient to justify the use of the name *C. waensis* to identify our specimen.

Both *C. baculifera* Marlier and *C. camerunensis* Marlier are also very similar to *C. waensis*, particularly in the general shape of the inferior appendages, which are elongate and narrow, with a characteristic subtruncate apex. All of these species also have elongated, curved, sensilla-bearing processes on the lateral lobes of tergum X, and a similar, basally broad, subtriangular ventral process on segment IX. We initially considered synonymizing all of these species. Restraint in doing so was based on the very acutely angled anteroventral margin of segment IX in the original illustration of *C. baculifera*, and the very elongate phallic spine featured in the original illustration of *C. camerunensis*. Since these kinds of differences are not usually attributable to intraspecific variation, a more critical evaluation, provided by comparison of holotype specimens, ideally in the context of a formal revision of the entire subgroup, should probably precede any synonymy.

Redescription. Adult. Overall color (in alcohol) pale yellowish brown. Head elongate (postocular parietal sclerite slightly shorter than diameter of eye). Palps elongate; maxillary palp with 1st segment very short (length subequal to width), 2nd segment elongate (slightly longer than 3rd), apex with cluster of stiff setae, 3rd segment moderately elongate (normal), 4th segment short ($\sim 2 \times 1^{\text{st}}$), 5th segment elongate (subequal to 3rd). Forewing length: male, 5.7 mm; female, 4.5–5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 distinctly sinuous, stem of R_s inflected at past midlength, with node extending into cell below, discoidal cell short, length slightly greater than width, basal fork not enlarged, forks I and II sessile, r crossvein diagonal, intersecting discoidal cell at approximately midlength, $r-m$ crossvein of forewing diagonal, slightly proximal to s , m crossvein very faint, proximal to $r-m$, very near basal fork of M, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 fused to subcosta basally, both veins intersecting wing margin, discoidal cell short, forks I and II elongate, sessile. Foreleg with apical tibial spur short; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII short, sternum and tergum subequal in length. Segment IX, in lateral view, relatively short, anterior margin distinctly, subangularly, produced in ventral $\frac{1}{4}$, dorsolaterally with very prominent, broadly rounded apodeme, nearly as projecting as ventral production, margin concave between; tergum, in dorsal view, very short and narrowly sclerotized, but continuous dorsally, or nearly so, forming excavation between apodemes; posterior margin obliquely and somewhat convexly widened from preanal appendage to ventral process; ventral process prominent, subtriangular, wide basally, only weakly projecting. Segment IX, in dorsal or ventral views, with anteroventral margin moderately, concavely excavated mesally. Lateral lobes of tergum X elongate, subtruncate rounded apically, somewhat dorsally produced in basal half, basodorsally with elongate, posteriorly oriented, digitate, sensilla-bearing process; lateral lobes, in dorsal view, subparallel; mesal lobe of tergum X membranous, approximately as long as lateral lobes. Preanal appendages short, constricted basally, knob-like. Inferior appendage, in lateral view, elongate, narrow, nearly uniform in width, distinctly dorsally flexed near base, apex slightly narrowed, forming subtruncate,

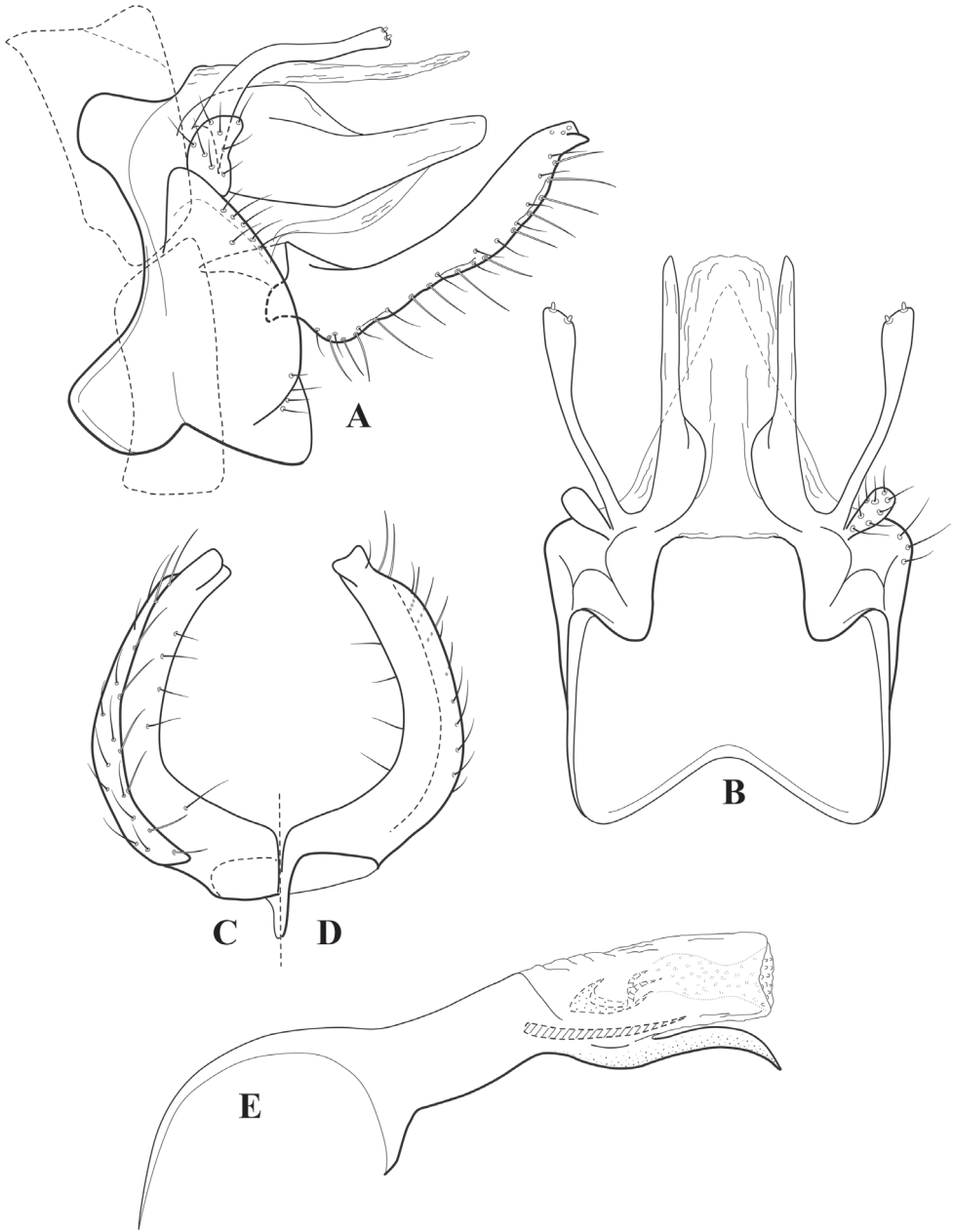


Figure 23. *Chimarra waensis* Gibon, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

weakly notched or bifid process; appendage, in dorsal or ventral views, more or less uniformly mesally curved, curvature moderate. Phallic apparatus with phallobase relatively short and tubular, with usual basodorsal expansion, apicoventral margin distinctly projecting and deflexed, apex acute and even more strongly ventrally curved;

endotheca with single, moderately elongate spine; phallotremal sclerite complex composed of short rod and ring structure, with small, indistinct apicolateral sclerites.

Distribution. Ghana, Ivory Coast.

The *leta* subgroup

Included species. *Chimarra amakyei* sp. nov.; and *Chimarra leta* Mosely, 1936.

Characters tentatively used to define the group include an elongate, narrow tergum X, with preanal appendages flattened and fused basally, sensilla of tergum X on a rounded mesally directed process, nearly linear arrangement of the *s*, *r-m*, and *m* crossveins of the forewing, and lack of a basal inflection of the inferior appendages. The latter two characters are probably plesiomorphic and also occur in the *cara* subgroup; thus, they do not necessarily indicate a relationship between the two subgroups. They are, however, unusual characters within the *marginata* Group as a whole. Like most members of the *fallax* subgroup, the inferior appendages are mounted relatively high above the ventral process of segment IX, which, however, is short, rather than elongate, and tergum X has a pair of ventral sclerotized periphallallic processes (or detached ventromesal lobes of tergum X, lacking sensilla). These similarities are likely convergent. Based on literature descriptions and illustrations, only *C. leta* and the following new species can be definitively placed in this subgroup.

Chimarra amakyei sp. nov.

<http://zoobank.org/7E3AB7DA-C910-461E-9057-754E790215CE>

Fig. 24A–E

Type material. Holotype. GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 3; 7°07'29"N, 0°35'31"E; 10 Mar. 1993; JS Amakye & J Kjørandsen leg.; sweep net; UMSP 000550018. **Paratypes.** GHANA – Volta Reg. • 3♂♂; same data as for holotype except station # 2^A; 8–11 Mar. 1993; Malaise trap; ZMBN.

Additional material. GHANA – Volta Reg. • 2♀♀; Wli, Agumatsa waterfall, station # 1^A; 7°07'29"N, 0°35'31"E; 12–21 Nov. 1993, J. Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for previous except station # 2^B; 5–14 Mar. 1993; JS Amakye & J. Kjørandsen leg.; ZMBN • 2♀♀; same collection data as for previous except station # 5^A; 10–13 Mar. 1993; ZMBN • 1♀; same collection data as for previous except station # 5^D; 9–12 Mar. 1993; ZMBN • 1♀; same collection data as for previous except station # 5C; 12–15 Mar. 1993, J Kjørandsen & JS Amakye leg.; UMSP.

Diagnosis. *Chimarra amakyei* sp. nov. is closely related to *Chimarra leta* Mosely. Like that species it has an elongate, narrow tergum X, with preanal appendages flattened and fused basally. It also has inferior appendages projecting approximately mid-laterally, above a small basally located ventral process. It differs diagnostically in that the apices of inferior appendages are tapering and acute, rather than subtruncate.

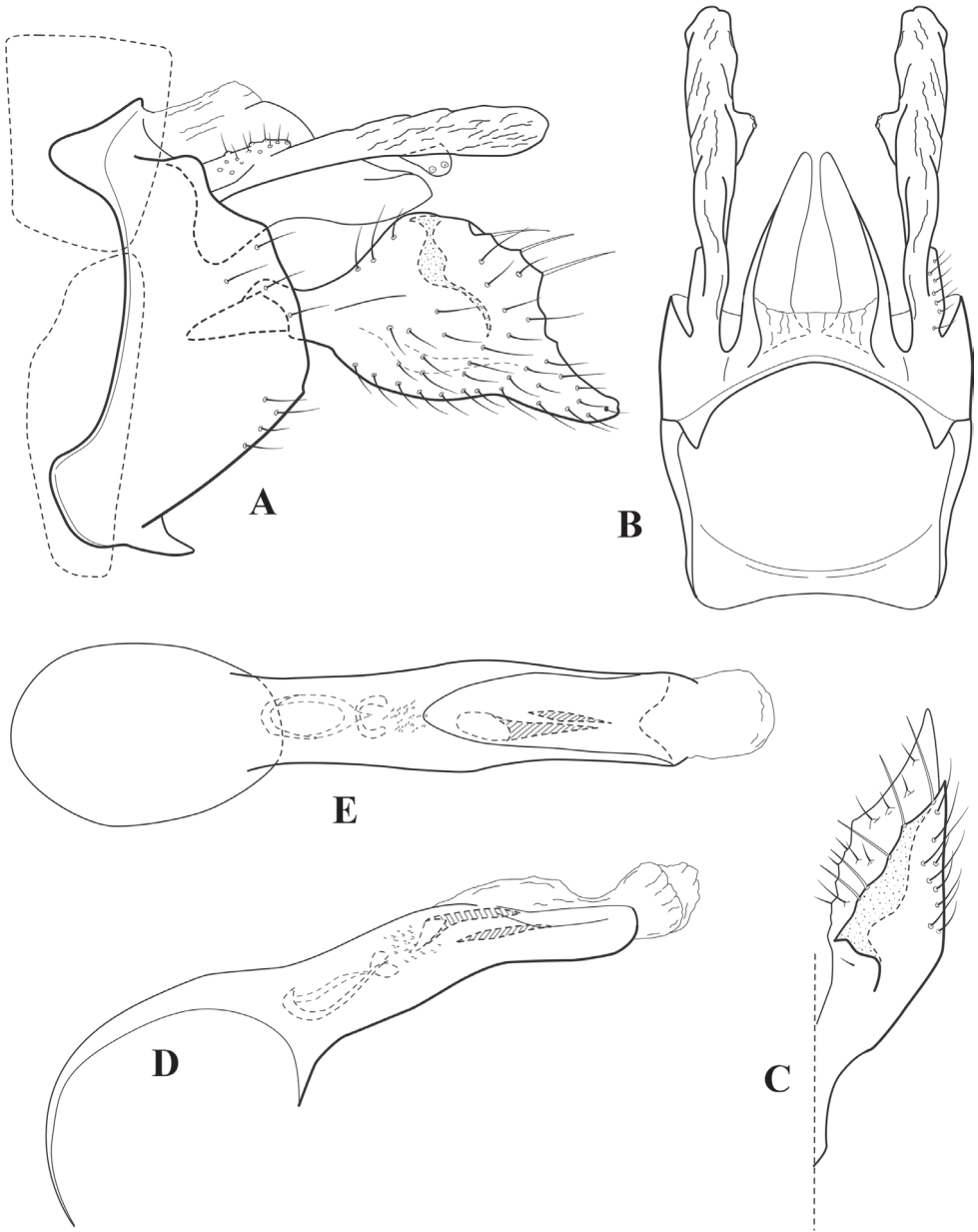


Figure 24. *Chimarra amakyei* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, dorsal **D** phallus, lateral **E** phallus, dorsal.

Description. Adult. Overall color (in alcohol) yellowish brown; vertex of head dark brown, setal warts very pale. Head relatively short (postocular parietal sclerite short). Palps moderately elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (distinctly shorter than 3rd), apex

with small cluster of stiff setae, 3rd segment elongate, 4th segment very short (shorter than 2nd), 5th segment elongate (slightly longer than 3rd). Forewing length: male, 4.8–5.3 mm; female, 4.5–5.3 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 sinuous, stem of R_s distinctly inflected at past midlength (without distinct node at inflection), basal fork of discoidal cell moderately enlarged, length of cell slightly greater than 2× width, forks I and II sessile, r crossvein strongly diagonal, intersecting discoidal cell at just past midlength, s , $r-m$, and m crossveins linear, s crossvein pigmented (like wing), $r-m$ and m crossveins hyaline (m very indistinct), 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 reduced, narrowly parallel to subcosta, fork I sessile, fork II subsessile, fork III distal and relatively wide, anal loop small. Forelegs with apical tibial spur short; male without enlarged tarsal claws, apical segments of tarsi narrow, claws very small and symmetrical.

Male genitalia. Segment VIII with sternum very short, tergum moderately expanded dorsally (~ 2× length of sternum at base). Segment IX, in lateral view, relatively short, anterior margin concave, dorsally with broadly rounded apodeme, anteroventrally with short angular projection at approximately basal ¼; posterior margin moderately produced midlaterally, basoventrally with very short, subtriangular, posteriorly projected ventral process, segment expanded and sloping dorsal to process, with inferior appendages inserted high above process, approximately midlaterally; as viewed dorsally, with tergum very narrow, but continuous, sternum subtruncate, slightly concave mesally. Lateral lobes of tergum X elongate, rugose and club-like, with small rounded, mesally directed process bearing two sensilla at past midlength; dorsum of tergum X short, membranous, continuous with paired, sclerotized, apically rounded, periphallalic processes surrounding phallic apparatus laterally and ventrally. Preanal appendages narrow and flattened, fused basally to lateral lobes. Inferior appendage without pronounced basal inflection, appendage narrow basally, dorsal margin with rounded expansion, tapering to acute, projecting apex; base of dorsal expansion with very short, sclerotized, mesally curved projection, continuous on mesal surface as sclerotized ridge. Phallic apparatus with relatively small, tubular phallobase with usual basodorsal expansion, apicodorsal margin with deep membranous invagination, ventral margin projecting, but without apicomesal projection; endotheca with two very small spines; phallotremal sclerite complex composed of reclinate, ring-like structure, with short rounded apicolateral projections.

Etymology. *Chimarra amakyei*, named for Joseph S. Amakye, who helped collect much of the material represented in this paper, in recognition of his efforts.

The *mazumbai* subgroup

Included species. *Chimarra mazumbai* sp. nov.; *Chimarra usambara* sp. nov.; and *C. wliensis* sp. nov.

Three species are assigned to this new group, the two from Tanzania very evidently closely related and the third from Ghana more speculatively associated. All of the species have scabrous lobes associated to terga IX or X, and relatively short phalli with a promi-

nent sclerotized ventral apex. The endotheca is relatively simple, short and untextured (without small spines). A single short spine is present in the endotheca, as well as a short phallotremal sclerite complex, composed of a short rod and ring structure. The ventral process of segment IX is also very short. Superficially, the species look very much like species in the *georgensis* Group, but venational characters, including the arrangement of the chord and the anal veins of the forewing, are typical of the *marginata* Group. It seems likely that the species included here represent a relatively basal lineage within this group.

***Chimarra mazumbai* sp. nov.**

<http://zoobank.org/A021CB84-FC3E-437E-A93E-14ECCCDEE586>

Fig. 25A–D

Type material. *Holotype*. TANZANIA – **Tanga Reg.** • ♂ (in alcohol); West Usambara Mts., Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 29–30 Nov. 1990; T Andersen leg.; Malaise trap; UMSP 000550020. *Paratypes*. TANZANIA – **Tanga Reg.** • 1♂; same data as for holotype except 14–20 Nov. 1990; UMSP • 21♂♂; same data as for holotype except 30 Oct. 1990–12 Feb. 1991; ZMBN.

Diagnosis. *Chimarra mazumbai* is very similar to *C. usambara* sp. nov. Both species have a pair of upturned, digitate processes on a short tergum X, and somewhat similar inferior appendages, as well as a relatively short segment IX, with a very small ventral process. *Chimarra mazumbai* can be distinguished by the shape of its inferior appendage, which has its dorsal process shorter, and also by having the digitate processes of tergum X less closely apposed.

Description. *Adult*. Overall color (in alcohol) dark brown. Head moderately elongate (postocular parietal sclerite ~1/2 diameter of eye). Palps elongate, maxillary palp with 1st segment short (length slightly greater than width), 2nd segment very elongate, with approximately a dozen elongate apical setae, 3rd segment elongate (subequal to 2nd), 4th segment short (< 1/2 length of 3rd), 5th segment elongate (slightly longer than 3rd). Forewing length: male, 6.5–8.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ not, or only very weakly, sinuous, stem of Rs with relatively weak inflection in apical half, with node at inflection, extending into cell below, basal fork of discoidal cell slightly enlarged, fork nearly symmetric, discoidal cell elongate, length ~ 2 1/2× width, forks I and II distinctly subsessile, *r* crossvein intersecting discoidal cell at base of fork I, *r-m* crossvein continuous with *s*, *m* crossvein proximal to *s* and *r-m* crossveins, approximately midway between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, very indistinct, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ fused to subcosta basally, both veins intersecting wing margin apically, forks I and II subsessile. Foreleg with apical tibial spur very short; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII short ventrally, tergum ~ 2× as long dorsally. Segment IX, in lateral view, relatively short, anterior margin relatively weakly, sinuously,

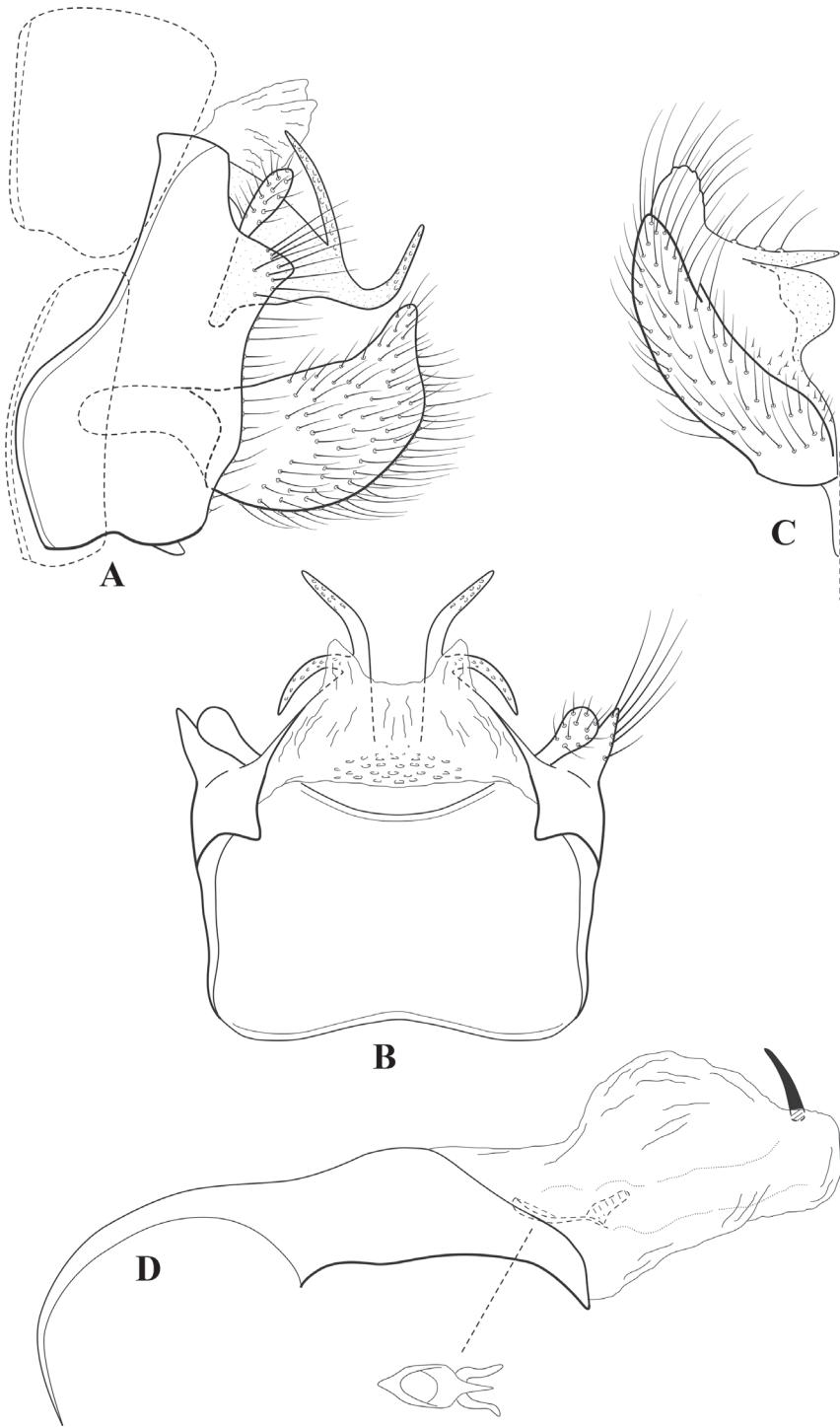


Figure 25. *Chimarra mazumbai* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral, with dorsal detail of phallotremal sclerite complex.

produced in ventral half, dorsolaterally with apodeme very small, almost absent; tergum, in dorsal view, obsolete between apodemes; posterior margin short dorsally, weakly produced below preanal appendages, nearly linear to ventral margin, ventral margin with very minute, short, ventrally projecting, process posteriorly. Segment IX, in dorsal or ventral views, with anteroventral margin subtruncate. Lateral lobes of tergum X very short, with pair of very narrow, digitate, dorsally projecting, apically acute processes, one apical and one at midlength, sensilla not apparent; mesal lobe of tergum X membranous, short, hardly projecting beyond base of lateral lobes. Preanal appendages short, rounded, knob-like, distinctly constricted basally. Inferior appendage, in lateral view, short, densely setose, strongly rounded basally, dorsally with short, rounded, dorsally flexed apex; in ventral view, with closely associated, narrow, acute, and rounded projections, visible on dorsomesal margin. Phallic apparatus with phallobase very short and tubular, with usual basodorsal expansion, apicoventral margin forming distinct, ventrally curved, projection; endotheca membranous and simple in structure, without minute spines, but with a single short apicomeral spine; phallotremal sclerite complex composed of very short rod and ring structure, with pair of small apical sclerites.

Etymology. *Chimarra mazumbai*, name used as a noun in apposition, for the name of the scenic type locality in the Usambara Mountains where the species was collected.

***Chimarra usambara* sp. nov.**

<http://zoobank.org/6D9524AF-CC86-460C-B9E1-011AE3246730>

Fig. 26A–E

Type material. *Holotype.* TANZANIA – **Tanga Reg.** • ♂ (in alcohol); East Usambara Mts, Sigi River, Amani; 21 Feb. 1959; 2,500 ft; MT Gillies leg.; INHS Trichoptera 50335. *Paratypes.* TANZANIA – **Tanga Reg.** • 1 ♀; same data as for holotype; INHS \$ 1 ♂; Amani; 16 Nov. 1959; MT Gillies leg.; INHS.

Diagnosis. *Chimarra usambara* is very similar to *C. mazumbai* sp. nov. and, like that species, has a short tergum X with a pair of upturned, spine-like processes. It is easily distinguished from *C. mazumbai* in that the spine-like processes of the tergum are more closely adpressed, and by the shape of its inferior appendage, which has a more distinctly defined and upturned, thumb-like dorsal process.

Description. *Adult.* Overall color (in alcohol) dark brown. Head moderately elongate (postocular parietal sclerite ~ 1/2 diameter of eye). Palps elongate, maxillary palp with 1st segment short (length subequal to width), 2nd segment very elongate, with approximately a dozen elongate apical setae, 3rd segment moderately elongate (shorter than 2nd), 4th segment short, 5th segment elongate (subequal to 2nd). Forewing length: male, 4.7 mm; female, 5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ not, or only very weakly, sinuous, stem of Rs with relatively weak inflection in apical half, with node at inflection, extending into cell below, basal fork of discoidal cell enlarged, fork very asymmetric, discoidal

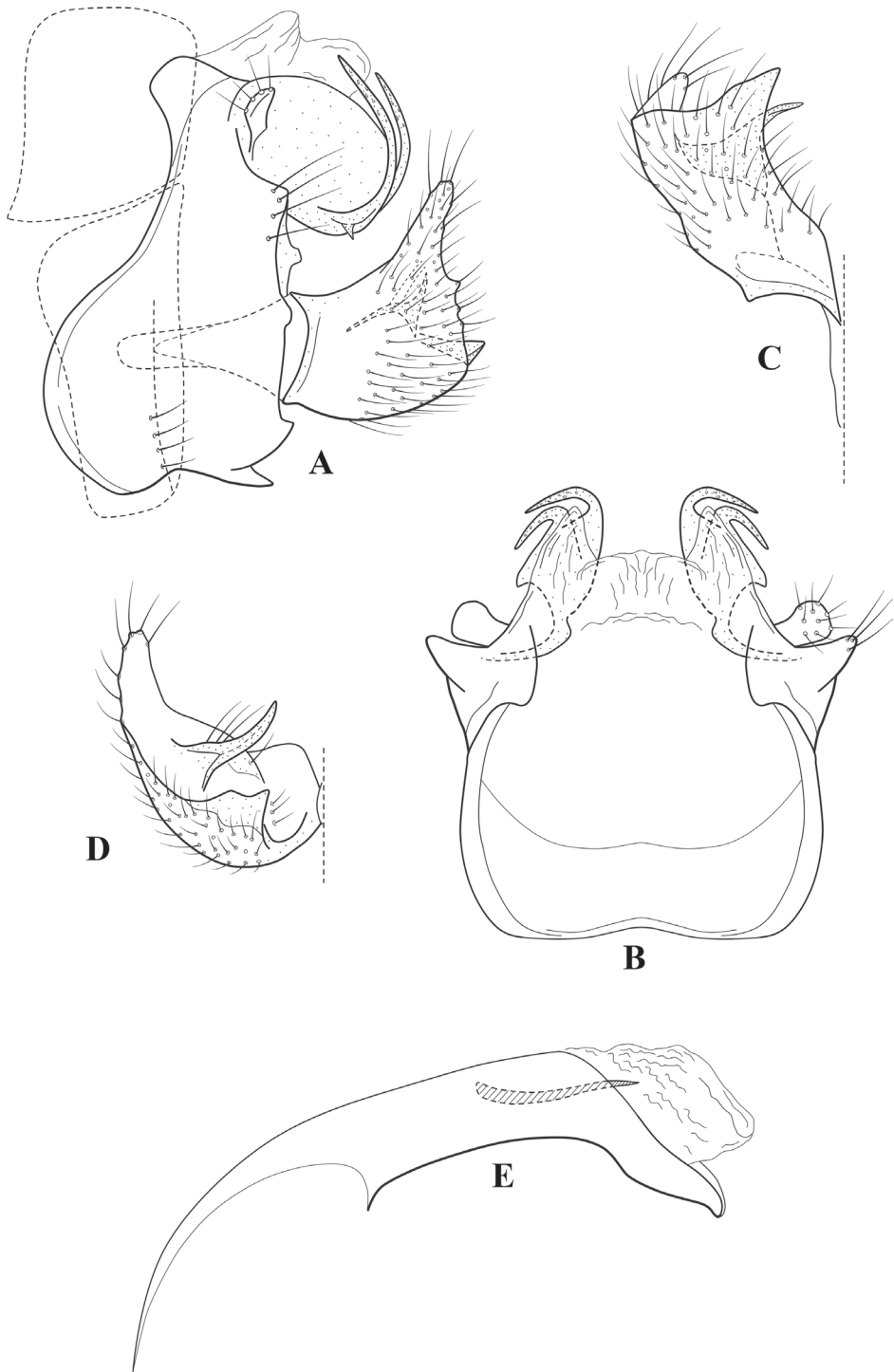


Figure 26. *Chimarra usambara* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, caudal **E** phallus, lateral.

cell with length $\sim 2\times$ its width, forks I and II slightly subsessile, r crossvein diagonal, intersecting discoidal cell at past midlength, just before fork I, $r-m$ crossvein continuous with s , m crossvein proximal to s and $r-m$ crossveins, approximately midway between basal fork of M and $r-m$ crossvein, s pigmented (like wing), $r-m$ and m crossveins hyaline, very indistinct, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile. Foreleg with apical tibial spur apparently absent; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII short ventrally, tergum somewhat wider dorsally. Segment IX, in lateral view, relatively short, anterior margin relatively weakly, sinuously produced in ventral half, dorsolaterally with distinct rounded apodeme; tergum, in dorsal view, obsolete between apodemes; posterior margin short dorsally, weakly produced below preanal appendages, nearly linear to ventral margin, ventral margin with short, small, posteriorly projecting, ventral process. Segment IX, in dorsal or ventral views, with anteroventral margin subtruncate. Lateral lobes of tergum X very short and rounded, with pair of closely apposed and very narrow, digitate, dorsally projecting, recurved, apically acute processes from apicoventral margin, projections slightly scabrous, sensilla not apparent; mesal lobe of tergum X membranous, short, hardly projecting beyond base of lateral lobes. Preanal appendages short, rounded, knob-like, distinctly constricted basally. Inferior appendage, in lateral view, short, densely setose, strongly rounded basally, dorsally with thumb-like, dorsally flexed projection; in ventral view, with short, acute, mesally curved, apicoventral projection, only indistinctly visible in lateral view; in caudal view, with narrow spine-like projection visible on mesal surface. Phallic apparatus with phallobase very short and tubular, with usual basodorsal expansion, apicoventral margin forming distinct, ventrally curved, projection; endotheca membranous and simple in structure, without spines; phallotremal sclerite complex composed of relatively short, simple, rod and ring structure, with associated sclerites absent or not apparent.

Etymology. *Chimarra usambara*, name used as an adjective, after the East Usambara Mountains of Tanzania, in which this species was collected.

***Chimarra wliensis* sp. nov.**

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Fig. 27A–E

Type material. Holotype. GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 2^A; 7°07'29"N, 0°35'31"E; 8–11 Mar. 1993; JS Amakye & J Kjærandsen leg.; Malaise trap; UMSP 000550021. **Paratypes.** GHANA – Volta Reg. • 1♂; same data as for holotype except station # 1^A; 5–14 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 3; 11–20 Nov. 1993; J Kjærandsen leg.; ZMBN. – **Western Reg.** • 1♂; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 12 Dec. 1993, T Andersen & J Kjærandsen leg.; sweep net; ZMBN.

Additional material. GHANA – Volta Reg. • 5♀♀; Wli, Agumatsa waterfall, station # 2^A; 7°07'29"N, 0°35'31"E; 5–14 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding except 8–11 Mar. 1993; UMSP • 1♀; same collection data as for preceding except station # 2^B; ZMBN • 1♀; same collection data as for preceding except station # 3; 17 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN.

Diagnosis. *Chimarra wliensis* is a very distinctive species, easily recognized by the curved, spine-like, and scabrous lateral lobes of tergum X and the shape of its inferior appendages, in addition to its venational attributes.

Superficial similarities would suggest a relationship to species in the *georgensis* Group, because of the scabrous dorsolateral processes on segment IX, as in the *evoluta* subgroup, and the sclerotized and divided lateral lobes of tergum X, as in the *georgensis* subgroup, as well as its rather simple and short phallobase, with a produced ventral apex. However, venational characters place this species within the *marginata* Group, since the anal veins have a distinct crossvein (2A apparently forked apically), the Rs vein of the forewing is distinctly curved, with the *s* crossvein pigmented (not hyaline), and the *m* crossvein is distinctly proximal to the *s* and *r-m* crossveins. In overall morphology the species is thus distinctive. It is conceivably related to *C. berghei* (Marlier), whose overall description makes it difficult to place; similarities to *C. wliensis* include, particularly, the arching dorsolateral lobes of tergum X; however, *C. berghei* differs significantly in the shape of its inferior appendages and it is possible that it is not very closely related.

Description. Adult. Overall color (in alcohol) medium brown, head and thorax not paler than body. Head elongate (postocular parietal sclerite nearly as long as diameter of eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment elongate (subequal to 3rd), apex with numerous elongate, stiff setae, 3rd segment elongate, 4th segment short (~ 1/3 length of 3rd), 5th segment elongate and narrow (subequal to 3rd). Forewing length: male, 5.7–6.5 mm; female, 6.5–7.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ somewhat curved, stem of Rs curved, bowed outward, without sclerotized node in cell below, basal fork of discoidal cell slightly enlarged, nearly evenly forked, length of cell ~ 2× width, forks I and II sessile, *r* crossvein diagonal, intersecting discoidal cell before fork, *s* crossvein pigmented, *r-m* and *m* hyaline, *s* and *r-m* crossveins continuous, *m* crossvein distinctly proximal; 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ obsolete (or fused to subcosta), forks I and II subsessile. Forelegs with apical tibial spur very short; male with apical segments of foreleg small and thread-like, not enlarged, tarsal claws symmetrical.

Male genitalia. Segment VIII short, tergum longer than sternum. Segment IX short, anterior margin expanded and rounded in ventral half, segment very short dorsally, anterodorsal margin with distinct rounded apodemes, posterodorsal margin with elongate, scabrous, posteriorly-curved, spine-like lateral processes, ventral process very short, subtriangular, more or less ventrally oriented, inferior appendages inserted

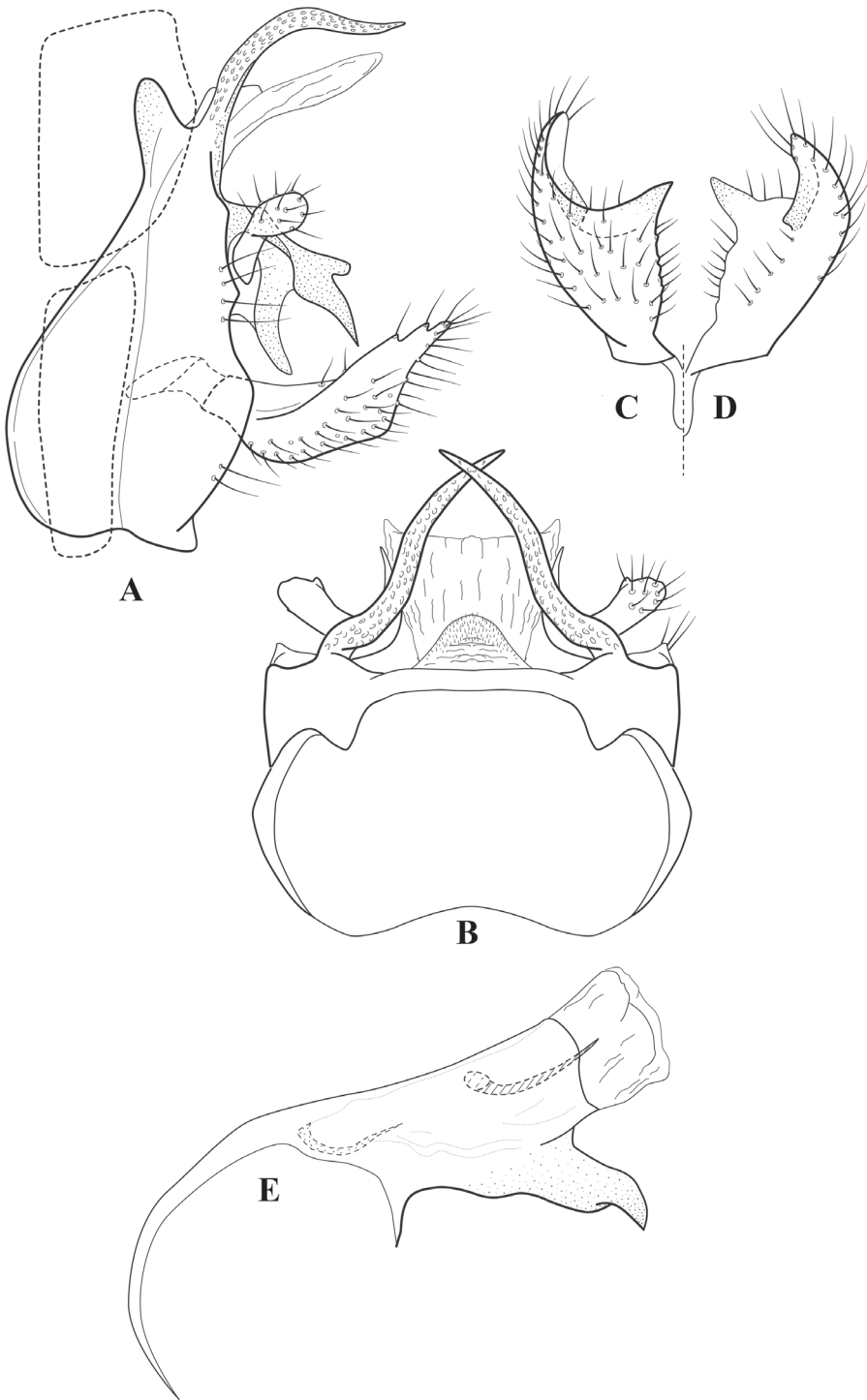


Figure 27. *Chimarra wliensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

distinctly above ventral margin of segment; as viewed dorsally, with tergum very narrow, but continuous, sternum short, broad, weakly concave mesally, scabrous dorsolateral processes of segment mesally curved, meeting mesally. Tergum X with mesal lobe membranous and with textured region at at base, lateral lobes (or periphalic processes?) strongly sclerotized and ventrally curved, divided apically into acute lobes, sensilla of lobes absent (or not evident). Preanal appendages short, knob-like, inserted membranously (not fused to segments IX or X). Inferior appendage with moderate basal inflection; as viewed laterally, more or less narrow, moderately elongate, apex acute; as viewed ventrally, with prominent, acute apicomesal projection (thus, ventral and apical projections subequal and separated by crescentic margin); mesal margin with short cusp, continuous with apical projection. Phallic apparatus with phallobase short and strongly sclerotized, with usual basodorsal expansion, apicoventral margin of phallobase projecting, sclerotized, acute, distinctly ventrally curved; endotheca apparently short, membranous, with single short spine; phallotremal sclerite complex composed of short rod and ring structure.

Etymology. *Chimarra wliensis*, used as an adjective, meaning “from Wli”, for the site where the holotype of this species was collected.

The *minima* subgroup

Included species. *Chimarra ambaja* Mosely, 1939; *C. angolensis* Marlier, 1965; *C. antsymeloka* Gibon, 2015; *C. assambae* Gibon, 2015; *C. bertrandi* Scott, 1974; *C. callasae* Gibon, 1982; *C. cereris* Barnard, 1934; *C. cognata* Kimmins, 1957; *C. intexta* Mosely, 1931; *C. koualaeensis* Johanson & Mary, 2009; *C. loffae* Gibon, 2015; *C. lufirae* Jacquemart, 1961; *C. minima* Ulmer, 1907; *C. prodhoni* Gibon, 1985; *C. sanagae* Gibon, 2015; *C. sassandrae* Gibon, 1982; *C. toubensis* Gibon, 1985; and *C. vulgaris* Gibon, 2015.

The *minima* subgroup was treated in a recent revision by Gibon (2015), and the reader is referred to that work for a comparative treatment and descriptions of the species. The only additional species assigned to the group is *C. koualaeensis* Johanson & Mary, 2009, due to its close morphological similarity. Four species of the subgroup were collected from Ghana and their distribution records are listed below. Illustrations of the species are included for comprehensive reasons.

Chimarra callasae Gibon, 1982

Fig. 28A–G

Chimarra callasae Gibon, 1982: 75–76, figs 3, 12–15.

Chimarra callasae Gibon: Gibon 2015: 335, 338, 346, fig. 3A–B (distribution [table, map]: Mali, Guinea, Sierra-Leone).

Material examined. GHANA – **Northern Reg.** • 1♂1♀; Bamboi, Black Volta; 8°08'50"N, 2°02'40"W; 25 Apr. 1991; T Andersen & JS Amakye leg.; light trap; UMSP.

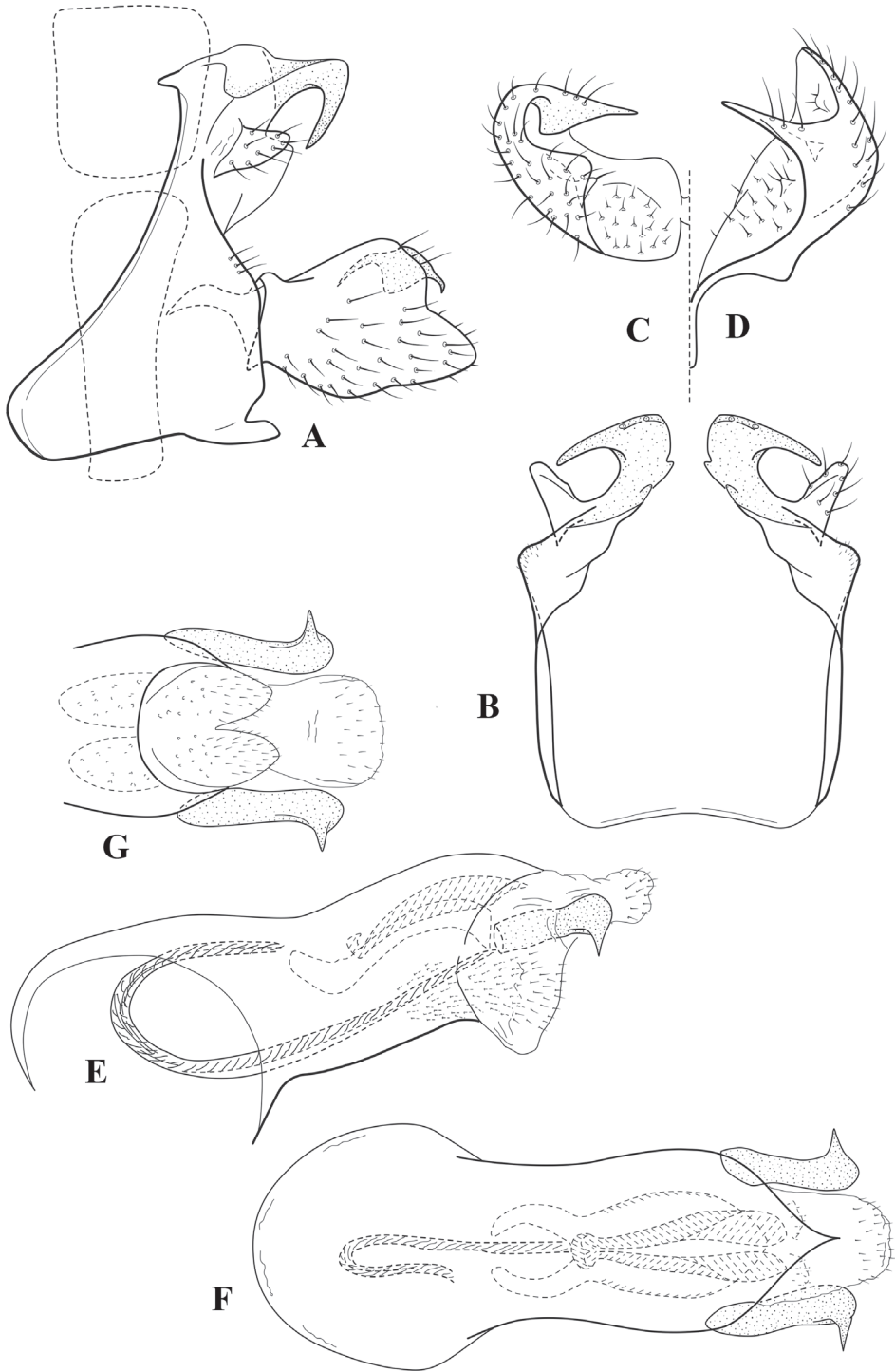


Figure 28. *Chimarra callasae* Gibon, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, dorsal **G** phallus apex, ventral

Diagnosis. *Chimarra callasae* is most readily diagnosed from other species in the subgroup by the short and apically strongly out-turned and acute lateral lobes of tergum X, by the shape of the two phallic spines, which are short, symmetrical, and have their apices more or less bird-head shaped, and also by the general shape of the inferior appendages.

Distribution. Ghana, Guinea, Mali, Sierra-Leone.

Chimarra intexta Mosely, 1931

Fig. 29A–F

Chimarrha intexta Mosely, 1931: 546–547, figs 6–9.

Chimarra intexta Mosely: Kimmins 1958: 359, 361, fig. 2 (distribution: Sierra Leone); Fischer 1961: 60; Gibon 1985: 25 (distribution: Ivory Coast); Gibon 2015: 335, 346 (distribution [table, map]: Sierra Leone, Ivory Coast, Guinea).

Material examined. GHANA – **Central Reg.** • 1♂; Kakum Forest Reserve; 5°21'N, 1°22'W; 8 Nov. 1994; T Andersen leg.; light trap; ZMBN • 1♀; same collection data as for preceding; UMSP. – **Greater Accra Reg.** • 1♂; Legon, Botanical Garden; 5°51'55"N, 0°11'15"W; 19 Nov. 1994; T Andersen leg.; light trap; ZMBN. – **Western Reg.** • 1♂; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 31 Mar. 1993; J Kjørandsen leg.; light trap; UMSP • 1♂2♀♀; same collection data as for preceding except 5 Dec. 1993; T Andersen & J Kjørandsen leg.; ZMBN.

Diagnosis. *Chimarra intexta* is most readily diagnosed from other species of the subgroup by the shape and form of the lateral lobes of tergum X, which are short, weakly sclerotized, and have the out-turned lateral apices only weakly angulate, and also by the general form of the inferior appendages, which have the dorsal process strongly mesally curved, elongate, and acute apically, and also have a small tooth or cusp on the ventromesal surface, visible in lateral view.

Distribution. Ghana, Guinea, Ivory Coast, Sierra-Leone.

Chimarra minima Ulmer, 1907

Fig. 30A–F

Chimarrha minima Ulmer, 1907: 43–44, fig. 64.

Chimarra minima Ulmer: Fischer 1961: 66; Gibon 2015: 335, 338, 348, fig. 3C–D (distribution, [table, map]: Togo, Ghana, Ivory Coast, Burkina Faso, Mali, Guinea, Cameroon).

Chimarra petri Gibbs, 1973: 369–371, figs 11–13, 21; Gibon 2015: 335 (as synonym of *C. minima* Ulmer).

Chimarra voltae Marlier, 1978: 288; Gibon 1985: 23 (as synonym of *C. petri* Gibbs).

Material examined. GHANA – **Brong Ahafo Reg.** • 1♂1♀; Asubende, River Pru; 8°01'18"N, 1°01'58"W; 25 Nov. 1990; JS Amakye leg.; light trap; ZMBN. – **Northern**

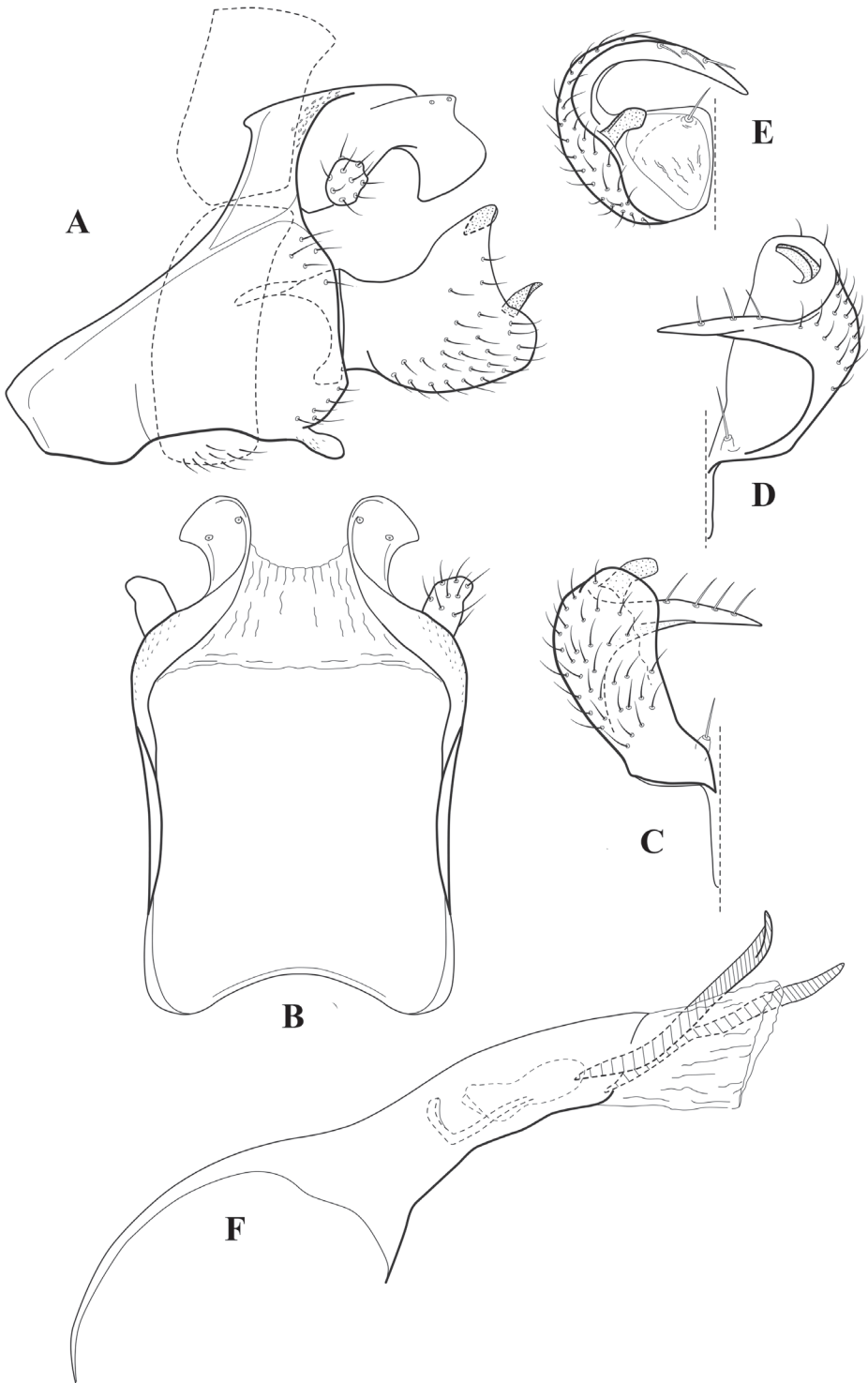


Figure 29. *Chimarra intexta* Mosely, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** inferior appendage, caudal **F** phallus, lateral.

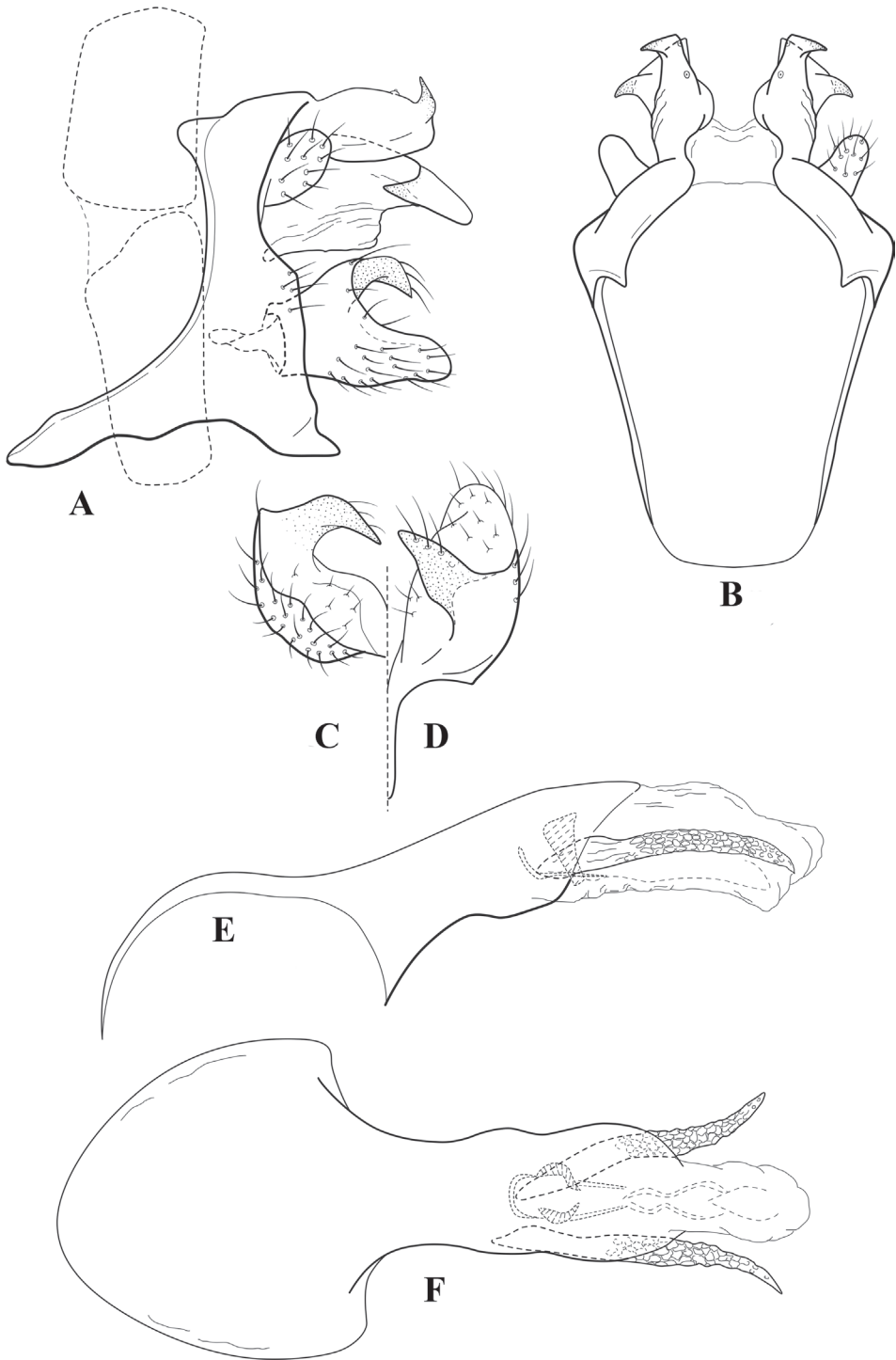


Figure 30. *Chimarra minima* Ulmer, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, dorsal.

Reg. • 7♂♂4♀♀; Bamboi, Black Volta; 8°08'50"N, 2°02'40"W; 25 Apr. 1991; JS Amakye leg.; light trap; ZMBN • 1♀; same collection data as for preceding; UMSP • 1♂; Sabari, Oti River; 9°17'41"N, 0°14'43"E; 10 Nov. 1993; T Andersen & J Kjørandsen leg.; light trap; ZMBN • 1♂; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra minima* is a very distinctive species, easily diagnosed by the form of the lateral lobes of tergum X, each of which is divided into a dorsal and ventral lobe, each ending in an acute apical projection, that of the dorsal lobe directed upward and that of the lower lobe directed laterally. The form of the inferior appendage is also diagnostic in that the ventral part is relatively projecting and rounded apically, and the dorsal process is relatively basal, prominent, and posteromesally curved, thus forming a C-shaped dorsal projection in apposition to the ventral apex. The paired phallic spines are also unusual in having a distinctly reticulated structure.

Distribution. Benin, Burkino Faso, Cameroon, Ghana, Guinea, Ivory Coast, Mali, Togo.

Chimarra sassandrae Gibon, 1982

Fig. 31A–F

Chimarra sassandrae Gibon, 1982: 76, fig. 4, 10–11.

Chimarra sassandrae Gibon: Gibon 1985: 24 (distribution: Ivory Coast); Gibon 2015: 335, 338, 346, fig. 3E (distribution [table, map]: Ivory Coast, Guinea, Mali, Togo, Cameroon).

Material examined. GHANA – **Brong Ahafo Reg.** • 14♂♂25♀♀; Asubende, River Pru; 8°01'18"N, 1°01'58"W; 24–25 Feb. 1990; JS Amakye leg.; light trap; ZMBN • 2♂♂; same collection data as for preceding except 18–19 Apr. 1991; Malaise trap; ZMBN. – **Northern Reg.** • 12♂♂7♀♀; Bamboi, Black Volta; 8°08'50"N, 2°02'40"W; 25 Apr. 1991; T Andersen & JS Amakye leg.; light trap; ZMBN • 9♂♂7♀♀; Sabari, Oti River; 9°17'41"N, 0°14'43"E; 27 Nov. 1990; JS Amakye leg.; light trap; ZMBN. – **Volta Reg.** • 1♂; Hohoe, Matvin Hotel; 7°09'43"N, 0°28'31"E; 11 Nov. 1993; J Kjørandsen leg.; at light; ZMBN • 1♂1♀; Kute, River Menu; 7°22'N, 0°36'E; 18 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN • 1♂; Wli, Agumatsa waterfall, station # 6; 7°07'29"N, 0°35'31"E; 20 Nov. 1993; J Kjørandsen leg.; light trap; UMSP • 8♂♂7♀♀; same collection data as for preceding except station # 10; 19 Nov. 1993; ZMBN • 8♂♂7♀♀; same collection data as for preceding except station # 12; 16 Nov. 1993; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra sassandrae* has a general similarity to *C. intexta*, especially in the general attributes of the structure of tergum X and the inferior appendages. It can be diagnosed by details in both structures. The short, weakly sclerotized dorsal part of the lateral lobe of tergum X lies flatter and does not curve downward, and its apical projections are more acute. The inferior appendages have the dorsal

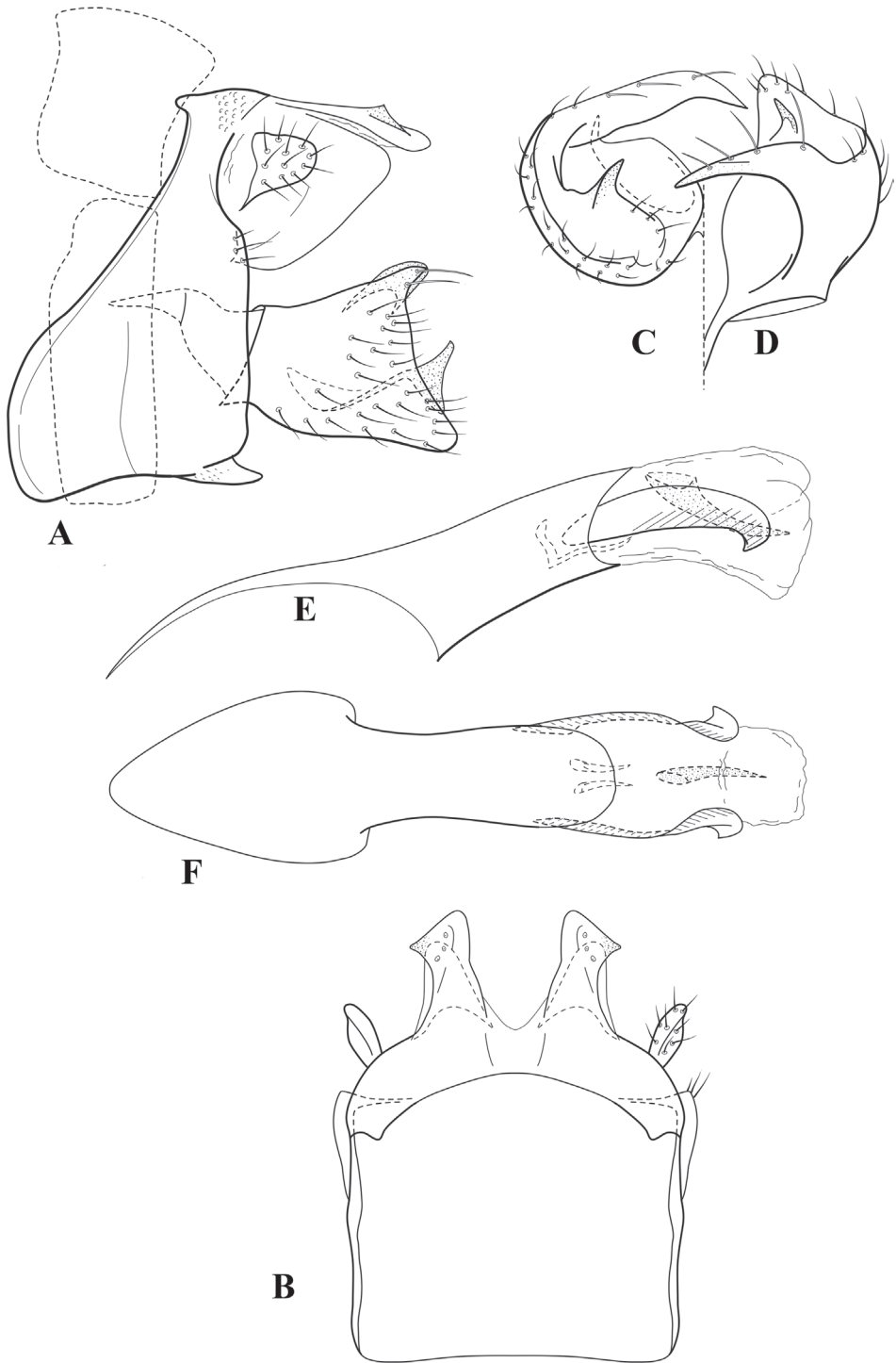


Figure 31. *Chimarra sassandrae* Gibon, ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, dorsal.

projection even more strongly mesally curved and ventromesal tooth or cusp is more prominent and acute apically. This gives the inferior appendage, in lateral view, a distinctly more subquadrate appearance and this provides the most readily discernable diagnostic difference for the two species. Additionally, the anteroventral margin of segment IX is less produced than in *C. intexta* and the shape of the phallic spines is different.

Distribution. Cameroon, Ghana, Guinea, Ivory Coast, Mali, Togo.

The *ruficeps* subgroup

Included species. *Chimarra chechewa* Wahlberg, Espeland & Johanson, 2014; *C. circumverta* Wahlberg, Espeland & Johanson, 2014; *C. clara* Mosely, 1938; *C. cornuta* Jacquemart & Statzner, 1981 (homonym of *C. cornuta* Ross, 1959); *C. dulensis* sp. nov.; *C. fuscipes* Kimmins, 1958; *C. kibiensis* sp. nov.; *C. lwirona* Statzner, 1976; *C. minacis* sp. nov.; *C. ruficeps* Ulmer, 1914; *C. tangaensis* sp. nov.; and *C. uncata* Morse, 1974.

This subgroup is probably closely related to the *fallax* subgroup. Members of both subgroups have the ventral process of segment IX of males distinctly narrow and elongate (length at least 2× width at base, and usually much greater than this). The apex of this process in lateral view, in species of the *ruficeps* subgroup, is distinctly enlarged due to the presence of a cluster of small spines or thickened setae on its ventral margin. This compares to species in the *fallax* subgroup in which the apex, in lateral view, is either acute or without modified setation. At least for species in which the character is discussed, the color pattern in species of the *ruficeps* subgroup includes a yellowish head and thorax and contrastingly darker wings. Another distinguishing feature is in the structure of the lateral lobes of tergum X. In members of the *ruficeps* subgroup, the lateral lobes are incised apically into dorsal and ventral lobes; the ventral lobes may converge ventrally beneath the phallus, but are not fused basally, as the periphallal processes often are in members of the *fallax* subgroup. As compared to species in the *fallax* subgroup, the overall shape of segment IX is also different, usually with the anteroventral margin distinctly produced and invaginated or concave mesally, rather than only moderately produced and truncate or weakly invaginated mesally. Also, the inferior appendages do not emerge so far above the ventral process as they do in many members of the *fallax* subgroup. Finally, the ventral margin of segment VIII is not modified and projecting as it is in members of the *fallax* subgroup.

The differences characterizing the *fallax* and *ruficeps* subgroups may be difficult to assess from literature descriptions; it is possible that they are not completely consistent for all species of the subgroups. Assigning a species to one subgroup or the other is therefore sometimes problematic and, in some cases, may be equivocal. However, the overall subjective differences do seem to warrant the recognition of two subgroups.

Chimarra cornuta Jacquemart & Statzner is a homonym of *C. cornuta* Ross from the New World and thus needs a new name. We prefer to defer this until the holotype is examined and a new illustration can be provided.

***Chimarra dulensis* sp. nov.**

<http://zoobank.org/EA7C917B-FEA2-41AC-A301-7AD5CF8E925C>

Fig. 32A–D

Type material. *Holotype*. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts, Dule; 4°51'S, 38°26'E; 26 Nov. 1990; T Andersen leg.; sweep net; UMSP 000550033.

Diagnosis. *Chimarra dulensis* most closely resembles *C. tangaensis* sp. nov., particularly in the overall shape of segment IX and shape of the inferior appendages, which are relatively short, with an acute dorsal apex. Both species also have an elongate, tube-shaped phallobase, with a projecting ventral apex and an endotheca with two elongate, symmetrical spines. The two species, however, are easily differentiated by the form of the lateral lobes of tergum X, which in *C. tangaensis* each have a dorsal spine-like projection, but in *C. dulensis* are simpler in form, elongate, with a more or less rounded, decurrent apex.

Description. *Adult*. Overall color (in alcohol) medium brown. Head elongate (postocular parietal sclerite nearly equal to diameter of eye). Palps relatively elongate, maxillary palp with 1st segment very short (slightly longer than wide), 2nd segment short (~ 2× 1st), apex with small cluster of stiff setae, 3rd segment elongate, almost 2× length of 2nd, 4th segment short (subequal to 2nd), 5th segment elongate (slightly longer than 3rd). Forewing length: male, 6.0 mm. Fore- and hind wing with forks I, II, III, and V present. Forewing with R₁ slightly sinuous, stem of Rs with inflection at past midlength (with distinct node at inflection, almost appearing as crossvein), basal fork of discoidal cell somewhat enlarged, fork asymmetric, discoidal cell short, length ~ 1 1/2× width, forks I and II elongate, slightly subsessile, *r* crossvein diagonal, intersecting discoidal cell before fork I; *s*, *r-m*, and *m* crossveins co-linear, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, but distinct, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ fused to subcosta basally, both veins intersecting wing margin, fork I sessile, fork II subsessile. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum short, without ventromesal projection, tergum hardly longer. Segment IX, in lateral view, with anteroventral margin greatly, angularly, produced, anterodorsal margin with prominent apodeme, margin between strongly concave; dorsomesal margin of segment strongly concave, very short, but continuously sclerotized; segment, in lateral view, very short dorsally, posterior margin obliquely and almost linearly widened to inferior appendage, ventral margin rounded, ventral process emerging well below inferior appendages, very elongate, digitate, with apex rounded in lateral view, apex with short spines or setae; anteroventral margin of segment, in dorsal or ventral views, very strongly concave. Lateral lobes of tergum X relatively elongate, simple in structure, apices rounded and distinctly ventrally curved; each lobe with short rounded basodorsal projection with two small sensilla; mesal lobe of tergum X very short, membranous, hardly projecting beyond basal sensilla-bearing projections. Preanal appendages short and

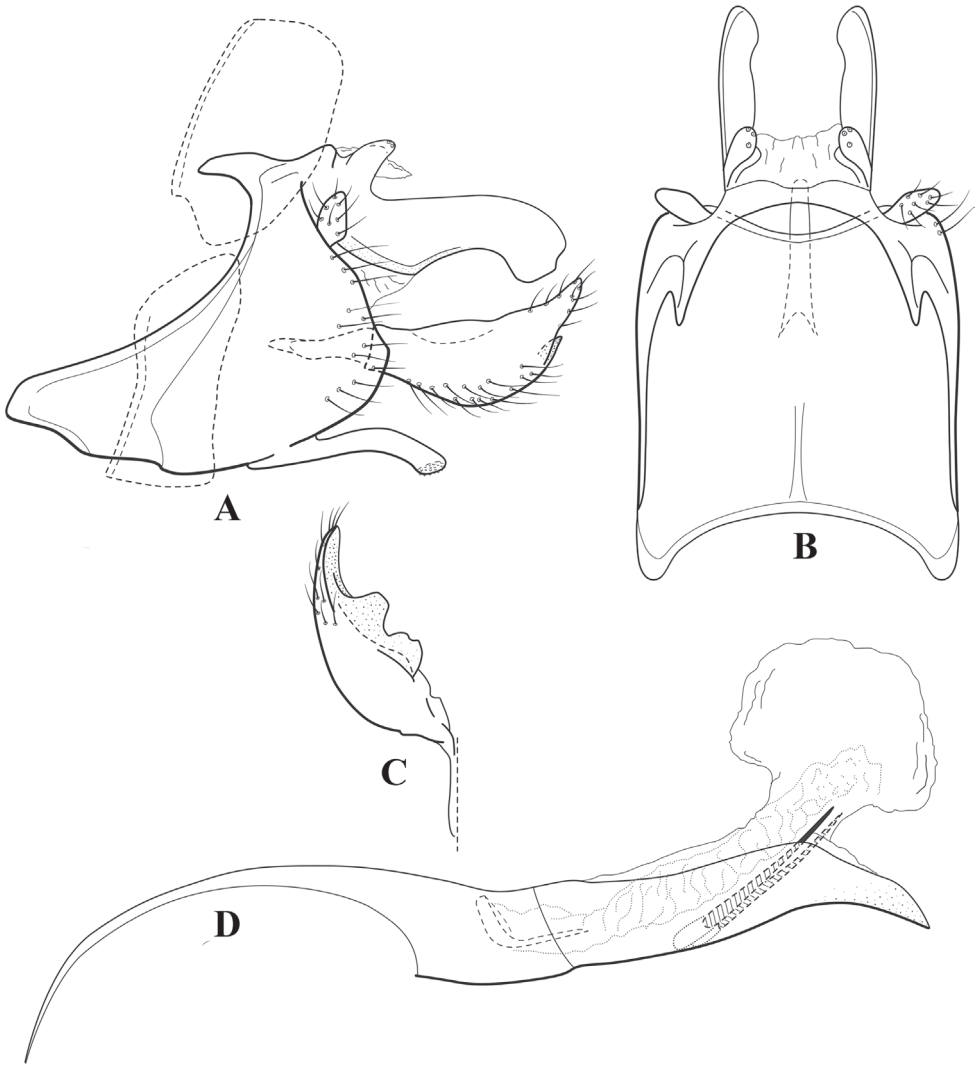


Figure 32. *Chimarra dulensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral.

knob-like, weakly constricted basally. Inferior appendage relatively short, rounded basally, with only weak basal inflection, apex narrowed, subacute, strongly posteriorly projecting; in ventral view, with pair of sclerotized cusps on mesal margin. Phallic apparatus with phallobase elongate, tubular, with usual basodorsal expansion, apicoventral margin acute, distinctly projecting and somewhat downturned; endotheca membranous and apparently elongate, with two moderately elongate, slender, symmetrically positioned spines, membrane not noticeably textured; phallosomal sclerite complex composed of a moderate length rod-and-ring structure, without obvious apical sclerites.

Etymology. *Chimarra dulensis*, name used as an adjective, meaning “from Dule,” for the name of the town near which the type species was collected.

***Chimarra kibiensis* sp. nov.**

<http://zoobank.org/F5993752-AC25-4017-AA14-7290CC5E8EF8>

Fig. 33A–G

Type material. *Holotype*. GHANA – **Eastern Reg.** • ♂ (in alcohol); Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjærandsen leg.; light trap; UMSP 000550030.

Additional material. GHANA – **Eastern Reg.** • 1♀; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjærandsen leg.; light trap; UMSP.

Diagnosis. *Chimarra kibiensis* is very similar to *C. minacis* sp. nov., as discussed in the diagnosis for that species, but the dorsal spine-like lobes of tergum X are shorter, and the ventral lobes of the tergum are longer, with the apices longer, more strongly ventrally curved, and also more sclerotized. Additionally, the inferior appendage in *C. kibiensis*, in lateral view, has an evident tooth on its posterior margin, whereas *C. minacis* has a pair of small mesal teeth or cusps; these are only readily evident in caudal view.

Description. *Adult*. Overall color (in alcohol) nearly uniformly yellowish brown, spurs slightly darker. Head moderate in length (postocular parietal sclerite slightly > 1/2 diameter of eye). Palps moderately elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (< 3 × 1st), apex with small cluster of stiff setae, 3rd segment elongate, almost 2 × length of 2nd, 4th segment very short (shorter than 2nd), 5th segment subequal to 3rd. Forewing length: male, 5.5 mm. Fore- and hind wing with forks I, II, III, and V present. Forewing with R₁ sinuous, stem of Rs inflected at past midlength (with small node at inflection), basal fork of discoidal cell somewhat enlarged, fork slightly asymmetric, length of cell ~ 2 × width, forks I and II subsessile, *r* crossvein diagonal, intersecting discoidal cell at approximately midlength, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ narrowly parallel to subcosta, forks I and II subsessile. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII short, tergum not wider, sternum without ventromesal projection. Segment IX, in lateral view, with anteroventral margin distinctly produced, anterodorsal margin with broadly rounded apodeme, margin between strongly concave; dorsomesal margin of segment very short, but continuously sclerotized; posterior margin strongly produced in ventral half, strongly narrowed dorsally above inferior appendages, segment very short dorsally; ventral process emerging from ventral margin, very elongate, digitate, with apex rounded in lateral view, apex with short spines or setae; anteroventral margin of segment, in dorsal or ventral views, concave. Lateral lobes of tergum X each divided laterally into dorsal and ventral lobes, dorsal lobes strongly upturned and spine-like,

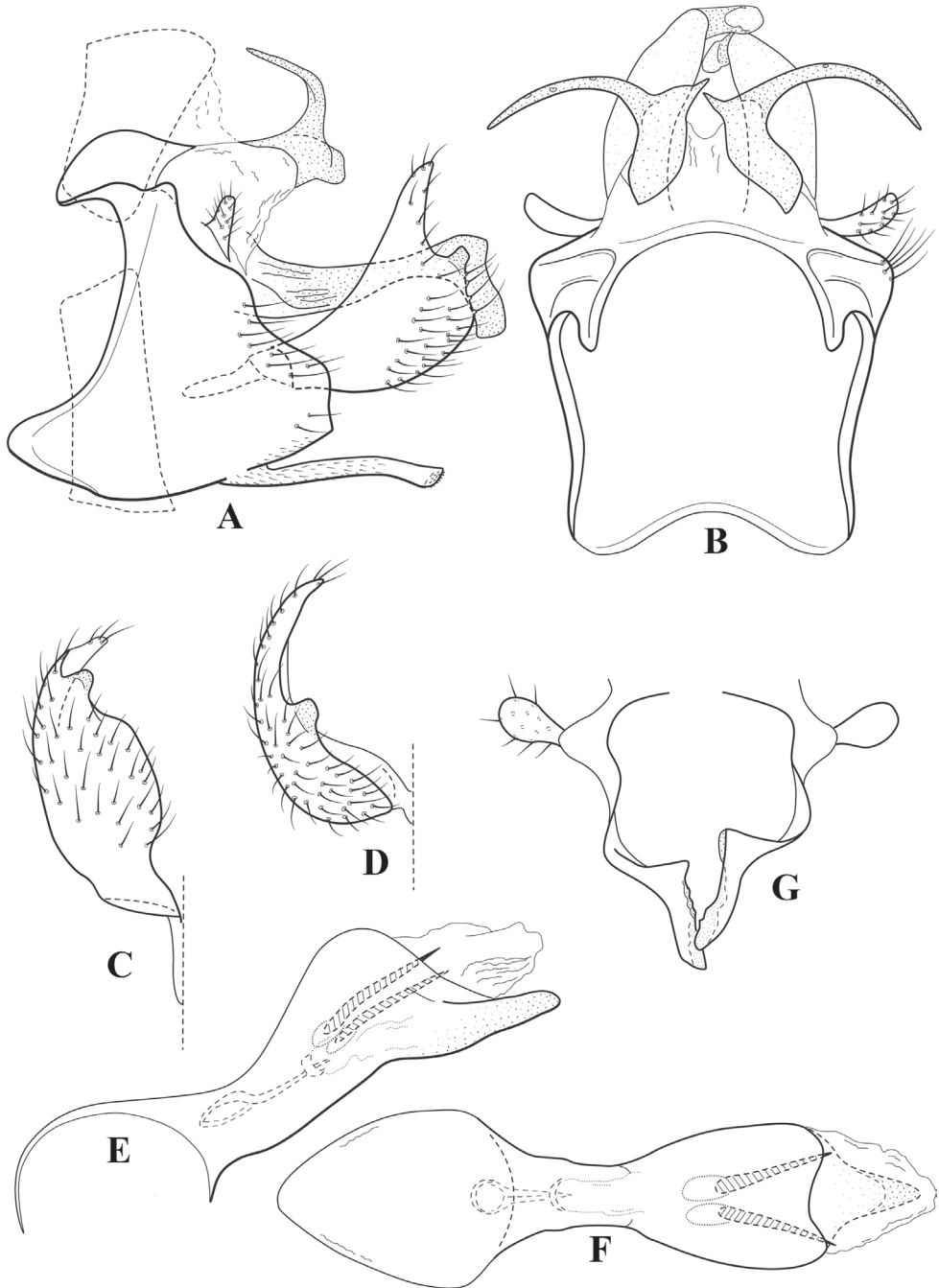


Figure 33. *Chimarra kibiensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, caudal **E** phallus, lateral **F** phallus, dorsal **G** ventral lobes of tergum X, caudal.

recurved and very strongly sclerotized, especially compared to base, almost appearing as separate structures; ventral lobes very elongate and strongly sclerotized, with apices strongly, angularly downturned, apices of lobes rounded. Preanal appendages short and knob-like, constricted basally. Inferior appendage with pronounced basal inflection, dorsally with moderately elongate, tapering dorsal projection, apex subacute; posteromesal margin with prominent sclerotized cusp, readily visible in lateral view. Phallic apparatus with phallobase moderately elongate, with usual basodorsal expansion, apical half strongly flared and vase-like, apicoventrally with short rounded, sclerotized projection; endotheca with two moderately elongate, slender, symmetrically positioned spines, phallotremal sclerite complex composed of short rod and ring structure, with small apical sclerite.

Etymology. *Chimarra kibiensis*, name used as an adjective (from Kibi), for the name of the town near where the type specimen was collected.

***Chimarra minacis* sp. nov.**

<http://zoobank.org/97E7A881-0991-47B9-840B-A7C27283BC77>

Fig. 34A–E

Type material. Holotype. GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 3; 7°07'29"N, 0°35'31"E; 10 Mar. 1993; JS Amakye & J Kjørandsen leg.; light trap; UMSP 000550079. **Paratypes.** GHANA – Volta Reg. • 1♂ (lacking abdomen); same data as for holotype except station # 2^B; 5–8 Mar. 1993; Malaise trap; UMSP • 3♂♂; same data as for holotype except 17 Nov. 1993; J Kjørandsen leg.; ZMBN • 2♂♂; same data as for holotype except station # 6; 20 Nov. 1993; J Kjørandsen leg.; ZMBN.

Diagnosis. *Chimarra minacis* is very closely related to *C. kibiensis* sp. nov. The differences between the two are relatively minor, but distinctive. The decision to recognize them as different species is admittedly subjective. Although it is conceivable that they may eventually be shown to be forms of a single species, the use of names in the meantime is meant to draw attention to the distinctiveness of the forms. Both species are readily recognized by the strongly upturned dorsal spine-like lobes of tergum X, with the elongate and apically downturned ventral lobes of the same tergum. *Chimarra cornuta* Jacquemart & Statzner also has spine-like lobes of tergum X, but in this species the lobes are not as upright, and the posterior margin of segment IX is not as produced in its ventral part as either of the two species discussed here. The primary difference of *C. minacis* from *C. kibiensis* is that the apices of the ventral lobes of tergum X are much more strongly developed and sclerotized in *C. kibiensis*, even resulting in some asymmetry of the lobes. Also, the sclerotized cusp or projection on the apical margin of the inferior appendage in *C. minacis* is not as strongly developed; notably it is not projecting or readily visible in lateral view; there is also a second small cusp found in *C. minacis*, not present in *C. kibiensis*.

Description. Adult. Overall color (in alcohol) nearly uniformly yellowish brown, spurs slightly darker. Head moderate in length (postocular parietal sclerite slightly > 1/2 diameter of eye). Palps moderately elongate; maxillary palp with 1st segment

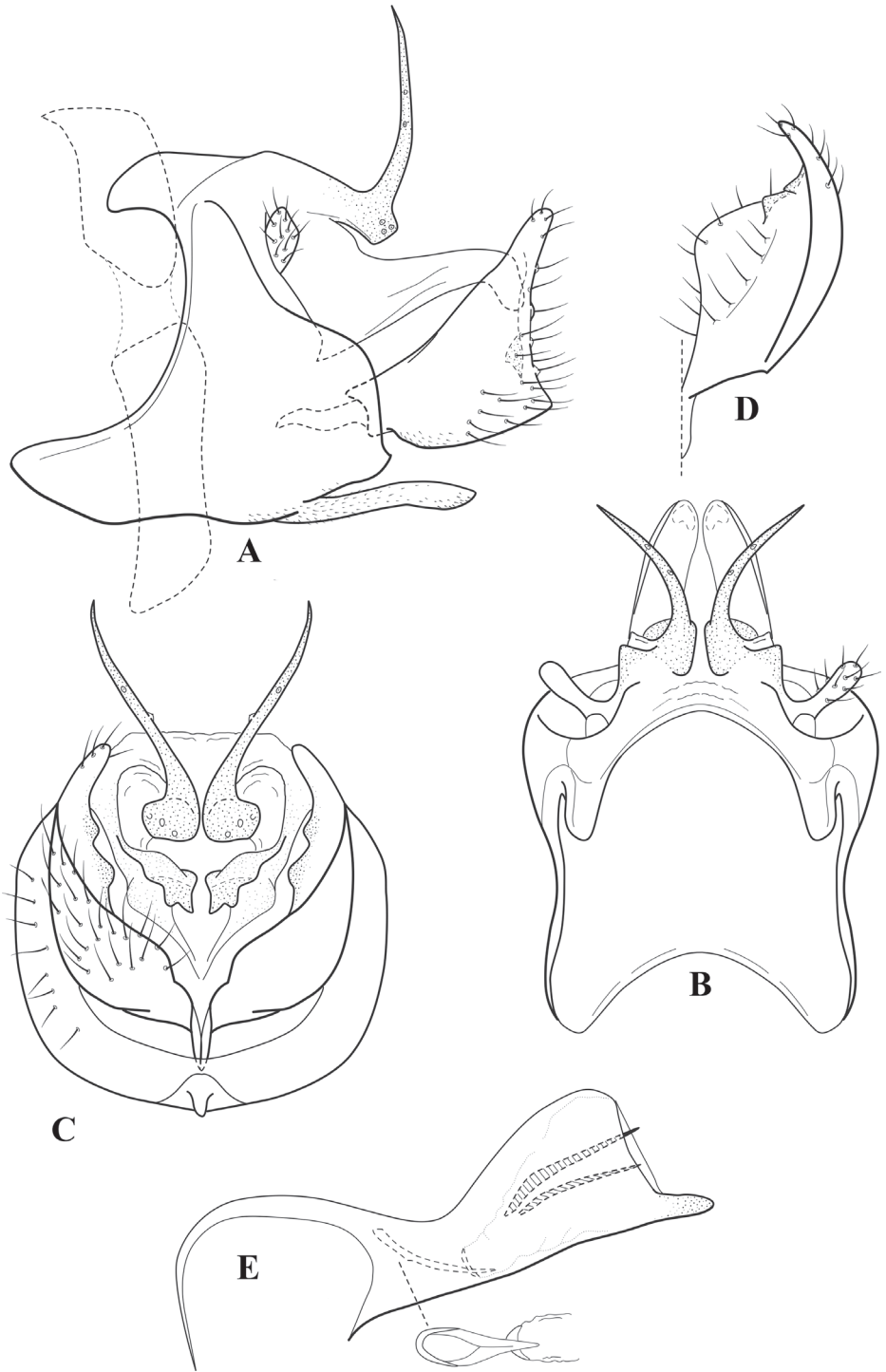


Figure 34. *Chimarra minacis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** caudal **D** inferior appendage, dorsal **E** phallus, lateral, with dorsal detail of phallotremal sclerite complex.

very short (approximately as long as wide), 2nd segment relatively short ($< 3 \times 1^{\text{st}}$), apex with small cluster of stiff setae, 3rd segment elongate, almost $2 \times$ length of 2nd, 4th segment very short (shorter than 2nd), 5th segment subequal to 3rd. Forewing length: male, 4.7–5.5 mm. Fore- and hind wing with forks I, II, III, and V present. Forewing with R_1 sinuous, stem of R_s inflected at past midlength (with small node at inflection), basal fork of discoidal cell distinctly enlarged, fork slightly asymmetric, length of cell $\sim 2 \times$ width, forks I and II subsessile, r crossvein diagonal, intersecting discoidal cell at approximately midlength, s and $r-m$, crossveins linear, m crossvein more proximal, s pigmented (like wing), $r-m$ and m crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R_1 narrowly parallel to subcosta, forks I and II subsessile. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII short, tergum not longer, sternum without ventromesal projection. Segment IX, in lateral view, with anteroventral margin greatly produced, anterodorsal margin with distinct and broadly rounded apodeme, margin between strongly concave; dorsomesal margin of segment very short, but continuously sclerotized; posterior margin strongly and truncately produced in ventral half, strongly narrowed dorsally above inferior appendages, segment very short dorsally; ventral process emerging from ventral margin, very elongate, digitate, with apex rounded in lateral view, apex with short spines or setae; anteroventral margin of segment, in dorsal or ventral views, very strongly concave. Lateral lobes of tergum X each divided laterally into dorsal and ventral lobes, dorsal lobes strongly upturned and spine-like, very strongly sclerotized, especially compared to base, almost appearing as separate structures; ventral lobes relatively elongate, with apices strongly, angularly downturned, apices of lobes rounded. Preanal appendages short and knob-like, constricted basally. Inferior appendage with pronounced basal inflection, dorsally with moderately elongate, tapering dorsal projection, apex subacute; posteromesal margin with a pair of small, sclerotized cusps, not or scarcely visible in lateral view. Phallic apparatus with phallobase moderately elongate, with usual basodorsal expansion, apical half strongly flared and vase-like, apicoventrally with short rounded, sclerotized projection; endotheca with two moderately elongate, slender, symmetrically positioned spines, membrane not noticeably textured, phallotremal sclerite complex composed of short rod and ring structure, with small apical sclerite.

Etymology. *Chimarra minaxis*, used as an adjective, from the Latin *minax*, meaning jutting out or threatening, for the upright spine-like processes on tergum X in this species.

***Chimarra tangaensis* sp. nov.**

<http://zoobank.org/C5D6476C-A2D5-4CA6-B8F4-D56548C5D090>

Fig. 35A–E

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts., Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 4–13 Dec. 1990; T Andersen leg.;

Malaise trap; UMSP 000550032. **Paratypes.** TANZANIA – Tanga Reg. • 5♂♂; same data as for holotype except 31 Oct. 1990–13 Jan. 1991; ZMBN.

Diagnosis. *Chimarra tangaensis* probably has its overall greatest similarity to *C. dulensis* sp. nov., particularly in the general shape of its inferior appendages, and in having an elongate, tubular phallobase with slender and symmetrically positioned phallic spines. It is easily distinguished by the more spine-like lateral lobes of tergum X. It is possible that the latter character reflects a closer relationship to the other new species of the *ruficeps* subgroup described here, which have the lobes even more dramatically developed into spine-like processes.

Description. Adult. Overall color (in alcohol) medium brown. Head relatively elongate (length of postocular parietal sclerite nearly equal to diameter of eye). Palps moderately elongate, maxillary palp with 1st segment very short (slightly longer than wide), 2nd segment short (~ 2× 1st), apex with small cluster of stiff setae, 3rd segment elongate, almost 2× length of 2nd, 4th segment short (subequal to 2nd), 5th segment elongate (slightly longer than 3rd). Forewing length: male, 7.5–8.5 mm. Fore- and hind wing with forks I, II, III, and V present. Forewing with R₁ slightly sinuous, stem of Rs weakly inflected at past midlength (with indistinct node at inflection, almost appearing as crossvein), basal fork of discoidal cell somewhat enlarged, fork almost symmetric, discoidal cell elongate, length ~ 2 1/2× width, forks I and II slightly sessile, *r* crossvein diagonal, intersecting discoidal cell at past midlength, before fork I, *s* and *r-m*, crossveins linear, *m* crossvein more proximal, ~ 1/2 way between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ fused to subcosta basally, both veins intersecting wing margin, forks I and II slightly sessile. Forelegs with apical tibial spur distinct; male with foretarsi unmodified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum short, without ventromesal projection, tergum slightly longer. Segment IX, in lateral view, with anteroventral margin greatly, subangularly, produced, anterodorsal margin with prominent apodeme, margin between strongly concave; dorsomesal margin of segment strongly concave, very short, but continuously sclerotized; segment, in lateral view, very short dorsally, posterior margin obliquely and almost linearly widened to inferior appendage, ventral margin rounded, ventral process emerging somewhat below inferior appendages, very elongate, digitate, with apex rounded in lateral view, apex with short spines or setae; anteroventral margin of segment, in dorsal or ventral views, very strongly concave. Lateral lobes of tergum X moderately elongate, divided into dorsal and ventral lobes, ventral lobes (possibly sclerotized extensions of periphallallic membrane) relatively lightly sclerotized, wide basally, subacute apically, dorsal lobes more distinctly sclerotized, with rounded and projecting basodorsal process and posteriorly projecting apical process, narrowing to a somewhat spine-like apex, sensilla not apparent; mesal lobe of tergum X short, membranous, only extending to basodorsal processes of dorsal lobes of lateral lobes. Preanal appendages short and knob-like, weakly constricted basally. Inferior appendage relatively short, rounded basally, with moderate basal inflection, apex narrowed, acute,

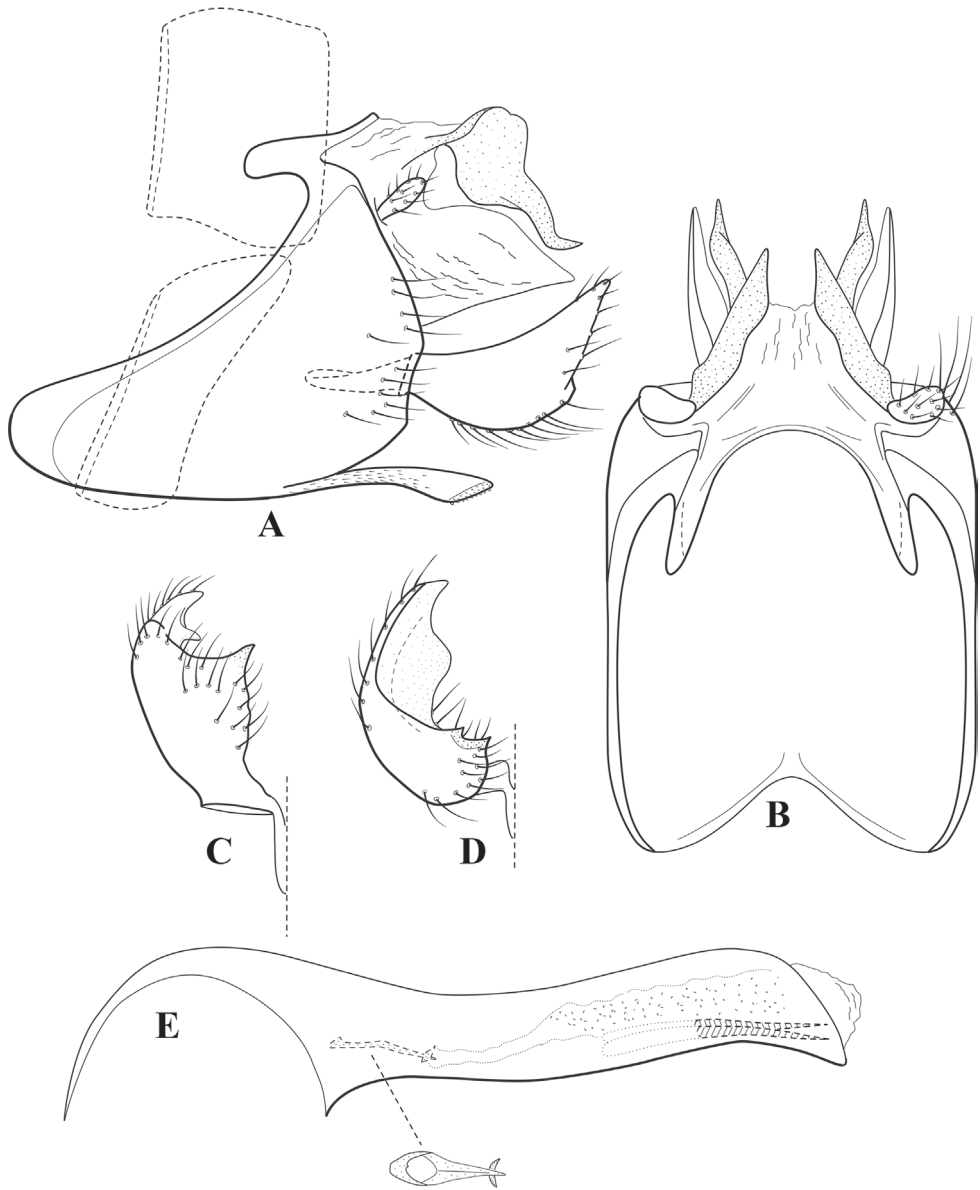


Figure 35. *Chimarra tangaensis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, caudal **E** phallus, lateral, with dorsal detail of phallotremal sclerite complex.

moderately posteriorly projecting; in caudal view, with rounded projection from dorsomesal margin. Phallic apparatus with phallobase elongate, tubular, with usual baso-dorsal expansion, apicoventral margin slightly projecting and somewhat downturned; endotheca membranous and apparently elongate, with two moderately elongate,

slender, symmetrically positioned spines, phallotremal sclerite complex composed of moderately elongate rod and ring structure, with small apical sclerites.

Etymology. *Chimarra tangaensis*, used as an adjective, meaning “from Tanga,” for the region in Tanzania in which this species was collected.

Species not assigned to subgroup

Chimarra multisensillata sp. nov.

<http://zoobank.org/5C9B0780-5053-4DAC-8E63-07D32C0F84BC>

Fig. 36A–F

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); East Usambara Mts, Fanusi; 28 Feb. 1959; 1,000 ft; MT Gillies leg.; INHS Trichoptera 50336.

Diagnosis. *Chimarra multisensillata* is a distinctive species, unlike any other described species, with several unusual characteristics. Its most diagnostic feature is the shape of the inferior appendage, which has a narrow, sclerotized, digitate projection on the dorsal margin at just past midlength, that is oriented more or less parallel to the appendage itself. Also distinctive is the overall form of the lateral lobes of tergum X, which are very elongate and simple in structure, with ~ 10 unraised sensilla scattered laterally along its length. Another unusual characteristic, for a species in the *marginata* Group, is the relatively elongate, tubular phallobase with two elongate, sclerotized, symmetrically arranged spines, possibly modified elements of the phallotremal sclerite complex. Finally, the shape of segment IX is also unusual in having its anterior margin uniformly concave and its ventral margin strongly produced, with lateral margins that are somewhat convergent, as viewed dorsally or ventrally.

Because of having multiple sensilla on tergum X, rather than just two, as is typical of species in the *marginata* Group, one might question its placement in the group. Its venational characters, however, are typical of species in the *marginata* Group. Nevertheless, it probably represents a relatively basal species in the lineage.

Description. Adult. Overall color (in alcohol) yellowish brown. Head relatively short (postocular parietal sclerite < 1/2 diameter of eye). Palps moderately elongate, maxillary palp with 1st segment short (length subequal to width), 2nd segment short (~ 2 × 1st), apex with small cluster of stiff setae, 3rd elongate (> 2 × as long as 2nd), 4th segment short (subequal to 2nd), 5th segment very elongate (longer than 3rd). Forewing length: male, 5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ distinctly sinuous, stem of Rs inflected at just past midlength, with small node at inflection, not extending into cell below, basal fork of discoidal cell enlarged, fork asymmetric, discoidal cell with length ~ 2 × width, fork I sessile, fork II stalked, *r* crossvein diagonal, intersecting discoidal cell at past midlength, *r-m* crossvein continuous with *s*, *m* crossvein proximal to *s* and *r-m* crossveins, approximately midway between basal fork of M and *r-m* crossvein, *s* pigmented (like wing), *r-m* and *m* crossveins hyaline, very faint, 2A with crossvein (apparently forked apically to 1A and 3A). Hind wing with R₁ fused to subcosta basally, both veins intersecting margin of wing,

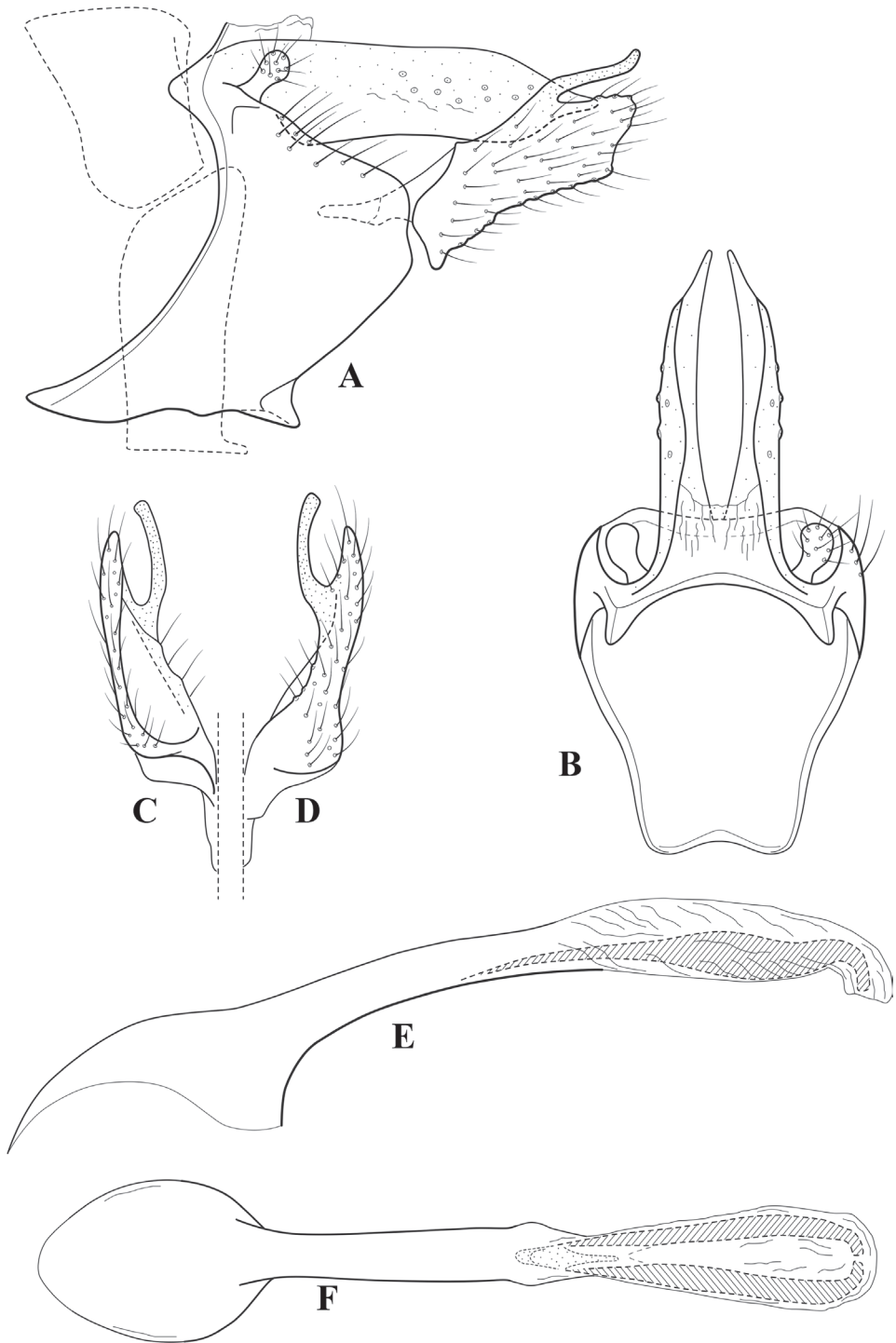


Figure 36. *Chimarra multisensillata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, dorsal.

fork I sessile, fork II stalked. Foreleg with apical tibial spur distinct; male with foretarsi unmodified, segments very narrow, claws small and symmetrical.

Male genitalia. Segment VIII with sternum relatively short, with short ventromesal projection, tergum approximately same length. Segment IX, in lateral view, relatively elongate, with anteroventral margin greatly produced, anterodorsal margin with small rounded apodeme, margin between strongly concave; dorsomesal margin of segment strongly concave, very short, but continuously sclerotized; segment, in lateral view, short dorsally, posterior margin greatly, convexly produced between preanal appendages and small, subtriangular ventral process, inferior appendage mounted at midheight; anteroventral margin of segment, in dorsal or ventral views, with lateral margins converging, mesal margin with weak concave emargination. Lateral lobes of tergum X elongate, parallel sided, tapering apically, simple in structure, lateral margin with ~ 10 unraised sensilla scattered along its length; mesal lobe of tergum X very short, membranous, much shorter than lateral lobes. Preanal appendages short and knob-like, distinctly constricted basally. Inferior appendage moderately elongate, projecting, without significant basal inflection, dorsal and ventral margins subparallel, with narrow, digitate, posteriorly projecting process at approximately midlength from dorsal margin, length of inferior appendage slightly $> 2\times$ its width, apex narrowing, rounded. Phallic apparatus with phallobase very elongate and narrowly tubular, with pair of very elongate, narrow sclerites, wider at midlength (possibly modified lateral sclerites of phallotremal sclerite complex), positioned apical to a more or less typical and moderately elongate rod and ring structure of phallotremal sclerite complex.

Etymology. *Chimarra multisensillata*, name used as an adjective, for the relatively numerous sensilla on the lateral lobes of tergum X, a very unusual characteristic for a species in the *marginata* Group.

The *georgensis* Group

This group was designated by Blahnik et al. (2012), when describing a new species from Vietnam. The group is otherwise only definitively known from Africa. *Chimarra georgensis* Barnard (1934), besides being the first described species in the group, is also the designated type species for the genus *Chimarrhafa* Lestage (1936), a genus synonymized with *Chimarra* by Ross (1956). Thus, *C. georgensis* has formal name priority over other species of the group, unless the genus *Vigarrha*, a monotypic genus from the Philippines, also synonymized under *Chimarra* by Ross (1956), can be demonstrated to belong to the group. Ross believed the two genera to be related. The issue is somewhat complicated and further discussed below in the characterization of the *georgensis* subgroup. African species of the group were listed by Gibon (2018) when describing a new species of the group from Madagascar. As recognized here, these species all belong to the *georgensis* subgroup. Another subgroup, the *evoluta* subgroup, is proposed in this paper, containing three described species and also additional species described herein.

The two subgroups of the *georgensis* Group are quite distinctive. The characters uniting them are a bit more difficult to characterize. Venational characters used to

characterize the group as a whole, including the absence of a crossvein in the anal veins of the fore wing (both 2A and 3A looped to the 1A), a linear arrangement of the *s*, *r-m*, and *m* crossveins of the forewing, and a straight (or nearly straight) *Rs* vein in the forewing, are probably all plesiomorphic characters, at least with respect to other subgenera within *Chimarra*. Both subgroups are also characterized by a loss of the R_1 vein of the hind wing (or its fusion to the subcosta). Thus, only a single vein of the two reaches the margin of the wing. However, this is not a unique character within *Chimarra*. It also characterizes most species of the subgenus *Otarrha* in the New World and seems to be a consistent character of the *minuta* Group of the subgenus *Chimarra* in Asia (whose relationship to the *georgensis* Group remains to be assessed). Since the subcosta and R_1 veins of the hind wing run narrowly parallel in many species of *Chimarra*, its loss is to be expected, especially in smaller species. It also makes determination of the character state difficult. The recent addition of photographs of wings in some publications of new species of *Chimarra*, as for instance, Johanson and Espeland (2010), Johanson et al. (2011), Johanson and Oláh (2012), and Gibon (2015), reveals that the loss or fusion of the R_1 vein in the hind wing characterizes many taxa in the *marginata* Group of the subgenus *Chimarra*, in addition to species of the *georgensis* Group, and also that the loss of fork I and fork III in the hind wing, either independently or together, is not uncommon. These are the most usual venational modifications occurring in the genus and seem to have occurred independently in various lineages or species. Nevertheless, loss of the R_1 vein of the forewing may be a synapomorphy for the taxa placed in the *georgensis* Group. In addition to this admittedly homoplasious character, most species of both the *georgensis* and *evoluta* subgroups are characterized by a rather short phallobase that is anchored in place by a sclerotization of the periphallalic membrane, forming a phallocrypt that holds the short phallobase in place (so that it is not easily removed). This is usually more evident in the *georgensis* subgroup. Members of both subgroups also have maxillary palps in which the terminal segment is unusually elongate. These characters, in combination, are suggestive enough to place both subgroups into a common taxon. We recognize that this placement deserves further evaluation.

The *georgensis* subgroup

Included species. *Chimarra ankylis* sp. nov.; *C. aurita* sp. nov.; *C. corneola* Blahnik, Arefina-Armitage & Armitage, 2012; *C. crescentis* sp. nov.; *C. furcata* Jacquemart, 1961; *C. georgensis* Barnard, 1934; *C. hoogstraali* Ross, 1956; *C. indicis* sp. nov.; *C. kabashana* (Marlier, 1943); *C. latidentis* sp. nov.; *C. leptodactylus* sp. nov.; *C. obuncata* sp. nov.; *C. polycentropoides* sp. nov.; *C. ralphi* sp. nov.; *C. serrella* sp. nov.; *C. triramosa* sp. nov.; *C. uncinata* sp. nov.; *C. vermitergata* sp. nov.; and *C. zombitsei* Gibon, 2018.

This subgroup has the R_1 vein of the hind wing either completely obsolete, or present basally, but obsolete or fused to the subcosta apically. Notably, only one vein intersects the wing margin. The venation of the hind wing is otherwise complete for *Chimarra*, with forks I, II, III, and V present. However, usually fork III is relatively narrowly

forked. All of the species seem to have a relatively short phallobase, with the ventral apex strongly projecting and downturned, and often modified. The most usual modification is for the apex to be bifid, or that is with a mesal invagination and lateral projections on either side. In the species from Tanzania, this ventral projection is apparently fused to the sclerotized periphallallic membrane, and thus it is difficult to say whether this is actually a phallic structure or independently derived and fused periphallallic processes. The former seems more likely. However, the situation is further complicated in that there is a sclerotized extension of the phallobase beyond this ventral projection, which may be due to a secondary sclerotization of the base of the endotheca in these species. All of the species in the *georgensis* subgroup from Ghana have males with enlarged and modified claws on the forelegs, whereas the four species from Tanzania placed in this subgroup have the claws small and unmodified. Since modified claws on the forelegs is a common feature throughout the genus *Chimarra*, including the *evoluta* subgroup, their absence in the species from Tanzania probably represents a loss. This character, in combination with the modified apex of the phallobase discussed above, can be taken as evidence for the monophyly of the Tanzanian species placed in this subgroup.

To date, only a single species of this subgroup has been reported from Asia (*Chimarra carneola* Blahnik, Arefina-Armitage & Armitage from Vietnam). However, *C. giacomazzoi* Malicky (2015a), described from Guangxi, China is very similar in morphology and probably also belongs here. Malicky stated, with the description of the species, that other species with a similar morphology exist, without stating their geographic location or whether they were currently described. *Chimarra potamophila* Mey (1995), described from Mindoro in the Philippines, also shares some of the features of this group and at least a superficial similarity. Unfortunately, venational characters of the species were not discussed in its initial description. Ross (1956) stated that *Vigarrha tibialis* Navás (1922), described from Luron (Luzon?) in the Philippines was related to the *Chimarrhafa* group from Africa. However, he placed both in the genus *Chimarra* and never discussed the morphological characters that he used to make his assessment. If related, the name *Vigarrha* (and its type species) would have name precedence in referring to this group. *Vigarrha tibialis* was based on a female specimen and only a hind wing was illustrated (Navás 1922: fig. 1). A male of the species was later illustrated by Ulmer (1930: fig. 7), based on specimens from Leyte and Mindanao, rather than Luzon. Thus, it is difficult to know whether the male illustrated actually represents the same species described by Navás. As illustrated by Navás (1922: fig. 1) *Vigarrha tibialis* possesses the R_1 vein in the hind wing but lacks fork III. Although the second character occurs in some species of the *evoluta* subgroup of Africa (with the additional loss of fork I), none of the known species of the *georgensis* Group have the R_1 vein of the hind wing present. Moreover, loss of this vein was a primary character used by Lestage (1936) to define the genus *Chimarrhafa*. Based on this conflicting evidence, both the existence of the *georgensis* Group or subgroup in the Philippines, and its possible relationship to the genus *Vigarrha*, is inconclusive and needs further investigation.

***Chimarra ankylis* sp. nov.**

<http://zoobank.org/EBBF7A2F-B3EE-4CF2-A487-805445ACCC82>

Fig. 37A–F

Type material. Holotype. TANZANIA –**Tanga Reg.** • ♂ (in alcohol); West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 26–29 Nov. 1990; T Andersen leg.; Malaise trap; UMSP 000550076. **Paratypes.** TANZANIA –**Tanga Reg.** • 10♂♂; same data as for holotype; UMSP • 35♂♂; same data as for holotype except 10 Nov. – 3 Dec. 1990; ZMBN.

Diagnosis. *Chimarra ankylis* is readily diagnosed by the distinctive characteristics of the lateral lobes of tergum X, which are very short and have both a short, acute, dorsally directed apical projection and a more prominent, acute, curved, basoventral projection. Also distinctive is a relatively elongate and very narrow lateral projection on each of the lateral lobes of tergum X, with an apical sensillum, in addition to several small sensilla basal to this structure. The inferior appendage is subovate, as viewed laterally, but has a short, subacute apex on its mesal surface as viewed ventrally. The phallobase, is both large and short, as is characteristic of the group, with its apicoven-tral projection relatively wide, sclerotized laterally, and with a small desclerotized notch mesally. The phallic spines, possibly actually components of a phallotremal sclerite complex, are relatively elongate and prominent.

Description. Adult. Overall color (in alcohol) dark brown. Head short (postocular parietal sclerite < 1/2 diameter of eye). Palps elongate; maxillary palp with 1st segment short (slightly longer than wide), 2nd segment moderately elongate (> 3× 1st), apex with cluster of ~ 8–10 stiff setae, 3rd segment elongate (distinctly longer than 2nd), 4th segment short (1/2 length of 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 5.0–6.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs straight, basal fork of discoidal cell not enlarged, evenly forked, length of cell ~ 2× width, forks I and II sessile, *r* crossvein diagonal, intersecting discoidal cell before apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete or fused to subcosta, forks I, and II distinctly subsessile, anal loop small. Forelegs with apical tibial spur short; male with foretarsi modified, tarsal claws enlarged and asymmetrically developed.

Male genitalia. Segment VIII very short, tergum slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, very short, anteroventral margin only slightly expanded in ventral 1/3, dorsal margin without apodemes, sternum with very short, rounded ventral process from ventral margin, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate, very shallowly emarginate mesally. Tergum X with mesal lobe short and membranous, lateral lobes very short and strongly sclerotized, each with short, acute apicodorsal projection and much larger, curved, basoventral, spine-like projection; preapical lateral margin with two or three small sensilla, one on a narrow digitate projection. Preanal appendages short

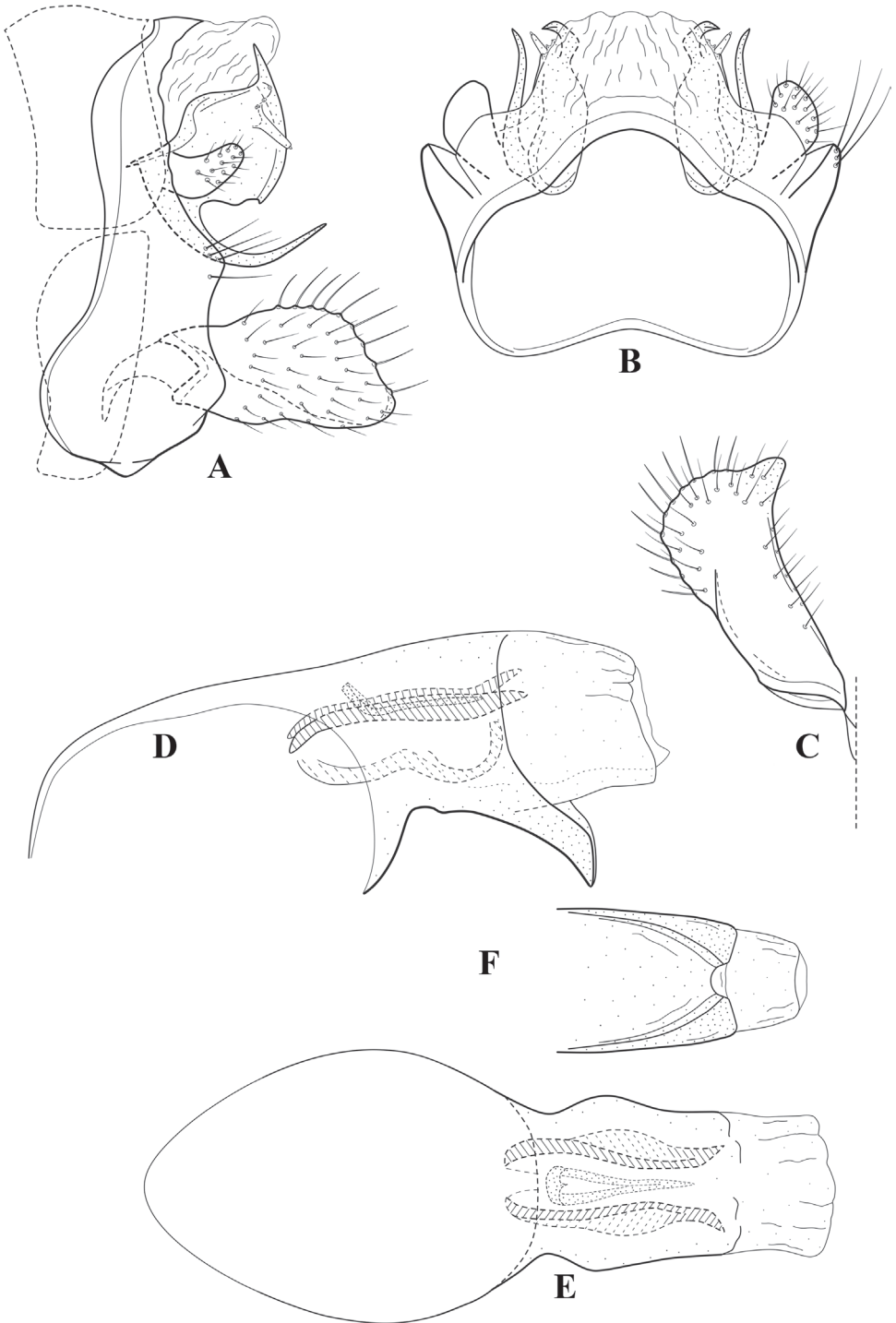


Figure 37. *Chimarra ankylis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral **E** phallus, dorsal **F** phallus apex, ventral.

and rounded, relatively prominent, constricted basally. Inferior appendage not or only weakly inflected basally, appendage relatively simple in structure, longer than wide, apicoventral margin somewhat projecting, forming subacute apicomesal projection, as viewed ventrally. Phallic apparatus with phallobase very short and wide, strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by sclerotized periphallalic membrane; apicoventral margin of phallobase very distinctly sclerotized and produced, downturned; apex, as viewed ventrally, relatively wide, with sclerotized lateral margins, apex subtruncate, only very shallowly emarginate mesally; endotheca simple and membranous. Armature of phallus relatively prominent, extending nearly length of phallobase, possibly entirely part of a modified phallotremal sclerite complex, composed of a moderate length rod-and-ring structure and enlarged pair of dorsolateral sclerites, appearing as pair of symmetrical spines.

Etymology. *Chimarra ankylis*, used as a noun in apposition, from the Greek word *ankylis*, a hook or barb, for the hooked ventral projection from the lateral lobes of tergum X in this species.

***Chimarra aurita* sp. nov.**

<http://zoobank.org/99E6C630-4634-4DF8-AC12-BA3543343DC1>

Fig. 38A–F

Type material. Holotype. GHANA – **Western Reg.** • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; UMSP 000550034. **Paratypes.** GHANA – **Western Reg.** • 2♂♂; same data as for holotype; ZMBN.

Additional material. GHANA– **Western Reg.** • 9♀♀; Ankasa Game Production Reserve; 5°15'N 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra aurita* is distinctive because of its enlarged and ear-like preanal appendages. As in other species of the subgroup, *C. aurita* is most readily diagnosed by characters of the inferior appendages, tergum X and phallobase in combination. The inferior appendages are short and ovate, with a mesally curved and spine-like projection on its dorsal margin and a short bifid cusp on its basomesal margin. The short lateral lobes of tergum X each terminates in a pair of digitate, sensillum-bearing processes, a longer ventrally curved one on its dorsal margin and a much shorter, dorsally-projecting process on its ventral margin. The short phallobase has a decurrent apex, appearing spine-like in lateral view, but with the apex actually broad, as viewed ventrally, and not divided mesally (or at most only weakly notched).

Description. Adult. Overall color (in alcohol) light brown or yellowish brown, undersides and appendages paler, setal warts of head not contrasting. Head short and rounded (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderate in length (~ 3× 1st), apex with cluster of ~ 8 stiff setae, 3rd segment elongate, distinctly longer

than 2nd, 4th segment short (shorter than 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.8–4.9 mm; female, 4.3–4.7 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs slightly inflected, basal fork of discoidal cell distinctly enlarged, evenly forked, length of cell ~ 2× width, forks I and II subsessile, *r* crossvein diagonal, intersecting discoidal cell before apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ evident basally, obsolete (or fused to subcosta) apically, forks I and II subsessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII very short, tergum approximately same length as sternum, sternum without posteroventral projection. Segment IX, in lateral view, relatively short, ventral margin somewhat projecting posteriorly, anteroventral margin only slightly expanded, constricted basally under sternum VIII, ventral process absent, dorsal margin without apodemes, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe short and membranous, lateral lobes short and divided apically into two digitate processes, each with single apical sensillum, dorsal process more elongate and slightly ventrally curved, ventral process very short. Preanal appendages prominent and moderately large, distinctly flattened, ear-shaped, slightly constricted basally, inserted membranously (not fused to segments IX or X). Inferior appendage without evident basal inflection; as viewed laterally, more or less ovate, subangulate apically, with short lateral setae and row of spaced, more elongate setae on dorsal margin; as viewed dorsally, with short, acute, sclerotized projection on dorsomesal margin, and prominent, apically forked cusp basoventrally on mesal surface. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallalic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, down-turned, apex produced into single acute mesal projection; endotheca short, membranous, with two short, curved, thick spines, one slightly larger than the other; phallotremal sclerite complex composed of short rod and ring structure, with pair of short apicolateral sclerites.

Etymology. *Chimarra aurita*, used as an adjective, from the Latin *auritus*, or eared, for the large, ear-like preanal appendages of this species.

***Chimarra crescentis* sp. nov.**

<http://zoobank.org/49EB1093-6FDF-4795-B9A2-3CE3A67CF65F>

Fig. 39A–F

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts, Dule; 4°51'S, 38°26'E; 26 Nov. 1990; T Andersen leg.; sweep net; UMSP

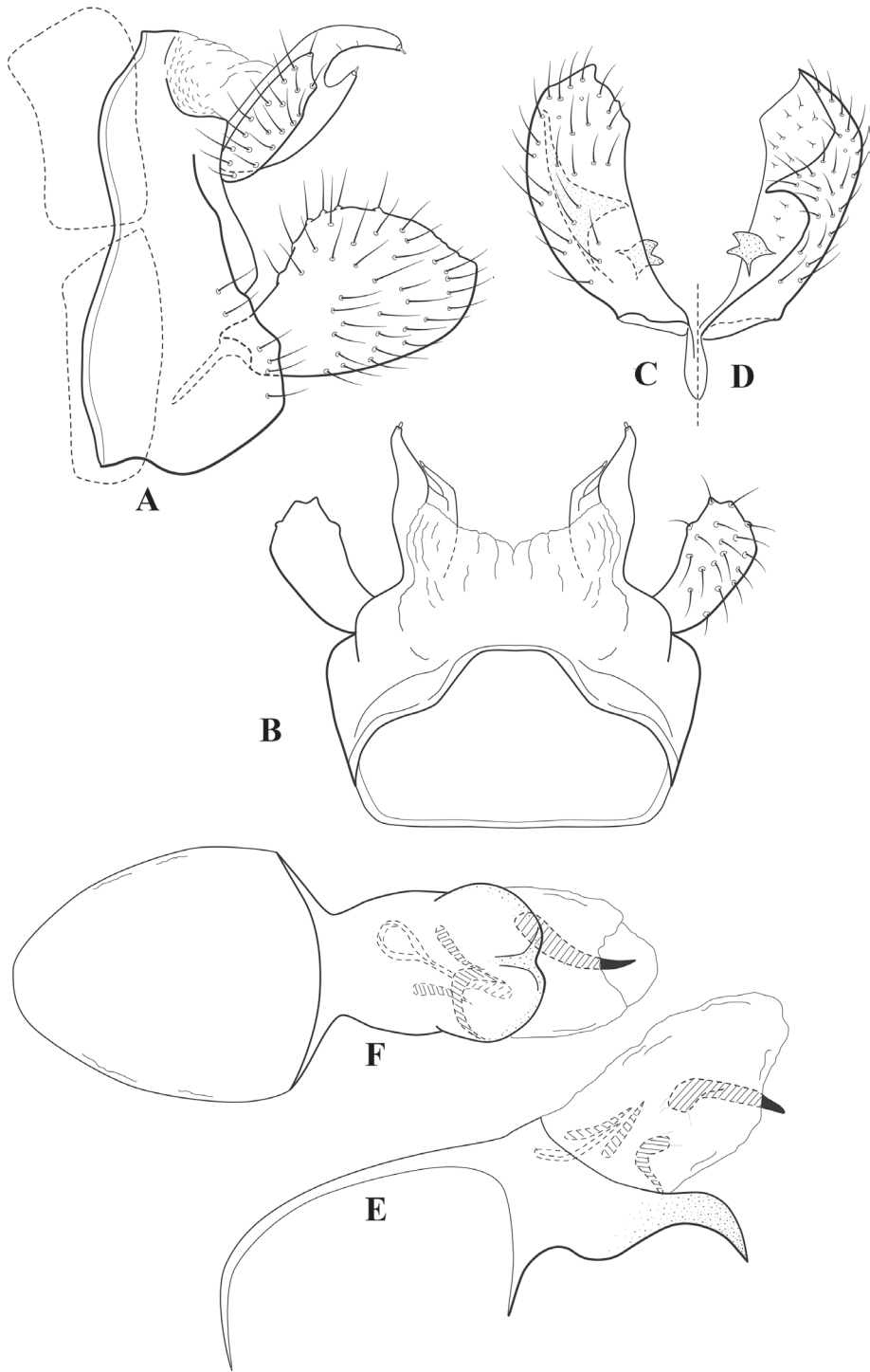


Figure 38. *Chimarra aurita* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, ventral.

000550035. **Paratypes.** TANZANIA – Tanga Reg. • 1♂; same data as for holotype; ZMBN • 1♂; INHS.

Diagnosis. *Chimarra crescentis* is related to the other new species of this subgroup from Tanzania, resembling them in the general structure of the phallus. It is easily distinguished from any other species by the shape of its inferior appendages, which, in lateral view, have acute dorsal and ventral apices separated by a broadly crescentic invagination.

Description. Adult. Overall color (in alcohol) medium brown to yellowish brown, setal warts of head slightly paler, weakly contrasting. Head short (postocular parietal sclerite relatively short, shorter than eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short ($\sim 2 \times 1^{\text{st}}$), apex with cluster of ~ 8 – 10 stiff setae, 3rd segment very elongate ($> 2 \times 2^{\text{nd}}$), 4th segment short (shorter than 2nd), 5th segment elongate and narrow (slightly longer than 3rd). Forewing length: male, 4.7–5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of R_s straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell $\sim 2 \times$ width, fork I sessile, fork II slightly subsessile, r crossvein diagonal, intersecting discoidal cell before apical fork, s , $r-m$, and m crossveins linear and hyaline (m crossvein somewhat diagonal), both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 evident basally, obsolete (or fused to subcosta) apically, forks I and II slightly subsessile, fork III distal and relatively wide, anal loop small. Forelegs with apical tibial spur short; male with tarsal claws not enlarged, claws symmetrical, tarsal segments narrow.

Male genitalia. Segment VIII very short, tergum longer than sternum, dorsal margin slightly projecting, sternum without posteroventral projection. Segment IX, in lateral view, short, anteroventral margin only slightly expanded, dorsal margin without apodemes, sternum with very short, rounded ventral process from posterior margin, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe short and membranous, lateral lobes short and strongly sclerotized, each with rounded basal part and mesally curved, spine-like dorsal projection; sensilla of lobes absent (or not evident). Preanal appendages very short and rounded, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage not or only weakly inflected basally, appendage narrow basally, expanded apically to produce widely forked, subequal, acute, dorsal and ventral lobes; mesal surface with irregular sclerotized cusp in basal half, probably articulating with sclerotized ventral projection of phallobase. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by sclerotized periphallalic membrane (and apparently fused to it); apicoventral margin of phallobase (or possibly projections from periphallalic membrane) very distinctly sclerotized and produced, down-turned, apex divided mesally, apparently articulating with cusped projections of mesal surface of inferior appendages; phallic apparatus distal to sclerotized ventral projection (possibly modified endotheca), with lightly sclerotized membranous region and bulbous sclerotized projection with rounded apical lobes (appearing as extension

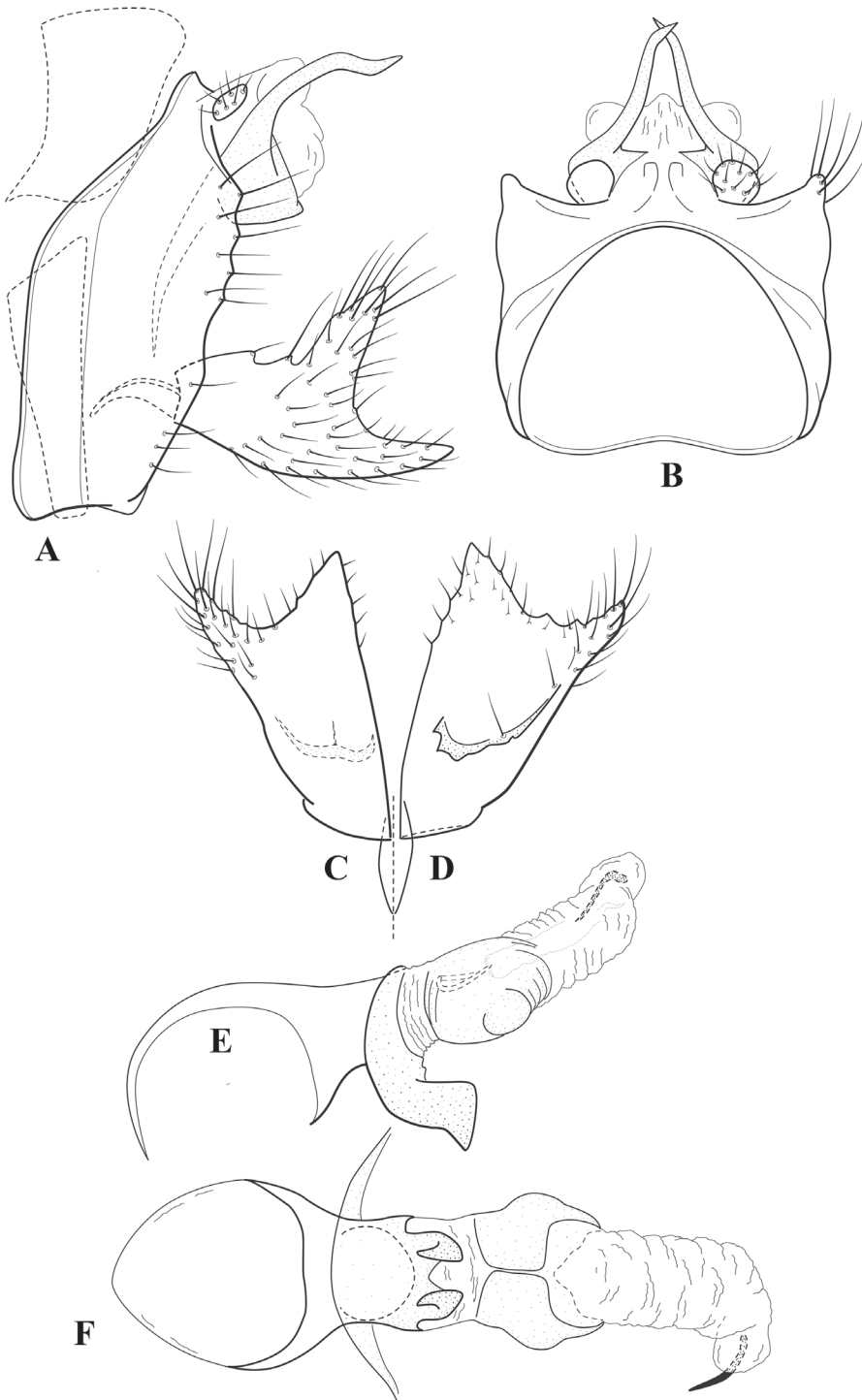


Figure 39. *Chimarra crescentis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, ventral.

of phallobase); endotheca with single short, curved apical spine; phallotremal sclerite complex composed of short rod and ring structure, rod very short.

Etymology. *Chimarra crescentis*, used as an adjective, for the crescentic apex of the inferior appendages in this species (derived via OF from the Latin *cresco*, to grow, for the figure of the moon in its first or last quarter).

***Chimarra indicis* sp. nov.**

<http://zoobank.org/D31D52C1-11C9-464D-A98B-85A18BC69929>

Fig. 40A–F

Type material. Holotype. GHANA – **Western Reg.** • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; UMSP 000550036. **Paratypes.** GHANA – **Western Reg.** • 4♂♂; same data as for holotype; ZMBN. – **Central Reg.** • 1♂; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN.

Additional material. GHANA – **Western Reg.** • 1♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; UMSP.

Diagnosis. *Chimarra indicis* appears to be somewhat similar to *C. georgensis* Barnard, particularly in a having an acute cusp on the ventral margin of the inferior appendage and in having each of the lateral lobes of tergum X with an elongate and short digitate process near its apex. A direct comparison is difficult because the genitalia of *C. georgensis* was drawn as fragmented parts. In general, *C. georgensis* is probably more directly related to *C. uncinata* sp. nov. and *C. serrella* sp. nov. because of the similarity in the structure of the phallobase in those species, with the apex decurrent and with two distinct apical points on each side and an acute projection on the dorsal margin where the apex begins to bend downward. Besides the differently formed apex of the phallobase in *C. indicis*, it also differs from *C. georgensis* in that the inferior appendage has an acute dorsal projection, and the lateral lobes of tergum X have a greater overall length, each lobe with two sensilla on short digitate processes, one basal and one curved and preapical, just before the elongate, acute, dorsally recurved apical projection.

Description. Adult. Overall color (in alcohol) light brown, undersides and appendages yellowish brown, vertex of head slightly darker, setal warts of head not distinctly contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (~ 3 × 1st), apex with cluster of ~ 6 setae, 3rd segment elongate, distinctly longer than 2nd, 4th segment short (shorter than 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.5–4.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell ~ 2 × width, fork I subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to

1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), forks I and II sessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur very short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII very short, tergum approximately same length as sternum, sternum without posteroventral projection. Segment IX, in lateral view, short, anteroventral margin only slightly expanded, dorsal margin without apodemes, ventral process very short, subtriangular, ventrally oriented, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe very short and membranous, lateral lobes projecting, distinctly sclerotized, produced apically into strongly dorsally curved spine-like projection (bent at approximately right angle), dorsal projection subequal to length of base before inflection, ventral margin of inflection with additional small spine; sensilla of lobes apparently reduced to two, on short nipple-like projections, one basodorsally and one dorsolaterally, before apical bend. Preanal appendages short and rounded, distinctly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with distinct basal inflection; as viewed laterally, narrow, with short, sclerotized projection from apex of ventral margin, appendage dorsally inflected and tapering from ventral projection, apex acute; as viewed ventrally, with acute sclerotized cusp on posterior margin (extended onto mesal surface), and additional small, irregular cusp basally on mesal surface. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, downturned, apex divided into pair of ventrally projecting spine-like processes; endotheca short, membranous, internally with pair of prominent recurved sclerites (possibly modified elements of phallosomal sclerite complex).

Etymology. *Chimarra indicis*, used as a noun in apposition, from the Latin *index*, a sign, token, or forefinger, for the notable upturned apex of tergum X in this species.

***Chimarra latidentis* sp. nov.**

<http://zoobank.org/3FAAEA83-9E81-41A9-9B86-8576F8A1F33A>

Fig. 41A–F

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 27–28 Oct. 1990; T Andersen leg.; Malaise trap; UMSP 000550038. **Paratypes.** TANZANIA – Tanga Reg. • 34♂♂; same data as for holotype except 27 Oct. 1990–12 Feb. 1991; ZMBN • 1♂; West Usambara Mts, Shokoi River; 4°46'S, 38°29'E; 24 Nov. 1990; T Andersen leg.; sweep net; UMSP.

Diagnosis. *Chimarra latidentis* is closely related to *C. leptodactylus* sp. nov. and *C. vermitergata* sp. nov. It is most similar to *C. vermitergata* in having the lateral lobes

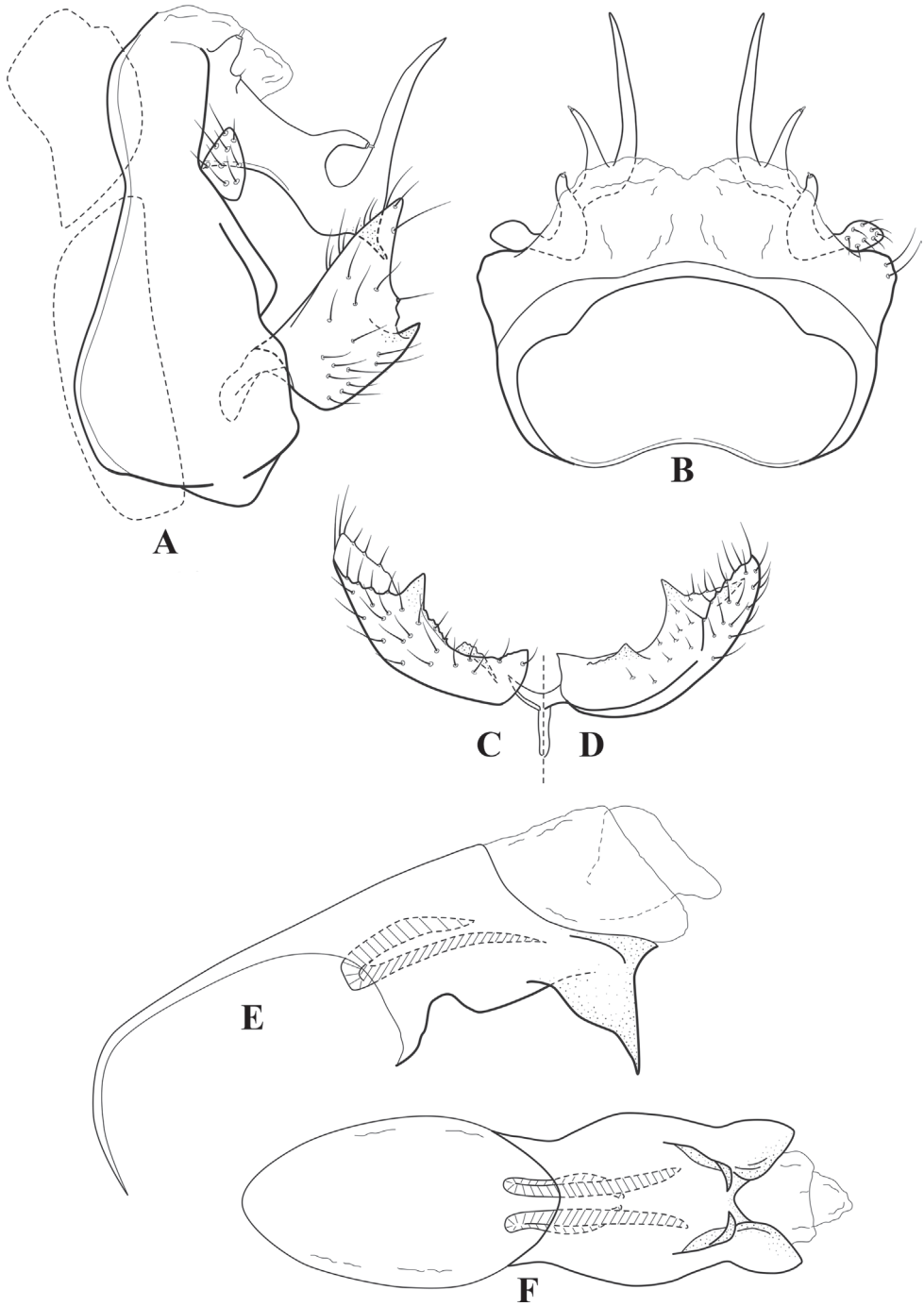


Figure 40. *Chimarra indicis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, ventral.

of tergum X formed into upright, spine-like processes, without a separated ventral projection. At least in the holotype of *C. latidentis*, these lobes are thicker, undivided and have their apices somewhat scabrous. The mesal cusps of the inferior appendages in *C. latidentis* are also wider, larger, and more prominent than in *C. vermitergata*, and the basal sclerotized portion of the endotheca, posterior to the sclerotized ventral apex of the phallobase, is more rounded.

Description. Adult. Overall color (in alcohol) medium brown to yellowish brown, head darker (dark brown), setal warts of head paler and somewhat contrasting. Head short (postocular parietal sclerite relatively short, shorter than eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short ($\sim 2 \times 1^{\text{st}}$), apex with cluster of ~ 8 stiff setae, 3rd segment very elongate (nearly $3 \times 2^{\text{nd}}$), 4th segment short (shorter than 2nd), 5th segment elongate and narrow (subequal to 3rd). Forewing length: male, 5.0–6.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of R_s straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, discoidal cell relatively elongate and narrow, length of cell nearly $3 \times$ width, fork I with long stem, fork II subsessile, r crossvein diagonal, intersecting discoidal cell near s crossvein, s , $r-m$, and m crossveins hyaline, s and $r-m$ linear, m crossvein somewhat proximal and diagonal, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), fork I with very short stem, fork II subsessile, fork III distal and very narrow, anal loop small. Forelegs with apical tibial spur short; male with tarsal claws not enlarged, claws symmetrical, tarsal segments narrow.

Male genitalia. Segment VIII with sternum very short, tergum $\sim 2 \times$ as long, dorsal margin projecting, sternum without posteroventral projection. Segment IX, in lateral view, short, anteroventral margin only slightly expanded, anterodorsal margin without apodemes, posterior margin angularly projecting below preanal appendages, sternum with very short, rounded ventral process from posterior margin, inferior appendages inserted somewhat above ventral margin; as viewed dorsally, with tergum very narrow, but continuous (or nearly so), sternum very short, subtruncate. Tergum X with mesal lobe short and membranous, lateral lobes short and sclerotized, each modified into short, up-turned spine-like projection from basoventral margin, apex of projection rugose; sensilla of lobes absent (or not evident). Preanal appendages very short and rounded, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with weak basal inflexion; as viewed laterally, short, with apicodorsal margin somewhat angulate and laterally projecting; as viewed ventrally, subtruncate apically, with mesal margins of opposite appendages proximate, then sharply bent; mesal surface with wide, sclerotized, tooth-like projection, apparently articulating with sclerotized ventral projection of phallobase. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by sclerotized periphallalic membrane (and apparently fused to it); apicoventral margin of phallobase (or projections from periphallalic membrane) very distinctly sclerotized and produced, down-turned, apex divided mesally, apparently articulating with tooth-like projections of mesal surface of inferior appendages; phallic apparatus distal to sclerotized ventral

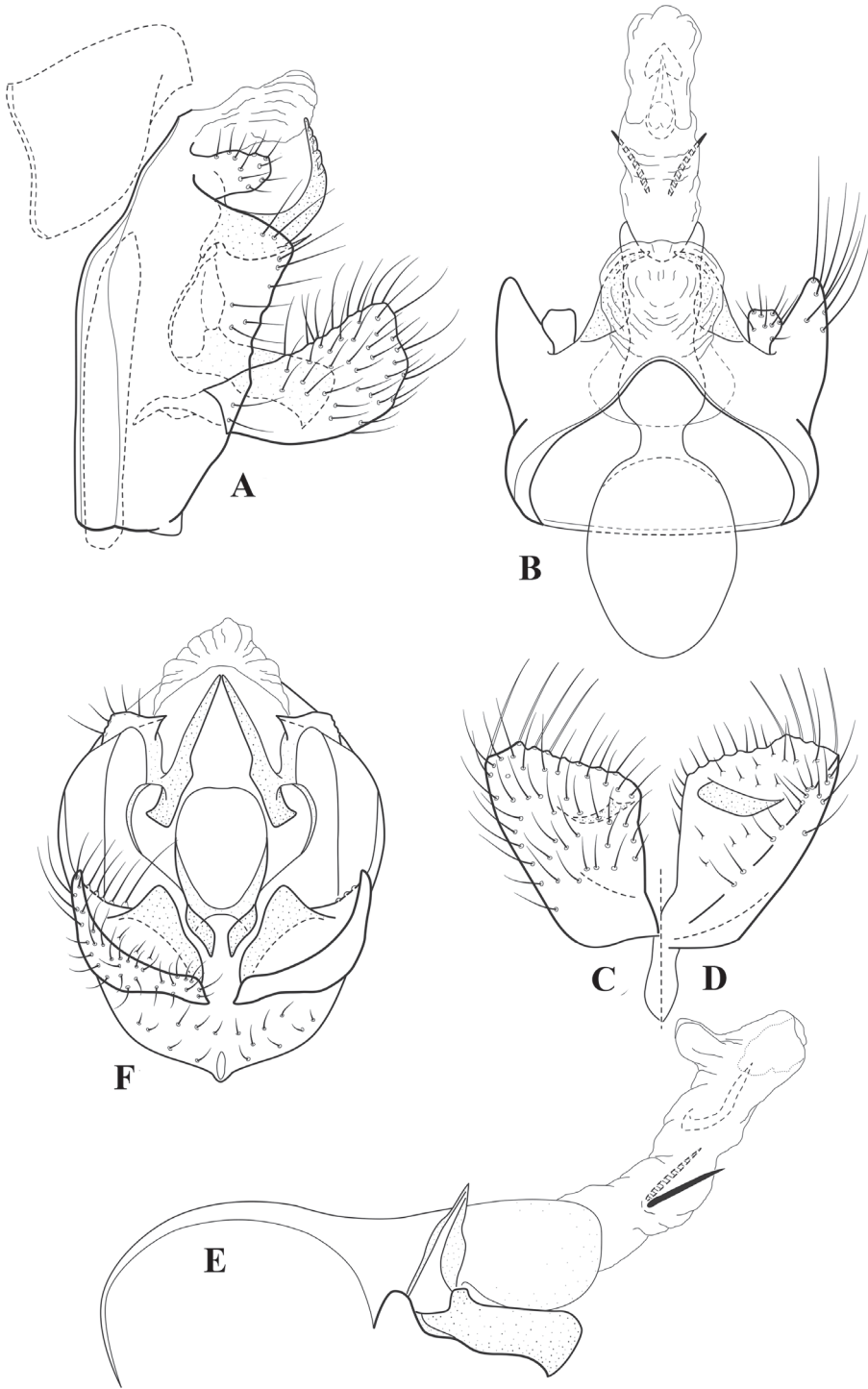


Figure 41. *Chimarra latidentis* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX, X, and phallus **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** caudal.

projection (possibly modified endotheca), forming short, sclerotized, bulbous extension of phallobase; endotheca approximately as long as phallobase, apicodorsally with pair of small membranous lobes, basally with pair of very short, symmetrically positioned spines; phallotremal sclerite complex composed of short rod and ring structure.

Etymology. *Chimarra latidentis*, used as a noun in apposition, from the Latin *latus*, meaning broad or wide, and *dens*, a tooth, for the relatively large, wide tooth-like cusp on the mesal surface of the inferior appendage.

***Chimarra leptodactylus* sp. nov.**

<http://zoobank.org/6C5E426B-C19E-44CA-9FEF-52D5DBB4D3B3>

Fig. 42A–F

Type material. Holotype. TANZANIA – **Tanga Reg.** • ♂ (in alcohol); West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 29 Nov. – 3 Dec. 1990; T Andersen leg.; Malaise trap; UMSP 000550040. **Paratypes.** TANZANIA – **Tanga Reg.** • 2♂♂; same data as for holotype except 20–26. Nov. 1990; ZMBN • 1♂; same data as for holotype except 3 Nov. 1990; sweep net; ZMBN • 1♂; West Usambara Mts, Mgwashi, Shokoi River; 4°46'S, 38°29'E; 24 Nov. 1990; T Andersen leg.; sweep net; UMSP.

Diagnosis. *Chimarra leptodactylus* is closely related to *C. latidentis* sp. nov. and *C. vermitergata* sp. nov. It is most readily diagnosed by the overall structure of the lateral lobes of tergum X, each of which has a narrow dorsomesal projection and a widely separated, acute, ventral projection, rather than a generally dorsally directed lobe or lobes.

Description. Adult. Overall color (in alcohol) medium brown, setal warts of head not contrasting. Head short (postocular parietal sclerite relatively short, shorter than eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short (~ 2 × 1st), apex with cluster of ~ 8 stiff setae, 3rd segment very elongate (~ 2 × 2nd), 4th segment short (shorter than 2nd), 5th segment elongate and narrow (subequal to 3rd). Forewing length: male, 5.5–6.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs straight, or nearly so, basal fork of discoidal cell distinctly enlarged, evenly forked, length of cell slightly > 2 × width, forks I and II sessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline (*m* crossvein somewhat diagonal), both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ evident basally, obsolete (or fused to subcosta) apically, forks I and II sessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur very short; male with tarsal claws not, or only slightly, enlarged, claws symmetrical, tarsal segments narrow.

Male genitalia. Segment VIII short, tergum longer than sternum, dorsal margin projecting, sternum without posteroventral projection. Segment IX, in lateral view, very short, anteroventral margin only slightly expanded, dorsal margin without apodemes, sternum with very short, rounded ventral process from posterior margin, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous (or nearly so), sternum short, subtruncate. Tergum X with mesal lobe short and membranous,

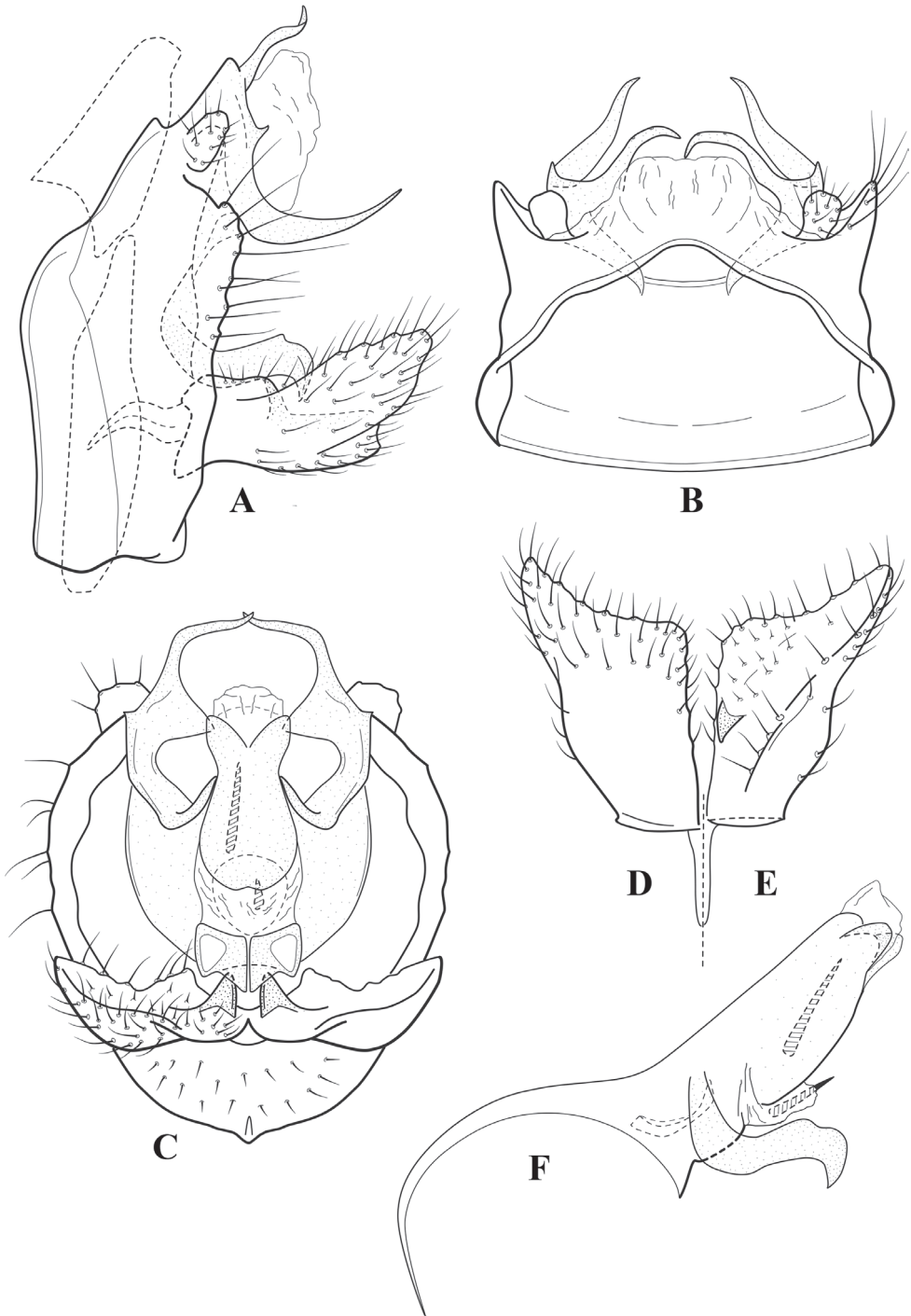


Figure 42. *Chimarra leptodactylus* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** caudal **D** inferior appendage, ventral **E** inferior appendage, dorsal **F** phallus, lateral.

lateral lobes short and sclerotized, each divided basally into dorsal and ventral spine-like processes, ventral processes larger and posteriorly curved, with short spine-like projection from dorsal margin in basal half, dorsal ones mesally curved; sensilla of lobes very small and reduced in number (possibly only 2 on each side, on apical half of dorsal lobe). Preanal appendages very short and rounded, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with weak basal inflection; as viewed laterally, with apices narrowed and laterally projecting; as viewed ventrally, with mesal margins of opposite appendages proximate, then sharply bent, with apices narrowing and laterally projecting; mesal surface with distinctly sclerotized, anteriorly projecting, spine-like projection in basal part, apparently articulating with sclerotized ventral projection of phallobase. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by sclerotized periphallallic membrane (and apparently fused to it); apicoventral margin of phallobase (or projections from periphallallic membrane) very distinctly sclerotized and produced, downturned, apex truncate and narrowly divided mesally, apparently articulating with spine-like projections of mesal surface of inferior appendages; phallic apparatus distal to sclerotized ventral projection (possibly modified endotheca), lightly sclerotized, tube-like, and narrowing, with short rounded apical lobes; endotheca with pair of short, asymmetrically positioned spines; phallotremal sclerite complex composed of short rod and ring structure.

Etymology. *Chimarra leptodactylus*, used as a noun in apposition, from the Greek words *leptos*, meaning thin, fine, small, or slender, and *daktylos*, a finger, for the narrow dorsal projection from each of the lateral lobes of tergum X.

***Chimarra obuncata* sp. nov.**

<http://zoobank.org/039AE4DE-6783-430F-84EA-11FEFD4D99D7>

Fig. 43A–G

Type material. Holotype. GHANA – **Western Reg.** • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 7–11 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; UMSP 000550042. **Paratype.** GHANA – **Western Reg.** • 1♂; same data as for holotype; ZMBN.

Additional material. GHANA – **Western Reg.** • 7♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN.

Diagnosis. *Chimarra obuncata* is easily identified by its short, rounded inferior appendages and the structure of tergum X, with its short sensillum-bearing processes. The structure of the phallobase, which is very short and has the apex tapered and subacute apically also distinguishes it from other species of the subgroup.

Description. Adult. Overall color (in alcohol) yellowish brown. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (distinctly shorter than 3rd), apex with cluster of stiff setae, 3rd segment elongate, 4th segment relatively

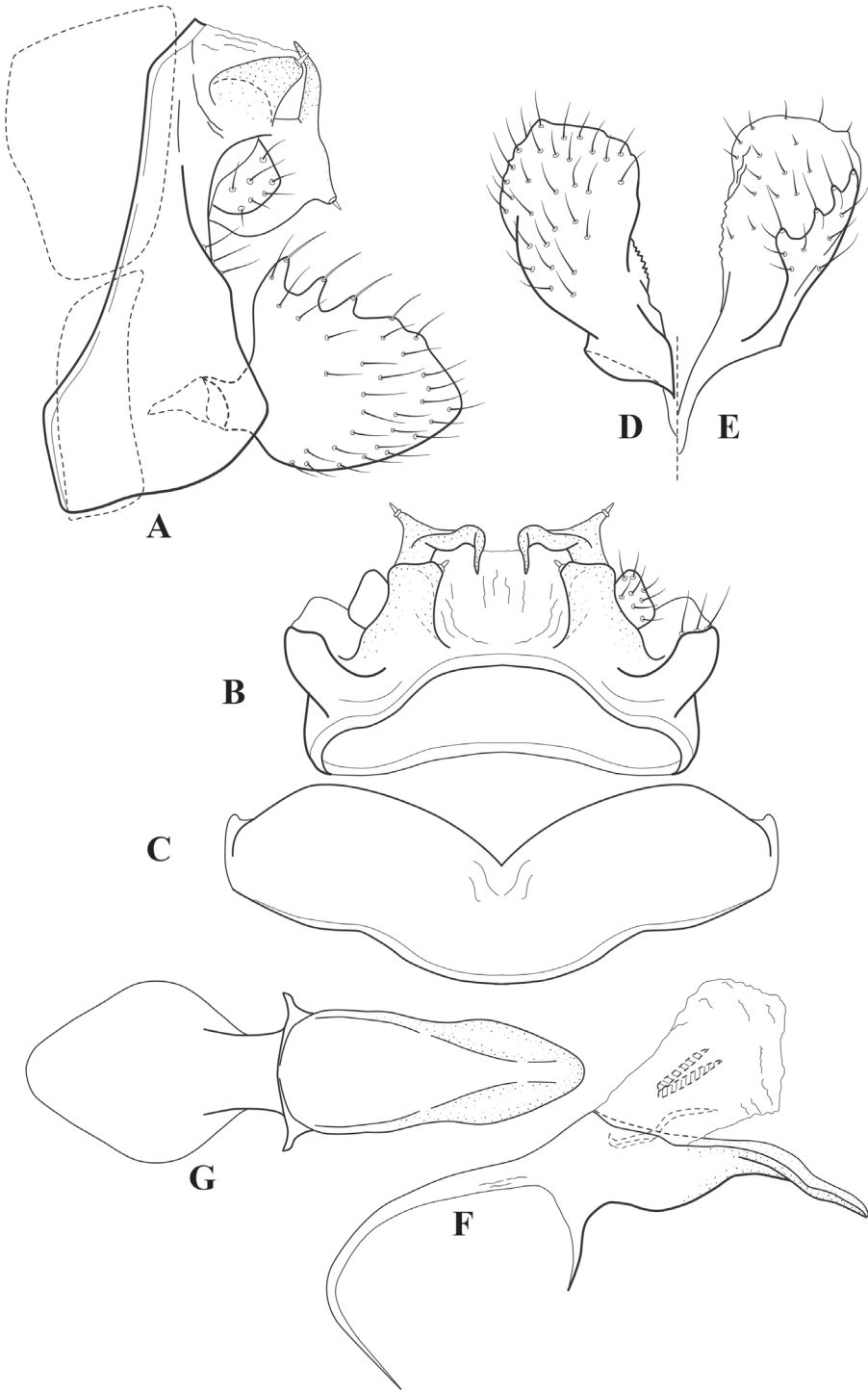


Figure 43. *Chimarra obuncata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** tergum VIII, dorsal **D** inferior appendage, ventral **E** inferior appendage, dorsal **F** phallus, lateral **G** phallus, ventral.

short (shorter than 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.5–3.8 mm; female, 3.7–4.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of R_s straight, or nearly so, basal fork of discoidal cell slightly enlarged, length of cell $\sim 2\times$ width, forks I and II subsessile, r crossvein diagonal, intersecting discoidal cell near apical fork, s , $r-m$, and m crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 faintly evident basally, obsolete or fused to subcosta distally, forks I and II subsessile, fork III distal and narrow, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical 2 segments of tarsi enlarged and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII with sternum very short, without posteroventral projection, tergum moderately expanded dorsally ($\sim 2\times$ length of sternum at base), dorsomesally with broad V-shaped emargination from posterior margin. Segment IX, in lateral view, short, segment widest ventrally, nearly linearly narrowing dorsally from approximately ventral $\frac{1}{4}$, dorsum very short, without apodemes; posterior margin not or scarcely produced, ventral process absent, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum very short, subtruncate. Lateral lobes of tergum X very short, each produced as pair of short, rounded dorsal and ventral sensillum-bearing processes, basodorsal pair mound-like, with apical sensilla somewhat mesally oriented, ventral pair more elongate, with apicoventral sensillum of each on short nipple-like process and somewhat laterally oriented, dorsal margin of ventral processes each with curved, dorsally directed, spine-like projection, dorsal lobe of tergum X short, membranous. Preanal appendages short and rounded, not (or hardly) constricted basally, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage without basal inflection; as viewed laterally, very short, rounded, basodorsal margin with short nipple-like projections, each bearing stout apical seta, mesal surface without projections. Phallic apparatus with phallobase very short, with usual basodorsal expansion, apicoventral margin very distinctly sclerotized and produced, somewhat downturned, subacutely narrowed, as viewed dorsally or ventrally; endotheca short, membranous, with two very small spines; phallotremal sclerite complex composed of short, reclinate ring and short rod.

Etymology. *Chimarra obuncata*, used as an adjective, from the Latin *obuncus*, meaning bent in or hooked, for the acute dorsal process of the very short tergum X in this species, which is dorsally projected and strongly mesally hooked inward.

***Chimarra polycentropoides* sp. nov.**

<http://zoobank.org/4B2DF6B6-A576-4D3E-94BB-D6ECD44D13BC>

Fig. 44A–E

Type material. Holotype. DEMOCRATIC REPUBLIC OF THE CONGO • ♂ (in alcohol); S slope of Mt Kahuzi; 5 Sept. 1957; 1,900 m a.s.l.; ES Ross & RE Leech leg.; INHS Trichoptera 50340.

Diagnosis. *Chimarra polycentropoides*, while similar in general aspects to other species of the *georgensis* subgroup, is distinctive because of its arched and spine-like lateral lobes of tergum X, and in having the ventromesal apex of the inferior appendage acutely produced, appearing as an upturned projection in lateral view. The general structure of the phallus and the absence of modified tarsal claws suggests a relationship to the species in the subgroup from Tanzania.

Description. Adult. Overall color (in alcohol) dark brown. Head short (postocular parietal sclerite $\sim 1/2$ diameter of eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short ($\sim 2 \times 1^{\text{st}}$), apex with cluster of ~ 8 –10 stiff setae, 3rd segment very elongate (almost $3 \times 2^{\text{nd}}$), 4th segment short (shorter than 2nd), 5th segment elongate and narrow (slightly longer than 3rd). Forewing length: male, 6.7 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of R_s straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell $\sim 2 \times$ width, forks I and II sessile, r crossvein diagonal, intersecting discoidal cell before apical fork, s , $r-m$, and m crossveins linear and hyaline (m crossvein very slightly proximal), both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 evident basally, obsolete (or fused to subcosta) apically, forks I and II sessile, anal loop small. Forelegs with apical tibial spur distinct; male with foretarsi not, or very little, modified, claws small and symmetrical.

Male genitalia. Segment VIII with sternum very short, without posteroventral projection, tergum moderately expanded dorsally. Segment IX, in lateral view, short, anterior margin nearly linear, without dorsolateral apodemes; segment very short dorsally, widening below preanal appendages, ventral process very small, subtriangular, not projecting, emerging from base of segment below inferior appendages; as viewed dorsally, with tergum very narrow, but continuous, anterior margin of sternum subtruncate. Lateral lobes of tergum X modified into elongate, arched, spine-like processes, apices slightly scabrous, ventral margin developed into short projecting lobe; mesal lobe of tergum X membranous, slightly textured, nearly as long as lateral lobes. Preanal appendages short, rounded, slightly constricted basally. Inferior appendage, in lateral view, without basal inflection, dorsal margin weakly produced at midlength, apex acutely projecting and upturned; as viewed ventrally, subquadrate, moderately widened apically, with apicomesal margin acutely produced. Phallic apparatus with phallobase very short, with usual basodorsal expansion, apicoventral margin very distinctly sclerotized, not bifid, forming a short, acute, preapical projection from ventral margin, as viewed laterally; endotheca, apparently, with basal part forming a weakly sclerotized extension of phallobase, apical membrane very short, with pair of short, symmetric spines; phallotremal sclerite complex not evident.

Etymology. *Chimarra polycentropoides*, name used as an adjective, for resemblance of this species to those in the genus *Polycentropus*, due to the similarity of the lateral lobes of tergum X to the dorsal spine-like structures of some species in that genus.

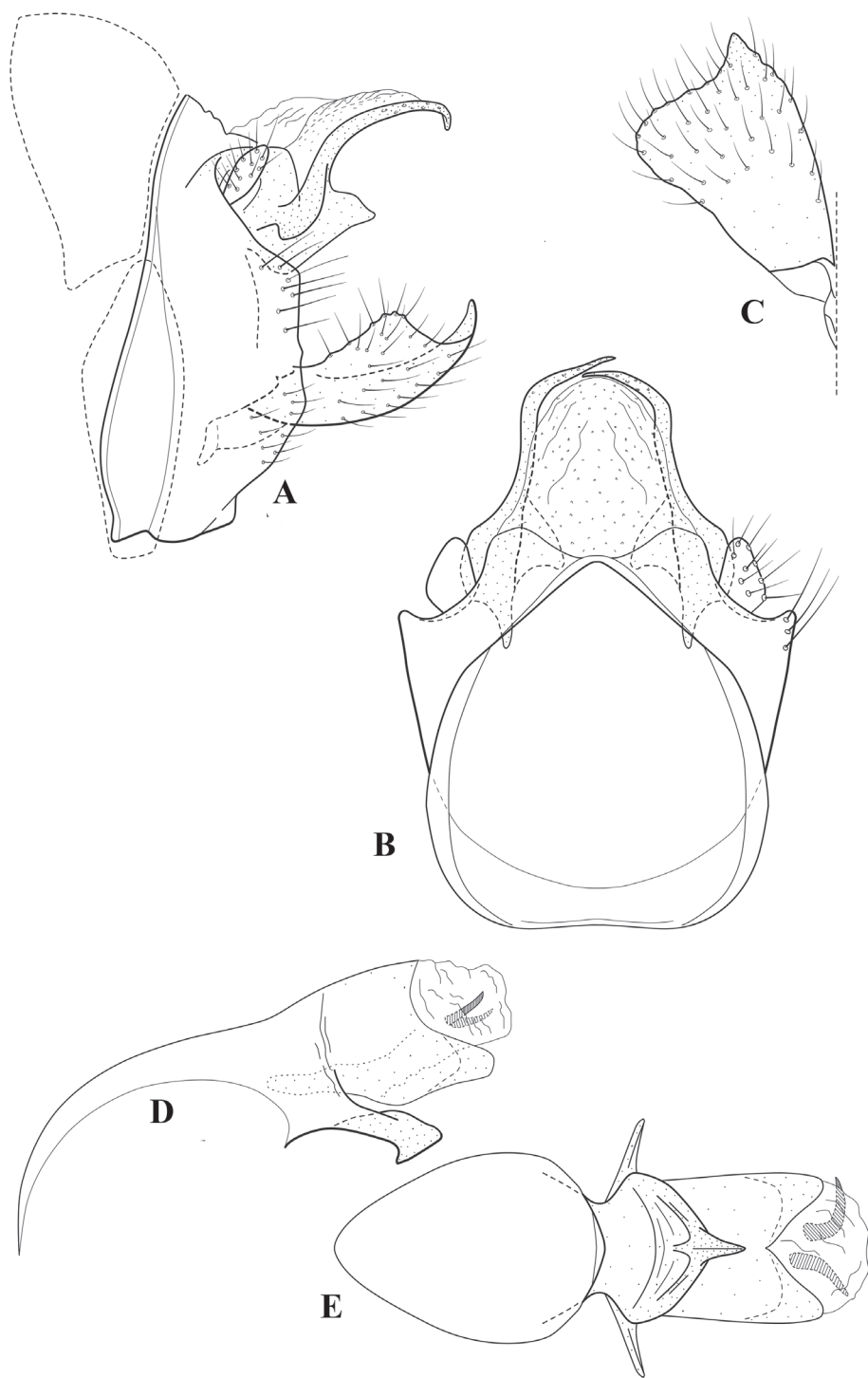


Figure 44. *Chimarra polycentropoides* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral **E** phallus, ventral.

***Chimarra ralphi* sp. nov.**

<http://zoobank.org/44E09354-0A8F-4932-BABA-7ADE04C845AC>

Fig. 45A–F

Type material. Holotype. GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 6; 7°07'29"N, 0°35'31"E; 11 Mar. 1993; JS Amakye & J Kjørandsen leg.; light trap; UMSP 000550041. **Paratypes.** GHANA – Western Reg. • 2♂♂; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN.

Additional material. GHANA – Volta Reg. • 1♀; Wli, Agumatsa waterfall, station # 6; 7°07'29"N, 0°35'31"E; 11–20 Nov. 1993; J Kjørandsen leg.; Malaise trap; ZMBN. – Western Reg. • 2♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra ralphi* is diagnosed by the unusual shape of its inferior appendages, each of which is very short, with the base rounded and with a short blunt, recurved projection on its dorsal margin; by the shape of the lateral lobes of tergum X, which are short and rounded apically, each with a short, ventrally curved spine-like projection on its dorsal margin and even shorter spine-like projection from its ventral margin; and by the form of the phallobase, with its apex deeply divided mesally and rather weakly down-curved.

Description. Adult. Overall color (in alcohol) light brown or yellowish brown, undersides and appendages paler, setal warts of head not contrasting. Head short and rounded (postocular parietal sclerite very short). Palps moderately elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (slightly greater than 2× width), apex with cluster of ~ 8 stiff setae, 3rd segment elongate (distinctly longer than 2nd), 4th segment short (subequal to 2nd), 5th segment elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.2–4.0 mm; female, 4.0–4.5 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs very slightly inflected, without node, basal fork of discoidal cell distinctly enlarged, evenly forked, length of cell ~ 2× width, forks I and II both subsessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), forks I and II subsessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII very short, tergum only slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, relatively short, ventral margin distinctly projecting posteriorly, anteroventral margin only slightly expanded, constricted basally under sternum VIII, ventral process absent, dorsal margin without apodemes, inferior appendages inserted near

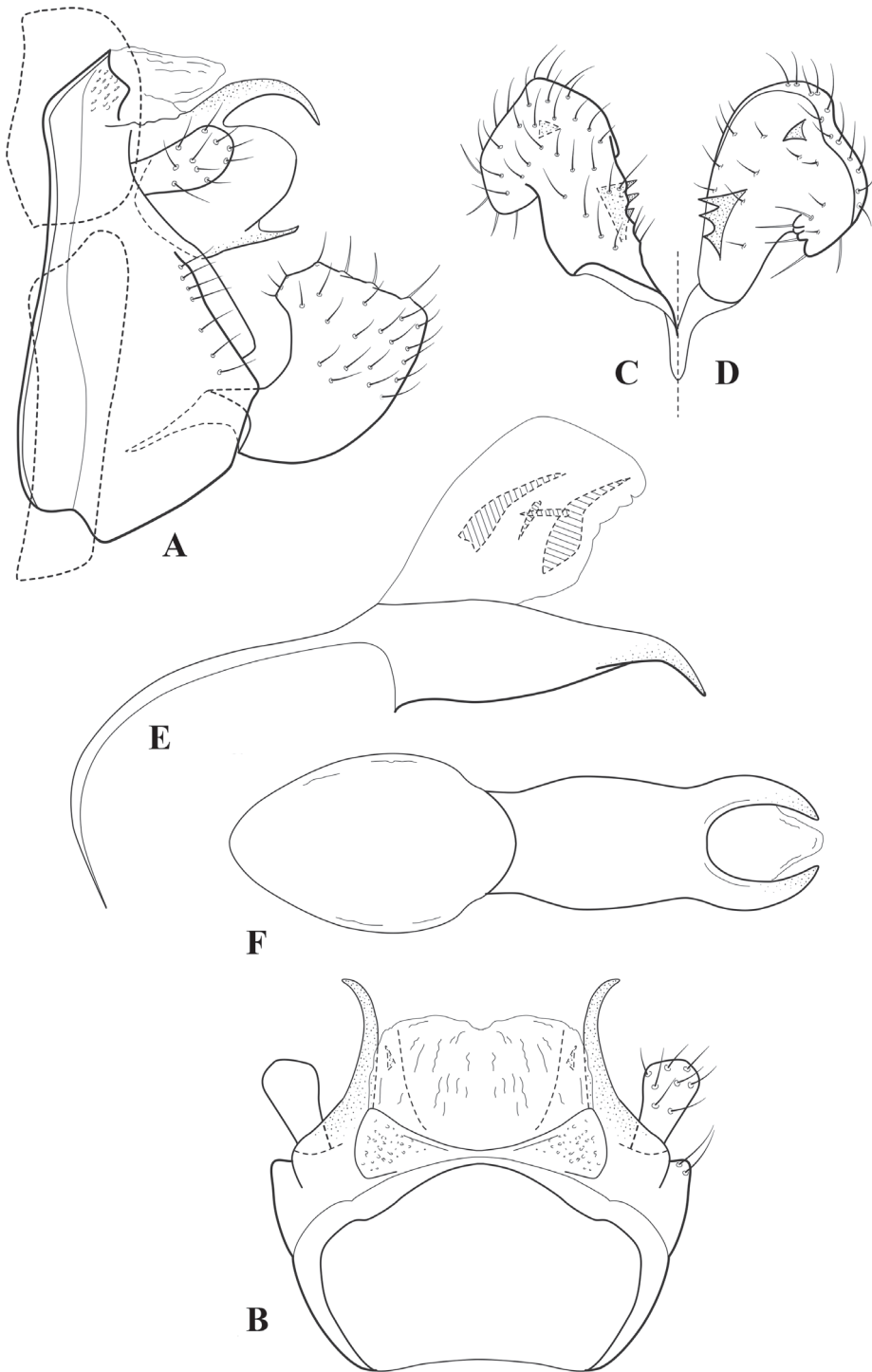


Figure 45. *Chimarra ralphi* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, ventral.

ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe short and membranous, lateral lobes short and rounded apically, lightly sclerotized, except ventral margin with more strongly sclerotized, spine-like process at approximately midlength and dorsal margin with projecting, sclerotized, hooked, spine-like process; sensilla of lobes apparently reduced to two on each side, on mesal surface of dorsal process, one basally and one at approximately midlength. Preanal appendages relatively short and knob-like (constricted basally), distinctly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with rounded basal inflection; as viewed laterally, short, more or less ovate, with short rounded dorsal projection at approximately midlength, basal inflection of projection very strong (nearly perpendicular), mesal margin of appendage with two distinct sclerotized cusps, one preapically and very small, the other basoventrally and somewhat larger. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallalic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, down-turned, apex with deep, concave mesal excavation, producing paired apical lobes; endotheca short, membranous, with pair of short, stout, sclerotized spines; phallotremal sclerite complex indistinct (not figured), apparently composed of reclinate ring and short rod, with pair of small apical spines.

Etymology. *Chimarra ralphi*, name used as an adjective in the genitive case and translated as Ralph's *Chimarra*, in honor of Ralph Holzenthal, the subject of this commemorative issue and in recognition of his many contributions to the systematics of Trichoptera, including many collaborations with both authors.

***Chimarra serrella* sp. nov.**

<http://zoobank.org/2523BCC1-2198-43C3-AA13-634041FE0CAA>

Fig. 46A–F

Type material. *Holotype.* GHANA – **Western Reg.** • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 31 Mar. 1993; JS Amakye & J Kjærandsen leg.; light trap; UMSP 000550043. *Paratypes.* GHANA – **Western Reg.** • 8♂♂; same data as for holotype except 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN.

Additional material. GHANA – **Western Reg.** • 9♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra serrella* is very similar to *C. uncinata* sp. nov. and the two undoubtedly constitute a pair of closely related sister species. The species resemble each other in the distinctive shape of the apex of the phallobase, and in the general shape of their inferior appendages, which are short, linear, and acute apically, as viewed laterally, but have the apex obliquely subtruncate, as viewed ventrally, with the ventromesal

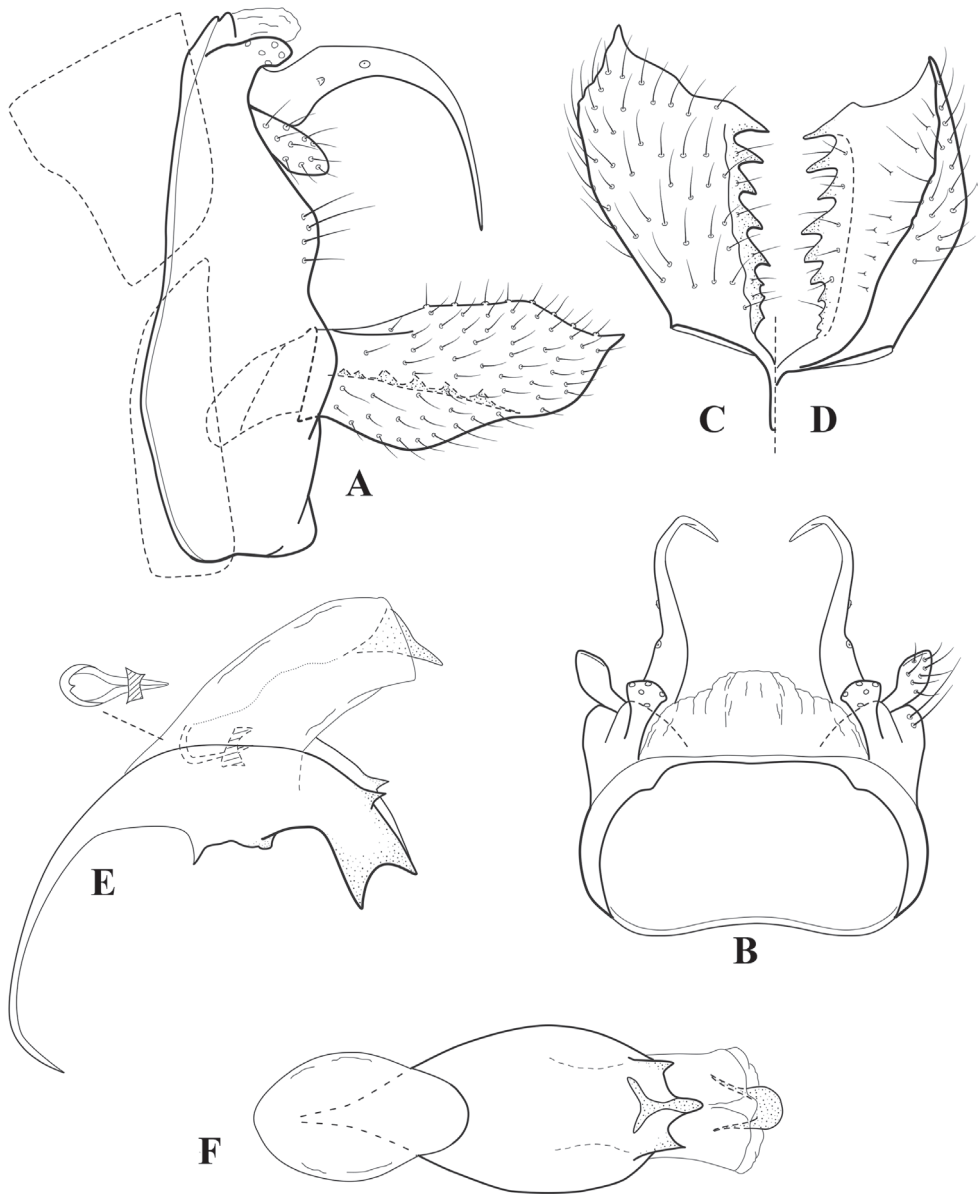


Figure 46. *Chimarna serrella* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, lateral **D** inferior appendage, ventral **E** phallus, dorsal, with dorsal detail of phallotremal sclerite complex **F** phallus, ventral.

margin distinctly serrate. Neither species has cusps or projections on the mesal surface of the inferior appendages. The most distinctive difference is in the shape of tergum X, which has its apex upturned and hooked in *C. uncinata*, and very narrow and strongly downturned in *C. serrella*. The apex of the inferior appendage, in lateral view, is also more acute in *C. serrella* than in *C. uncinata*.

Description. Adult. Overall color (in alcohol) light brown, underside and appendages yellowish brown, setal warts of head not distinctly contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderate ($\sim 3 \times 1^{\text{st}}$), apex with cluster of ~ 6 – 8 stiff setae, 3rd segment elongate, 4th segment short (shorter than 2nd), 5th segment elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.5–4.0 mm; female, 3.7–4.4 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell $\sim 2 \times$ width, fork I subsessile, fork II sessile, r crossvein diagonal, intersecting discoidal cell before apical fork, s , $r-m$, and m crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), forks I and II subsessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur very short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII short, tergum longer than sternum, sternum without posteroventral process. Segment IX, in lateral view, very short, anteroventral margin only slightly projecting, dorsal margin without apodemes, but with pair of short, rounded, multi-sensillate projections from posterior margin, ventral process very short, subtriangular, not or scarcely projecting, inferior appendages inserted slightly above ventral margin of segment; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe very short and membranous, lateral lobes short and distinctly sclerotized, produced apically into tapering, ventrally recurved, spine-like projections; sensilla of lobes very small, reduced in number, possibly only two, on basal part of tergum. Preanal appendages short, oblong, somewhat ventrally projecting, inserted membranously (not fused to segments IX or X). Inferior appendage with very weak basal inflection; as viewed laterally, more or less ovate, acutely angulate apically, with short lateral setae, setae slightly longer and spaced on dorsal margin; as viewed ventrally, with apex obliquely truncate, with longitudinal ridge near mesal margin, mesal margin distinctly serrate. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallalic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, down-turned, apex produced into short apical spine-like processes, ventral one weakly divided, dorsolateral margin of apex with additional short spine-like projection on each side; endotheca short, membranous, with small, lightly sclerotized apical spine, apex bluntly rounded, as viewed ventrally; phallotremal sclerite complex composed of short rod and ring structure, with indistinct apicolateral sclerite.

Etymology. *Chimarra serrella*, used as a noun in apposition, from the Latin diminutive for *serra*, a saw, in reference to the very serrate ventromesal margin of the inferior appendages in this species.

***Chimarra triramosa* sp. nov.**

<http://zoobank.org/E9134C4F-47C0-40FF-8CF9-66987226CAF1>

Fig. 47A–E

Type material. Holotype. GHANA – **Volta Reg.** • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 12^A; 7°07'29"N, 0°35'31"E; 13–16 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; UMSP 000550045. **Paratypes.** GHANA – **Volta Reg.** • 3♂♂; same data as for holotype except station # 5^A; 4–13 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 5^B; 10–13 Mar. 1993; ZMBN • 2♂♂; same data as for holotype except station # 6^B; 12–15 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 7^A; 10–13 Mar. 1993; ZMBN • 3♂♂; same data as for holotype except station # 8^A; 7–13 Mar. 1993; ZMBN • 3♂♂; same data as for holotype except station # 8^B; ZMBN • 3♂♂; same data as for holotype except station # 9^A; 10–13 Mar. 1993; ZMBN • 13♂♂; same data as for holotype except station # 9^B; 4–13 Mar. 1993; ZMBN • 281♂♂; same data as for holotype except station # 10^A; ZMBN • 10♂♂; same data as for holotype except station # 11^A; ZMBN • 5♂♂; same data as for holotype except station # 12^A; 7–13 Mar. 1993; ZMBN • 2♂♂; same data as for holotype except station # 12^B; 7–16 Mar. 1993; ZMBN • 7♂♂; same data as for holotype except station # 6; 11 Mar. 1993; light trap; ZMBN • 286♂♂; same data as for holotype except station # 10; 8 Mar. 1993; light trap; ZMBN • 3♂♂; same data as for holotype except 19 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN • 45♂♂; same data as for holotype except 8 Mar. 1993; sweep net; ZMBN. – **Eastern Reg.** • 2♂♂; Boti Falls; 6°11'40"N, 0°13'05"W; 28 Oct. – 4 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN • 4♂♂; Kibi, Subri stream; 6°10'N 0°33'W; 5 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN.

Additional material. GHANA – **Eastern Reg.** • 4♀♀; Kibi, Subri stream; 6°10'N, 0°33'W; 5 Nov. 1993; J Kjørandsen leg.; light trap; ZMBN. – **Volta Reg.** • 2♀♀; Wli, Agumatsa waterfall, station # 5^B; 7°07'29"N, 0°35'31"E; 10–13 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; ZMBN • 3♀♀; same collection data as for preceding except station # 6^B; 12–15 Mar. 1993; ZMBN • 2♀♀; same collection data as for preceding except station # 8^B; 7–13 Mar. 1993; ZMBN • 2♀♀; same collection data as for preceding except station # 9^A; 10–13 Mar. 1993; ZMBN • 6♀♀; same collection data as for preceding except station # 9^B; 4–13 Mar. 1993; ZMBN • 230♀♀; same collection data as for preceding except station # 10^A; ZMBN • 2♀♀; same collection data as for preceding except station # 10^B; 10–13 Mar. 1993; ZMBN • 6♀♀; same collection data as for preceding except station # 11^A; 4–13 Mar. 1993; ZMBN • 2♀♀; same collection data as for preceding except station # 12^A; 7–13 Mar. 1993; ZMBN • 2♀♀; same collection data as for preceding except station # 12^B; 7–16 Mar. 1993; ZMBN • 70♀♀; same collection data as for preceding except station # 10; 8 Mar. 1993; light trap; ZMBN • 1♀; same collection data as for preceding except station # 12; 16 Nov. 1993; J Kjørandsen leg.; ZMBN • 1♀; same collection data as for preceding except 19 Nov. 1993; UMSP.

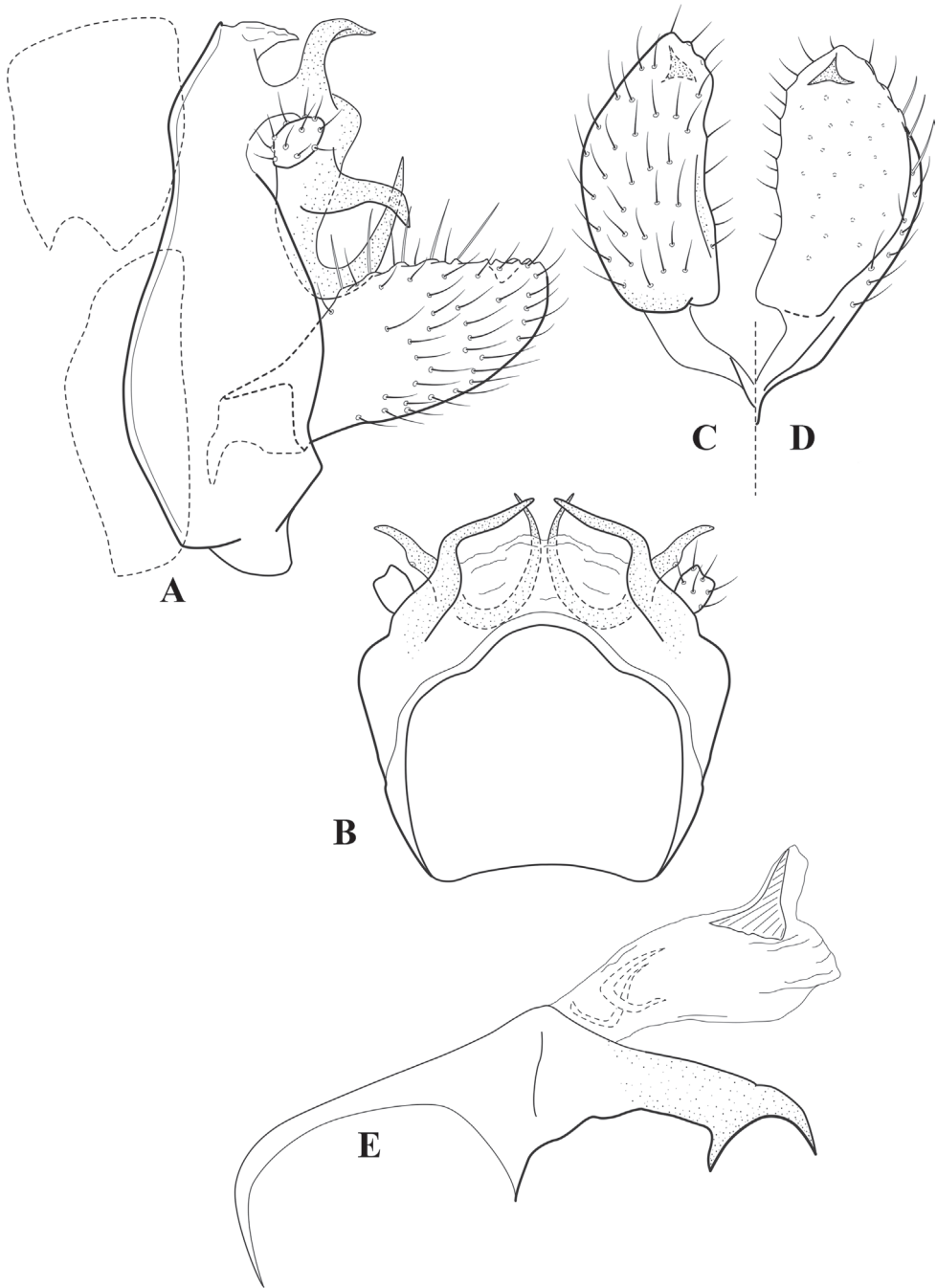


Figure 47. *Chimarra triramosa* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

Diagnosis. *Chimarra triramosa* is most readily diagnosed by its ovate inferior appendages, each with a short preapical projection on its mesal surface; lateral lobes of tergum X, each of which is divided into three pairs of short, curved spine-like projections; and especially by the short phallobase, with a decurved and mesally divided ventral apex, each half of which, in turn, has its apex crescentic, forming an additional two apical projections, in lateral view.

Description. Adult. Overall color (in alcohol) light brown, underside and appendages yellowish brown, setal warts of head pale, contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (slightly shorter than 3rd), apex with cluster of ~ 6–8 stiff setae, 3rd segment elongate, 4th segment short (shorter than 2nd), 5th segment very elongate and narrow (slightly shorter than 3rd and 4th combined); both sets of palps with evident longitudinal row of more elongate setae on dorsomesal surface, graded and shortened on apical segments. Forewing length: male, 3.2–4.0 mm; female, 4.0–5.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell ~ 2× width, forks I and II subsessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), forks I and II subsessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur very short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII very short, tergum slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, very short, anteroventral margin only slightly expanded, dorsal margin without apodemes, ventral process very short, subtriangular, more or less ventrally oriented, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe very short and membranous, lateral lobes very short and strongly sclerotized, somewhat variable in structure, each produced into three more or less spine-like lobes, one curved ventrally, with apex recurved dorsally, one intermediate and laterally curved lobe, often subtruncate apically, and one dorsomesally curved lobe; sensilla of lobes very small and reduced in number (possibly only two, one on posterobasal margin of dorsal lobe, other either apically or preapically on lateral lobe). Preanal appendages short and rounded, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage without basal inflection; as viewed laterally, ovately rounded, subtruncate apically, with short lateral setae and row of spaced, more elongate setae on dorsal margin; mesal surface with distinctly sclerotized, short, preapical spine-like projection. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallallic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, down-turned, apex divided mesally, with each half of divided apex produced into pair of apical and preapical spine-like processes (thus with four

apical spine-like projections); endotheca short, membranous, with pair of apical, lightly sclerotized, subtriangular spines (possibly connected mesally); phallotremal sclerite complex composed of short rod and ring structure, with indistinct lateral sclerite.

Etymology. *Chimarra triramosa*, used as an adjective, from the Latin *ramus*, or branch, for the 3-branched tergum X of this species, which is one of its most defining characters.

***Chimarra uncinata* sp. nov.**

<http://zoobank.org/F8D2E59B-0617-4308-9DD0-32517239ACB4>

Fig. 48A–F

Type material. *Holotype.* GHANA – **Volta Reg.** • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 12^A; 7°07'29"N, 0°35'31"E; 7–16 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; UMSP 000550047. *Paratypes.* GHANA – **Volta Reg.** • 1♂; same data as for holotype; ZMBN • 1♂; same data as for holotype except station # 10^B; 10–13 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 12^B; 13–16 Mar. 1993; ZMBN.

Additional material. GHANA – **Volta Reg.** • 1♀; Volta Region, Wli, Agumatsa waterfall, station # 12^A; 7°07'29"N, 0°35'31"E; 7–10 Mar. 1993, JS Amakye & J Kjørandsen leg.; Malaise trap; UMSP.

Diagnosis. *Chimarra uncinata* is most readily diagnosed, in combination, by its short inferior appendages, with the ventromesal margins very irregular and serrate, lateral lobes of tergum X, each of which has its apex hook-like, upturned and acute and also has short sensillate lobes on the basodorsal and basoventral margins, and by the form of the phallobase, which is short and has its apex sharply decurrent, with the apex bifid in both lateral and caudal views and with an additional short spine on each side of the dorsal margin just prior to the decurrent apex. It is most similar to *C. serrella* sp. nov., which also has the ventromesal margin of the inferior appendages serrate, but differs in the structure of tergum X.

Description. *Adult.* Overall color (in alcohol) light brown, underside and appendages yellowish brown, vertex of head darker, setal warts of head pale, contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (slightly shorter than 3rd), apex with cluster of ~ 6–8 stiff setae, 3rd segment elongate, 4th segment short (shorter than 2nd), 5th segment very elongate and narrow (slightly shorter than 3rd and 4th combined). Forewing length: male, 3.2–3.8 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R₁ straight, stem of Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell ~ 2× width, fork I subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), forks I and II subsessile, fork III distal and relatively narrow, anal loop small. Forelegs with apical tibial spur very short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

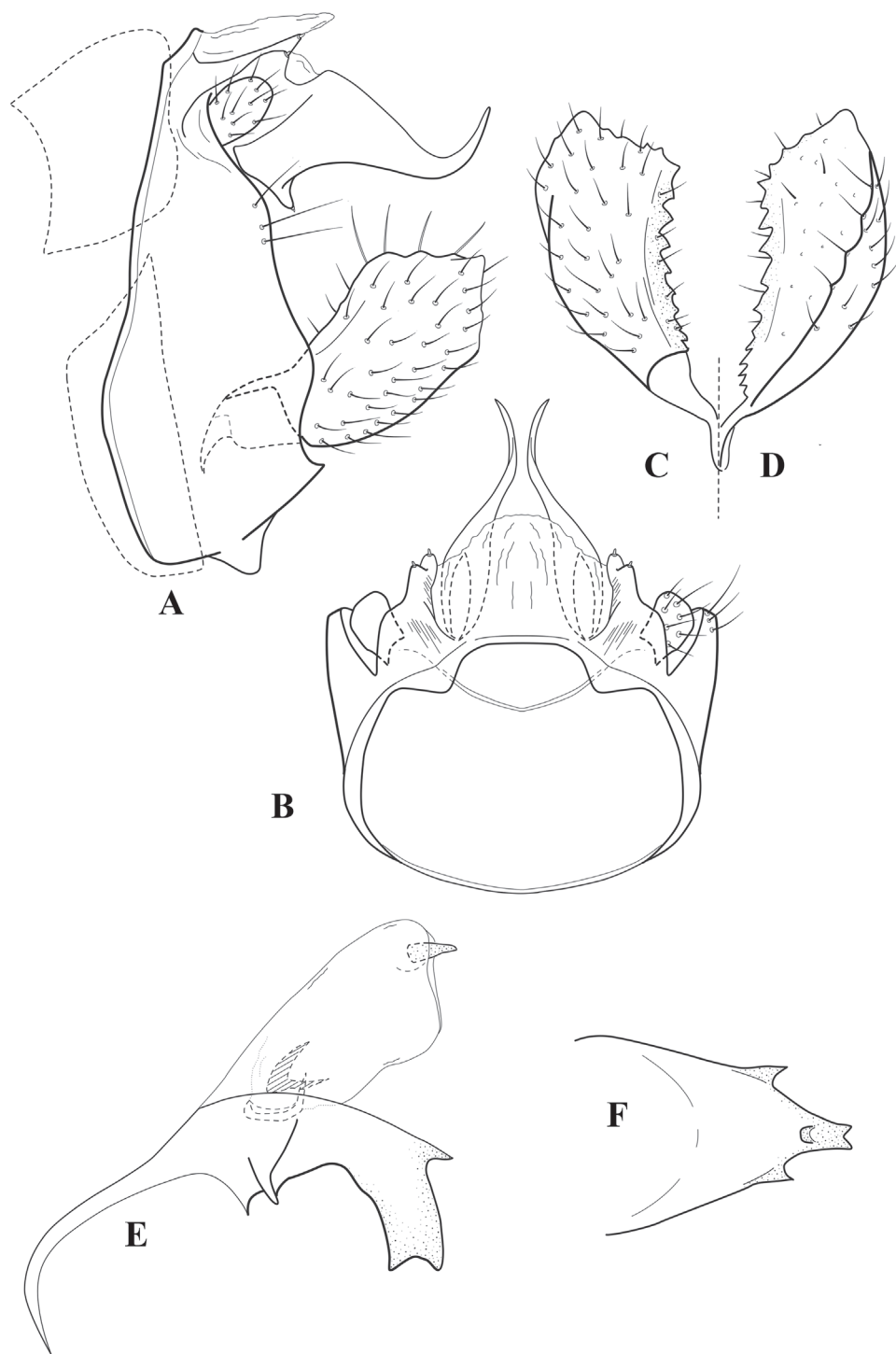


Figure 48. *Chimarra uncinata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus apex, ventral.

Male genitalia. Segment VIII very short, tergum slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, very short, anteroventral margin only slightly expanded, dorsal margin without apodemes, ventral process very short, subtriangular, more or less ventrally oriented, inferior appendages inserted near ventral margin; as viewed dorsally, with tergum very narrow, but continuous, sternum short, subtruncate. Tergum X with mesal lobe very short and membranous, lateral lobes short and distinctly sclerotized, produced apically into dorsally recurved spine-like projections; sensilla of lobes very small, reduced in number, on short nipple-like basal projections, one dorsally with two or three sensilla and one ventrally with single apical sensillum. Preanal appendages short and rounded, distinctly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with very weak basal inflection; as viewed laterally, more or less ovate, subangulate apically, with short lateral setae and row of spaced, more elongate setae on dorsal margin; as viewed ventrally, with longitudinal ridge near mesal margin, mesal margin distinctly serrate. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by semi-sclerotized periphallic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase very distinctly sclerotized and produced, down-turned, apex produced into short apical and preapical spine-like processes, apical one weakly divided, dorsolateral margin of apex with additional short spine-like projection on each side; endotheca short, membranous, with very small, lightly sclerotized apical spine; phallotremal sclerite complex composed of short rod and ring structure, with indistinct lateral sclerite.

Etymology. *Chimarra uncinata*, used as an adjective, from the Latin *uncus*, or hook, for the hooked apex of tergum X in this species, which is a useful identifying character.

***Chimarra vermitergata* sp. nov.**

<http://zoobank.org/3AFD8372-63B3-433C-9B04-D72CDD682FDE>

Fig. 49A–E

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts, Gologolo; 4°41'S, 38°13'E; 25 Nov. 1990; T Andersen leg.; sweep net; UMSP 000550049. **Paratypes.** TANZANIA – Tanga Reg. • 1♂; same data as for holotype; ZMBN • 1♂; West Usambara Mts, Mazumbai, Kaputu Stream; 4°48'S, 38°30'E; 4–13 Jan. 1991; T Andersen leg.; Malaise trap; ZMBN • 2♂♂; same collection data as for preceding except 5 Nov. 1990; sweep net; ZMBN.

Diagnosis. *Chimarra vermitergata* has an overall similarity to both *C. leptodactylus* sp. nov. and *C. latidentis* sp. nov. It is most similar to *C. latidentis*; only a direct comparison of the genitalia offers convincing evidence that they are different species. The most evident difference, as apparent from the accompanying illustrations, is in the more divided and less scabrous lateral lobe of tergum X in *C. vermitergata*. However, this is a relatively minor difference, and it is difficult to know how constant this

character may be from the limited material available. A synopsis of the differences between *C. vermitergata* and *C. latidentis* include: a somewhat more elongate inferior appendage, with a shorter, less prominent cusp on the mesal surface; structural details of the lateral lobes of tergum X, which have the spine-like basal projections narrow and divided in *C. vermitergata* and with the apices less evidently scabrous than in *C. latidentis*; and a phallic apparatus with a narrow, tube-like, and lightly sclerotized basal portion of the endotheca apical to the deflexed and paired ventral projections of the phallobase, rather than one that is short and bulbous. In combination, these differences provide sufficient evidence that the two should be considered different species.

Description. Adult. Overall color (in alcohol) medium brown to yellowish brown, head slightly darker, setal warts of head not, or hardly, contrasting. Head short (postocular parietal sclerite relatively short, shorter than eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment short ($\sim 2 \times 1^{\text{st}}$), apex with cluster of ~ 8 stiff setae, 3rd segment very elongate ($> 2 \times 2^{\text{nd}}$), 4th segment short (shorter than 2nd), 5th segment elongate and narrow (slightly longer than 3rd). Forewing length: male, 7.0 mm. Fore- and hind wings with forks I, II, III, and V present. Forewing with R_1 straight, stem of Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, discoidal cell slightly longer than $2 \times$ width, forks I and II sessile, r crossvein diagonal, intersecting discoidal cell just before fork I, s , $r-m$, and m crossveins more or less linear and hyaline (m crossvein somewhat diagonal), both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 evident basally, obsolete (or fused to subcosta) apically, fork I sessile, fork II slightly subsessile, fork III distal and relatively wide, anal loop small. Forelegs with apical tibial spur short; male with tarsal claws not enlarged, claws symmetrical, tarsal segments narrow.

Male genitalia. Segment VIII with sternum very short, tergum $\sim 2 \times$ as long, dorsal margin projecting, sternum without posteroventral projection. Segment IX, in lateral view, short, anteroventral margin only slightly expanded, anterodorsal margin without apodemes, posterior margin angularly projecting below preanal appendages, sternum with very short, subtriangular ventral process from posterior margin, inferior appendages inserted somewhat above ventral margin; as viewed dorsally, with tergum very narrow, but continuous (or nearly so), sternum very short, subtruncate. Tergum X with mesal lobe short and membranous, lateral lobes short and sclerotized, each modified into several narrow, upturned spine-like projections, dorsal ones longest, mesally curved and with two sensilla near apex. Preanal appendages short and rounded, slightly flattened, inserted membranously (not fused to segments IX or X). Inferior appendage with weak basal inflection; as viewed laterally, short, with apicodorsal margin somewhat angulate and laterally projecting; as viewed ventrally, subtruncate apically, with mesal margins of opposite appendages proximate, then sharply bent; mesal surface with sclerotized, anteriorly projecting, cusp-like projection, apparently articulating with sclerotized ventral projection of phallobase. Phallic apparatus with phallobase very short and strongly sclerotized, with usual basodorsal expansion, securely anchored within segment by sclerotized periphallallic membrane (and apparently fused

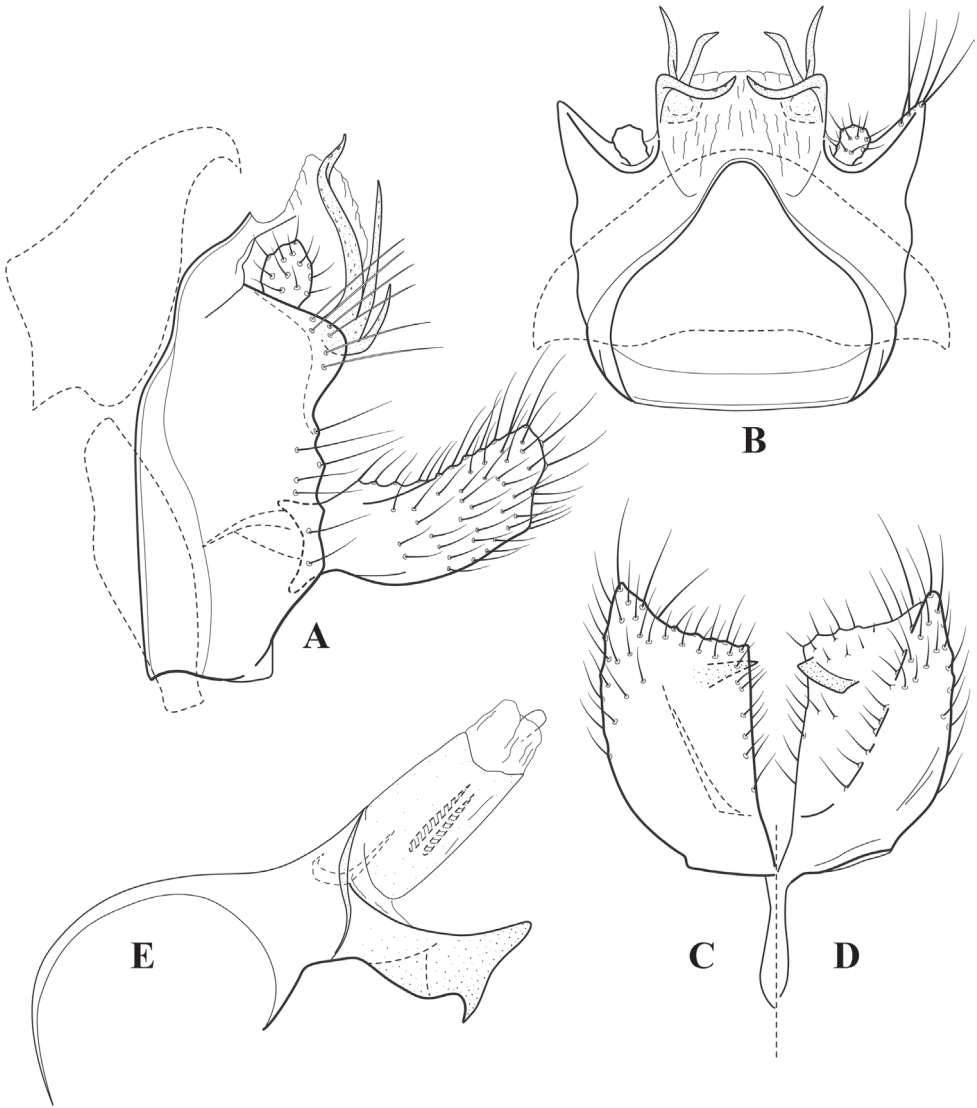


Figure 49. *Chimarra vermitergata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

to it); apicoventral margin of phallobase (or projections from periphallalic membrane) very distinctly sclerotized and produced, down-turned, apex divided mesally, apparently articulating with spine-like projections of mesal surface of inferior appendages; phallic apparatus distal to sclerotized ventral projection (possibly modified endotheca), forming narrow sclerotized tube, apparently as extension of phallobase; endotheca with pair of very short, symmetrically positioned spines; phallotremal sclerite complex composed of short rod and ring structure.

Etymology. *Chimarra vermitergata*, used as an adjective, from the Latin *vermis*, a worm, and *tergum*, a back, for the narrow, irregular, and worm-like divisions of tergum X of this species.

The *evoluta* subgroup

Included species. *Chimarra aciculata* Morse, 1974; *C. evoluta* Kimmins, 1957; *C. foliata* Kimmins, 1959; *C. giboni* sp. nov.; *C. lobulata* sp. nov.; *C. mgwashi* sp. nov.; *C. parafoliata* sp. nov.; and *C. pectinella* sp. nov.

This subgroup is distinguished from the *georgensis* subgroup by its more reduced venation (absence of forks I and III in the hind wing, in addition to the fused R_1 and subcosta veins), and by the presence of elongate and often scabrous dorsal processes from the dorsal margin of segment IX. Since tergum X is fused with and continuous with the posterior margin of segment IX, it is conceivable that these processes actually have their origin as a basally divided lobe from the lateral lobes of tergum X. The apparent lateral lobes of tergum X are simpler in overall structure than in species of the *georgensis* subgroup, lacking the scabrous or acute and divided lobes present in this subgroup, and generally with two rather evident sensilla on each lobe, one apical and one preapical.

Chimarra giboni sp. nov.

<http://zoobank.org/2DD1B8CE-7038-4454-8F5F-07A2662A70CD>

Fig. 50A–D

Type material. Holotype. GHANA – **Western Reg.** • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; UMSP 000550050. **Paratypes.** GHANA – **Western Reg.** • 4♂♂; same data as for holotype; ZMBN. – **Central Reg.** • 3♂♂; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN.

Additional material. GHANA – **Central Reg.** • 9♀♀; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP. – **Western Reg.** • 69♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. This species is probably most closely related to *Chimarra foliata* Kimmins and *C. parafoliata* sp. nov., resembling both in having foliate basal projections on the lateral lobes of tergum X and in having the posterior margin of segment IX strongly produced at the level of the inferior appendage. It differs in the much more elongate and apically projecting inferior appendages, without a mesal tooth or cusp, and in that the posterior projection of segment IX is at, or nearly at, the ventral margin of the segment.

Description. Adult. Overall color (in alcohol) yellowish brown, vertex of head slightly darker. Head short (postocular parietal sclerite short). Palps elongate; maxillary

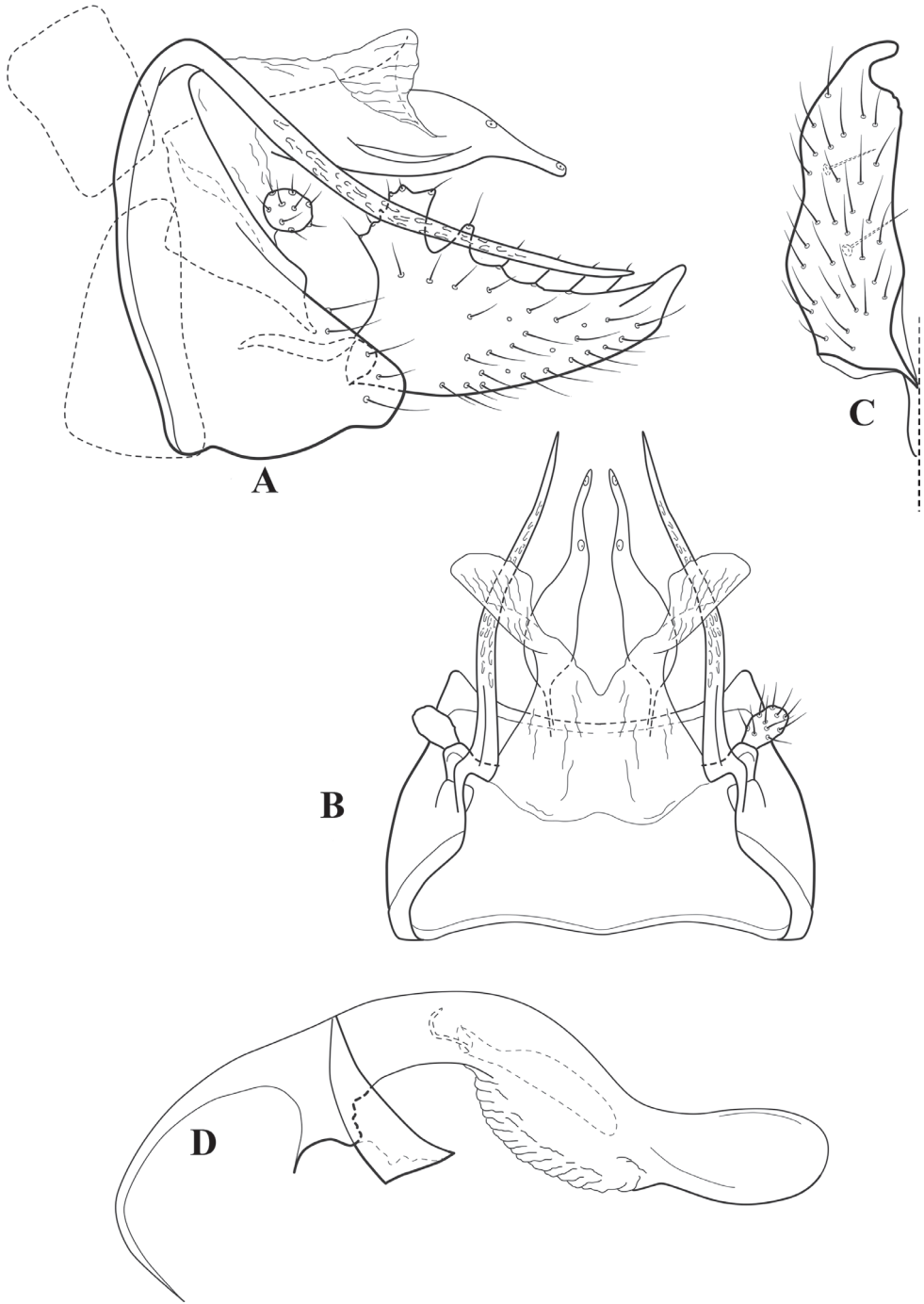


Figure 50. *Chimarra giboni* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral.

palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate ($\sim 3 \times 1^{\text{st}}$), apex with cluster of ~ 8 –10 stiff setae, 3rd segment moderately elongate, slightly longer than 2nd, 4th segment short ($\sim \frac{1}{2}$ length of 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 3.2–4.0 mm; female, 3.5–4.5 mm. Forewing forks I, II, III, and V present; hind wing with forks II and V only. Forewing with R_1 nearly straight, stem of R_s very weakly inflected, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell $\sim 2 \times$ width, forks I and II sessile, r crossvein not evident, s , $r-m$, and m crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), fork II sessile, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII short, sternum without posteroventral projection. Segment IX, in lateral view, with anterior margin nearly straight, ventral margin very distinctly expanded, forming projection point for attachment of inferior appendages, segment narrowing and convergent dorsally, dorsal margin without apodemes, but with paired, elongate, narrow, scabrous, posteroventrally directed processes from posterolateral margin, apices of processes acute, ventral process of segment apparently obsolete; as viewed dorsally, with tergum discontinuous mesally, posterior processes widely separated basally. Tergum X with membranous mesal lobe, divided mesally, lateral lobes with expanded foliate basal lobes and narrow, projecting apices; sensilla two on each lobe, one preapical and one apical, on narrow projection. Preanal appendages small and knob-like, rounded, constricted basally, inserted membranously (not fused to segments IX or X). Inferior appendage, as viewed laterally, relatively elongate, subtriangular, with basodorsal expansion, gradually narrowing to acute apex, without cusp or tooth on mesal margin; as viewed ventrally, with apex narrowed and mesally curved. Phallic apparatus with phallobase short, well anchored within segment by semi-sclerotized periphallalic membrane (attached to lateral margin of segment IX); apex of phallobase and endotheca not well demarcated, endotheca apparently weakly sclerotized, forming looped structure with rounded apex; phallotremal sclerite complex small and indistinct, composed of short rod and ring structure and weakly sclerotized apical structure.

Etymology. We take pleasure in naming this species *Chimarra giboni* for François-Marie Gibon, in recognition of his many contributions to the taxonomy of Trichoptera in Africa and Madagascar, and especially the genus *Chimarra*.

***Chimarra lobulata* sp. nov.**

<http://zoobank.org/6E004EBF-33C6-4C0C-A2AA-5D8F25118D37>

Fig. 51A–F

Type material. Holotype. GHANA – Western Reg. • ♂ (in alcohol); Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; UMSP 000550052.

Additional material. GHANA – **Western Reg.** • 2♀♀; Ankasa Game Production Reserve; 5°15'N, 2°37'W; 6–12 Dec. 1993; T Andersen & J Kjærandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra lobulata* is closely related to *C. pectinella* sp. nov., as evidenced by the shape of segment IX, including the mesally proximate posterior processes, shape of tergum X, and the paired apicoventral lobes of the phallobase. It differs diagnostically in the much more prominent apicolateral lobes of the phallobase, as well as in the shape of the interior appendages, which have the posterodorsal margin projecting and lack cusps on the mesal margin.

Description. Adult. Overall color (in alcohol) light brown to yellowish brown, head slightly darker, setal warts of head pale, contrasting. Head relatively short (postocular parietal sclerite short), slightly flattened. Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (~ 3× 1st, slightly shorter than 3rd), apex with cluster of ~ 8 stiff setae, 3rd segment moderately elongate, 4th segment short (~ 1/2 length of 2nd), 5th segment very elongate and narrow (slightly longer than 3rd and 4th combined). Forewing length: male, 4.0 mm; female, 4.0–4.3 mm. Forewing forks I, II, III, and V present; hind wing with forks II and V only. Forewing with R₁ nearly straight, stem of Rs weakly, but distinctly inflected, basal fork of discoidal cell enlarged, asymmetrically forked, length of cell slightly > 2× width, fork I subsessile, fork II sessile, *r* crossvein diagonal, intersecting discoidal cell near apical fork, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), fork II sessile, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII moderate in length, tergum slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, relatively long, narrowed dorsally at about level of preanal appendages, ventral margin not, or hardly, expanded, dorsal margin without apodemes, but with paired, elongate, narrow, scabrous, posteroventrally-directed processes from posterior margin, apices of processes acute, ventral process absent; as viewed dorsally, with tergum discontinuous mesally, posterior processes proximate mesally, bowed outward, sternum subtruncate. Tergum X without evident mesal lobe, lateral lobes divided mesally, moderately elongate and narrow, with narrow, projecting apex; sensilla probably only two on each lobe, one apical and the other preapical. Preanal appendages very small and rounded, inserted membranously (not fused to segments IX or X). Inferior appendage, as viewed laterally relatively short and wide, without distinct basal inflection, apicodorsal margin distinctly projecting; as viewed caudally, with slight mesal curvature, apex rounded, mesal surface without cusp, but ventromesal margin distinctly sclerotized. Phallic apparatus with phallobase relatively short, lightly sclerotized, with usual basodorsal expansion, apparently well anchored within segment by semi-sclerotized periphallallic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase sclerotized, with lobate, ventrally projecting lobes, mesal margin between lobes

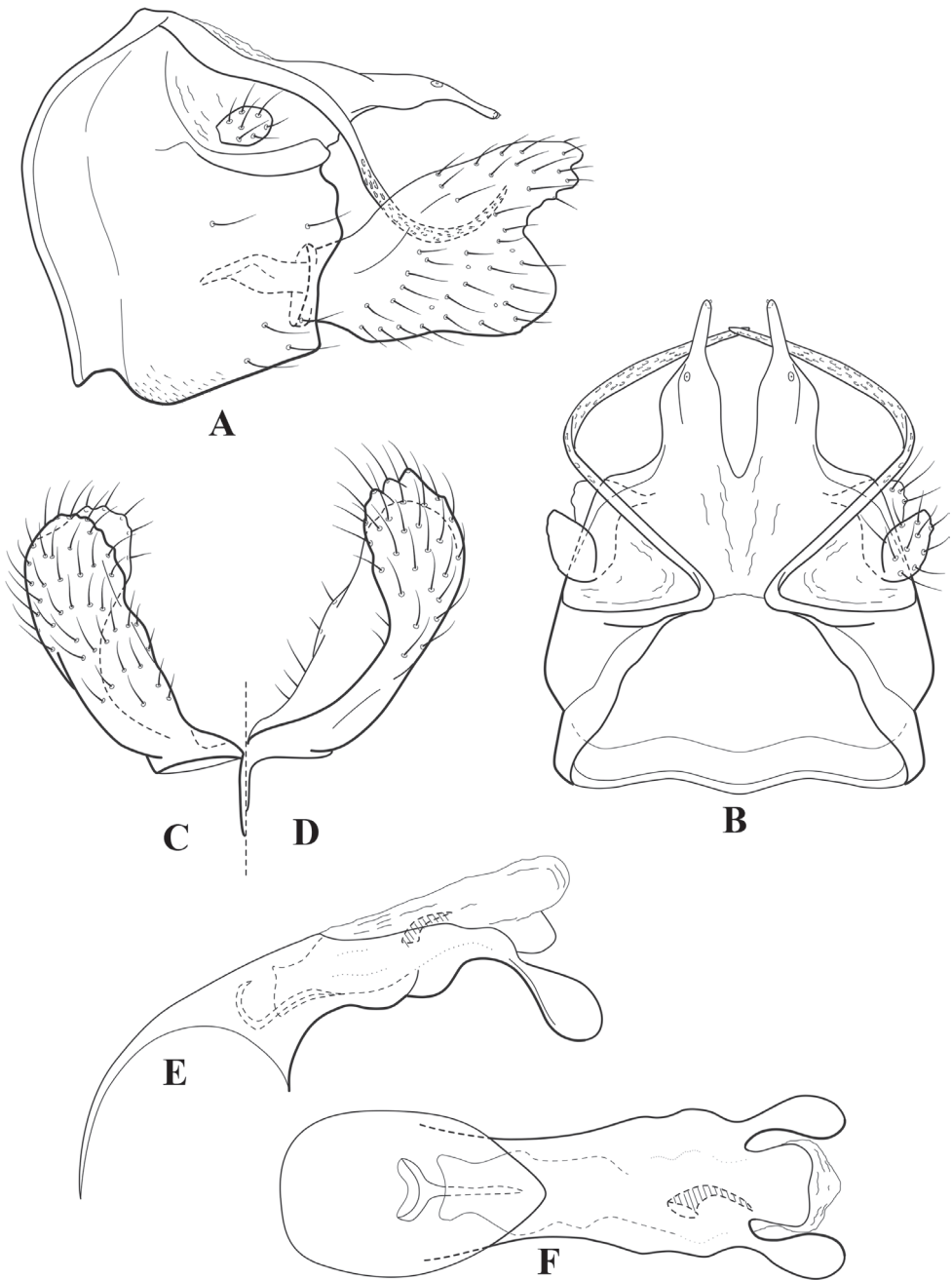


Figure 51. *Chimarra lobulata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus, ventral.

slightly projecting and truncate; endotheca with short, curved spine; phallotremal sclerite complex large, composed of relatively elongate rod and ring structure, with lightly sclerotized apical structure.

Etymology. *Chimarra lobulata*, used as an adjective, from the Latin *lobus*, a rounded projection or protuberance, and referring to the lobulate apex of the phallobase in this species.

***Chimarra mgwashi* sp. nov.**

<http://zoobank.org/6FDC2AA0-73A5-43EA-87C3-BC6889272C62>

Fig. 52A–E

Type material. Holotype. TANZANIA – Tanga Reg. • ♂ (in alcohol); West Usambara Mts, Mgwashi, Shokoi River; 4°46'S, 38°29'E; 24 Nov. 1990; T Andersen leg.; sweep net; UMSP 000550054.

Diagnosis. *Chimarra mgwashi* sp. nov. is most similar to *C. aciculata* Morse and *C. evoluta* Kimmins, particularly in the general shape of segment IX and inferior appendages. Diagnostic differences from *C. aciculata* include the overall shape of the inferior appendage, in lateral view, which in *C. mgwashi* has its dorsal process more basal and not hooked or curved mesally, and the shape of the phallobase, which, in *C. mgwashi*, is very short and obscured by the strongly sclerotized lateral projections of the phallocrypt. The most useful diagnostic feature separating *C. mgwashi* from *C. evoluta* is the shape of the apex of the inferior appendage in ventral view, which is subtruncate in *C. mgwashi*, but narrowed and mesally hooked in *C. evoluta*.

Description. Adult. Overall color (in alcohol) dark brown. Head short (postocular parietal sclerite short, < 1/2 diameter of eye). Palps elongate, maxillary palp with 1st segment very short (slightly longer than wide), 2nd segment moderate (~ 2 × 1st), apex with cluster of ~ 8–10 stiff setae, 3rd segment elongate (~ 1½ × 2nd), 4th segment short (~ 1/2 length of 3rd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 5.2 mm. Forewing forks I, II, III, and V present; hind wing with forks II and V only. Forewing with R₁ nearly straight, stem of Rs very weakly inflected in middle, basal fork of discoidal cell enlarged, evenly forked, length of cell ~ 2½ × width, forks I and II sessile, r crossvein not evident, s, r-m, and m crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), fork II slightly sessile, anal loop small. Forelegs with apical tibial spur short; male with foretarsi modified, tarsal claws enlarged and asymmetrically developed.

Male genitalia. Segment VIII short, sternum without posteroventral projection. Segment IX, in lateral view, very short, with anterior margin nearly straight, without dorsolateral apodemes, posterior margin somewhat expanded at attachment point of inferior appendages; dorsal margin with paired, elongate, narrow, scabrous, posteroventrally directed processes from anterolateral margin, apices of processes acute; ventral process of segment from ventral margin, very small, rounded, ventrally directed; as viewed dorsally, with tergum discontinuous mesally, posterior processes widely separated basally. Tergum X with relatively short membranous mesal lobe, divided mesally, lateral lobes, as viewed laterally, with dorsal margin more sclerotized, forming two rounded projections, the more distal one with two sensilla. Preanal appendages rounded, mound-like, fused

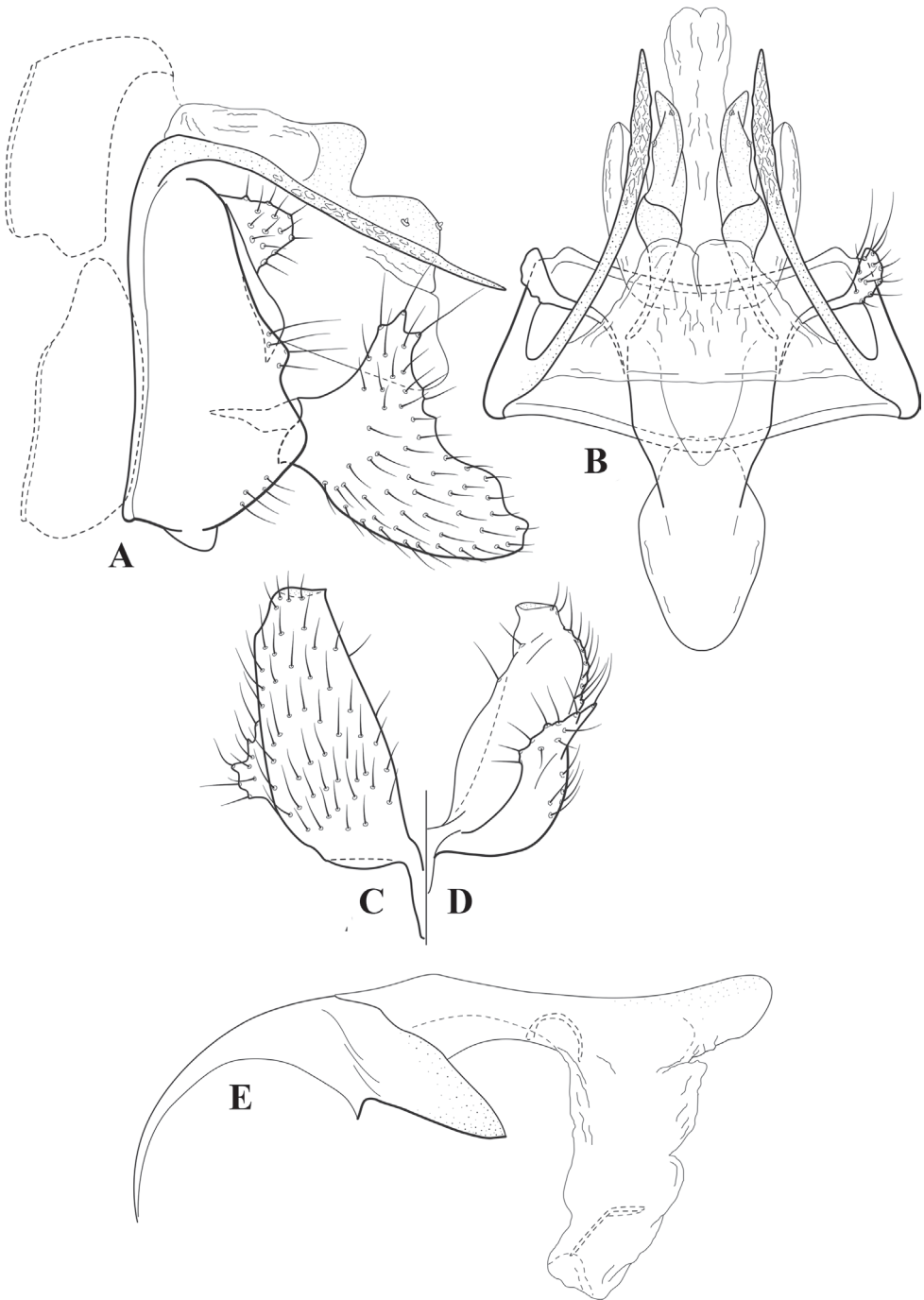


Figure 52. *Chimarra mgwashi* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X and base of phallus **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral.

basally. Inferior appendage, as viewed laterally, moderately elongate, narrowing apically, with short, tapering, basodorsal expansion; as viewed dorsally, without cusp or tooth on mesal margin, apex truncate. Phallic apparatus with phallobase very short, with usual basodorsal expansion, well anchored within segment by sclerotized periphallic membrane (attached to lateral margin of segment IX), appearing as sclerotized lateral wings, ventral apex of phallobase not projecting, continuous with endotheca; endotheca membranous, with slightly sclerotized dorsal lobe, phallic spines apparently absent; phal-lotremal sclerite complex composed of short, rather indistinct, rod and ring structure.

Etymology. *Chimarra mgwashi*, used as a noun in apposition, and named for the site in Tanzania where the holotype specimen was collected.

***Chimarra parafoliata* sp. nov.**

<http://zoobank.org/4BFE5A74-ABBC-4E77-BB6D-2A2B80E54C7D>

Fig. 53A–F

Type material. Holotype. GHANA – Eastern Reg. • ♂ (in alcohol); Kibi, Subri stream; 6°10'N, 0°33'W; 4 Feb. 1993; J Kjørandsen leg.; at light; UMSP 000550067.

Diagnosis. This species is undoubtedly closely related to *Chimarra foliata* Kimmins and *C. giboni* sp. nov. as evidenced by its foliate dorsal lobes of tergum X. It is most similar to *C. foliata* in the overall structure of its inferior appendages and in the general shape of segment IX, which has its posteroventral margin expanded at the level of the inferior appendages, and by the general lobate and semi-sclerotized structure of the endotheca. It differs diagnostically in the shape of its inferior appendages, which have a broader basodorsal lobe and also an acute ventral apex, as viewed laterally. The semi-sclerotized endotheca also seems to be somewhat different in shape, more elongate in *C. parafoliata* than in *C. foliata*, but the constancy and significance of this difference is difficult to assess.

Description. Adult. Overall color (in alcohol) yellowish brown, head slightly darker, setal warts of head pale, contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate (~ 3× 1st), apex with cluster of ~ 8–10 stiff setae, 3rd segment moderately elongate, slightly longer than 2nd, 4th segment short (~ 1/2 length of 2nd), 5th segment very elongate and narrow (subequal to 3rd and 4th combined). Forewing length: male, 4.0 mm. Forewing forks I, II, III, and V present; hind wing with forks II and V only. Forewing with R₁ nearly straight, stem of Rs weakly inflected, basal fork of discoidal cell distinctly enlarged, evenly forked, length of cell slightly > 2× width, forks I and II sessile, *r* crossvein not evident, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), fork II sessile, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

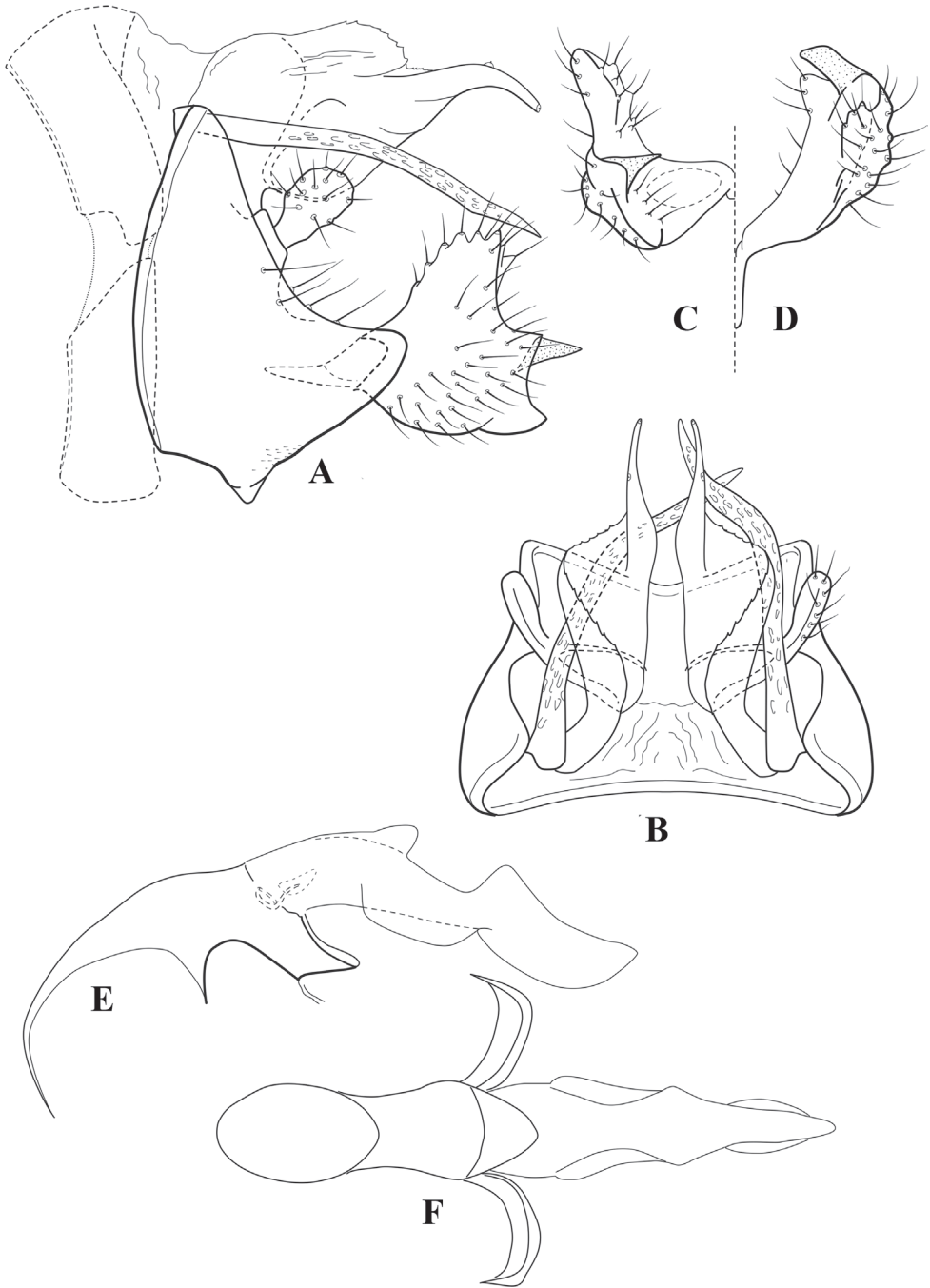


Figure 53. *Chimarra parafoliata* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, caudal **D** inferior appendage, dorsal **E** phallus, dorsal **F** phallus, lateral/ventral.

Male genitalia. Segment VIII short, dorsal margin of tergum slightly expanded, sternum without posteroventral projection. Segment IX, in lateral view, with anterior margin nearly straight, ventral margin very distinctly expanded at level of inferior appendages, segment narrowing and convergent dorsally, dorsal margin without apodemes, but with paired, elongate, narrow, scabrous, posteriorly-directed processes from posterolateral margin, apices of processes acute, ventral process very short, ventrally projecting; as viewed dorsally, with tergum discontinuous mesally, posterior processes widely separated basally, mesally curved apically, sternum short, subtruncate. Tergum X with short membranous mesal lobe, lateral lobes with expanded foliate basal lobes and narrow, projecting apices; sensilla probably only two on each lobe, one apical and one preapical on narrow apical projection. Preanal appendages moderately large and knob-like, distinctly flattened, constricted basally, inserted membranously (not fused to segments IX or X). Inferior appendage, as viewed laterally, relatively short, convexly rounded basally, dorsally with rounded projection with marginal setae, apically with short, angular projections on ventral margin and midlaterally, the latter with sclerotized cusp projecting from mesal margin. Phallic apparatus with phallobase short, ventral apex short and deflexed, rounded apically, well anchored within segment by semi-sclerotized periphallic membrane (attached to lateral margin of segment IX); endotheca elongate, lightly sclerotized, with evident structure including dorsal, lateral, and apical lobes; phallotremal sclerite complex indistinct, apparently composed of short rod and ring structure.

Etymology. *Chimarra parafoliata*, the species name meaning alongside or next to, because of the great similarity of this species to *C. foliata* Kimmins.

***Chimarra pectinella* sp. nov.**

<http://zoobank.org/78E8A2D4-C9C6-4C10-8B2E-3F9829E988C8>

Fig. 54A–F

Type material. Holotype. GHANA – **Central Reg.** • ♂ (in alcohol); Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; UMSP 000550061.

Additional material. GHANA – **Central Reg.** • 2♀♀; Kakum Forest Reserve; 5°21'N, 1°22'W; 8–15 Nov. 1994; T Andersen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra pectinella* is probably closest to *C. lobulata* sp. nov., as evidenced by the similarity in the shapes of segment IX and tergum X of both species. Both species also have the dorsal processes of segment IX very narrowly separated mesally. *Chimarra pectinella* differs in the shape of its inferior appendages, with the setae on the apical margin on almost lobe-like projections, and by having a comb-like row of spines on the dorsal processes of segment IX, which, unlike *C. lobulata* lack a scabrous surface texture. It also differs in the shorter, smaller, and less ventrally curved apicoventral lobes

of the phallobase, and by having a distinct cusp or tooth on the mesal surface of the inferior appendages.

Description. Adult. Overall color (in alcohol) yellowish brown, head slightly darker, setal warts of head pale, contrasting. Head short (postocular parietal sclerite short). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment moderately elongate ($\sim 3 \times$ 1st, slightly shorter than 3rd), apex with cluster of ~ 8 stiff setae, 3rd segment moderately elongate, 4th segment short ($\sim \frac{1}{2}$ length of 2nd), 5th segment very elongate and narrow (slightly longer than 3rd and 4th combined). Forewing length: male, 4.0 mm; female, 4.5–4.8 mm. Forewing forks I, II, III, and V present; hind wing with forks II and V only. Forewing with R_1 nearly straight, stem of R_s weakly inflected, basal fork of discoidal cell distinctly enlarged, evenly forked, length of cell slightly $> 2 \times$ width, fork I subsessile, fork II sessile, fork III with veins crossed (both forewings of male, possibly aberration, female with normal fork), r crossvein diagonal, intersecting discoidal cell near apical fork, s , $r-m$, and m crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), fork II sessile, anal loop small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII moderate in length, tergum slightly longer than sternum, sternum without posteroventral projection. Segment IX, in lateral view, relatively long, narrowed dorsally at approximately level of preanal appendages, ventral margin only slightly expanded, dorsal margin without apodemes, but with paired, elongate, narrow, posteriorly directed processes from posterior margin, each with row of short spines on dorsal margin, apices of processes acute, ventral process absent; as viewed dorsally, with tergum discontinuous mesally, posterior processes proximate mesally, bowed outward, sternum short, subtruncate. Tergum X without evident mesal lobe, lateral lobes divided mesally, moderately elongate and narrow, with narrow, projecting apex; sensilla probably only two on each lobe, one apical and the other preapical. Preanal appendages very small and rounded, inserted membranously (not fused to segments IX or X). Inferior appendage with only weak basal inflection, widened apically, apical margin with short nipple-like projections, each with elongate seta; as viewed caudally, with slight mesal curvature, apex rounded, mesal surface with distinctly sclerotized cusp. Phallic apparatus with phallobase moderately elongate, lightly sclerotized, with usual basodorsal expansion, apparently well anchored within segment by semi-sclerotized periphallic membrane (attached to lateral margin of segment IX), apicoventral margin of phallobase sclerotized and slightly projecting, mesal margin with U-shaped invagination, producing short paired, sclerotized processes; endotheca with very short spine; phallotremal sclerite complex large, composed of relatively elongate rod and ring structure, with lightly sclerotized apical structure.

Etymology. *Chimarra pectinella*, used as an adjective and derived from the Latin *pecten*, a comb, in reference to the row of comb-like spines on the dorsolateral lobes of segment IX in this species.

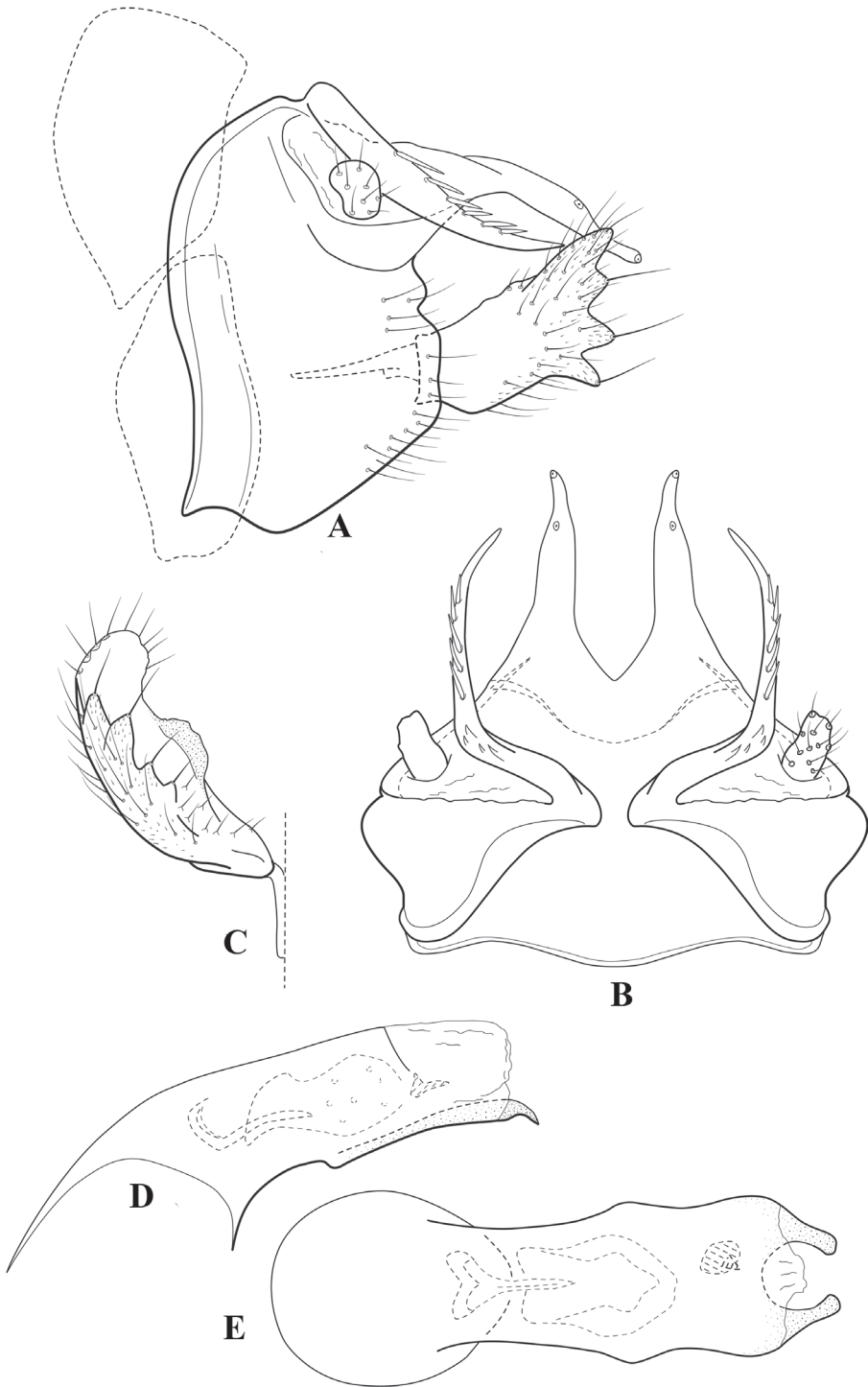


Figure 54. *Chimarra pectinella* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** inferior appendage, ventral **D** phallus, lateral **E** phallus, ventral.

Species not assigned to subgroup

Chimarra agumatsa sp. nov.

<http://zoobank.org/71853F1C-53D9-43C0-AC0D-652E87E34878>

Fig. 55A–F

Type material. *Holotype*. GHANA – **Volta Reg.** • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 2^B; 7°07'29"N, 0°35'31"E; 5–8 Mar. 1993; JS Amakye & J Kjørandsen leg.; Malaise trap; UMSP 000550055. *Paratypes*. GHANA – **Volta Reg.** • 2♂♂; same data as for holotype except 8–11 Mar. 1993; ZMBN • 6♂♂; same data as for holotype except station # 1^B; 5–14 Mar. 1993; ZMBN • 2♂♂; same data as for holotype except station # 5^C; 6–9 Mar. 1993; ZMBN • 1♂; same data as for holotype except station # 6; 11–20 Nov. 1993; J Kjørandsen leg.; ZMBN.

Additional material. GHANA – **Volta Reg.** • 1♀ Wli, Agumatsa waterfall, station # 6; 7°07'29"N, 0°35'31"E; 11–20 Nov. 1993; J Kjørandsen leg.; Malaise trap; ZMBN • 1♀; same collection data as for preceding; UMSP.

Diagnosis. *Chimarra agumatsa* shows its relationship to species of the *georgensis* Group in having an elongate apical segment of its maxillary palps and in its primitive venation (straight Rs vein of the forewing, linear, unpigmented chord, and absence of a “fork” or crossvein in the anal veins). It would appear to have its greatest affinity to members of the *georgensis* subgroup, especially in having the phallobase relatively short, with its apex somewhat bifid. However, it is distinctive in a number of ways, including the absence of a tergum X, loss of fork III in the hind wing, and in having the phallus less sclerosely anchored than is typical in members of the *georgensis* Group in general. For this reason, we have left the species unassigned to subgroup.

Chimarra agumatsa is easily diagnosed by the characters discussed above, in addition to the distinctive shape of its inferior appendages, which are very short, with both the ventral and dorsal margins incurved. It is apparently most similar to *C. ino* Marlier, whose inferior appendages have more or less the same structure but have the projections from the ventral margin more elongate and projecting. Both species lack fork III in the hind wing. The quality of the original illustration of *C. ino* make other characters difficult to compare.

Description. Adult. Overall color (in alcohol) yellowish brown, vertex of head slightly darker, appendages yellowish. Head moderately elongate (postocular parietal nearly as long as diameter of eye). Palps elongate; maxillary palp with 1st segment very short (approximately as long as wide), 2nd segment relatively short (~ 3× length of 1st), apex with cluster of ~ 8–10 stiff setae, 3rd segment elongate, almost 2× length of 2nd, 4th segment short (slightly shorter than 2nd), 5th segment very elongate (nearly length of 3rd and 4th combined). Forewing length: male, 4.0–5.0 mm; female, 4.0 mm. Forewing forks I, II, III, and V present; hind wing with forks I, II and V. Forewing with R₁ nearly straight, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell ~ 2× width, fork I subsessile, fork II sessile, *r* crossvein intersecting discoidal cell at past midlength, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R₁ obsolete (or fused to subcosta), forks I and II sessile, anal loop

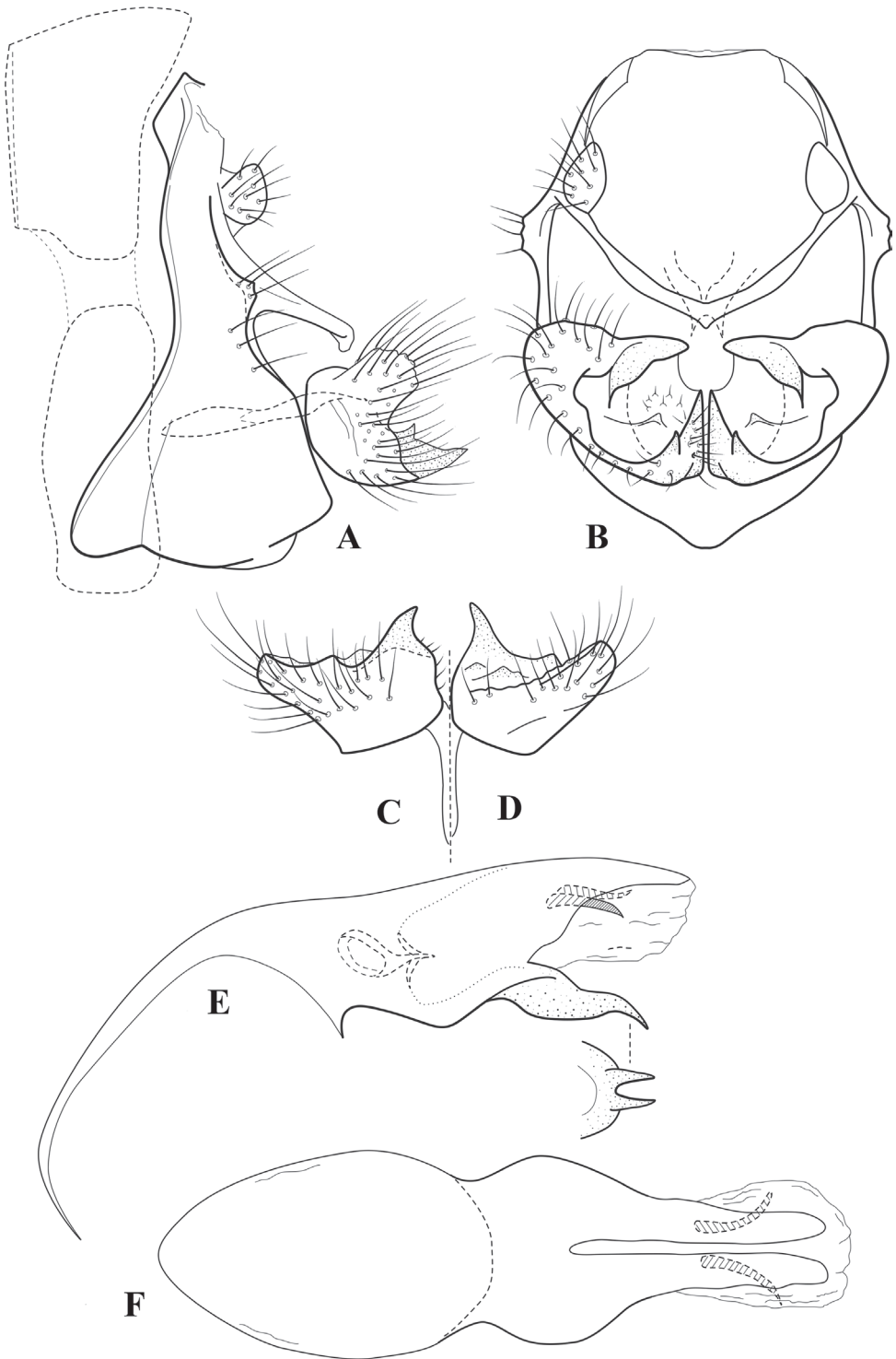


Figure 55. *Chimarra agumatsa* sp. nov., ♂ genitalia **A** lateral **B** caudal **C** inferior appendage, ventral **D** inferior appendage, dorsal **E** phallus, lateral, with ventral view of phallobase apex **F** phallus, dorsal.

small. Forelegs with apical tibial spur short; male with modified tarsal claws, apical three segments of tarsi short and flattened, claws asymmetrical, outer one elongate and twisted.

Male genitalia. Segment VIII short, sternum without posteroventral projection. Segment IX, in lateral view, subtriangular, anteroventral and postroventral margins both moderately produced, strongly converging dorsally, dorsal margin obsolete, or nearly so, anterior margin without apodemes. Ventral process of segment greatly reduced, rounded, ventrally projecting, width at base greater than length. Tergum X apparently absent, but with narrow, converging lateral processes below preanal appendages, subtending phallus and fused apicomesally. Preanal appendages small and knob-like, rounded, slightly constricted basally, apparently fused to segment IX. Inferior appendage very short, with dorsal margin enrolled and rounded, as viewed laterally, forming a projecting cusp on the mesal surface; ventral margin of appendage projecting, acute, and mesally curved, forming short spine-like projection on mesal margin. Phallic apparatus with phallobase relatively short, not (or not evidently) anchored by sclerotized periphallic membrane; ventral apex of phallobase, as viewed laterally, projecting and acute, as viewed ventrally, weakly bifid apically; dorsal margin of phallobase, as viewed laterally, distinctly projecting, subequal in length to ventral projection, but with mesal margin forming an elongate, narrow, desclerotized strip over much of its length, as viewed dorsally; endotheca apparently short and simple in structure, with a pair of short, curved, symmetrically oriented phallic spines; phallotremal sclerite complex small and indistinct, composed of short rod and ring structure.

Etymology. *Chimarra agumatsa*, the name considered a noun in apposition, for the name of the scenic waterfalls near which the holotype specimen was collected.

***Chimarra kjaerandseni* sp. nov.**

<http://zoobank.org/611EDC60-4653-4ECD-9B39-E6B05AE840D7>

Fig. 56A–G

Type material. *Holotype* GHANA – Volta Reg. • ♂ (in alcohol); Wli, Agumatsa waterfall, station # 5^C; 7°07'29"N, 0°35'31"E; 9–12 Mar. 1993; JS Amakye & J Kjaerandsen leg.; Malaise trap; UMSP 000550057.

Additional material. GHANA – Volta Reg. • 1 ♀; Wli, Agumatsa waterfall, station # 6; 7°07'29"N, 0°35'31"E; 20 Nov. 1993; J Kjaerandsen leg.; light trap; UMSP.

Diagnosis. *Chimarra kjaerandseni* is a unique and enigmatic species, very different from the other species placed in the *georgensis* Group, but sharing some of the diagnostic characters, including a maxillary palp with a relatively elongate terminal segment and primitive venational characters, including a forewing with a straight Rs vein, a linear, unpigmented chord, and absence of a “fork” or crossvein in the anal veins. Like the species in the *evoluta* subgroup, it lacks fork I and III in the hind wing. However, none of the genitalic characters are particularly suggestive of a relationship with this subgroup, since it lacks either the elongate processes from the dorsal margin of segment IX or modified ventral apex of the phallobase that characterize other

species in the subgroup. Because of this, and despite the very suggestive hind wing venational loss characters, we prefer to consider this species unassigned to subgroup in the *georgensis* Group.

General diagnostic characters of the species include the general shape of segment IX, which is relatively elongate and lacks anterodorsal apodemes, the ventrally projecting ventral process of the same segment, the simple lateral lobes of tergum X, and the short curved inferior appendages. Additionally, the numerous small spines in the phallus, its relative length, absence of a projecting ventral apex on the phallobase, as well as the relatively desclerotized posteromesal margin of segment VIII are also all useful diagnostic characters, not found in any other species of the *georgensis* Group.

Description. Adult. Overall color (in alcohol) yellowish brown, vertex of head slightly darker, appendages yellowish. Head relatively short (postocular parietal sclerite $\sim 1/2$ length of eye). Palps relatively elongate; maxillary palp with 1st segment short and stout (approximately as long as wide), 2nd segment moderately elongate ($\sim 3 \times 1^{\text{st}}$), apex with cluster of 6–8 stiff setae, 3rd segment slightly longer than 2nd, 4th segment short ($\sim 1/2$ length of 3rd), 5th segment relatively elongate and very narrow (somewhat shorter than 3rd and 4th combined). Forewing length: male, 4.0 mm. Forewing with forks I, II, III, and V present; hind wing with forks II and V only. Forewing with Rs straight, or nearly so, basal fork of discoidal cell slightly enlarged, evenly forked, length of cell $\sim 2 \times$ width, fork I subsessile, II sessile, *r* crossvein not evident, *s*, *r-m*, and *m* crossveins linear and hyaline, both 2A and 3A looped to 1A (2A without apical fork). Hind wing with R_1 obsolete (or fused to subcosta), fork II slightly subsessile, anal loop small. Forelegs with apical tibial spur very short; male with modified tarsal claws, apical tarsal segment enlarged and flattened, claws asymmetrical, outer one elongate and slightly twisted.

Male genitalia. Segment VIII short, sternum without posteroventral projection, tergum slightly longer, with very distinct membranous posteromesal invagination. Segment IX, in lateral view, relatively elongate ventrally, anteroventral margin moderately expanded, posterior margin subparallel to anterior margin to point just above inferior appendage, then angularly narrowing dorsally; as viewed dorsally, with dorsal margin short, but continuous, anteroventral margin subtruncate. Ventral process of segment IX ventrally projecting, subtriangular, closer to anterior than posterior margin. Lateral lobes of tergum short and broad, subparallel, widely separated dorsally, with membranous lobe between, lobes converging anteroventrally, apices of lobes each with angular, beak-like, ventral projection, sensilla absent or indistinct. Preanal appendages prominent, rounded and knob-like, slightly constricted basally, apparently fused to segment IX. Inferior appendage, as viewed laterally, short and simple in shape, distinctly inflected basally, longer than wide, slightly tapering, apex rounded, mesally curved as viewed dorsally or ventrally, without cusp or tooth on mesal margin. Phallic apparatus with phallobase moderately elongate, tubular, without distinctly sclerotized periphallallic membrane, ventral apex of phallobase not projecting. Endotheca at least moderately elongate, textured with small spine-like projections and several clusters of short spines, phallotremal sclerite complex small and indistinct, forming short rod and ring structure.

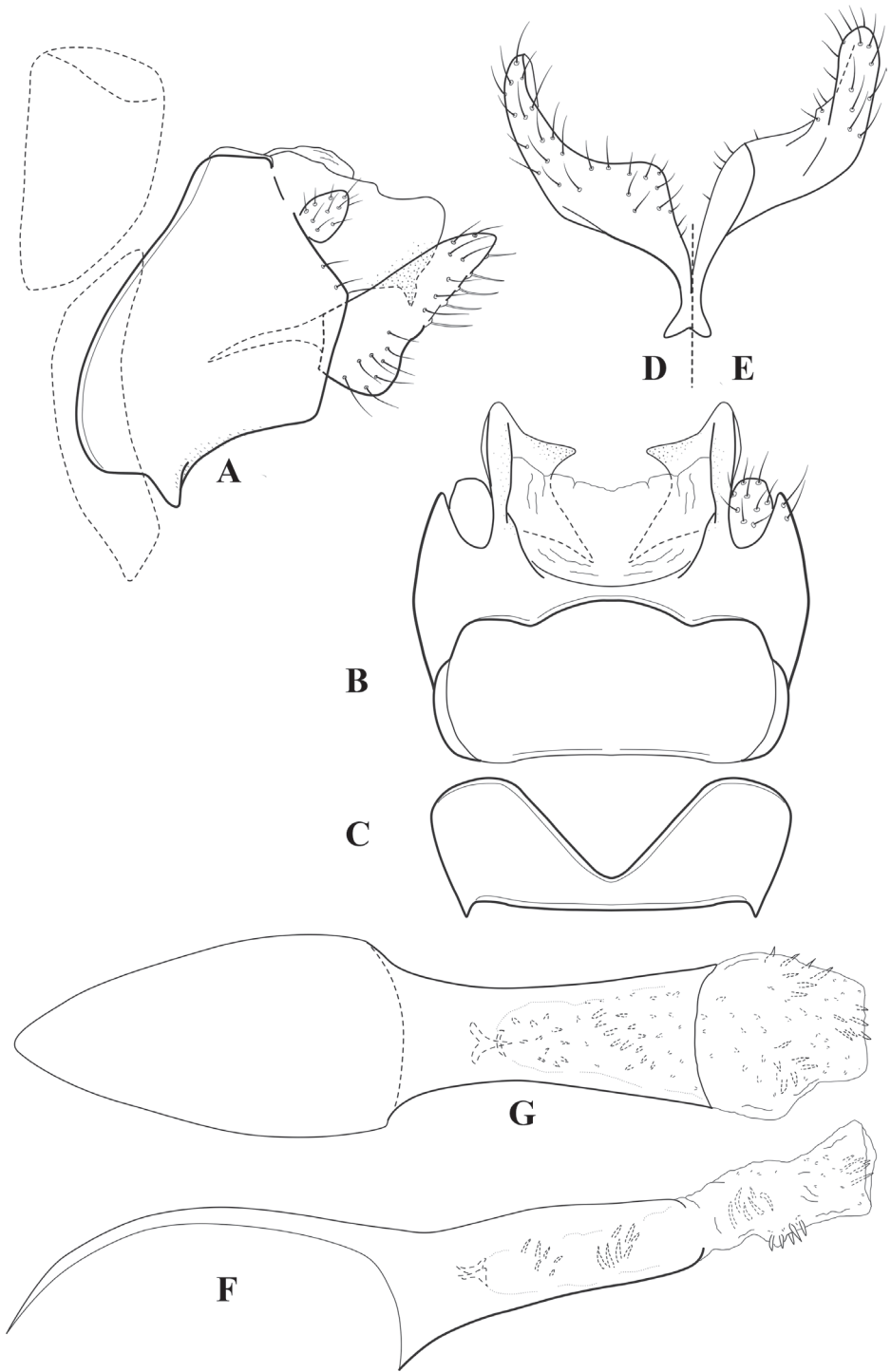


Figure 56. *Chimarra kjaerandseni* sp. nov., ♂ genitalia **A** lateral **B** dorsal, segments IX and X **C** tergum VIII, dorsal **D** inferior appendage, ventral **E** inferior appendage, dorsal **F** phallus, lateral **G** phallus, dorsal.

Etymology. We are pleased to name this species for Jostein Kjærandsen, who participated in the collecting expedition that generated much of the material that the current study is based on, in addition to doing an initial sorting of the material and initiating the study.

Acknowledgements

The project in Tanzania was a joint project between the Faculty of Forestry, Sokoine University of Agriculture (SUA) and the University Museum of Bergen. The second author is indebted to Jørn Bjørndalen, Kjell Arne Johanson, Geir E.E. Sølvi and the other members of the team for help and company during the field work. Financial support was given by the Norwegian Research Council (NFR), the Norwegian Agency for Development Cooperation (Norad) and the University of Bergen. The project in Ghana was a joint project between the Department of Zoology, University of Ghana; Institute of Aquatic Entomology, CSIR, Accra, Ghana, and the University Museum of Bergen. We are indebted Joseph S. Amakye, Institute of Aquatic Entomology, and the other members of the team. Financial support was granted by the Norwegian Universities' Committee for Research and Education (NUFU) and by the Norwegian Research Council (NFR). Special thanks are extended to Jostein Kjærandsen who collected much of the material and did much of the initial sorting.

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Three new species of *Xiphocentron* Brauer, 1870 (Trichoptera, Xiphocentronidae) from Mexico

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Abstract

Three new species of the genus *Xiphocentron* (Trichoptera, Xiphocentronidae) are described from Nearctic and Neotropical regions of Mexico. *Xiphocentron* (*Glyphocentron*) *flinti* sp. nov. has a very unique morphology distinguished by the presence of long spines on the preapical and apical margin of tergum X. *Xiphocentron* (*Antillotrichia*) *holzenthali* sp. nov. is diagnosed by tergum IX, with the apical margin bearing a narrow, rounded, mesal emargination and by a spiny projection near the basal plate. These species are the first records of the family in northwestern Mexico. *Xiphocentron* (*Antillotrichia*) *pineroi* sp. nov. is recognized, when observed in lateral view, by its less elongate genitalia and the sinuous mesal sclerite of the inferior appendage. Additionally, we provide detailed illustrations of *Xiphocentron* (*Antillotrichia*) *rhamnes* Schmid, and an updated list of the distribution of the genus *Xiphocentron* in Mexico.

Keywords

Aquatic insects, caddisflies, Mexico, Neotropical, taxonomy

Introduction

The family Xiphocentronidae Ross, 1949 is comprised of 195 species distributed in eight genera (as *Caenocentron* Schmid, 1982 was elevated to genus status) (Vilarino et al. in press). The family was erected by Ross (1949); subsequently it was placed in the family Psychomyiidae Walker, 1852 by Edwards (1961) and treated as a subfamily. Schmid (1982) in a world revision of the group resurrected the family status of Xiphocentronidae. The Xiphocentronidae are organized in two subfamilies: Proxiphocentroninae Schmid, 1982 and Xiphocentroninae Schmid, 1982 (Vilarino et al. 2018). The genus *Xiphocentron* Brauer, 1870 includes the majority of the species of the family, with 53 extant species and two subspecies widely distributed in the Neotropics (Holzenthal and Calor 2017; Vilarino and Bispo 2020) and one fossil species described from Chiapas, Mexico (Wichard et al. 2006). The genus *Xiphocentron* is subdivided into five subgenera: *Glyphocentron* Schmid, 1982, *Rhamphocentron* Schmid, 1982, *Sphagocentron* Schmid, 1982, *Xiphocentron* Schmid, 1982, and *Antillotrichia* Banks, 1941 (Holzenthal and Calor 2017; Vilarino et al. 2018). The greatest diversity of subgenera is found in Mesoamerica, with only *Antillotrichia* occurring in South America and the Antilles (Vilarino and Bispo 2020). Representatives of all the subgenera occur in Mexico, and most of the distribution records of the subgenera *Rhamphocentron* and *Xiphocentron* are from Mexico. As a result of the continuing studies of the caddisfly fauna, 18 extant *Xiphocentron* and one fossil species are known to occur in Mexico (including the species here described) (Table 1). The genus *Xiphocentron* Brauer, 1870 has a wide distribution in Mexico. We have collections from the northern states of Chihuahua and San Luis Potosí, the central states of Puebla, Oaxaca, Michoacán, Ciudad de México, and Estado de México, and the southern part of the country, including the states of Veracruz, Chiapas, and Tabasco (Table 1). Because caddisflies of the genus *Xiphocentron* are diurnal (Flint 1968; Schmid 1982), often a limited number of individuals are collected when using only light traps. Rocha et al. (2017), for instance, reported that they collected two new species of *Xiphocentron*, using only the light trap method, although one of them was described with just a single type specimen.

Methods

The specimens of the genus *Xiphocentron* studied here were borrowed from the collections of the National Museum of Natural History, Smithsonian Institution in Washington, DC, and from the Colección Nacional de Insectos, Instituto de Biología de la Universidad Nacional Autónoma de México.

For the description of wing venation, we followed Vilarino and Bispo (2020). For the study of the internal structure of the male genitalia, we put the entire adults or an abdomen into a small container with a solution of 10% of KOH, and then kept on a hot plate at 100 °C for 10 minutes, in order to clear the genitalia. After that, the specimens were kept in 10% acetic acid for 10 min to stop the clearing reaction (Prather 2003). Subsequently, the specimens were placed on microscope slides with a drop of glycerin for the observation of the male genitalia. We used a dissection microscope (LEICA

Table 1. Distribution of the genus *Xiphocentron* Brauer, 1870 in Mexico. Chihuahua (Chi.), Nuevo León (NL), San Luis Potosí (SLP), Michoacán (Mich.), Estado de México (Edo. Mex.), Ciudad de México (CDMEX), Puebla (Pue.), Veracruz (Ver.), Oaxaca (Oax.), Tabasco (Tab.), Chiapas (Chis.), († fossil), (♣ New Distribution).

Species	States
<i>X. (Xiphocentron) asilas</i> Schmid, 1982	SLP
<i>X. (Xiphocentron) aureum</i> Flint, 1967	Edo. Mex., ♣ Ver.
<i>X. (Xiphocentron) bilimekii</i> Brauer, 1871	MEXICO
<i>X. (Xiphocentron) polemon</i> Schmid, 1982	CDMEX
<i>X. (Xiphocentron) tarquon</i> Schmid, 1982	Chis., Tab., Ver.
<i>X. (Xiphocentron) chiapasi</i> Wichard, Solórzano- Kraemer, Luer, 2006	Chis. †
<i>X. (Xiphocentron) numanus</i> Schmid, 1982	Oax.
<i>X. (Sphagocentron) julus</i> Schmid, 1982	Oax.
<i>X. (Rhaphocentron) erato</i> Schmid, 1982	SLP
<i>X. (Rhaphocentron) alecto</i> Schmid, 1982	NL, Chi., SLP
<i>X. (Rhaphocentron) lavinia</i> Schmid, 1982	Chis.
<i>X. (Rhaphocentron) mexico</i> Ross, 1949	NL, SLP, Tab.
<i>X. (Rhaphocentron) messapus</i> Schmid, 1982	Chis.
<i>X. (Glyphocentron) flinti</i> sp. nov.	Chi.
<i>X. (Antillotrichia) mezencius</i> Schmid, 1982	Pue.
<i>X. (Antillotrichia) rhamnes</i> Schmid, 1982	Mich., Oax.
<i>X. (Antillotrichia) serestus</i> Schmid, 1982	Mich., Oax.
<i>X. (Antillotrichia) holzenthali</i> sp. nov.	Chi.
<i>X. (Antillotrichia) pineroi</i> sp. nov.	Tab.

Model EZ4) and a ZEISS compound microscope with camera lucida for observation and creation of the drawings, the latter subsequently digitized on the computer using Adobe Illustrator CS6. Morphological terminology and style of the description of the male genitalia, follows that presented by Muñoz and Holzenthal (1997) and Schmid (1982). Distribution maps were generated using ArcGIS v. 10.2 (ESRI 2013). Distributional data for Xiphocentronidae was compiled from the literature.

The type materials are deposited as indicated in each species description, in the collections: National Museum of Natural History, Smithsonian Institution in Washington, DC (USNM), and Colección Nacional de Insectos, Instituto de Biología de la Universidad Nacional Autónoma de México (CNIN, formerly IBUNAM).

Results

Family Xiphocentronidae Ross, 1949

Genus *Xiphocentron* Brauer, 1870

Xiphocentron (Glyphocentron) flinti Bueno, Vilarino & Barba, sp. nov.

<http://zoobank.org/5BE15179-7CA0-4F3D-A475-D275022D2985>

Figures 1, 2, 6

Diagnosis. This new species is very distinct from all other *Xiphocentron* species. The group of long, mesally situated setae on the basal portion of the inferior appendages has some resemblance to species in the subgenus *Xiphocentron*, whereas the complex

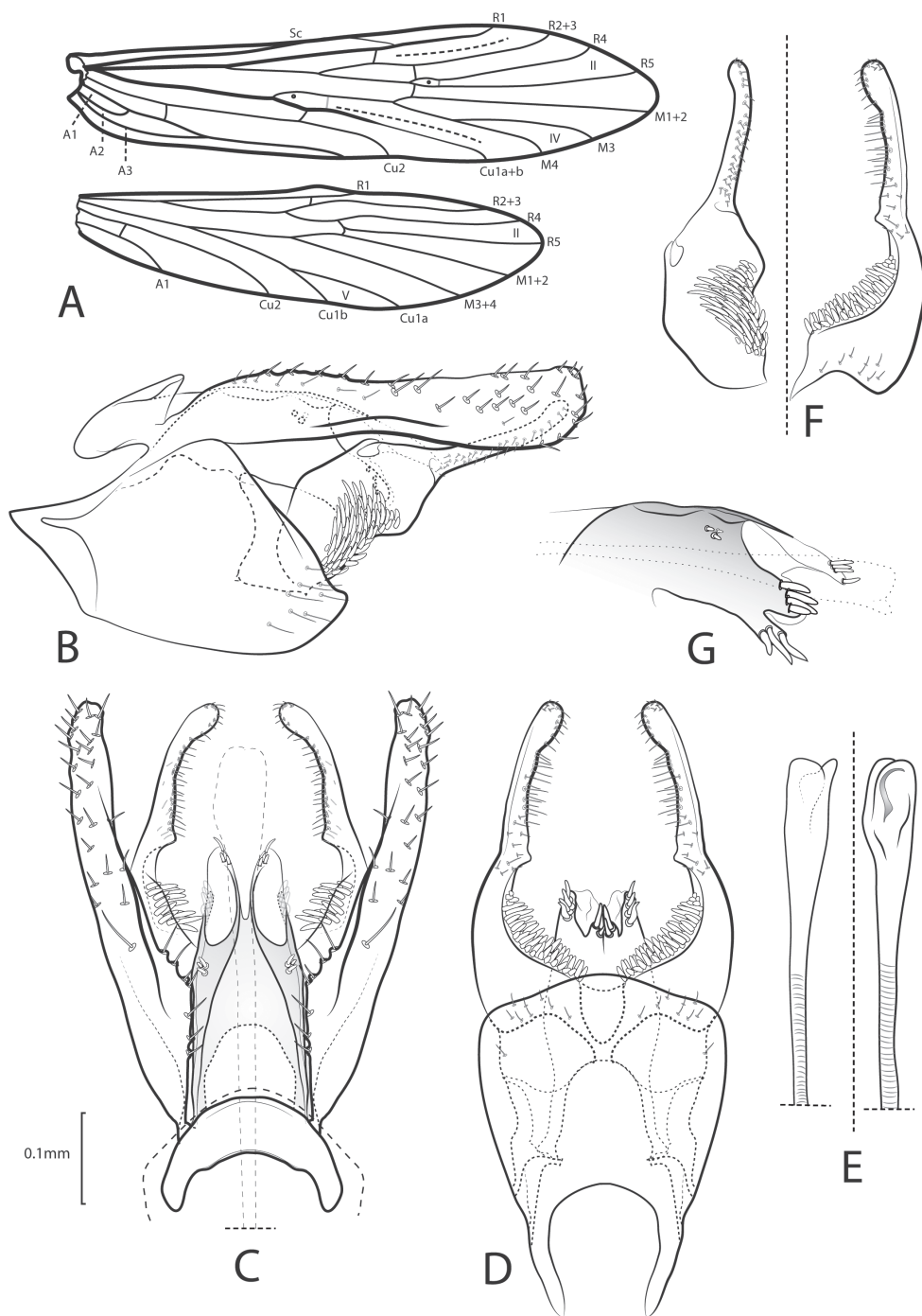


Figure 1. *Xiphocentron (Glyphocentron) flinti* sp. nov., holotype, adult, ♂ **A** forewing and hindwing. Male genitalia **B** left lateral **C** dorsal **D** ventral **E** phallus, apex in lateral and dorsal view **F** detail of right inferior appendage mesal surface, lateral and ventral view **G** detail of segment X left lateral.

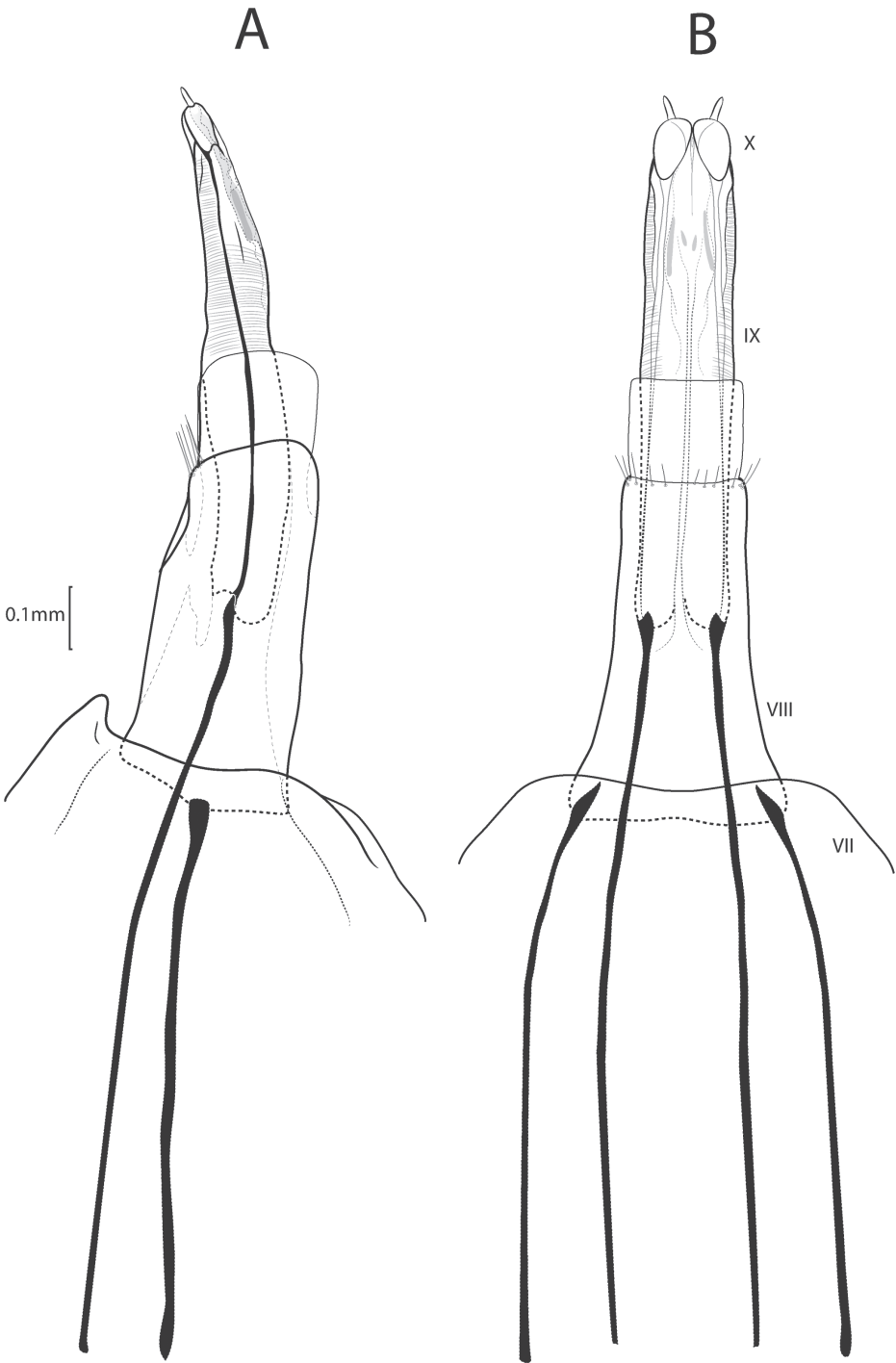


Figure 2. *Xiphocentron* (*Glyphocentron*) *flinti* sp. nov., paratype, adult, ♀, genitalia **A** lateral **B** dorsal view.

tergum X is similar to species in the subgenus *Glyphocentron*. *Xiphocentron* (*G.*) *flinti* sp. nov. can be distinguished from all the species of the family by the unique tergum X which bears long spines on the preapical and apical margin and visible in both dorsal and ventral views.

Description. Adult. Forewing length 4.8–9.0 mm, $n = 16$; fork II and fork IV present; Sc reaching C subapically, meeting R1 apically; fork II sessile at discoidal cell, with crossvein between R5 and M1+2; thyridial cell shorter than discoidal cell; three anal veins present (Fig. 1). Hindwing with fork II and fork V present. Color fuscous. Tibial spur formula 2–4–3. Hind tibia apical spurs not modified. Sternum V bearing pair of reticulated regions.

Male genitalia. Tergum IX small, ellipsoidal; in lateral view, rounded ventrally, narrow dorsally, anterior margin straight; in dorsal view anterior margin with wide, deep, U-shaped mesal emargination; apical margin rounded. Sternum IX subtriangular, in lateral view, about two times as long as high; anterior margin with elongate, wide, mesal apodeme; ventral margin rounded; posterior margin rounded; in ventral view, anterior margin with deep, U-shaped emargination, enlarging apically; posterior margin rounded. Tergum X in lateral view, subrectangular, narrow basally, wide mesally, with a group of spinelike setae, preapically rectilinear, apically bifurcated in two lobes, ventral lobe longer with group of long spinelike setae, dorsal lobe shorter with apical spinelike setae, anterior margin curved; in dorsal view, subtriangular, wide basally, narrow apically, lateral surface sclerotized, mesally membranous; apex with deep cleft, forming two rounded membranous lobes, bearing preapical spinelike setae, apices divergent; in ventral view, apex with two long mesal spinelike setae. Preanal appendages long, dorsal margin crenulate, in lateral view, broad, parallel-sided, with longitudinal ridge, apex rounded; in dorsal view, enlarged basally, narrowed at middle. Inferior appendage short, approximately half length of preanal appendages, basal section with a group of long spinelike setae; in lateral view, basal section broad, apical section narrow; in ventral view, basal section subtriangular, with a line of large spinelike setae, apical section long and thin, curved mesad; basal plate short, shorter than half sternum IX length. Phallus, long, slender, tubular, apex enlarged, with narrow curved sclerite.

Female genitalia. VIII segment long and narrow, synscleritous dorsally, internally with a pair of long slender apodemes from anterior margin; intersegmental membrane nearly as long as IX segment when extended. IX segment long and slender, with a pair of internal apodemes arising from anterior margin; apex with a pair of slender processes.

Type material. Holotype: ♂ MEXICO, Chihuahua, Ruta San Rafael-Cuiteco, 27°26'13"N, 108°00'32"W, elev. 1707 m, 30.VIII.2005, J. Bueno and R. Barba leg. pinned with abdomen in glycerin (CNIN). **Paratypes:** ibid., Chihuahua, Riito, Hwy. 16, 10 mi E. Yepachic 28°10'26"N, 108°10'36"W, elev. 2086 m, 28.VI.1987, R. Baumann, B. Kondratieff, Sargent and Wells leg. 8♂ 8♀ in alcohol (USNM); ibid., small stream Cascada de Basaseachic, 28°10'52"N, 108°12'44"W, elev. 1950 m, 28.VI.1987, B. Kondratieff and R. Baumann leg. 1♂ in alcohol (USNM); ibid., Cascada de Basaseachic, 22.VIII.1986, B. Kondratieff leg. 1♂ pinned (USNMENTO1518156); ibid.,

fork Arroyo Bandera near Jct. Río Chuhuichupa, 25.VI.1987, B. Kondratieff and R. Baumann leg. 1♂ 1♀ in alcohol (USNM).

Etymology. We dedicated this species, with sadness and love, to the memory of a great entomologist, Dr Oliver S. Flint Jr, who passed away on May 18, 2019.

Distribution. All the specimens were collected at Sierra Tarahumara, the mountain region of Chihuahua State (Fig. 6).

Remarks. The affinities of *Xiphocentron* (*Glyphocentron*) *flinti* sp. nov. are not very clear. The preanal appendages present a mesal ridge, a character present in the species of the genus *Melanotrichia*. The long setae on the basal portion of the inferior appendages in this species are similar to species within the subgenus *X. (Xiphocentron)* or even to *Cnodocentron* (*Caenocentron*). The complex tergum X with apical points puts it closer to the subgenus *X. (Glyphocentron)*. The new species lacks other diagnostic characters of *Melanotrichia* (fan-like spine line), *Cnodocentron* (bifurcate inferior appendage), or *X. (Xiphocentron)* (modified hind leg spurs, and presence of forewing fork I); therefore, we are placing it within subgenus *X. (Glyphocentron)*, for which the diagnostic character is the presence of points on tergum X (Schmid 1982).

***Xiphocentron* (*Antillotrichia*) *holzenthali* Bueno, Vilarino & Barba, sp. nov.**

<http://zoobank.org/919102E4-F494-4B38-8FD2-C327ECC42FCE>

Figures 3, 6

Diagnosis. This new species is very similar to *Xiphocentron* (*Antillotrichia*) *serestus* Schmid, 1982. However, *Xiphocentron* (*Antillotrichia*) *holzenthali* sp. nov. can be separated from *X. (Antillotrichia) serestus* by the shape of the tergum IX, as viewed dorsally; in *X. (Antillotrichia) holzenthali* sp. nov. the apical margin has a narrow, rounded, mesal emargination, while in *X. (Antillotrichia) serestus* the mesal emargination is wide and shallow. In the new species, the apical margin of sternum IX, in ventral view, has a narrow, rounded, mesal emargination, while in *X. (Antillotrichia) serestus* this margin has a trilobed mesal emargination. Also, in the new species the inferior appendage, in ventral view, has a spiny projection near the basal plate, which is absent in *X. (Antillotrichia) serestus*.

Description. Adult. Forewing length 6–7 mm, $n = 5$. Color in alcohol pale. Tibial spur formula 2–4–3. Hind tibia apical spurs not modified. Sternum V bearing pair of reticulated regions.

Male genitalia. Tergum IX semicircular; in lateral view, wide basally, narrow apically; dorsal margin curved; ventral margin nearly straight; in dorsal view anterior margin with deep V-shaped central incision; apical margin with narrow, rounded, mesal emargination. Sternum IX ovate, in lateral view, about twice as long as high; anterior margin with slender, pointed, mesal apodeme; ventral margin rounded; dorsal margin subtriangular; in ventral view, enlarging preapically; anterior margin rectilinear; posterior margin with small mesal emargination. Tergum X in lateral view, rectangular, narrow, acute apically; in dorsal view, subtriangular, wide basally, narrow apically; lat-

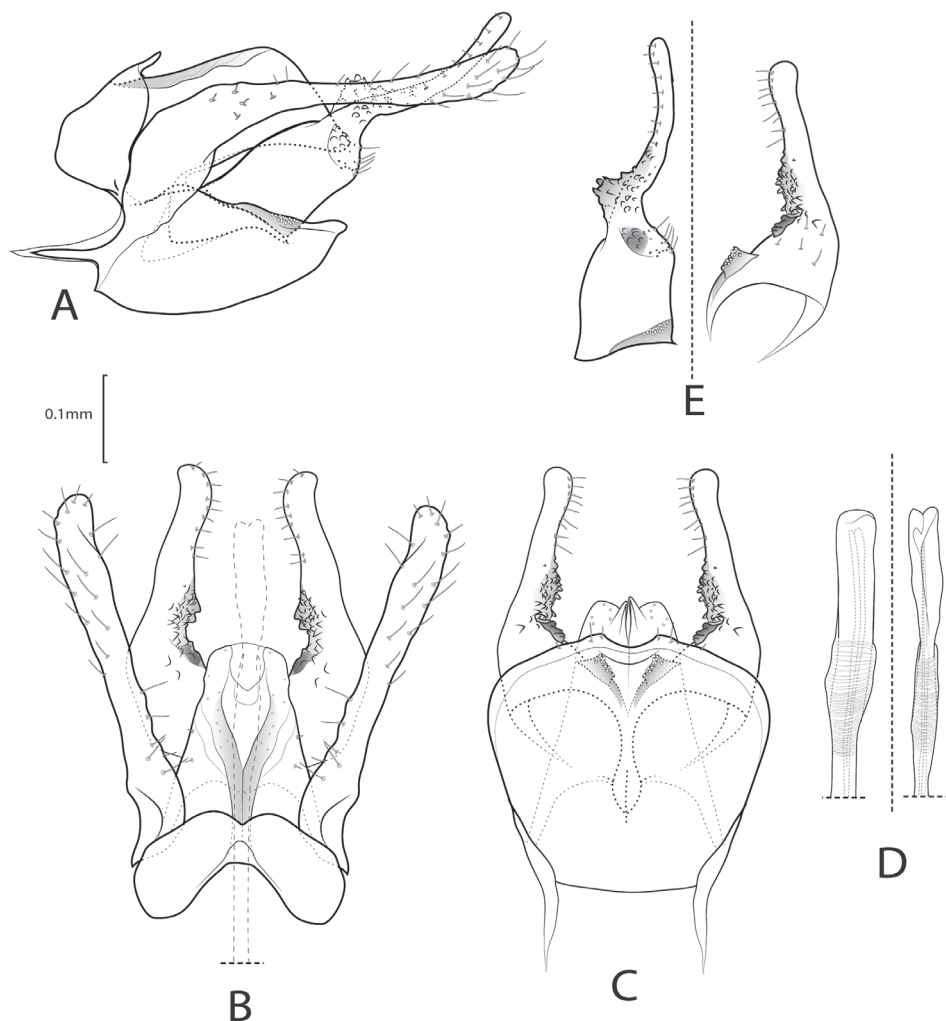


Figure 3. *Xiphocentron (Antillotrichia) holzenthali* sp. nov., holotype, adult, ♂, genitalia **A** left lateral **B** dorsal **C** ventral **D** phallus left lateral and dorsal **E** detail of right inferior appendage mesal surface, lateral and ventral view.

eral surface sclerotized, each sclerotized side fused mesally; apex with deep, V-shaped emargination; in ventral view, subtriangular, wide basally, narrow, cleft apically. Preanal appendages long, margins crenulate, surface weakly setose; in lateral view, broad basally, parallel-sided, narrow preapically, apex rounded. Inferior appendages, in lateral view long, approximately same length as preanal appendages, weakly setose; widest basally and mesally, apical section narrower, slender, upturned, and curved; mesal surface, with short, thick, peglike setae, separated in two, small patches, visible in ventral and dorsal view; in ventral view with spiny projection near basal plate; basal plate long, about as long as half sternum IX length. Phallus long, slender, tubular, slender apically.

Female genitalia (not illustrated). VIII segment narrowly divided dorsally, internally with pair of long slender apodemes from anterior margin; intersegmental membrane nearly as long as IX segment when extended. IX segment long and slender with pair of internal apodemes arising from anterior margin; apex with pair of slender processes.

Type material. *Holotype*: ♂ MEXICO: Chihuahua, Jct. E & W Forks Arroyo Toro, Toro Basin 28°06'35"N, 107°37'28"W, elev. 2425 m, 23.VI. 1987, B. Kondratieff and R. Baumann leg. in glycerin (USNM). *Paratypes*: ibid., 1♂1♀ in glycerin (USNM); Chihuahua, Arroyo Chuchupate, Trib. Río Chuhuichup 28°48'08"N, 107°24'43"W, elev. 2426 m, 23.VI.1987, B. Kondratieff and R. Baumann leg. 2♂ in glycerin (USNM).

Etymology. We name this species in honor of Dr Ralph Holzenthal in recognition of his great contribution to the knowledge of the systematics and distribution of Neotropical caddisflies.

Distribution. All the specimens were collected at Sierra Tarahumara, the mountainous region of Chihuahua State (Fig. 6).

***Xiphocentron (Antillotrichia) pineroi* Bueno, Vilarino & Barba, sp. nov.**

<http://zoobank.org/27C736E6-3A0A-4383-A5CF-A15EB24D1612>

Figures 4, 6

Diagnosis. This new species is similar to other species with a mesal sclerite on the inferior appendages. The new species is particularly similar to *Xiphocentron (Antillotrichia) surinamense* Flint, 1974, and *Xiphocentron (Antillotrichia) pintada* Flint, 1983 due to the shape of tergum IX and the mesal sclerite. *Xiphocentron (Antillotrichia) pineroi* sp. nov. can be distinguished from *X. (Antillotrichia) surinamense* by the longer and thinner sternum IX, preanal and inferior appendages in lateral view. It is distinguished from *X. (Antillotrichia) pintada* by its longer, sinuous mesal sclerite in lateral view, and by the deeper mesal emargination of sternum IX in dorsal view.

Description. Adult. Forewing length 6.0 mm. Color in alcohol pale. Tibial spur formula 2–4–3. Hind tibia apical spurs not modified. Sternum V bearing pair of reticulated regions.

Male genitalia. Tergum IX in lateral view, ovate, anterior margin rounded, posterior margin rectilinear, dorsal margin produced posterad. In dorsal view anterior margin with narrow, V-shaped, mesal emargination. Apical margin with acute mesal emargination. Sternum IX ovate, in lateral view, about twice as long as high; anterior margin with elongate, slender, pointed, mesal apodeme; ventral margin convex; dorsal margin subtriangular; in ventral view, anterior margin rectilinear; posterior margin with short, rounded, mesal emargination. Tergum X, in lateral view, cylindrical, narrow basally, mesally wider, circular apically. In dorsal view, subtriangular, wide basally, narrow apically; lateral surface sclerotized, each sclerotized side fused mesally; apex with deep, V-shaped emargination, forming two lobes; in ventral view, subtriangular, wide basally, narrow and cleft apically, forming two apicomeral pro-

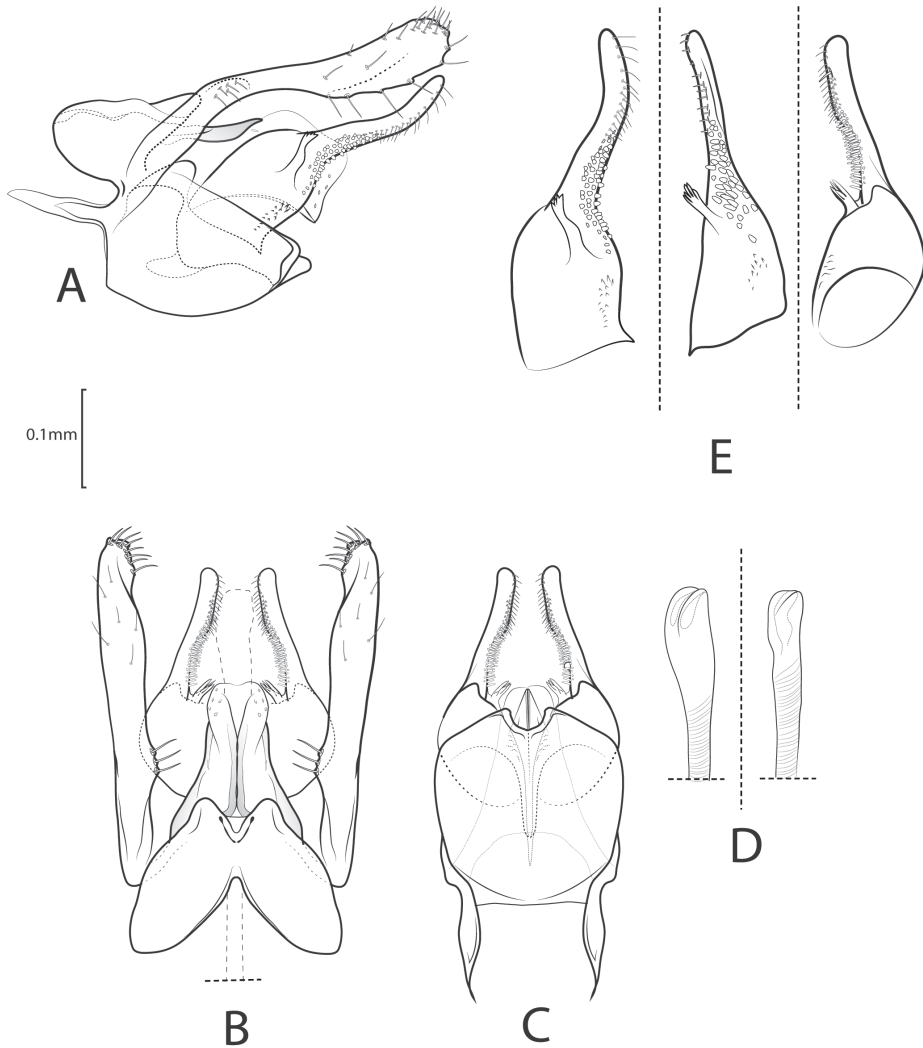


Figure 4. *Xiphocentron* (*Antillotrichia*) *pineroi* sp. nov., holotype, adult, ♂, genitalia **A** left lateral **B** dorsal **C** ventral **D** phallus apex, left lateral and dorsal **E** detail of right inferior appendage mesal surface, lateral, ventro-lateral, and ventral view.

jections. Preanal appendages elongated, about twice as long as segment X and setose. In lateral view, basally directed posterodorsally, then bent posterad, constricted at mid-length, apex rounded. In dorsal view, narrowed at base and sinuous, rectangular preapically, apex rounded, rugose. Inferior appendages long, shorter than preanal appendages, basal section with narrow and sinuous sclerite bearing small spines at apex; in lateral view, basal section broad, apical section longer than basal region, slender; in dorsal view, apex rectangular, basal section rounded; mesal surface with

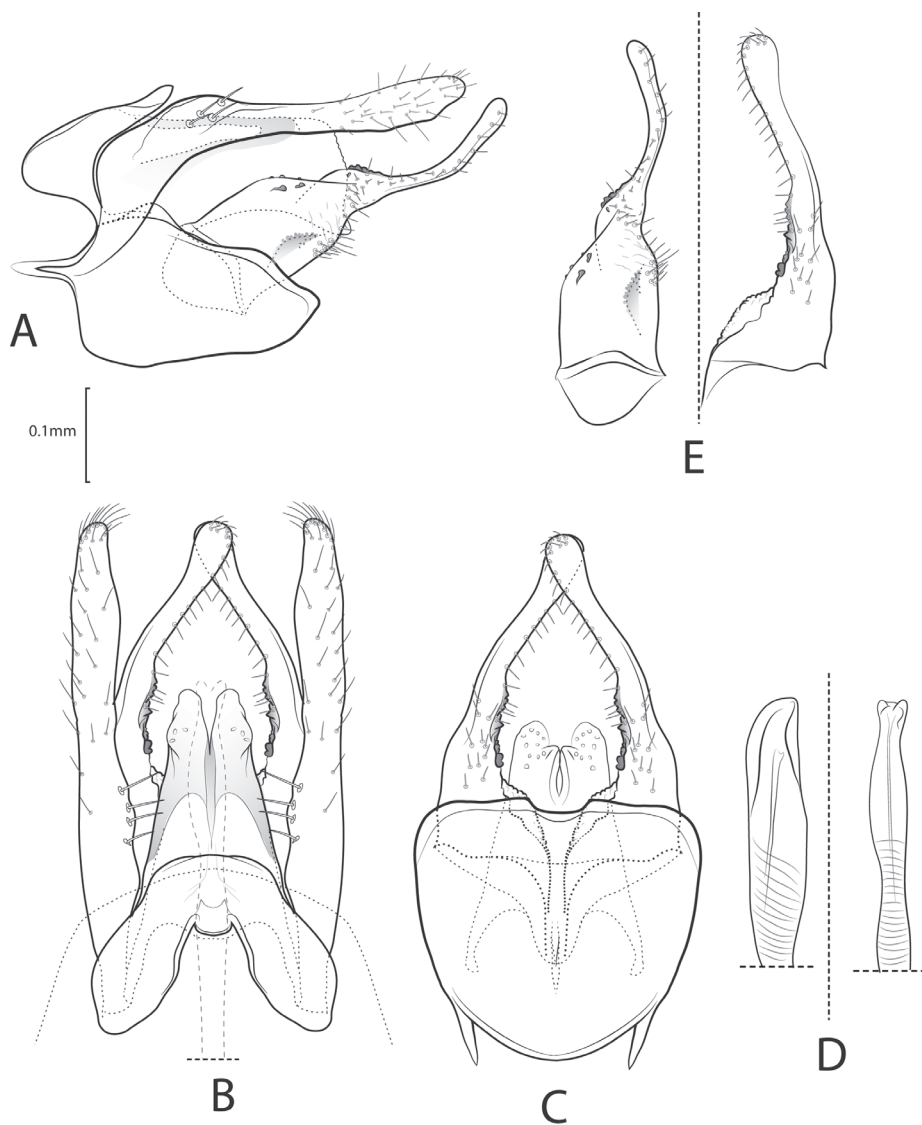


Figure 5. *Xiphocentron* (*Antillotrichia*) *rhamnes* Schmid, 1982, adult, ♂, genitalia **A** left lateral **B** dorsal **C** ventral **D** phallus apex, left lateral and dorsal **E** detail of right inferior appendage mesal surface, lateral, and ventral view.

row of several short spine-like setae and narrow sclerite; in ventral basal section rugose near basal plate; basal plate long, about as long as half sternum IX length. Phallus long, slender, tubular, apex enlarged.

Female. Unknown.

Type material. Holotype: ♂ **MEXICO: Tabasco,** Mpio. Huimanguillo Ejido Villa de Guadalupe 1a Secc. Cascada Cerro de Las Flores Rta. Malpasito-Carlos A. Madrazo

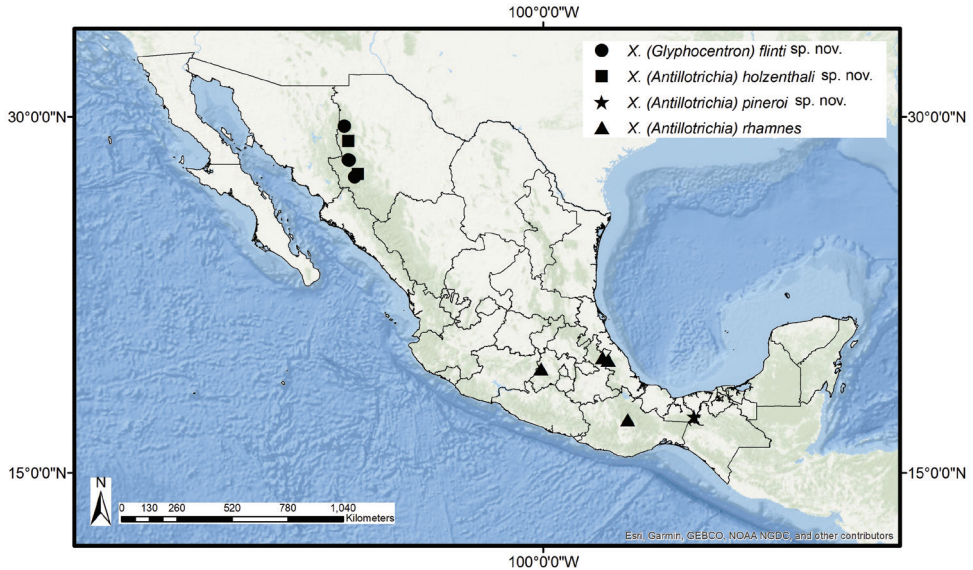


Figure 6. Mexican distribution of the new species of *Xiphocentron* and *X. (Antillotrichia) rhamnes* Schmid, 1982.

17°21'39"N, 93°37'29"W, elev. 540 m, 16.III.2000, J. Bueno, R. Barba, A. Rojas leg. in glycerin (CNIN).

Etymology. We take great pleasure in naming this species for Dr Daniel Ignacio Piñero-Dalmau in recognition of his great contributions to the knowledge of the genetics of populations and conservation of Mexican plants.

Distribution. The holotype was collected at a waterfall in a rain forest in Tabasco State (Fig. 6).

Xiphocentron (Antillotrichia) rhamnes Schmid, 1982

Figures 5, 6

Material analyzed. **MEXICO: Veracruz,** N. Huatusco, 19°8'53"N, 96°58'1"W, elev. 1344 m, 31.VII.1966, O.S. Flint and M.A. Ortiz leg. 1♂ pinned (USNM-ENTO1028628) [holotype]. **Estado de México,** Mpio. Villa de Allende, km 60 Carr. Toluca-Valle de Bravo San Cayetano, 19°22'14"N, 100°5'15"W, elev. 2516 m, 13.VI.2003, M. Razo and L. Oñate leg. 2♂ pinned (CNIN). **Puebla,** Mpio. Progreso, Río San Juan 5.8 km N de Tlatlauquitepec, 19°50'14"N, 97°30'48"W, elev. 2003 m, 28.VI.1996, A. Contreras and R. Barba leg. 1♂ in glycerin (CNIN). **Oaxaca,** Santa María de Yavesia, 17°13'36"N, 96°25'35"W, elev. 2062 m, 16.VIII.2001, J. Bueno, R. Barba and A. Ibarra leg. 9 ♂♂ in glycerin (CNIN) [specimen illustrated]. **Veracruz,** Altotonga, Río Pancho Pozas 19°44'42"N, 97°14'52"W, elev. 2008 m, 25.VII.1994, B. Kondratieff and R. Baumann leg. 1♂ in glycerin (CNIN).

Distribution. Mexico; Estado de México, Puebla, Oaxaca, and Veracruz states (Fig. 6).

Remarks. In the original description, Schmid (1982) did not provide the full depiction of the dorsal and ventral view of the male genitalia of this species. Therefore, some characters cannot be observed, such as the shape of the anterior margin of the tergum IX in dorsal view and the basal crenulate area of the inferior appendage in ventral view. The holotype is fixed in a permanent slide in dorso-lateral view. To avoid damaging it, we illustrated another identified specimen (from Oaxaca) and analyzed the holotype with material from the same province of the holotype (Veracruz) and other regions of Mexico.

Discussion

According to the biogeographic provinces proposed by Morrone et al. (2017), *X. (Antillotrichia) holzenthali* sp. nov. and *X. (Glyphocentron) flinti* sp. nov. are distributed in the Nearctic region of Mexico (Fig. 6), particularly in the province of Sierra Madre Occidental (in the Gran Meseta and Cañones Chihuahuenses and Sierras and Subcañadas del Norte subprovinces). This province presents the largest mountain system in the country, with altitudes of 2000–2500 m a.s.l. (Morrone et al. 2017). The collection sites of *X. (Antillotrichia) holzenthali* sp. nov. are located at 2060 m on average, and *X. (Glyphocentron) flinti* sp. nov. at 1809 m. Both species are distributed in places with Subhumid Temperate Climate (Cw) (García and CONABIO 1998) and vegetation consisting of conifer and oak forests. These species are the first representatives of the family Xiphocentronidae recorded from northwestern Mexico. The biogeographical analysis of *Caenocentron* suggests that these western mountain ranges were an important dispersal area of early radiations during the Oligocene (Vilarino et al. in press); this might also be true for the radiation of other groups within Xiphocentronidae. The distribution of *X. (Antillotrichia) rhamnes* is found within the Mexican Transition Zone in the Transverse Volcanic Province and the Province of Sierra Madre del Sur, at an average altitude of 2133 m, which is characterized by a subhumid temperate climate (Cw) and vegetation commonly consisting of coniferous and oak forests. *Xiphocentron (Antillotrichia) pineroi* sp. nov. is the southernmost occurring of these species and is distributed in the Neotropical region, where it occurs in the Veracruz Province but is restricted to the Sierra Norte de Chiapas subprovince. The type locality has an altitude of approximately 740 m, a tropical rainforest climate (Af) (García and CONABIO 1998), and a tropical evergreen forest vegetation type.

Conclusion

Previously, 15 extant (Bueno-Soria 2010) and one fossil (Wichard et al. 2006) species of *Xiphocentron* were known from Mexico. With the addition of three new species

described here, the number of *Xiphocentron* species known from Mexico is now 19. However, many species are still only known from their type locality, and many regions remain poorly explored for the genus, particularly the Sierra Madre Occidental and Sierra Madre del Sur along the Pacific Coast. Therefore, more collections are necessary to obtain a better idea of the distribution and actual diversity of the genus *Xiphocentron* in Mexico.

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Caddisflies (Trichoptera) checklist and a new species of *Helicopsyche* von Siebold, 1856, from the Brejo de Altitude de Triunfo, a relict rainforest within the Caatinga domain, Northeast Brazil

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Abstract

Brejos de Altitude are evergreen seasonal forests, associated with plateau regions in the middle of the Caatinga domain in Northeast Brazil, which possibly acted as biological corridors between the Atlantic Forest and the Amazon rainforest during the Pleistocene. The first entomological survey in the highest point in the state of Pernambuco, Brazil, the Brejo de Altitude de Triunfo, was implemented and resulted in a checklist of caddisflies with six families, nine genera, and eleven species, including a new species. *Helicopsyche ralphi* **sp. nov.** is described and illustrated, based on all semaphoronts. A key to Brazilian *Helicopsyche* (*Feropsyche*) Johanson, 1998 species is also provided. In addition to the caddisfly survey in the Brejos de Altitude, the results include new records for the state, region, and also for the country. Thus, this study updates the number of species in the Brazilian Northeast region and Pernambuco state to 169 species and 43 species, respectively.

Keywords

Aquatic insects, distribution, *Helicopsyche* (*Feropsyche*), larvae, semaphoronts, snail-case caddisfly, taxonomy

Introduction

The Caatinga domain is a mosaic of xerophyte forest of 912,529 km² in Northeastern Brazil (da Silva et al. 2017), delimited by the Atlantic Forest, Amazon rainforest and Cerrado domains. Previously, the area that today comprises Caatinga was a connection between the Atlantic Forest and Amazon rainforest (Santos et al. 2007; Batalha-Filho et al. 2013). The palynological profile from the late Pleistocene (0.9 Mya) in the Caatinga domain revealed a high concentration of pollen of taxa found in the present Atlantic Forest and Amazon rainforest, probably reflecting a connection of these domains during this period (Costa et al. 2017; Ledo and Colli 2017). The initial separation of these regions possibly occurred because of the Andean uplift, which changed the climate and consequently the vegetation of South America (Morley 2000). These changes led to the modification and emergence of a “dry diagonal”, an area with more xeric habitats, separating the two forests (Costa et al. 2017). This splitting process started in the Miocene (5.6–23 Mya), but the total separation occurred only in the early Pleistocene (the last 5.5 Mya) (Batalha-Filho et al. 2013; Costa et al. 2017; Ledo and Colli 2017). Subsequently, the Caatinga domain has been characterized by a xerophyte forest mosaic, with some islands of humid tropical forests, named Brejos de Altitude (Andrade-Lima 1982; Ledo and Colli 2017). Possibly due to this recent separation many sister species and lineages have disjunct distributions in the Atlantic Forest and Amazon rainforest (Borges-Nojosa and Caramaschi 2003; Batalha-Filho et al. 2013; Ledo and Colli 2017; Silveira et al. 2019).

Brejos de Altitude represent forest refuges enclaved in the Caatinga domain (Pereira-Filho and Montingelli 2011). These areas are a mosaic composed of Atlantic Forest and Amazon biotic components, and they have climatic, edaphic, and topographical features different from their semiarid surroundings (Borges-Nojosa and Caramaschi 2003), and harbor a peculiar biodiversity of amphibians and reptiles (e.g., Pereira-Filho and Montingelli 2011; Castro et al. 2019a, b; Quirino et al. 2019), insects (e.g., Silva et al. 2007; Santos et al. 2011; Silva et al. 2019), and plants (e.g., Rodal et al. 2005; Machado et al. 2012; Araujo et al. 2019). The Brejos de Altitude possibly originated from climatic fluctuations that occurred during the Pleistocene, allowing the expansion of Atlantic Forest into currently semiarid locations in areas with a favorable microclimate during the shrinkage process (Behling et al. 2000; Auler et al. 2004; Silveira et al. 2019).

Brejos de Altitude environments also play an important role in freshwater flow, and as a consequence of orographic rains, several headwater streams emerge from them (Andrade-Lima 1982; Araújo et al. 2007). Headwater streams represent essential habitats for taxa primarily associated with these environments, such as some families of Trichoptera (Richardson 2019).

Trichoptera is the most diverse order of strictly aquatic insects, with ~ 16,300 extant species, 632 genera and 63 families (Morse 2022). Of these, ~ 3,300 species, 25 families, and 155 genera were recorded in the Neotropical region (Holzenthal and Calor 2017; Morse et al. 2019). In Brazil, ~ 900 species of Trichoptera are recorded

(Santos et al. 2022). Although our knowledge of caddisflies from Brazil has increased in the last years (Vilarino and Calor 2017), the Atlantic Forest and Amazon rainforest contain the most concentrated species records, possibly as a consequence of research groups established in these regions for a longer time. On the other hand, our knowledge of caddisflies from the Caatinga has increased, with 77 species (14 endemic) now known (Santos et al. 2022). Currently there are 39 species of Trichoptera reported for Pernambuco state (Souza et al. 2013a; Gomes and Calor 2019; Pereira et al. 2020), of which three are representatives of Helicopsychidae: *Helicopsyche* (*Cochliopsyche*) *clara* (Ulmer, 1905), *Helicopsyche* (*Feropsyche*) *tapadas* Denning, 1966, and *Helicopsyche* (*Feropsyche*) *vergelana* Ross, 1956 (Souza et al. 2013a; Pereira et al. 2020). In all Brejos de Altitude, only three caddisfly species [*Macrostemum hyalinum* (Pictet, 1836), *Oxyethira tica* Holzenthal & Harris, 1992, and *Atopsyche antisuya* Schmid, 1989] have been recorded, in França et al. (2013), Souza and Santos (2017), and Gomes and Calor (2019), respectively.

Trichoptera are holometabolic insects, presenting an egg, larva (generally five instars), pupa and adult stage (Holzenthal et al. 2015). For most insects, the morphology of females and immatures is little known, because descriptions and identification tools have a male bias (Yeo et al. 2018). This shortfall of knowledge of the semaphoronts (Haeckelian shortfall) (Faria et al. 2020) is exaggerated in *Helicopsyche*, where only 19 immature stages and 63 adult females of the 130 valid species from the Neotropical region are known (four immatures and 13 adult females from Brazil), but most have no description of these semaphoronts (only 17 immatures and 25 adult females have descriptions) (Johanson 2002; Holzenthal and Calor 2017; Morse 2022). The subgenus *H.* (*Feropsyche*) has knowledge shortfalls of the species (Linnean shortfalls), since ~40% were described only in the 21st century (e.g., Johanson 2003; Johanson and Malm 2006; Johanson and Holzenthal 2010; Rueda-Martín and Miranda 2015; Vilarino and Calor 2017; Dumas and Nessimian 2019), and many species to be described. Considering the significant reduction of vegetation in the Brazilian Northeast Atlantic Forest, the Brejos de Altitude constitute areas of high priority for conservation (SOS Mata Atlântica & INPE 2019; Pereira-Filho et al. 2020). Here we present the first study of caddisfly fauna from a Brejo de Altitude with a commented checklist. Additionally, we present the description of *Helicopsyche ralphi* sp. nov., based on adult males and females and immature stages, and a key to Brazilian *Helicopsyche* (*Feropsyche*) species.

Materials and methods

The Brejo de Altitude de Triunfo (07°50'17"S, 38°06'06"W) is located in the Baixo Pajeú region and represents the highest altitude mountain in the Pernambuco state, Brazil, with altitude of 500–1,260 m. The area is predominantly composed of seasonal semideciduous forest, exhibiting average rainfall of 1,222 mm/year, with higher rainfall occurring in March and April (Tabarelli and Santos 2004). Specimens were collected between 2017 to 2019 from the following sites: (A) Pico do Papagaio stream;

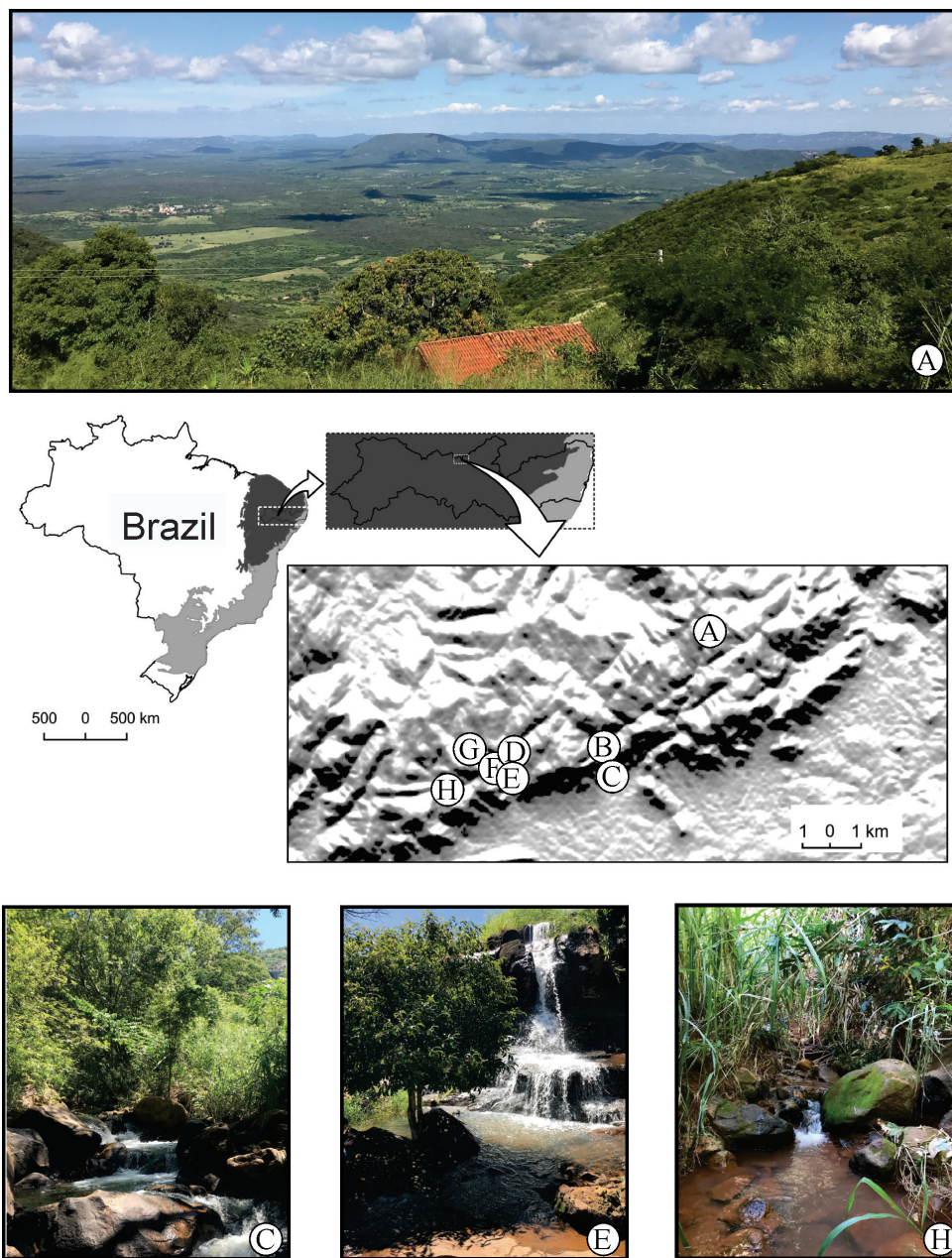


Figure 1. Distribution map of the sampling sites in the Brejo de Altitude de Triunfo, Pernambuco state, Brazil
A Pico do Papagaio stream **B** Grito stream **C** Laje stream **D, E, F** Pinga stream **G** Alfinim stream **H** Icó stream.

(B) Grito stream; (C) Laje stream; (D, E, and F) Pinga stream; (G) Alfinim stream, and (H) Icó stream (Fig. 1, Table 1). Adults were collected by means of light bulbs (ultraviolet and white lights) attached to a white sheet, UV light pan trap (Calor and

Table 1. Collection data from Brejo de Altitude de Triunfo, with the sample of each collection site, geographic coordinates, elevation, date, traps (LPT = UV Light Pan Trap, MAL = Malaise and WSA = White Sheet Attraction), and acronyms of collectors.

Sample	Collection sites	Geographic coordinates	Elevation (a.s.l.)	Date	Trap	Acronyms of collectors
A1	Pico do Papagaio stream	7°49'36"S, 38°3'32"W	1050 m	02.v.2019	LPT	ACS, RP
B1	Grito stream	7°51'41"S, 38°5'25"W	740 m	07.viii.2018	LPT	ACS
B2		7°51'41"S, 38°5'25"W	740 m	09.viii.2018	LPT	ACS
B3		7°51'41"S, 38°5'25"W	740 m	09.x.2018	LPT	ACS
C1	Laje stream	7°52'13"S, 38°5'18"W	580 m	07.viii.2018	LPT	ACS
C2		7°52'13"S, 38°5'18"W	580 m	08.ix.2018	LPT	ACS
C3		7°52'13"S, 38°5'18"W	580 m	10.x.2018	LPT	ACS
C4		7°52'13"S, 38°5'18"W	580 m	i.2019	MAL	ACS
C5		7°52'28,2"S, 38°8'15,6"W	570 m	02.v.2019	LPT	ACS, RP
C6		7°52'28,5"S, 38°8'13,6"W	560 m	02.v.2019	LPT	ACS, RP
C7		7°52'28,5"S, 38°8'15,3"W	860 m	03.v.2019	LPT	ACS, RP
D1	Pinga stream	7°52'3"S, 38°7'13"W	890 m	16.xii.2017	LPT	ACS
D2		7°52'3"S, 38°7'13"W	890 m	18.xii.2017	LPT	ACS
D3		7°52'3"S, 38°7'13"W	890 m	21.ix.2017	LPT	ACS
D4		7°52'3"S, 38°7'13"W	890 m	07.ii.2018	LPT	ACS
D5		7°52'3"S, 38°7'13"W	890 m	09.ii.2018	LPT	ACS
D6		7°52'3"S, 38°7'13"W	890 m	06.viii.2018	WSA	ACS
D7		7°52'3"S, 38°7'13"W	890 m	06.viii.2018	LPT	ACS
D8		7°52'3"S, 38°7'13"W	890 m	07.viii.2018	LPT	ACS
D9		7°52'3"S, 38°7'13"W	890 m	21.viii.2018	LPT	ACS
D10		7°52'3"S, 38°7'13"W	890 m	ix.2018	MAL	ACS
D11		7°52'3"S, 38°7'13"W	890 m	09.x.2018	LPT	ACS
D12		7°52'3"S, 38°7'13"W	890 m	03.ii.2019	LPT	ACS
D13		7°52'3"S, 38°7'13"W	890 m	07.ii.2019	LPT	ACS
D14		7°52'3"S, 38°7'13"W	890 m	09.ii.2019	LPT	ACS
D15		7°52'3"S, 38°7'13"W	890 m	10.ii.2019	LPT	ACS
D16		7°52'3"S, 38°7'13"W	890 m	11.iii.2019	LPT	ACS
D17		7°52'3"S, 38°7'13"W	890 m	16.iv.2019	LPT	ACS
D18		7°52'5,5"S, 38°7'15,6"W	870 m	01.v.2019	LPT	ACS, RP
D19		7°52'4,7"S, 38°7'15,3"W	860 m	01.v.2019	LPT	ACS, RP
D20		7°52'5,5"S, 38°7'15,7"W	865 m	01.v.2019	LPT	ACS, RP
D21		7°52'3,2"S, 38°7'13,8"W	840 m	01.v.2019	LPT	ACS, RP
D22		7°52'3,2"S, 38°7'13,8"W	840 m	02.v.2019	LPT	ACS, RP
E1	Alfinim stream	7°51'44"S, 38°7'52"W	940 m	08.viii.2018	LPT	ACS
E2		7°51'44"S, 38°7'52"W	940 m	08.viii.2018	WSA	ACS
F1	Icó stream	7°52'28,8"S 38°8'15,8"W	800 m	01.v.2019	LPT	ACS, RP
F2		7°52'28,5"S, 38°8'15,3"W	810 m	02.v.2019	LPT	ACS, RP
F3		7°52'28,5"S, 38°8'15,8"W	800 m	02.v.2019	LPT	ACS, RP

Mariano 2017), and Malaise trap. Immature stages were collected manually. All specimens were preserved in 80% ethanol. For each collector, an acronym was designated, as follows: ACS for Amanda Cavalcante-Silva and RP for Rafael Pereira.

The map with collection sites was created using QGIS 3.4.15 and finalized in Corel Draw X5. The species distribution data were obtained from Holzenthal and Calor (2017) for the Neotropical region and Queiroz et al. (2020) and Santos et al. (2022) for Brazil. New records for Pernambuco state are indicated in the species distribution. Genitalia of males and females were diaphanized in 10% KOH solution

or lactic acid (Betten 1934; Blahnik and Holzenthal 2004; Blahnik et al. 2007) and stored in microtubes with glycerin. Association between immature and adult stages was done using the metamorphotype method (Milne 1938).

The illustrations were made with the aid of a microscope equipped with a camera lucida, scanned, and finalized in Adobe Illustrator CS6. Microphotographs were made with a Leica stereoscope equipped with a digital camera, Nikon model DS-Fi1 and finalized in Corel Draw X5. Descriptions were made using the DELTA system (Dallwitz et al. 1999). The terminology applied to the morphological structures of adults follows Johanson (1998), with adaptations of Holzenthal et al. (2016), and immature follows Monson et al. (1988) and Waringer et al. (2017). The type specimens will be deposited at the following institutions: Museu de Zoologia da Universidade São Paulo, São Paulo (MZSP), Museu de História Natural da Bahia, Universidade Federal da Bahia, Salvador (UFBA), Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (DZRJ), and Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), as indicated in the material examined section.

Results

Helicopsyche (Feropsyche) ralphi sp. nov.

<http://zoobank.org/15602B59-C063-4007-82C0-9141BD06D2BE>

Figs 2–7

Material examined. Holotype. BRAZIL, 1 male; Pernambuco, Triunfo, Pinga stream; 7°52'3"S, 38°7'13"W, el. 890 m; 21.ix.2017; Cavalcante-Silva, A. leg.; UV light pan trap (MZSP). **Paratypes.** Same data as holotype, except 5 males; Grito stream; 7°51'41"S, 38°5'25"W, el. 740 m; 09.viii.2018 (UFBA); same except 3 males; Laje stream; 7°52'13"S, 38°5'18"W, el. 580 m; 07.viii.2018 (DZRJ); same except 6 males; Pinga stream; 7°52'3"S, 38°7'13"W, el. 890 m; 21.ix.2017 (MZSP); same except 6 males (INPA); same except 1 female; 7°52'3"S, 38°7'13"W, el. 890 m; 03.ii.2019 (MZSP); same except 5 females; 7°52'5,5"S, 38°7'15,6"W, el. 870 m; 01.v.2019; Cavalcante-Silva, A, Pereira, R. leg. (MZSP); same except 6 females; 7°52'5,5"S, 38°7'15,7"W, el. 865 m; 01.v.2019 (UFBA); same except 6 females (DZRJ); same except 6 females (INPA).

Diagnosis. The new species is distinguished from all other congeners by the following characters of the male genitalia: inferior appendage subtriangular, acuminate in posterior region, basomesal lobe subtriangular ~ 1/2 the length of the inferior appendage, in lateral view, trapezoid, with spine-like setae in posterior margin, in ventral view; abdominal segment X slender, slightly cleft at the apex, in dorsal view. The characters of the genitalia of new species are morphologically similar to *Helicopsyche flinti* Johanson (1999). The new species presents abdominal segment X with a rounded apex, and a medial row of spine-like setae, in dorsal view (while *H. flinti* presents abdominal

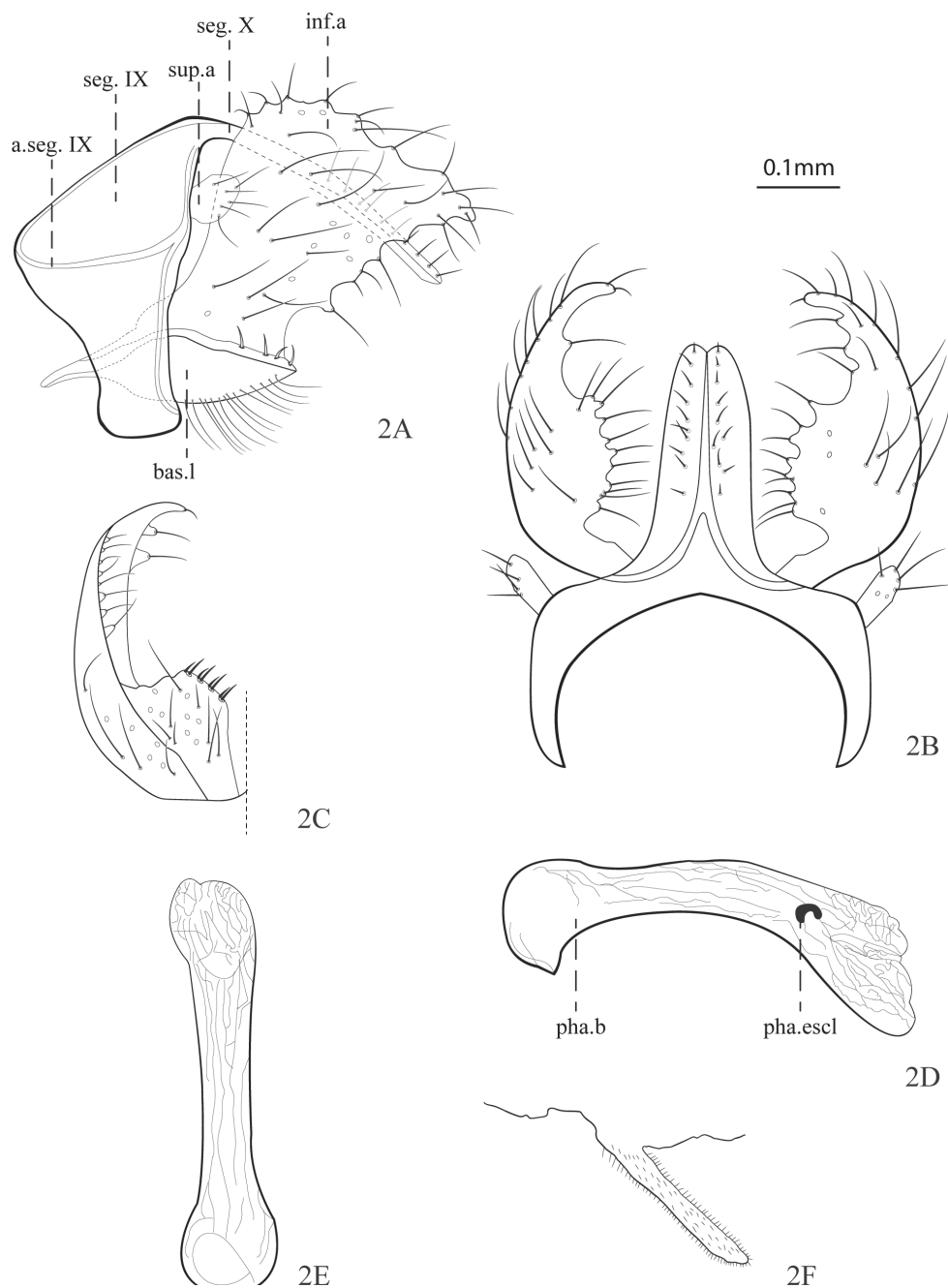


Figure 2. *Helicopsyche ralphi* sp. nov., male **A** genitalia, lateral view **B** segments IX and X and inferior appendages, dorsal view **C** inferior appendage, ventral view **D** phallus, lateral view **E** phallus, ventral view **F** sternum VI, lateral view. Abbreviations: seg. IX = abdominal segment IX; a.seg. IX = apodeme of abdominal segment IX; sup.a = superior appendage; seg. X = abdominal segment X; bas.l = basomesal lobe; inf.a = inferior appendage; pha.b = phallobase; pha.scl. = phallotremal sclerite.

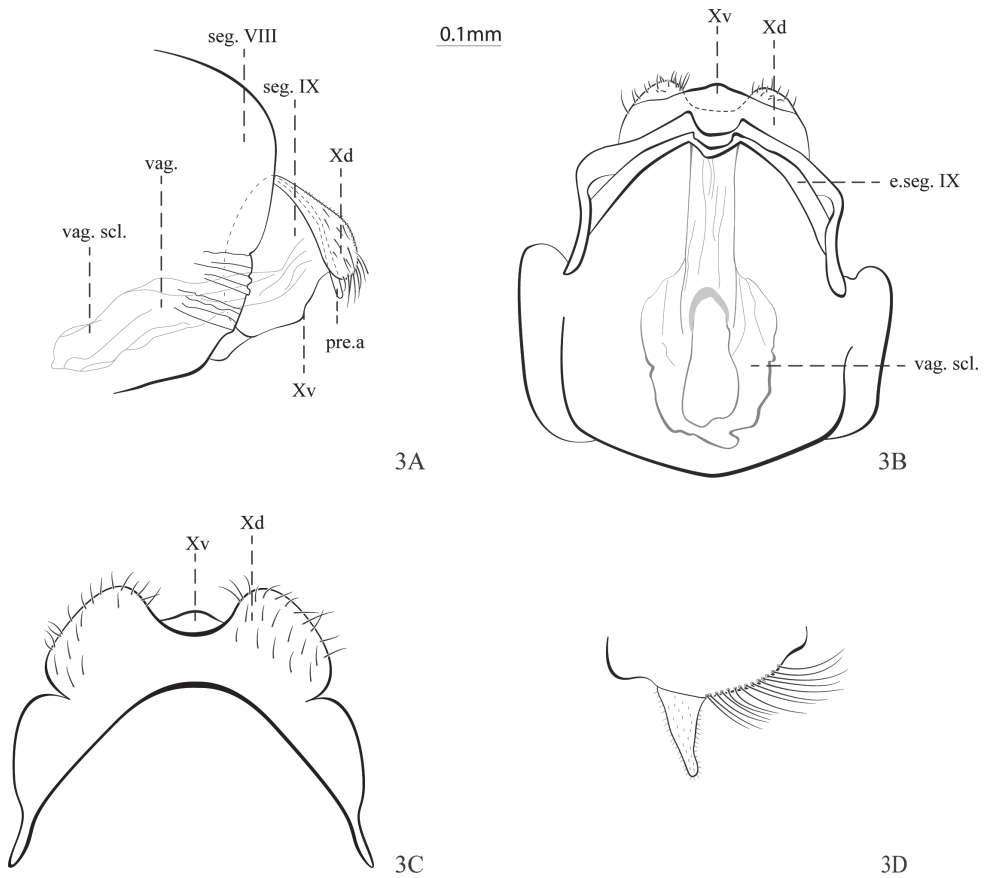


Figure 3. *Helicopsyche ralphi* sp. nov., female **A** genitalia, lateral view **B** genitalia, ventral view **C** genitalia, dorsal view **D** sternum VI, lateral view. Abbreviations: seg. VIII = abdominal segment VIII; seg. IX = abdominal segment IX; e.seg. IX = external part of abdominal segment IX; pre.a = preanal appendage; Xd = dorsal branch abdominal segment X; Xv = ventral branch abdominal segment X; vag. = vagina; vag. scl. = vaginal sclerite.

segment X with apex nearly straight, side row of spine-like setae), and inferior appendage with strongly projecting mesal margin, forming a large, rounded lobe, in dorsal view (while *H. flinti* presents an inferior appendage without a large mesal lobe).

Description. Adults (Fig. 4): length of forewing 4.1–5.2 mm ($n = 20$). Wings: forewing without discoidal cell, without medial cell, with thyridial cells; hind wing without discoidal cell, without thyridial cell. Head: brownish; antennae yellowish, shorter than forewing length, scape yellowish, shorter than head length, covered with long setae (Fig. 4E–G). Thorax: pronotum brownish, with warts, filiform, covered with small and ferruginous setae; mesoscutum brownish, with mesoscutal warts spherical and not covered with setae; mesoscutellum brownish, with mesoscutellar warts spherical and not covered with setae (Fig. 4G); legs yellowish, tibial spur formula 2,2,4.

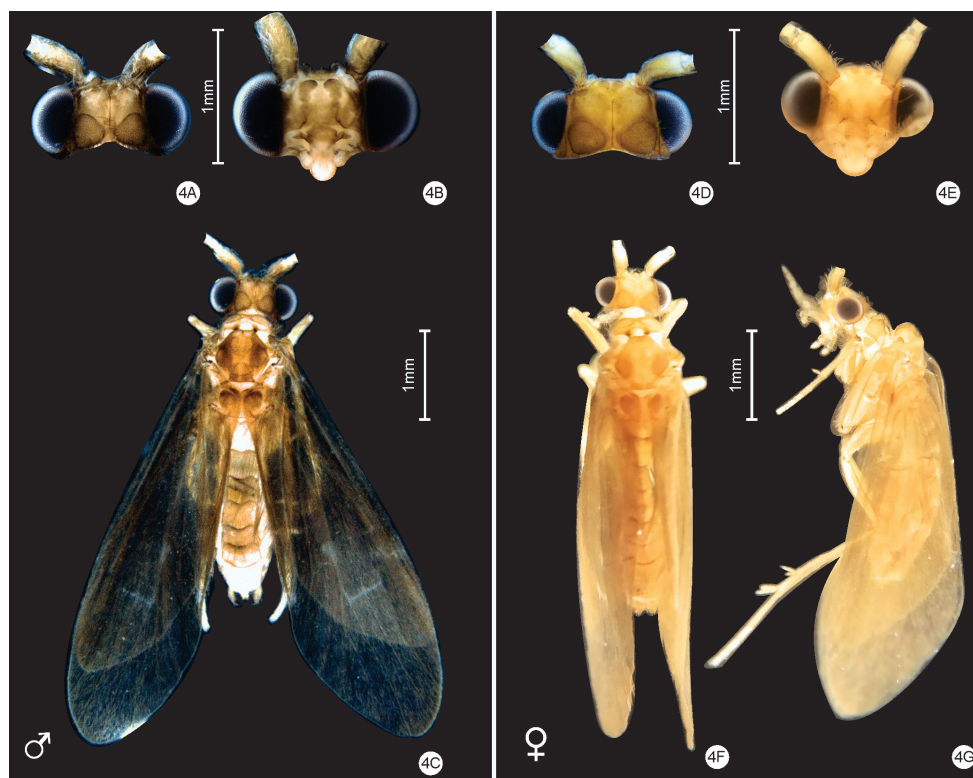


Figure 4. *Helicopsyche ralphi* sp. nov., adult **A** male head, dorsal view **B** male head, frontal view **C** male habitus, dorsal view **D** female head, dorsal view **E** female head, frontal view **F** female habitus, dorsal view **G** female habitus, lateral view.

Male (Figs 2, 4A–C): body length ~ 3.3–4.6 mm ($n = 20$).

Head: interantennal warts present, brownish, spherical, covered with small setae; posteroantennal warts present, brownish, club shaped, covered with long setae; cephalic warts present, brownish, subtriangular, covered with long setae; postocular warts present, filiform, brownish, covered with long setae (Fig. 4A–C); maxillary palps yellowish, with two segments, covered with long ferruginous setae; labial palps yellowish, with three segments, covered with long ferruginous setae. Abdomen: abdominal sternum VI process present, almost same length as segment, tubular, apically rounded, covered with small microtrichiae (Fig. 2F).

Genitalia. Abdominal segment IX with slightly concave anteroventral margin in ventral half; apodeme well developed laterally, located midlaterally on segment; posterior margin nearly straight, in lateral view (Fig. 2A), anterior margin strongly concave, in dorsal view (Fig. 2B); preanal appendages setose, rounded in lateral view (Fig. 2A), clavate in dorsal view (Fig. 2B). Abdominal segment X tubular, dorsal margin slightly curved, in lateral view (Fig. 2A); slender, mesodorsal borders inverted Y-shaped, bearing two rows of short setae, near the center, in dorsal view (Fig. 2B). Inferior append-

age subtriangular, acuminate in posterior region, in lateral view (Fig. 2A); anterior margin slightly convex, posterior margin undulated and tapered apex, in dorsal view (Fig. 2B); basomesal lobe of inferior appendage, in lateral view well developed, with ventral margin covered with long setae and dorsal margin with spine-like setae, in ventral view (Fig. 2C). Phallus tubular, phallobase rounded, ventral view (Fig. 2E), acuminate at anteroventral border, in lateral view (Fig. 2D), slightly down curved; phallotremal sclerite conspicuous, moon shaped in lateral view (Fig. 2D).

Female (Figs 3, 4D–G): body length ~ 3.9–5.4 mm ($n = 20$).

Head: interantennal warts present, brownish, spherical, covered with small setae; postero-antennal warts present, brownish, covered with long setae; cephalic warts present, brownish, subtriangular, covered with long setae (Fig. 4D–F); postocular warts present, filiform, brownish, covered with long setae (Fig. 4F); maxillary palps yellowish, with 5-segments, covered with long and yellowish setae; labial palps yellowish, with 3-segments, covered with long yellowish setae (Fig. 4G). Abdomen: abdominal sternum VI process present, ~ 1/3 segment length, tubular and apically rounded, covered with small microtrichiae (Fig. 3D).

Genitalia. Abdominal segment IX is well separated from abdominal segment VIII and indistinctly separated from abdominal segment X, anterior margin convex, in lateral view (Fig. 3A); external part of abdominal segment IX apically incised, in ventral view (Fig. 3B). Preanal appendage long and filiform, in lateral view (Fig. 3A). Abdominal segment X with two branches; dorsal branch narrow, base with apex broad, rounded and covered with long setae, in lateral view (Fig. 3A), bilobed with U-shaped with apical incision, in dorsal view (Fig. 3C); ventral branch with sinuous margin, in lateral view (Fig. 3A), and apex obtuse in ventral and dorsal view (Fig. 3B, C). Vagina with thick anterior margin, in ventral view (Fig. 3B); vaginal sclerite slender along its length, in lateral view (Fig. 3A), finger-shaped projection on the anterior margin, internal sclerite long, with sclerotized lateral margins, in ventral view (Fig. 3B).

Larva (5th instar) (Figs 5A–L, 6C): Body total length 2.9–3.6 mm ($n = 10$).

Head: oval, with anterior margin 1.3 × broader than posterior margin, in dorsal view (Fig. 5A), mostly light brown, with pale region on anterolateral margin of the head capsule until antenna region, around stemmata, medial region of frontoclypeus margin, and posteromedial region of head capsule, in dorsal view (Fig. 5A), with lateral region light brown, in ventral view (Fig. 5B), cardo and anterior ventral apotome dark brown, six and eight brown muscle scars in left and right, respectively, in dorsal view (Fig. 5A), head capsule with muscle scar light brown in posterolateral region, in dorsal view (Fig. 5A), with frontal area flattened, muscle scars in basal region, cardo and ventral apotome sclerotized, ventral view (Fig. 5B); with muscle scar light brown in posterior region, in lateral view (Fig. 5C); frontoclypeus and adjacent areas nearly flat and margined with semicircular carina, frontoclypeal suture with strongly delimited margin, frontoclypeal with one muscle scar brown in medial region, and three in posterior region, in dorsal view (Fig. 5A); labrum translucent, with short setae covering the anterior margin, in ventral view (Fig. 5B); mandibles asymmetrical, each internal margin with pale, long, thin setae; left mandible with three teeth, the apical tooth trilobed,

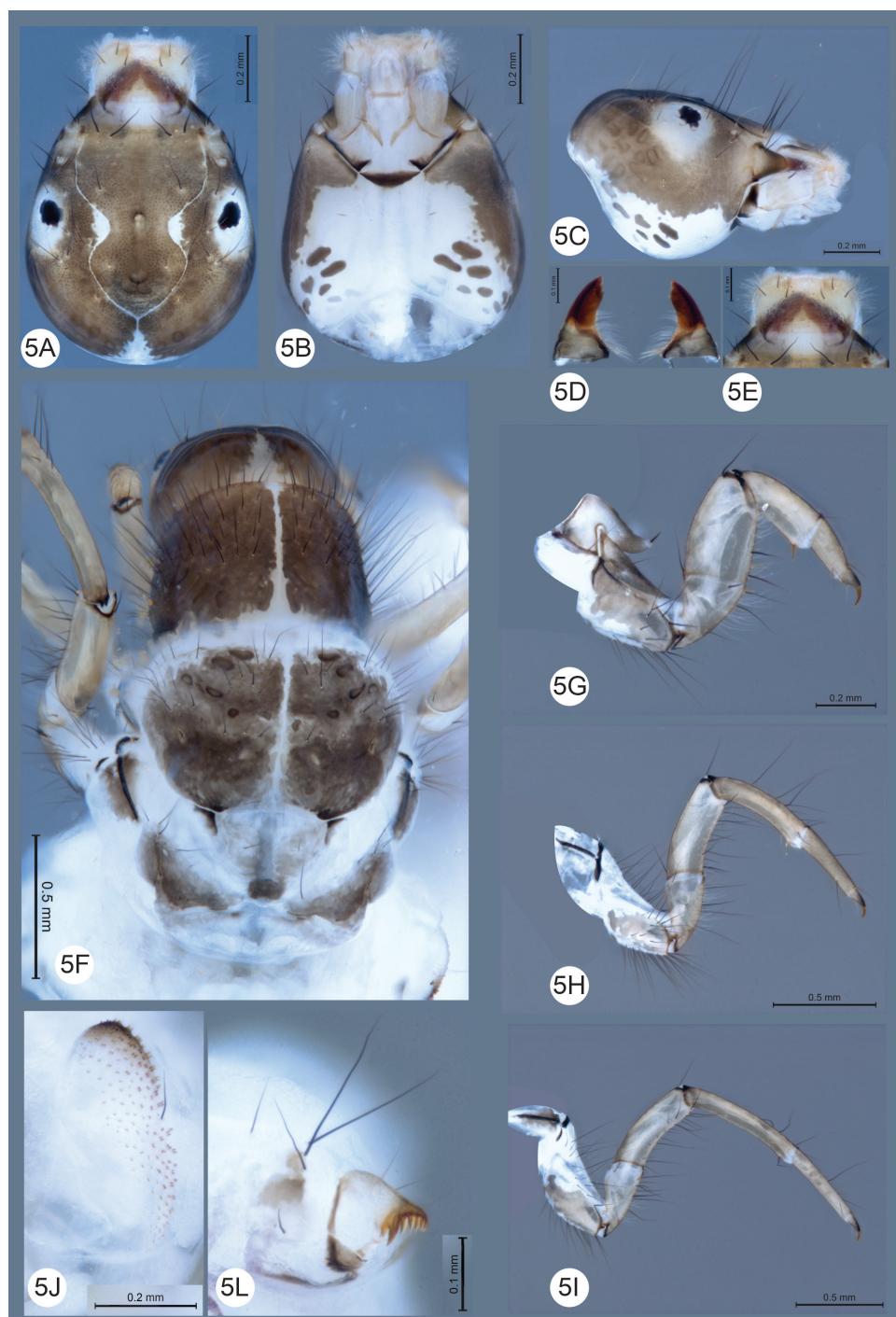


Figure 5. *Helicopsyche ralphi* sp. nov., larva **A** head, dorsal view **B** head, ventral view **C** head, left lateral view **D** mandibles, dorsal view **E** labrum, dorsal view **F** notos, dorsal view **G** proleg, lateral view **H** meso-leg, lateral view **I** metaleg, lateral view **J** lateral hump **L** anal legs.

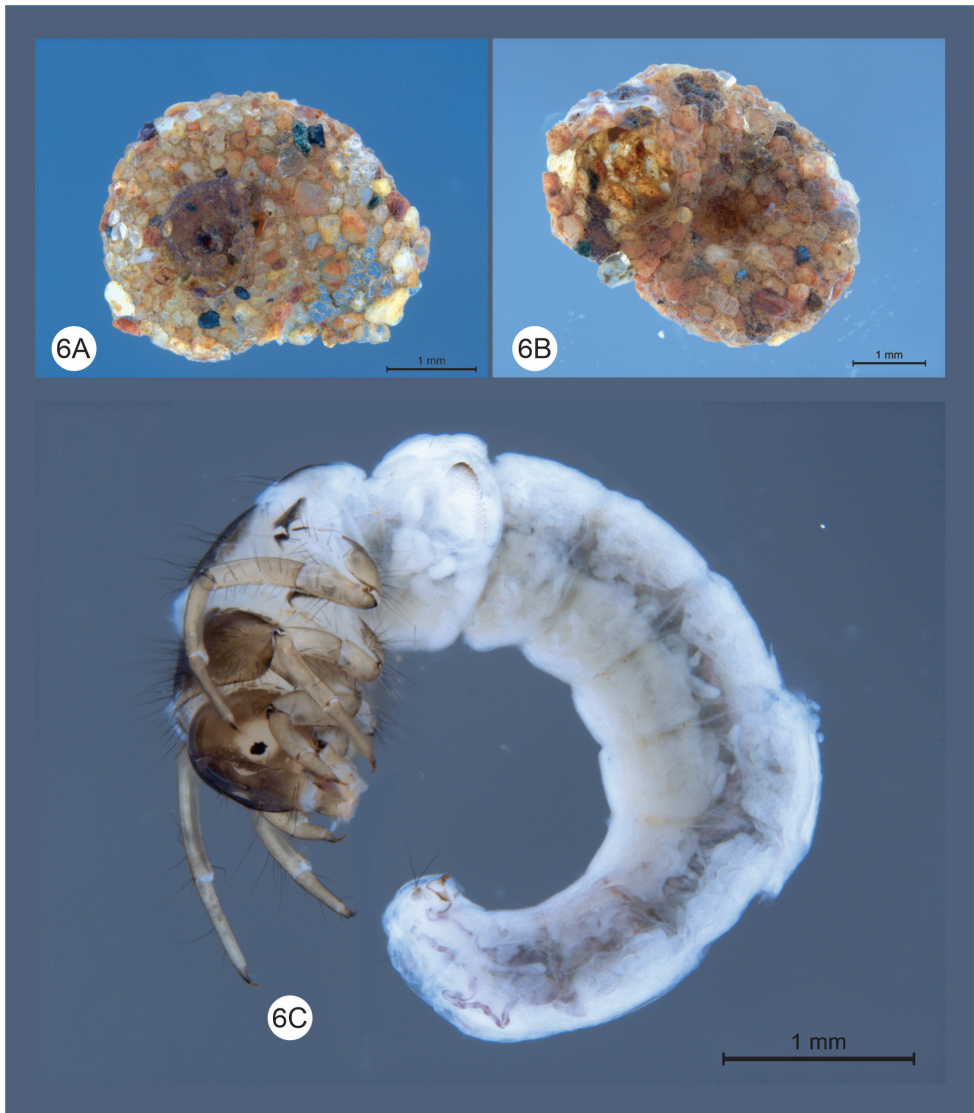


Figure 6. *Helicopsyche ralphi* sp. nov., larvae and case **A** larval case, dorsal view **B** larval case, ventral view **C** larval lateral habitus.

mesal and basal tooth acute; right mandible with three teeth, the apical tooth trilobed, mesal and basal tooth obtuse, in dorsal view (Fig. 5D–E); chaetotaxy of head as in Figure 5A–E. Thorax: pronotum brown with dark muscle scars, anterior region with row of long setae at margin, covered long setae to near medial region, posterior margin sinuous and lighter with few and scattered setae, in dorsal view (Fig. 5F), trochantin almost as long as foreleg coxae, finger shaped with one spinelike setae in apex (Fig. 5G); mesonotum lighter than pronotum, with pale regions in medial region, muscle scars in

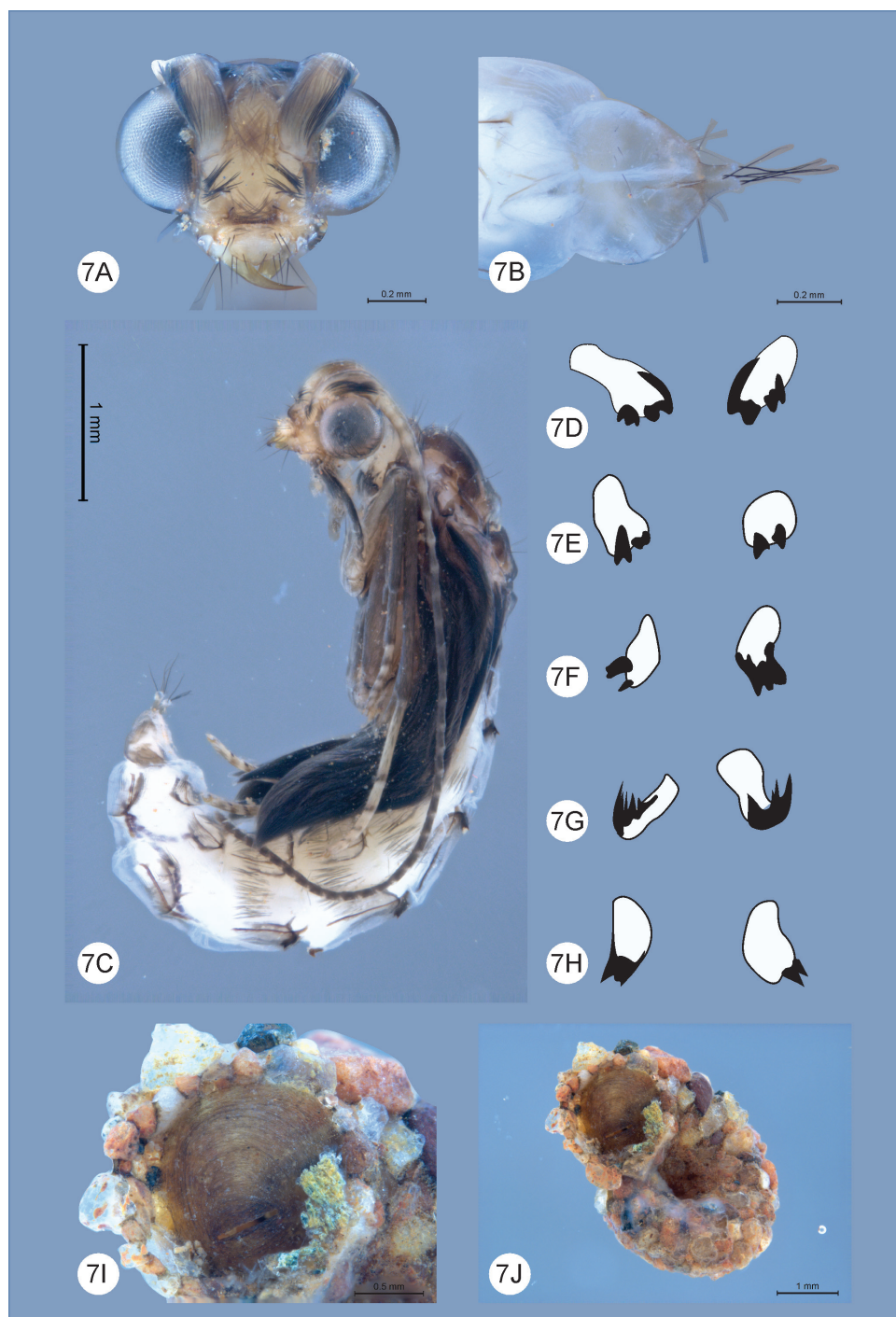


Figure 7. *Helicopsyche ralphi* sp. nov., pupa and case **A** pupa front **B** abdominal segment IX and anal processes, dorsal view **C** pupa lateral habitus **D–H** abdominal segments I–V, dorsal, with details of dorsal hook plates **I** pupa case, ventral view **J** pupa case with sieve membrane highlighted, ventral view.

dark brown shades, four pairs in anterior region and one pair in posterior region, posterior margins angulate, in dorsal view (Fig. 5F); metanotum with three pairs of sclerites, two pairs of anteromesal (sa1) sclerites small, one pairs anterior subtriangular, and one pairs irregular bearing one setae and one pair of posterior subtriangular sclerites (fused sa2 and sa3 sclerites), each bearing single seta posteromesally (sa2) and several setae anterolateral (sa3), in dorsal view (Fig. 5F); lateral hump oval, apical region mostly dark, one short setae in anteromedial region (Fig. 5J); thoracic legs with chaetotaxy as in Figure 5G–I; The foreleg has a length equivalent to 2/3 of the midleg and 1/2 of the hindleg, foreleg segments robust and short, mid and hind leg segments filiform and long (Fig. 5I). Abdomen: anal prolegs each with lateral sclerites curved, anal claw elongates, with accessory parallel teeth pectinate, arranged like comb (Fig. 5L).

Larval case (Figs 6A–B, 7I–J): length 2.9–3.6 mm ($n = 10$). Made with cemented sand grains, forming a snail-like, helical case, case with two 1/2 whorls at the end of the phase, with umbilicus open and deep.

Pupa (Fig. 7A–J): body length 3.3–4.1 mm ($n = 10$). Generally dark brown, almost black, with yellowish abdomen; Head: mandibles curved with wide bases, each with length $2.5 \times$ basal width, apex pointed and internal margin smooth (Fig. 7A). Abdomen: paired anterior dorsal hook plates on segments II–V, pair of posterior dorsal hook plates on segment IV asymmetrical; general morphology of dorsal hook plates as in (Fig. 5C–H); terminal abdominal segment rounded, with two divergent digitate processes, each process bearing one subapical and three apical setae (Fig. 7B).

Etymology. This species is named in honor of Dr. Ralph W. Holzenthal, for his outstanding contribution to the study of Neotropical caddisflies, and also as an acknowledgment for collaboration and his contributing to the training of young researchers.

Material additional. A1 (1 female), C6 (643 males); C7 (10 larvae, 10 pupae); D2 (34 males); D7 (1 male); D17 (14 males); D18 (379 males); D18 (49 females); D20 (32 females); D22 (1 larvae); E1 (1 male); F2 (30 males); F3 (17 males) (UFBA) (Table 1).

Distribution. Brazil (Pernambuco state).

Key to Brazilian species of *Helicopsyche* (*Feropsyche*), except *H. braziliensis* (Swainson, 1840) and *H. helicoidella* (Vallot, 1855)

Helicopsyche braziliensis (Swainson, 1840) and *H. helicoidella* (Vallot, 1855) are not included in the key because their males are not known.

- | | | |
|---|--|----|
| 1 | Inferior appendage with distal region rounded, in lateral view (Dumas and Nessimian 2019: fig. 2A) | 2 |
| – | Inferior appendage with distal region acuminate, in lateral view (Johanson 2002: fig. 21A) | 11 |
| 2 | Abdominal segment X with projections (Dumas and Nessimian 2019: fig. 2A) | 3 |
| – | Abdominal segment X without projections (Holzenthal et al. 2016: fig. 2B).
..... | 6 |

- 3 Abdominal segment IX with anterior lobe rounded, anterodorsal margin notched, in lateral view (Dumas and Nessimian 2019: fig. 4A); abdominal segment X with apical cleft V-shaped, in dorsal view (Dumas and Nessimian 2019: fig. 8B) **4**
- Abdominal segment IX with anterior lobe acuminate, anterodorsal margin nearly straight, in lateral view (Dumas and Nessimian 2019: fig. 1A); abdominal segment X with apical cleft U-shaped, in dorsal view (Holzenthal et al. 2016: fig. 2B) **5**
- 4 Abdominal segment X rectangular with projections less developed, in dorsal view (Dumas and Nessimian 2019: fig. 4B); inferior appendage with rounded apex and without projections, in ventral view (Dumas and Nessimian 2019: fig. 4C) ***H. luziae* Dumas & Nessimian, 2019**
- Abdominal segment X deltoid with pair of large tab-like midlength projections, in dorsal view (Dumas and Nessimian 2019: fig. 8B); inferior appendage with acuminate apex and with finger shaped projection, in ventral view (Dumas and Nessimian 2019: fig. 8C) ***H. planorboides* Machado, 1957**
- 5 Inferior appendage with length equal to or shorter than abdominal segment X, basal lobe nearly as wide as distal lobe, in lateral view (Dumas and Nessimian 2019: fig. 1A); basomesal lobe trapezoid and unprojected, in lateral view (Dumas and Nessimian 2019: fig. 1A) ***H. bendego* Dumas & Nessimian, 2019**
- Inferior appendage longer than abdominal segment X, basal lobe narrower than distal lobe, in lateral view (Holzenthal et al. 2016: fig. 2A); basomesal lobe finger shaped and projected, in lateral view (Holzenthal et al. 2016: fig. 2A) ***H. guara* Holzenthal, Blahnik & Calor, 2016**
- 6 Inferior appendage longer than abdominal segment X, distal lobe narrow and longer, in lateral view (Johanson 2002: figs 8D, 11D) **7**
- Inferior appendage with length equal to or shorter than abdominal segment X, distal lobe wide and short, in lateral view (Holzenthal et al. 2016: fig. 1A) ... **8**
- 7 Abdominal segment X with a row of setae going from base to the apex, in dorsal view (Johanson 2002: fig. 8E); inferior appendage shorter than abdominal segment X, in dorsal view (Johanson 2002: fig. 8E) ***H. vergelana* Ross, 1956**
- Abdominal segment X with a row of setae going from middle to the apex, in dorsal view (Johanson 2002: fig. 11E); inferior appendage equal or longer than abdominal segment X, in dorsal view (Johanson 2002: fig. 11E) ***H. tapadas* Denning, 1966**
- 8 Abdominal segment X with apical cleft, in dorsal view (Holzenthal et al. 2016: fig. 1B); inferior appendage with base and apex with subequal width, in ventral view (Holzenthal et al. 2016: fig. 1C) **9**
- Abdominal segment X without apical cleft, in dorsal view (Dumas and Nessimian 2019: fig. 2B); inferior appendage with wide base and apex without subequal width, in ventral view (Silva et al. 2014: fig. 1B) **10**

- 9 Inferior appendages bear very prominent spine-like setae on their apicomesal face and mesally at midlength, in ventral view (Holzenthal et al. 2016: fig. 1C); basomesal lobe oval and short, in ventral view (Holzenthal et al. 2016: fig. 1C) ***H. angeloi* Holzenthal, Blahnik & Calor, 2016**
- Inferior appendages without setae on their apicomesal face and mesally at midlength, in ventral view (Johanson and Malm 2006: fig. 49); basomesal lobe finger-shaped and ~ 1/2 the length of the inferior appendage, in ventral view (Johanson and Malm 2006: fig. 49) ***H. cipoensis* Johanson & Malm, 2006**
- 10 Abdominal segment X with apical cleft V-shaped, in dorsal view (Dumas and Nessimian 2019: fig. 2B); inferior appendages with half the length of the abdominal segment X, and with well-developed and strongly rounded protuberance, in dorsal view (Dumas and Nessimian 2019: fig. 2B) ***H. daome* Dumas & Nessimian, 2019**
- Abdominal segment X with deep and short apical cleft U-shaped, in dorsal view (Silva et al. 2014: fig. 1A); inferior appendages with subequal length than abdominal segment X, and without rounded protuberance (Silva et al. 2014: fig. 1B) ***H. timbira* Silva, Santos & Nessimian, 2014**
- 11 Basomesal lobe not or very little projected on anterobasal margin of the inferior appendage, in lateral view (Gama-Neto et al. 2019: fig. 3C) **12**
- Basomesal lobe well projected on anterobasal margin of the inferior appendage, in lateral view (Gama-Neto et al. 2019: fig. 2C) **21**
- 12 Abdominal segment X with projections (Holzenthal et al. 2016: fig. 3B) **13**
- Abdominal segment X without projections **14**
- 13 Inferior appendage deltoid, in lateral view; basomesal lobe unprojected, in ventral view (Holzenthal et al. 2016: fig. 3C) ***H. lazzariae* Holzenthal, Blahnik & Calor, 2016**
- Inferior appendage globose with distal finger shaped projection and ventro-medial setose projection, in lateral view (Gama-Neto et al. 2019: fig. 3D); basomesal lobe triangular and well projected, in ventral view ***H. inflata* Gama-Neto, Ribeiro & Passos, 2019**
- 14 Abdominal segment X subretangular with apex nearly straight, in dorsal view (Johanson 2002: fig. 46E) **15**
- Abdominal segment X ovaled with apex rounded, in dorsal view (Dumas and Nessimian 2019: fig. 3B) **16**
- 15 Abdominal segment IX with broad base, in lateral view (Dumas and Nessimian 2019: fig. 5A); abdominal segment X with acuminate apex, in lateral view (Dumas and Nessimian 2019: fig. 5A), and without apical cleft, in dorsal view (Dumas and Nessimian 2019: fig. 5B) ***H. petri* Dumas & Nessimian, 2019**
- Abdominal segment IX with short base, in lateral view; abdominal segment X with rounded apex, in lateral view (Johanson 2002: fig. 46D), and with shallow, short apical cleft, in dorsal view (Johanson 2002: fig. 46E) ***H. monda* Flint, 1983**

- 16 Inferior appendage with a wide concavity in the posterobasal margin; basomesal lobe square with almost straight margins, in ventral view (Johanson 2002: fig. 45F) **17**
- Inferior appendage nearly straight or with a short convexity in posterobasal margin; basomesal lobe finger shaped with rounded margins, in ventral view (Dumas and Nessimian 2019: fig. 6C) **19**
- 17 Abdominal segment X with lateral margin nearly straight, subapical cluster of setae and apex with a deep, and long cleft, in dorsal view (Johanson and Holzenthal 2004: fig. 18) ***H. succincta* Johanson & Holzenthal, 2004**
- Abdominal segment X with lateral margin convex, with a row of setae going from base to the apex, and apical shallow, short cleft, in dorsal view (Vilarino and Calor 2017: fig. 4B) **18**
- 18 Inferior appendage subrectangular, with a large lobe inner face, in dorsal view, (Johanson 2002: fig. 45E); basomesal lobe wide and $\sim 1/2$ the length of the inferior appendage, in ventral view (Johanson 2002: fig. 45F) ***H. valligera* Flint, 1983**
- Inferior appendage in boomerang shape, without large lobe inner face, in dorsal view (Vilarino and Calor 2017: fig. 18); basomesal lobe very short of the length of the inferior appendage, in ventral view (Vilarino and Calor 2017: fig. 4D) ***H. guariru* Vilarino & Calor, 2017**
- 19 Inferior appendage subrectangular with wide basal lobe almost as wide as distal lobe, in lateral view (Johanson 2002: fig. 21A); basomesal lobe $\sim 1/2$ the length of the inferior appendage, in ventral view (Johanson 2002: fig. 21B) ***H. muelleri* Banks, 1920**
- Inferior appendage subtriangular, basal lobe narrow and distal lobe wide; basomesal lobe less than half the length of the inferior appendage, in ventral view (Dumas and Nessimian 2019: fig. 3C) **20**
- 20 Abdominal segment X and Inferior appendages subequal in length, with clusters setae on apex, in dorsal view (Dumas and Nessimian 2019: fig. 6B); inferior appendage deltoid with distal finger shaped projection, in lateral view (Dumas and Nessimian 2019: fig. 6A); basomesal lobe globose and bifid, (Dumas and Nessimian 2019: fig. 6C) ***H. shaamunensu* Dumas & Nessimian, 2019**
- Abdominal segment X shorter than inferior appendage in length, with a row of setae going from base to the apex, in dorsal view (Dumas and Nessimian 2019: fig. 3D); inferior appendage triangular with distal lobe long with acuminate apex, in lateral view (Dumas and Nessimian 2019: fig. 3A); basomesal lobe finger shaped, in ventral view (Dumas and Nessimian 2019: fig. 3C) ***H. dinoprata* Dumas & Nessimian, 2019**
- 21 Basomesal lobe filiform shaped with a cluster of spine-like setae in distal region, in lateral view (Souza et al. 2017: fig. 1A), apex rounded covered with spine-like setae, in ventral view (Gama-Neto et al. 2019: fig. 2D) **22**
- Basomesal lobe subtriangular with a cluster of spine-like setae in dorsal and ventral margin, in lateral view (Fig. 2A), apex nearly straight covered with spine-like setae, in ventral view (Fig. 2C) **23**

- 22 Abdominal segment IX with anterior lobe acuminate, in lateral view (Souza et al. 2017: fig. 1A); abdominal segment X rectangular, row of setae going from base to the apex, apex nearly straight with shallow and short cleft, in dorsal view (Souza et al. 2017: fig. 1D); inferior appendage with nearly straight posterior margin and with setose projection and shorter apicodorsal projection, in lateral view (Souza et al. 2017: fig. 1A)
 ***H. catoles* Souza, Gomes & Calor, 2017**
- Abdominal segment IX with anterior lobe rounded, in lateral view (Gama-Neto et al. 2019: fig. 2C); abdominal segment X oval, subapical cluster of setae, apex rounded without cleft, in dorsal view (Gama-Neto et al. 2019: fig. 2E); inferior appendage with wide concavity on posterior margin and without setose projection and longer apicodorsal projection, in lateral view (Gama-Neto et al. 2019: fig. 2C)
 ***H. carajas* Gama-Neto, Ribeiro & Passos, 2019**
- 23 Abdominal segment IX with anterodorsal margin notched, in lateral view (Johanson and Malm 2006: fig. 29); abdominal segment X with shallow and long cleft, in dorsal view (Johanson and Malm 2006: fig. 30); inferior appendage truncated with apical tooth, in ventral view; basomesal lobe short and subtriangular, in ventral view (Johanson and Malm 2006: fig. 31)
 ***H. paprockii* Johanson & Malm, 2006**
- Abdominal segment IX with anterodorsal margin nearly straight, in lateral view (Fig. 2A); abdominal segment X with short or without cleft, in dorsal view; inferior appendage with apical projection finger shaped, in ventral view (Fig. 2C); basomesal lobe wide and trapezoid, ventral view (Fig. 2C) **24**
- 24 Abdominal segment X with apex rounded, medial row of spine-like setae, in dorsal view (Fig. 2B); inferior appendage with inner margin strongly projected mesad, forming a rounded large lobe, in dorsal view (Fig. 2B)
 ***H. ralphi* sp. nov.**
- Abdominal segment X with apex nearly straight, side row of spine-like setae, in dorsal view (Johanson 1999: fig. 4); inferior appendage without large lobe inner face, in dorsal view (Johanson 1999: fig. 4)
 ***H. flinti* Johanson, 1999**

Caddisflies from Brejo de Altitude de Triunfo

HYDROPSHYCHIDAE

Smicridea (*Smicridea*) *palifera* Flint

Smicridea (*Smicridea*) *palifera* Flint, 1981: 23 [type locality: Venezuela, Aragua, Maracay, El Limón; NMNH; male; female].

Material examined. BRAZIL: Pernambuco: B2 (71 males, 9 females); C1 (4 males, 2 females); C5 (4 males); C6 (2 males, 3 females); D4 (1 female); D5 (1 female); D6

(4 males, 3 females); D7 (27 males, 15 females); D10 (1 female); D11 (3 males, 1 female); D15 (1 male); D17 (1 male); D18 (3 males); D19 (3 males, 2 females); D20 (6 males, 10 females); F1 (1 female).

Distribution. Brazil (AL, ES, MA, MT, MG, PB, PE, RJ, RO), Grenada, and Venezuela.

Remarks. This species differs from all other species in the *Smicridea nigripennis* group due to the presence of a simple aedeagus, with only a sclerotized spine, and large rounded lobe in segment X (Flint 1981). *Smicridea (Smicridea) palifera* presents a wide distribution in Brazil, except in the south of the country (Santos et al. 2022). In the Northeast region it has been registered in four states (altitude range of 53 m and 814 m) (Souza et al. 2013a; Desidério et al. 2017; Desidério et al. 2020). It was recorded in the Caatinga domain, Pernambuco state (Souza et al. 2013a) and later the Cerrado and Atlantic Forest domains (Desidério et al. 2017; Desidério et al. 2020). This is the first record in *Brejo de Altitude*.

LEPTOCERIDAE

Oecetis excisa Ulmer

Oecetis excisa Ulmer, 1907: 15 [type locality: Argentina, Chaco de Santa Fé, Las Garzas, Río Las Garzas, 25 km W Ocampo; MNHNP; male].

Material examined. BRAZIL: Pernambuco: B2 (1 male, 1 female); B3 (1 male); C1 (2 males, 8 females); C3 (1 male); C5 (1 male); D3 (17 males); D5 (1 female); D9 (20 females); D10 (1 male); D11 (1 male, 2 females); D12 (16 males, 4 females); D21 (1 female); E1 (1 male).

Distribution. Argentina, Bolivia, Brazil (BA, CE, GO, MS, MT, PA, PB, PE, RN, SP), Mexico, Paraguay, and Venezuela.

Remarks. The examined specimens match the description of Ulmer (i.e., tibial spur formula 1,2,2), unlike specimens examined by Quinteiro and Calor (2015), for states of Bahia, Mato Grosso, Paraíba, and Rio Grande do Norte, which presented tibial spur formula 0,2,2. This species is widely distributed in Brazil, including several records in the Northeast region (Quinteiro and Calor, 2015; Desidério et al. 2017). Souza et al. (2013a) recorded the occurrence of the species in the Caatinga domain, Amaraji municipality, Pernambuco state (altitude 320 m). This study provides the first record of species in *Brejo de Altitude*.

PHILOPOTAMIDAE

Chimarra potiguar Queiroz, Dias & Calor

Chimarra potiguar Queiroz, Dias & Calor, 2020: 101 [type locality: Brazil, Rio Grande do Norte, Portalegre, Pinga Stream, MZUSP; male].

Material examined. BRAZIL: Pernambuco: C1 (4 males, 17 females); C2 (1 male); C4 (2 males); C5 (5 males); C6 (7 males, 4 females); D1 (3 males); D2 (54 males,

55 females); D7 (6 males, 7 females); D10 (6 males, 5 females); D11 (2 males, 2 females); D12 (2 females); D13 (1 female); D14 (2 females); D16 (1 male, 3 females); D17 (2 males, 2 females); D18 (39 males, 18 females); D19 (28 males, 10 females); D20 (52 males, 42 females); D21 (4 males, 3 females); E1 (11 females); E2 (2 females).

Distribution. Brazil (RN, PE [new record]).

Remarks. The occurrence of this species was recorded only for the Brejo de Altitude de Portalegre, Rio Grande do Norte state (altitude of 642 m) (Queiroz et al. 2020). The record in Brejo de Altitude de Triunfo (altitude range 580–940 m) is also the first record for Pernambuco state.

POLYCENTROPODIDAE

Cyrnellus fraternus (Banks)

Cyrnellus fraternus (Banks, 1905): 17 [type locality: United States, Maryland, Plummer's Island; MCZ; female].

Material examined. BRAZIL: Pernambuco: C3 (1 male); D2 (4 males); D7 (1 male); D11 (3 males); D12 (4 males); D13 (4 males); D14 (7 males); D16 (8 males); D17 (1 male); D21 (1 male).

Distribution. Argentina, Brazil (AM, BA, ES, MA, MG, MS, MT, PA, PE [new record], PI, PR, RJ, SC), Costa Rica, El Salvador, Ecuador, Mexico, Nicaragua, Panama, Paraguay, Suriname, United States, Uruguay, and Venezuela.

Remarks. *Cyrnellus* Banks contains 12 species in the Neotropical region, and is widely distributed in North, Central, and South America (Morse 2022). *Cyrnellus fraternus* has a distribution from the USA to Argentina, being the most widely distributed caddisfly on the continent (see Holzenthal and Calor 2017). Currently, it has a known distribution in several regions of Brazil and in the Northeast is registered for the Caatinga and Cerrado domains (Dumas et al. 2010; Takiya et al. 2016; Desidério et al. 2017). In this study the species distribution is extended, representing the first record for the state of Pernambuco.

Cyrnellus mammillatus Flint

Cyrnellus mammillatus Flint, 1971: 30 [type locality: Brazil [Edo. Amazonas], Lago des Rio Luna am oberen Teil; NMNH; male].

Material examined. BRAZIL: Pernambuco: B2 (6 males); D12 (3 males).

Distribution. Argentina, Brazil (AM, MA, MG, MS, PA, PE, PI, PR, RJ, SP), Ecuador, Paraguay, Peru, and Uruguay.

Remarks. In the Northeast of Brazil, the occurrence of this species was recorded for the Caatinga and Cerrado domains (altitude range 60–448 m) (Souza et al.

2013a; Desidério et al. 2017; Moreno et al. 2020). This study expands its occurrence for rainforest islands of higher elevations (altitude range 580–940 m) on Brejo de Altitude.

Cyrnellus kozepes Oláh

Cyrnellus kozepes Oláh, 2016: 159 [type locality: Argentina, Corrientes Province, Carlos Pellegrini Posada, Aguape, 28°32'26"S, 57°10'20"W; male].

Material examined. BRAZIL: Pernambuco: D14 (1 male).

Distribution. Argentina and Brazil (PE [new record]).

Remarks. Previously recorded only for Argentina (type locality) (Oláh 2016). This study extends the known distribution of this species and provides the first record for Brazil. This disjunct distribution may be the result of omission errors, the article describing the species is difficult to access and the illustration provided lacks details. In order to avoid future the errors, omission we provide an illustration richer in details.

HYDROPTILIDAE

Metrichia peluda Santos, Takiya & Nessimian

Metrichia peluda Santos, Takiya & Nessimian, 2016: 35 [type locality: Brazil, Rio de Janeiro, Itatiaia, 1st order tributary of Rio Palmital, 22°25'40"S, 44°32'46"W, el. 584 m; DZRJ; male].

Material examined. BRAZIL: Pernambuco: D3 (7 males); D7 (1 male).

Distribution. Brazil (PE [new record], RJ).

Remarks. Previously recorded only from the type locality, domain of the Atlantic Forest (Southeast region of Brazil), the known distribution of this species is extended into the Northeast region with this study.

Neotrichia feolai Santos & Nessimian

Neotrichia feolai Santos & Nessimian, 2009: 766 [type locality: Brazil, Amazonas, Rio Preto da Eva (tributary to Rio Preto da Eva, 02°38'14,6"S, 59°44'09,9"W); INPA; male].

Material examined. BRAZIL: Pernambuco: D3 (2 males).

Distribution. Brazil (AM, PE) and Venezuela.

Remarks. This species was previously recorded only for the Amazon rainforest (Northern region of Brazil) and Venezuela (Santos et al. 2022). Subsequently, Souza et al. (2013b) recorded it for the Caatinga, Northeast Brazil. This study reports this species for the first time in Atlantic Forest (Brejo de Altitude).

***Oxyethira tica* Holzenthal & Harris**

Oxyethira tica Holzenthal & Harris, 1992: 168 [type locality: Costa Rica, Guanacaste, Parque Nacional Santa Rosa, Quebrada El Duende near La Casona, 10.838°N, 85.614°W; NMNH; male; female].

Material examined. BRAZIL: Pernambuco: B2 (9 males); C1 (2 males); D3 (32 males); D7 (2 males).

Distribution. Brazil (AL, AM, BA, CE, MA, MG, PB, PE, PI, RJ, SE), Costa Rica, Dominica, Ecuador, French Guiana, Grenada, Guadeloupe, Honduras, Martinique, Mexico, Nicaragua, Panama, St. Lucia, St. Vincent, Trinidad, and Venezuela.

Remarks. Holzenthal and Harris' (1992) description matches the specimens examined, except for the number of segments in the antennae (33 segments) in the specimens observed. Previously reported for the North and Southeast regions of Brazil Takiya et al. (2016) recorded the presence of the species for the Northeast region, Caatinga domain (Ceará state) and Souza and Santos (2017) extended the distribution for the Atlantic Forest and Cerrado domains (states of Alagoas, Bahia, Maranhão, Paraíba, and Sergipe) and *Brejo de Altitude de Bonito* (Pernambuco state).

***Hydroptila zerbinae* Souza, Santos & Takiya**

Hydroptila zerbinae Souza, Santos & Takiya, 2014: 641 [type locality: Brazil, Pernambuco, Vicência Cachoeira do Engenho Embú, 07°37'22"S, 35°22'51"W, el. 186 m; DZRJ; male].

Material examined. BRAZIL: Pernambuco: B1 (1 male); B2 (26 males); C1 (243 males); C3 (1 male); D7 (2 males); D8 (1 male).

Distribution. Brazil (AL, BA, PE).

Remarks. Previously recorded only in the Brazilian Northeast region, Caatinga and Atlantic Forest domains (states of Alagoas, Bahia, and Pernambuco) (Souza et al. 2014). This study expands its occurrence to the Brejos de Altitude.

Discussion

The new species described here is an important step forward for the knowledge of Trichoptera in the Brejos de Altitude of Northeastern Brazil. Furthermore, the species presented here composes a small group of 12 of the 177 species of *Helicopsyche* (*Feropsyche*) that have all the semaphoronts described. Knowing and describing all semaphoronts represents a qualitative gain of information mainly for morphology-based systematics (to differentiate similar or cryptic species), and quantitative gain

of characters for phylogenetic analyses, since different semaphoronts may represent distinct evolutionary scenarios (Farias et al. 2020).

This study is the first on the caddisfly biodiversity in the Brejos de Altitude, and it includes new species record from Brazil (*Cyrnellus kozepes*), and new records for the Brazilian Northeast region (*Cyrnellus kozepes* and *Metrichia peluda*), and Pernambuco state (*Chimarra potiguar*, *Cyrnellus kozepes*, *Cyrnellus fraternus*, and *Metrichia peluda*), as well as a new species, *Helicopsyche ralphi* sp. nov. Including the species previously recorded for Brazilian Northeast region (Santos et al. 2022) and Pernambuco state (França et al. 2013; Souza et al. 2013a, 2013b; Souza and Santos 2017; Gomes and Calor 2019; Pereira-Filho et al. 2020), 169 and 43 species have now been recorded from the Brazilian Northeast region and Pernambuco state, respectively. All species in this study, except *Chimarra potiguar* and *Oxyethira tica*, constitute new records from the Brejos de Altitude. Among the species listed here, *S. palifera*, *Oecetis excisa*, *Cyrnellus fraternus*, *Cyrnellus mammillatus*, and *Oxyethira tica* present disjunct distributions in the Atlantic Forest and Amazon rainforest. On the other hand, *Chimarra potiguar*, *Metrichia peluda*, and *Helicopsyche zerbinae* have known distributions from the Atlantic Forest, and *Neotrichia feolai* was known only from the Amazon rainforest (Santos et al. 2022). In this way, Brejo de Altitude de Triunfo seems to be a refuge for caddisflies with distributions in the Atlantic Forest and Amazon rainforest. The presence of Trichoptera with disjunct distributions in the Brejo de Altitude de Triunfo corresponds to a pattern registered for other taxa (e.g., Borges-Nojosa and Caramaschi 2003; Castro et al. 2019a; Silveira et al. 2019; Pereira-Filho et al. 2020).

Our results are helpful in guiding further studies in understanding the historical relationships between the Atlantic Forest and Amazon rainforest through the Brejos de Altitude. The shared distribution of these caddisfly species can be the result of past connections, when these enclaves acted as biological corridors between the Atlantic Forest and Amazon rainforest, harboring species from both domains, as proposed by some authors (e.g., Auler et al. 2004; Batalha-Filho et al. 2013; Silveira et al. 2019). In addition, our studies contribute to conservation strategies for the Brejos de Altitude. These areas are highly degraded due to deforestation, illegal hunting, and habitat fragmentation (Pereira-Filho et al. 2017). According to SOS Mata Atlântica & INPE (2019) and Pereira-Filho et al. (2020), these enclaves should be considered as the most threatened sector of the Atlantic Forest and conservation efforts are urgent.

Among the 43 Brejos de Altitude (Tabarelli and Santos 2004), except for this paper, there are only four caddisfly species recorded from these “islands of humid tropical forests” in the Caatinga domain. Three of them from Brejo de Altitude de Bonito, Pernambuco state (*Macrostemum hyalinum*, *Oxyethira tica*, and *Atopsyche antisuya*) (França et al. 2013; Souza and Santos 2017; Gomes and Calor 2019), and one from Brejo de Altitude de Portalegre, Rio Grande do Norte state (*Chimarra potiguar*) (Queiroz et al. 2020). Despite the increase in the number of species with this study, the number of collection sites remains insufficient, consequently taxonomic inventories and description of new species are important to fill gaps in taxonomic and biogeographic knowledge at the Brejos de Altitude.

Conclusions

The present paper identified eleven caddisfly species from the Brejo de Altitude de Triunfo, Pernambuco state. These data revealed four new distributional records for Pernambuco state (*Chimarra potiguar*, *Cyrnellus fraternus*, *Cyrnellus kozepes*, and *Metrichia peluda*), two of them for Brazilian Northeast region (*Cyrnellus kozepes* and *Metrichia peluda*), and one for Brazil (*Cyrnellus kozepes*). Previously, 39 species were registered for Pernambuco state and as a product of this survey, the records are updated to 43 species. Furthermore, this inventory is a pioneer in Brejos de Altitude, thus showing the lack of knowledge of the fauna of Trichoptera in these locations, which possibly have the dynamics of populations influenced by the isolation of these enclaves.

In addition, a new species of *Helicopsyche* (*Feropsyche*) is described, including all semaphoronts. In this way, this description represents a qualitative gain of information mainly for systematics based on morphology (Farias et al. 2020), as it presents a new source of characters for phylogenetic studies and also increases the accuracy in the identification of immatures and females, also useful in ecological studies.

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Caddisflies (Trichoptera) of Mongolia: an updated checklist with faunistic and biogeographical notes

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Abstract

To establish the biogeographic affinities of the caddisfly fauna of Mongolia, published records and results of our faunistic studies were analyzed. This study captured more than 47,000 adults collected from 386 locations beside lakes, ponds, streams/rivers, and springs in ten sub-basins of Mongolia using Malaise traps, aerial sweeping, and ultraviolet lights. In total, 201 species have been recorded, and approximately 269 species may occur in Mongolia according to our estimation. In a comparison of species richness for the family level, the Limnephilidae and Leptoceridae were the richest in species. The families Brachycentridae, Glossosomatidae, and Psychomyiidae had low species richness, but they included the most dominant species in terms of abundance and/or the percentage of occurrence in the samples from multiple sub-basins. Comparing the sub-basins, the Selenge had the highest Shannon diversity ($H' = 3.3$) and the Gobi sub-basin had the lowest ($H' = 1.5$). According to the Jaccard index of similarity, caddisfly species assemblages of Mongolia's ten sub-basins were divided into two main groups: One group includes the Selenge, Shishkhed, Bulgan, Tes, and Depression of Great Lakes sub-basins; the other group includes the Kherlen, Onon, Khalkh Gol, Valley of Lakes, and Gobi sub-basins. The majority of Mongolian species were composed of East Palearctic taxa, with a small percentage of West Palearctic and Nearctic representatives and an even smaller percentage from the Oriental region, suggesting that the Mongolian Gobi Desert is, and has been, a significant barrier to the distribution of caddisfly species between China and Mongolia.

Keywords

East Palearctic, habitats, regional affinities, river sub-basin, species abundance, species diversity, species richness

Introduction

Mongolia is a large, land-locked country located in the southeastern East Palearctic Region (Morse 2021) for which knowledge of the freshwater fauna was poorly known. An understanding of a regional and local fauna is important for assessing ecosystem services and informing conservation management, especially for large areas with little faunistic research such as Mongolia. Survey efforts provide basic knowledge of faunal diversity within regional or local scales (Gelhaus et al. 2008; Heino 2009; Morse 2016) with cumulative diversity increasing as spatial and temporal scales of studies increase (Dodds 2002). Our long-term series of surveys for aquatic invertebrate diversity in Mongolia confirms these observations and expands the faunal and biogeographical knowledge of the country. Our four surveys occurred during 2002–2005 as the Hovsgol_GEF (Dynamics of biodiversity loss and permafrost melt in Lake Hovsgol, National Park, Mongolia), during 2003–2006 as the SRP (Selenge River Basin Project), during 2008–2011 as the MAIS (Mongolian Aquatic Insect Survey funded by US-NSF), and during 2016–2019 as the MACRO (Macroecological Riverine Synthesis funded by US-NSF) projects conducted as expeditions to study the aquatic insects in Mongolia.

Caddisflies (Trichoptera) constitute one of the major aquatic insect groups (Morse et al. 2019a). They are found in both lotic (streams and springs) and lentic (lakes, ponds, pools, and marshes) habitats (Wiggins 1996) and are great contributors to ecosystem functioning as shredding consumers of leaf litter (e.g., Limnephilidae), scrapers of periphyton (e.g., Apataniidae, Glossosomatidae, Psychomyiidae), filterers of suspended organic particles and tiny prey (e.g., Brachycentridae), and predators (e.g., Leptoceridae, Rhyacophilidae). In turn, they are an important component of the diet for fish and other invertebrates (Dodds 2002; Morse et al. 2019a, 2019b). Immature stages of caddisflies are well-studied and generally intolerant of environmental pollution, and thus, they are used as bioindicators in freshwater biomonitoring (Barbour et al. 1999; Dodds 2002).

The order Trichoptera includes more than 16,775 species belonging to 52 families in two monophyletic suborders, Integripalpia and Annulipalpia (Thomas et al. 2020; unpublished data). Trichoptera constitute the seventh most species-rich order of insects (Thomas et al. 2020). The fauna of the East Palearctic Biogeographic Region includes at least 1,244 species of caddisflies (Morse 2016; unpublished data).

The Trichoptera of Mongolia have been studied from the early 19th century and were extensively investigated by foreign and Mongolian researchers through many expedition surveys, especially in the past 20 years (Chuluunbat et al. 2016). According to their investigations, 198 species have been recorded. For our checklist, we have reviewed 64 taxonomic publications which reported Mongolian caddisfly species and their distribution. We also include specimens collected and identified from our expeditions throughout the northern and western parts of the country from 2003 through 2011. The spatial distribution of species is reported and compared by provinces (or “aimags” in Mongolian), which is an administrative subdivision for the country and commonly reported and interpreted in previous publications (e.g., Chuluunbat et al. 2016).

In this study, we characterize caddisfly biogeographical distribution in ten major river basins and provide a revised and annotated checklist for the Trichoptera fauna in Mongolia. We assess the species richness and diversity of caddisflies in ten sub-basins (biogeographical regions), hypothesizing that they will be conspicuously different, and compare the similarities of species among the sub-basins and with the adjacent regions of neighboring countries.

Materials and methods

Study area

Mongolia is located in Central Asia, covering 1,564,118 km². The area is characterized by an extreme continental climate with four distinct seasons including a long, cold, dry winter and short, hot summer; average annual precipitation is 220 mm (Natsagdorj 2014).

Mongolian surface water network is divided into three different major basins. The Mongolian northern Arctic Ocean Basin (**AOB**) contains the highest density or 52% of the country's surface water network (Davaa 2015), including the following nine major rivers: the Orkhon, (the longest river in Mongolia), Ider, Tuul, Kharaa, Yoroo, Eg, Delgermurun, and Shishkhed Rivers, which are all tributaries of the Selenge River (Davaa and Oyunbaatar 2017); samples examined in this study were from all these rivers. The Yolt and two other streams are tributaries of the Hurimt River, which is a headwater of the Black Irtysh River (Shagdar 2006); no samples were taken from the Hurimt River itself. The AOB includes five major lakes: Hovsgol, Dood Tsagaan, Sangiin Dalai, Terkhiin Tsagaan, and Ugii.

The Central Asian Internal Drainage Basin (**CAIB**) covers a vast area from the western Altai Mountains to the eastern Dornod Steppe and 32% of the surface water network. It includes the following five major lakes: Uvs, Khyargas, Khar Us, Khar, and Airag. It also includes the following 11 rivers: the Khovd, Zavkhan, Baidrag, Buyant, Bulgan, Uyench, Bodonch, Sagsai, Ongi, Tes, and Tuin Rivers (Davaa 2015; Davaa and Oyunbaatar 2017); samples were collected from all these lakes and rivers.

The Pacific Ocean Basin (**POB**) contains 16% of Mongolia's surface water network and includes the Kherlen, Onon, Ulz, Khalkh Gol, Numrug, and Degee Rivers; samples were from all six of these rivers. Kherlen River is the longest river in the basin and provides an inflow for Dalai Lake in China. The three major lakes are the Buir, Yakhi, and Khukh (Davaa and Oyunbaatar 2017).

According to Dulma (1979), Sokolov (1983), and Mendsaikhan et al. (2017), those three basins are further divided into nine sub-basins. However, their subdivisions were based entirely on the biogeography of fish distributions and does not include scattered water bodies in the Gobi that are without a fish fauna. Therefore, based on the distribution of aquatic beetles throughout Mongolia, ten regional sub-basins were proposed and published by Enkhnasan and Boldgiv (2019) by adding the Gobi sub-basin. These ten regional sub-basins include the Tes, Valley of Lakes, Depression of

Great Lakes, and Gobi sub-basins in the CAIB; the Selenge, Shishkhed, and Bulgan in the AOB; and the Kherlen, Onon and Khalkh Gol sub-basins in the POB. According to Dulma (1979), Sokolov (1983), Mendsaikhan et al. (2017), and Enkhnasan and Boldgiv (2019), the divisions for hydrobiological studies suggest that the Bulgan River is in the AOB; in contrast, the hydrological classification by Davaa (2015) and others (Davaa and Oyunbaatar 2017) places the Bulgan River in the CAIB; we include the Bulgan River in the AOB.

Database

The database was compiled from two main sources: caddisfly records published in papers cited by Chuluunbat et al. (2016) and caddisfly specimens collected by our own surveys and those kept in private collections (Prof. Bayartogtokh and Dr Puntsagdulam). In our previous publication (Chuluunbat et al. 2016), we used specimens collected during our own expeditions from 2003 through 2011. In this paper, additional specimens collected through 2020 and other personal collections were considered. That is to say, an enormous amount of species-level data collected by our long-term series of surveys (Hovsgol_GEF 2002–2005, SRP 2003–2006, MAIS 2008–2011, MACRO 2016–2019), preserved in private collections, and reported in previous publications since the early 20th century were compiled in the current paper. One of our goals was to determine the estimated species richness; thus we needed species abundance data. Most of the early publications simply listed species without any individual numbers and without precise collection data due to lack of both precise positioning tools and standard transliteration of geographical names. We databased any species abundances reported in publications; however, if species were only listed without number of specimens, we counted the number of individuals as “one.” We realize that this procedure may have underestimated the abundance of these species, which in turn might overestimate species richness. In the literature sources, if species distribution or location information was provided without any details for an exact location, then we added the species records to our nearest collection sites that have geographical details. Non-verifiable records, not supported with voucher specimens, were omitted from the database.

A total of 47,931 individuals from 386 sampling sites were databased as distributed in ten regional sub-basins (Fig. 1) and four different types of water bodies or habitats (lakes, ponds/pools, rivers/streams, and springs). The river/stream type represents 1st to 7th orders of streams and rivers (Table 1).

We have followed the regional sub-basin classification of Enkhnasan and Boldgiv (2019), defining ten sub-basins in Mongolia. For the world geographical divisions we adopted the seven biogeographic regions of the Trichoptera World Checklist (Morse 2021).

To document similarities of species assemblages for the adjacent neighboring countries, we compared faunistic data for Russia by Ivanov (2011), for China by Yang et al. (2016), and for Kazakhstan by Smirnova et al. (2016). The Mongolian caddisfly fauna was also compared to adjacent regions including the Altay Mountains, Sayan Mountains, Pribaikalie Region, and Chita Region of Russia; the Xinjiang, Gansu, and Inner

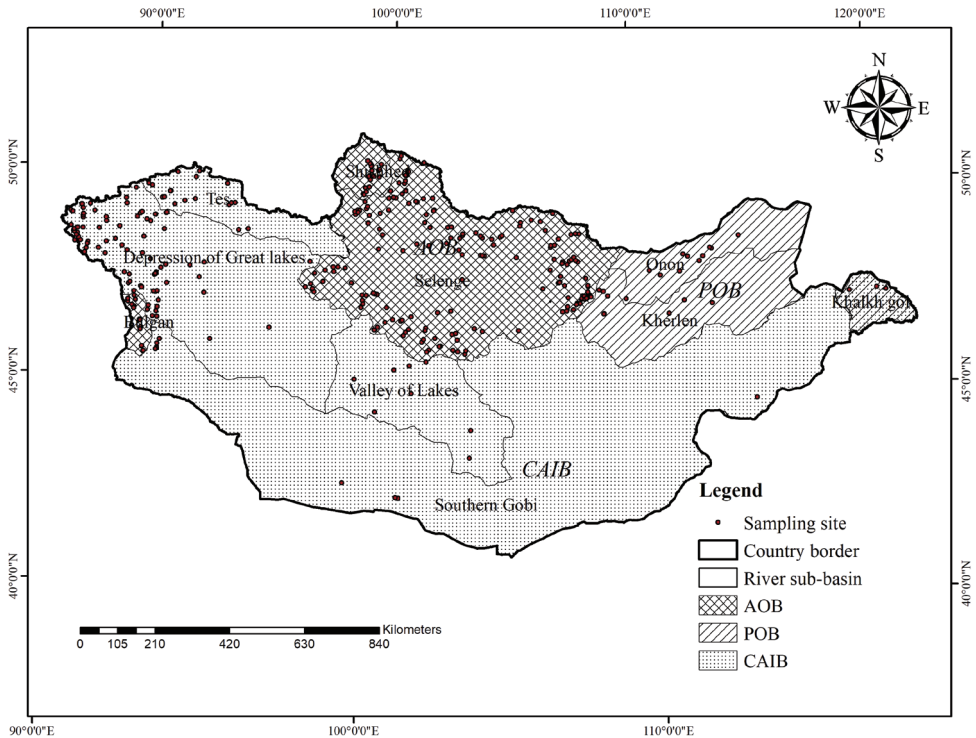


Figure 1. Mongolian watershed basins and ten sub-basins with 386 sampling sites. Abbreviations: AOB = Arctic Ocean Basin, CAIB = Central Asian Internal Basin, POB = Pacific Ocean Basin.

Mongolian regions of China; and the Irtysh and Balkhash-Alakol regions of Kazakhstan. Lake Baikal species in Russia are excluded from comparison analyses because of the high level of endemism in the lake. Thus, we have compared 754 species of caddisflies from the above nine regions of their respective three countries for similarity analyses.

Sampling and identifications

In our surveys, we used various collecting techniques such as aerial nets, light traps when air temperature was above 10 °C with no wind (McCafferty 1981), and two Townes-style Malaise traps (Townes 1972) placed at the edge of the water, one on bare ground and the other in tall grass or bushes. Malaise traps were placed for the duration of a week for Hovsgol_GEF samples in the rivers of the eastern shore of Lake Hovsgol, 12 hours for SRP and MAIS samples, and two hours for MACRO samples. Adult caddisfly identifications were accomplished under dissecting microscopes, using identification keys by Lehr (1997), Malicky (2004), and other authors. Verification of determinations for the most common 95 caddisfly species belonging to 41 genera and 13 families was accomplished through comparisons of their mtCOI barcodes with those of sequenced species from other countries maintained at the Canadian Centre for DNA Barcoding,

Table 1. Numbers of habitat types of water bodies sampled in ten sub-basins of Mongolia. Key: AOB = Arctic Ocean Basin, CAIB = Central Asian Internal Basin, POB = Pacific Ocean Basin.

No.	Sub-basins	Lake	Pond/Pool	River/stream	Spring	Total
1	Selenge (AOB)	18	7	152	14	191
2	Shishkhed (AOB)	4	3	9	2	18
3	Bulgan (AOB)	2	0	22	2	26
4	Tes (CAIB)	5	0	16	1	22
5	Depression of Great Lakes (CAIB)	16	2	65	7	90
6	Valley of Lakes (CAIB)	0	0	6	1	7
7	Kherlen (POB)	2	0	8	2	12
8	Onon (POB)	0	0	12	0	12
9	Khalkh Gol (POB)	1	0	2	0	3
10	Gobi (CAIB)	1	0	1	3	5
11	Total	49	12	293	32	386

Biodiversity Institute of Ontario, University of Guelph, under the Trichoptera Project of the Barcode of Life Database (BOLD Systems 2013). Sequences of the mtCOI gene for the 95 sequenced species in our studies are recorded in GenBank (Zhou et al. 2016).

Statistical analysis

An abundance-based species accumulation curve was used to predict rarified species richness. Chao 1 was used as an estimator to show the relationship of sample sizes and numbers of species. EstimateS 9.1.0 software was used to calculate the Chao1, and 100 runs were performed to see the singletons (**S1**, one specimen of a species), doubletons (**S2**, two specimens of a species), and unique species (**SU**, species occurring at only one site) (Colwell 2013) at each collection location. Shannon’s index of diversity (**H**) (Shannon and Weaver 1949), evenness (**J**) (Pielou 1966), and Berger-Parker dominance index (**Dd**) (Berger and Parker 1970) were calculated for the ten sub-basins and for the country. Similarity of assemblages among the sub-basins was determined based on presence-absence data quantified by the Jaccard index method using Ward distance with the vegan package of R3.6.1 software (R Development Core team 2010).

Results

Based on the results of our data mining (species data from previously published literature) and our survey investigations, we found 201 caddisfly species representing 72 genera and 16 families in Mongolia (Appendix). Families with the most diverse genera and species were Limnephilidae (23 genera, 62 species) and Leptoceridae (7, 32); families with the least diverse genera and species were Psychomyiidae (1, 3), Goeridae (2, 3), Thremmatidae (1, 1), and Stenopsychidae (1, 1) (Fig. 2). The genera with the highest number of species were *Limnephilus* (25 species), *Ceraclea* (11), *Rhyacophila* (10), *Hydropsyche* (9), *Apatania* (8), *Agrypnia* (7), and *Glossosoma* (6) (Fig. 2, Appendix). In terms of abundance, families Brachycentridae and Psychomyiidae were most abundant (Table 2).

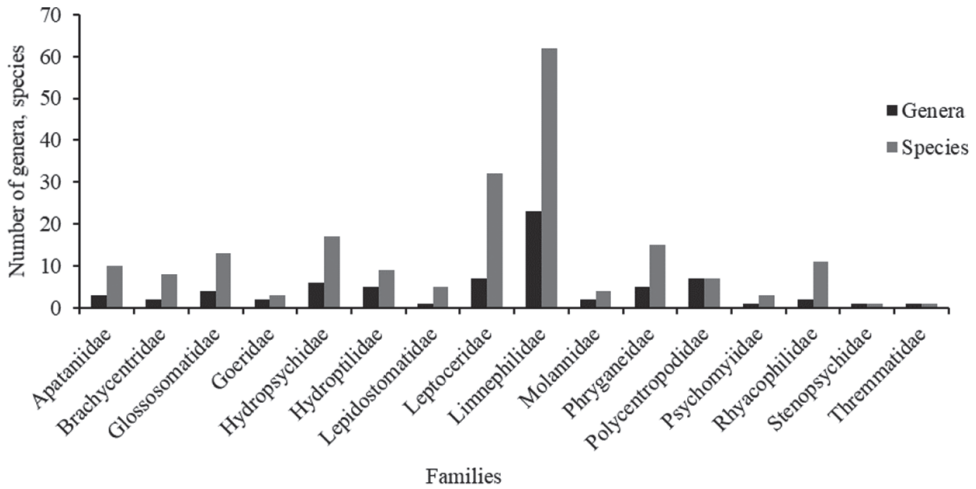


Figure 2. Number of genera and species of caddisfly families in Mongolia.

Species diversity (H') was highest in the Selenge River sub-basin (3.33) and the Depression of Great Lakes sub-basin (2.57), while evenness (J') was highest in the Khalkh Gol sub-basin (0.79) and the Gobi sub-basin (0.78) (Table 2).

Species in families Brachycentridae, Glossosomatidae, and Psychomyiidae were most abundant (Table 2, Appendix). *Brachycentrus americanus* (Banks, 1899) was the most dominant species in the Tes (31%) and Valley of Lakes (48%) sub-basins, with both of these sub-basins belonging to the CAIB. *Padunia bikinensis* Martynov, 1934, was the dominant species in the Kherlen and Onon sub-basins (38% and 54%, respectively), both belonging to the POB; and *Psychomyia flavida* Hagen 1861 was the dominant species in the Depression of Great Lakes sub-basin (28%) and all of Mongolia (16%). Other species were dominant in the other five sub-basins (Table 2).

Abundance-based species accumulation analysis estimated that species of caddisflies occurring in Mongolia is 269 (Table 2). Among the 201 currently recorded species, 53 were represented by a single specimen at some sites (S1) and 16 were represented by two specimens at some sites (S2). In our study, 69 species occurred uniquely at a single site in Mongolia (SU) (Table 2).

Caddisfly species richness varied greatly among the four different habitat types of water bodies. From 386 sampling sites, the highest species numbers (178 species) were from the various types of rivers. The next most-diverse habitat was lakes with 106 species. Springs and ponds were inhabited by 47 and 40 species, respectively (Fig. 3).

The regional distribution and richness of caddisflies in Mongolia varied in the ten sub-basins, ranging from 7 to 157 species. The highest numbers of species and genera of caddisflies occur in the Selenge River sub-basin (157 species, 54 genera), followed by the Depression of Great Lakes (88 species, 41 genera), the Tes and Shishkhed River sub-basins (50 and 49 species, respectively, in 26 genera), the Bulgan River sub-basin (39 species in 20 genera), Kherlen River sub-basin (38 species in 21 genera), the Onon

Table 2. Richness and diversity measurements of caddisflies for Mongolia and its ten sub-basins. Key: Sub-basins = sub-basin names, Sites = collection sites, N = number of individuals, Sobs = observed number of species, Chao1 = estimated number of species, S1 = singleton species, S2 = doubleton species, SU = unique species, H' = Shannon-Weaver diversity index, J' = Pielou's evenness, Dd = Berger-Parker dominance index (by percentage of dominant species), dominant species for the sub-basin and Mongolia. AOB = Arctic Ocean Basin, CAIB = Central Asian Internal Basin, POB = Pacific Ocean Basin.

No.	Sub-basins	Sites	N	Sobs	Chao1	S1	S2	SU	H'	J'	Dd	Dominant species
1	Selenge (AOB)	191	19287	157	211	46	10	61	3,33	0,65	16%	<i>Rhyacophila egijnica</i>
2	Shishkhed (AOB)	18	1635	51	63	13	5	25	2,48	0,63	30%	<i>Apatania majuscula</i>
3	Bulgan (AOB)	26	4999	39	54	13	1	16	2,36	0,64	21%	<i>Psychomyia minima</i>
4	Tes (CAIB)	22	2243	52	75	20	7	29	2,29	0,57	31%	<i>Brachycentrus americanus</i>
5	Depression of Great Lakes (CAIB)	90	17306	88	110	16	4	25	2,57	0,57	28%	<i>Psychomyia flavida</i>
6	Valley of Lakes (CAIB)	7	215	15	22	2	3	9	1,79	0,66	48%	<i>Brachycentrus americanus</i>
7	Kherlen (POB)	12	1357	38	45	12	8	22	1,81	0,49	38%	<i>Padunia bikinensis</i>
8	Onon (POB)	12	719	34	43	12	6	18	1,77	0,5	54%	<i>Padunia bikinensis</i>
9	Khalkh Gol (POB)	3	64	17	21	8	5	11	2,26	0,79	22%	<i>Oecetis ochracea</i>
10	Gobi (CAIB)	5	106	7	11	1	0	7	1,52	0,78	34%	<i>Colpotautius incisus</i>
11	Mongolia	386	47931	201	269	53	16	69	3,38	0,63	16%	<i>Psychomyia flavida</i>

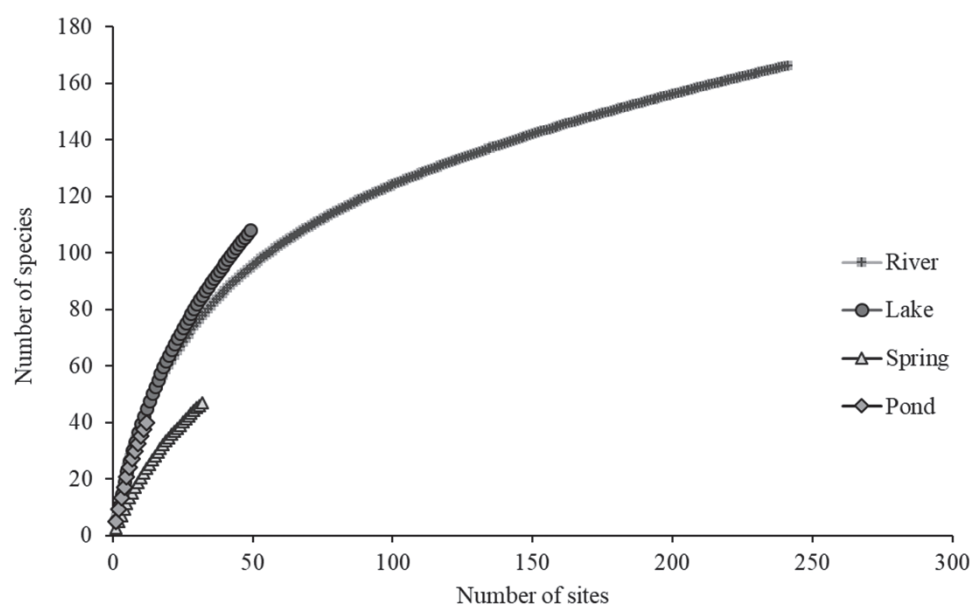


Figure 3. Caddisfly species richness collected from different numbers of sites from four different types of water bodies.

River sub-basin (34 species in 24 genera), Khalkh Gol (17 species in 13 genera), the Valley of Lakes sub-basin (15 species in 10 genera), and the sub-basin with the lowest species richness was the Gobi sub-basin (7 species in 4 genera) (Table 2, Fig. 4).

Based on the distribution of 201 species of caddisflies in the ten sub-basins of Mongolia, similarities of caddisfly assemblages among sub-basins are shown in Fig. 5. The

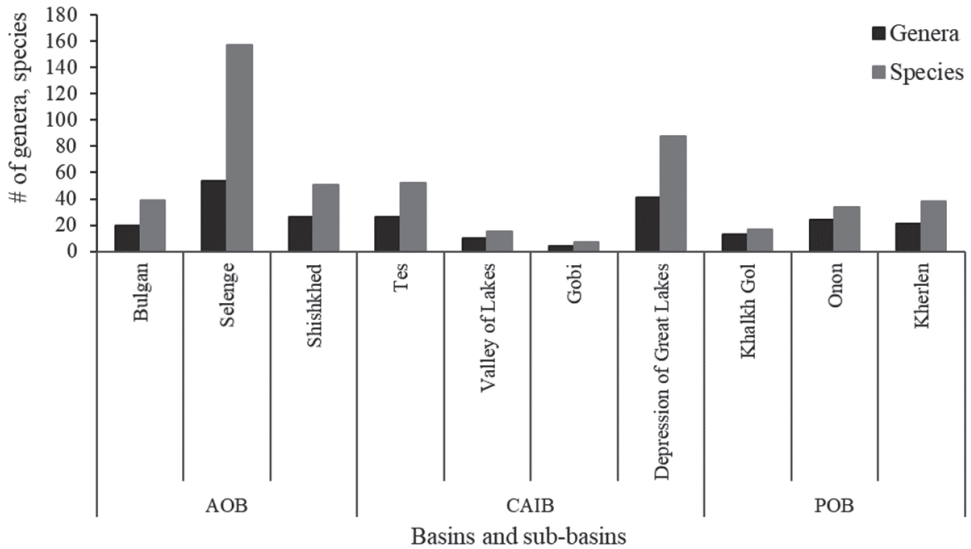


Figure 4. Richness of genera and species of caddisflies distributed in ten sub-basins of Mongolia. Abbreviations: AOB = Arctic Ocean Basin, CAIB = Central Asian Internal Basin, POB = Pacific Ocean Basin.

Onon, Kherlen, and Khalkh Gol sub-basins (POB) were more similar to the CAIB's Valley of Lakes and Gobi sub-basins as one cluster, whereas the Shishkhd, Selenge, and Bulgan river sub-basins (AOB) were similar to the CAIB's Tes and Depression of Great Lakes sub-basins in another group. The interesting results of this clustering showed that the CAIB's sub-basins were divided into two clusters. The Valley of Lakes and Gobi sub-basins were more similar to those of the POB, the Tes and Depression of Great Lakes sub-basins were more similar to those of the AOB. That is, the caddisfly assemblages in the AOB and the POB were most dissimilar geographically, with the CAIB partially similar to each of them (Fig. 5).

China, Kazakhstan, and Russia are large countries bordering Mongolia on the south, west, and north, respectively. To assess similarities with these surrounding countries, we selected their closest regions. Species assemblages for the neighboring regions were clustered into three groups. The first group was composed of Chinese Gansu and Inner Mongolia. The second group was composed of Russian Chita region and Kazakhstan's Balkhash-Alakol and Chinese Xinjiang region. Finally, Russian Pribaikalie, Altay, and Sayan Mountains, Kazakhstan's Irtysh basin, and Mongolia were clustered into one group (Fig. 6). Mongolian caddisfly species were most similar to those of the Russian and Kazakhstan faunas and least similar to the Chinese fauna (Fig. 6).

Most caddisfly species of Mongolia also inhabit other parts of the East Palearctic Biogeographic Region (98%). Among those, 31% occur also in Europe and northern Africa (WP). Another 20% of the Mongolian species are Holarctic, occurring also in the Nearctic and West Palearctic Regions. Six percent of the Mongolian-East Palearctic species occur also in the Oriental Region, 4% occur also in the Nearctic, and 1% occur

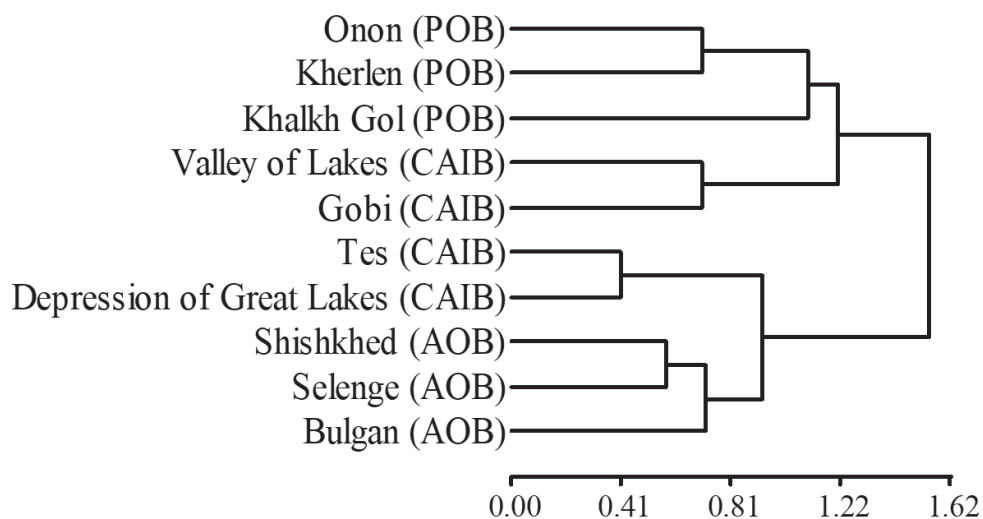


Figure 5. Similarities of caddisfly assemblages among ten sub-basins. Abbreviations: AOB = Arctic Ocean Basin, CAIB = Central Asian Internal Basin, POB = Pacific Ocean Basin.

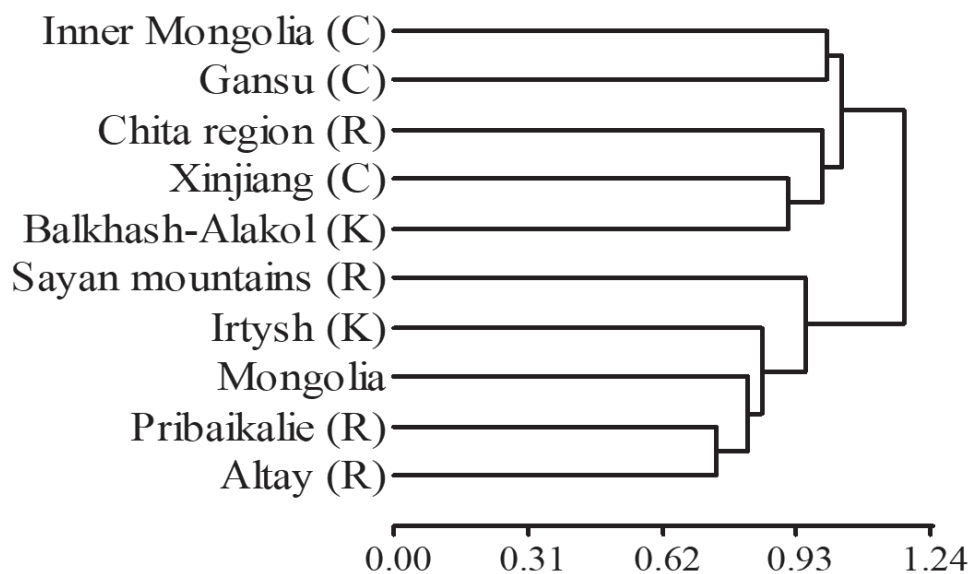


Figure 6. Caddisfly fauna similarities among Mongolia and nine adjacent regions of China (C), Kazakhstan (K), and Russia (R).

in all three of these latter regions (Fig. 7). Caddisfly endemism is very rare for Mongolia (Fig. 7). Endemic species (**) and new country reports (*) are highlighted in the species list (Appendix). The list includes the following five new records for the country:

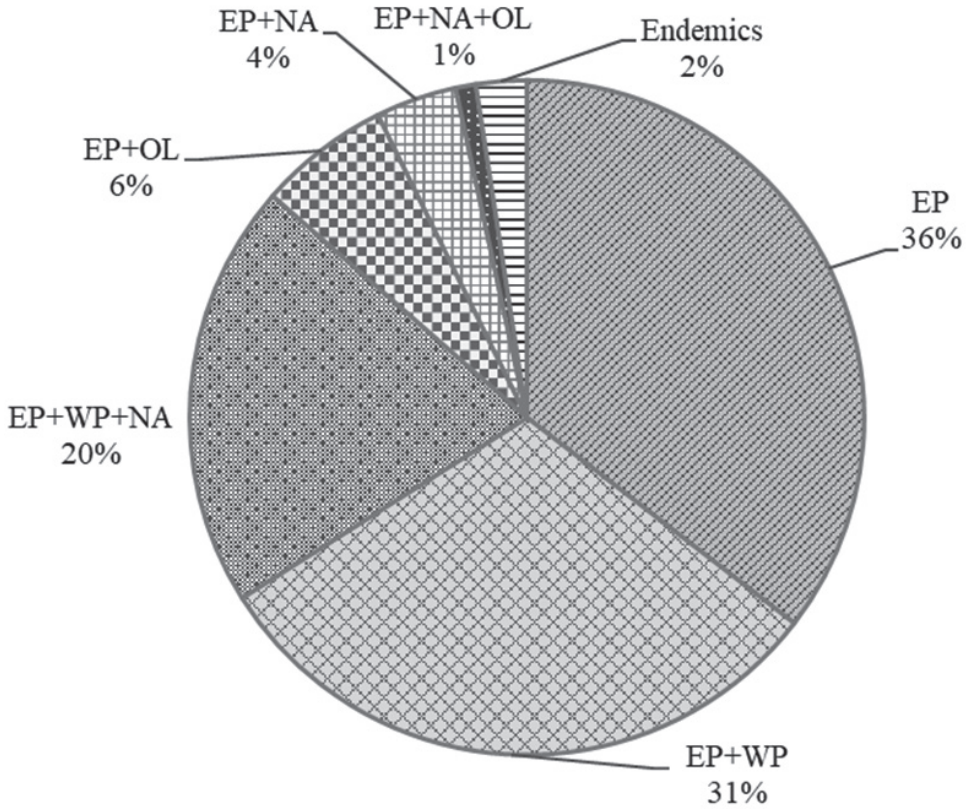


Figure 7. Mongolian caddisfly species composition according to world biogeographic regions (Morse 2021): East Palearctic (EP), Nearctic (NA), Oriental (OL), and West Palearctic (WP).

1. *Asynarchus sachalinensis* Martynov, 1914: Tov Province, Erdene Soum, Upper Tuul River, 47.94981°N, 107.45511°E, elev. 1593 m, 2004.vi.29. coll. MAIS team, 1 male, det. S. Chuluunbat.

2. *Cheumatopsyche infascia* Martynov, 1934: Dornod Province, Khalkh Gol, 31 km east of from Khalkh Gol Soum, 47.52556°N, 118.98538°E, elev. 736 m, 2006.vi.22, coll. J. Puntsagdulam, D. Altanchimeg, 2 males, 11 females, det. S. Chuluunbat.

3. *Oecetis nigropunctata* Ulmer, 1908: Khentii Province, Batnorov Soum, Bayanbulag, 47.91561°N, 111.50480°E, elev. 1328 m, 2020.vi.28, coll. B. Bayartogtokh, light trap, 1 male, 4 females, det. S. Chuluunbat.

4. *Drusus* sp.: Khovd Province, Duut Soum, Tsagaan Burgas Gol, 47.55936°N, 91.76095°E, elev. 1865 m, 2008.vii.15, coll. MAIS team, 7 males, 2 females, det. S. Chuluunbat.

5. *Nyctiophylax* sp.: Uvs Province, Zuungobi Soum, Nariin Gol, 50.05245°N, 94.15410°E, elev. 923m, 2009.vii.22, coll. MAIS team, 1 male, det. S. Chuluunbat.

Discussion

Survey investigations contribute to knowledge of a regional fauna. Up to the late 1900s and early 2000s, Mongolian Trichoptera were investigated mostly by foreign scientists who recorded 129 species (Morse et al. 2006). Starting in early 2000, regional scientific expeditions surveyed various parts of Mongolia intensively and expanded the caddisfly species list up to 198 (Chuluunbat et al. 2016). We are currently adding five new country records to this list. Two subspecies (*Limnephilus extricatus sibiricus* Mey, 1991, is a subspecies of *Limnephilus extricatus* McLachlan, 1865; *Phryganea grandis rotundata* Ulmer, 1905, is a subspecies of *Phryganea grandis* Linnaeus, 1758) are not shown as distinct taxa in the Mongolian species list (Appendix) and remain uncounted as species by Morse (2021). These findings result in a list of 201 species in Mongolia. This total number of documented species relative to the estimated 269 species indicates that (a) more survey work is needed in Mongolia to fully document the country's caddisfly fauna and (b) the estimated number of species may have been overestimated due to lack of precise abundance data for some species as reported in previous literature.

A new synonym and changes in two species names are also reflected and updated from the list of Chuluunbat et al. (2016). *Stenopsyche marmorata* Navás, 1920, is a synonym of *Stenopsyche griseipennis* McLachlan, 1866, according to Kuranishi & Tanida (2016). *Micropterna sequax* McLachlan, 1875, was reported as *Stenophylax sequax* (McLachlan, 1875); *Synagapetus inaequispinosus* (Schmid, 1970) was reported as *Agapetus inaequispinosus* (Schmid, 1970) by Chuluunbat et al. (2016).

Different numbers of endemic species from Mongolia have been reported. By 2006, a single endemic species was reported in Lake Hovsgol, *Limnephilus hovsgolicus* Morse, 1999 (Morse et al. 2006; Chuluunbat et al. 2016). However, Puntsagdulam et al. (2017) reported 7 endemic species of caddisflies for Mongolia: *Agapetus inaequispinosus* (Schmid, 1970); *Neureclipsis mongolica* Schmid, 1968; *Rhyacophila egijnica* Schmid, 1968; *Triaenodes kaszabi* Schmid, 1968; *Hydroptila pectinifera* Schmid, 1970; *Apataniana impexa* Schmid, 1968; with *Limnephilus hovsgolicus*. However, *Agapetus inaequispinosus* (Schmid, 1970) is now acknowledged as *Synagapetus inaequispinosus* (Schmid, 1970) and has been reported from Russia (Ivanov 2011) and Japan (Kuranishi & Tanida 2016). *Neureclipsis mongolica* Schmid, 1968, is a synonym of *Neucentropus mandjuricus* (Martynov, 1907) and has been reported also from China (Yang et al. 2016). *Rhyacophila egijnica* Schmid, 1968, has been reported from Russia (Ivanov 2011). *Triaenodes kaszabi* Schmid, 1968, is a synonym of *Triaenodes jakutanus* Martynov, 1910, and reported from Russia (Ivanov 2011) and North America (Manuel 2010). *Hydroptila pectinifera* Schmid, 1970, has not been reported from any other country yet and the type locality is the Delgermurun River, Burenkhaan Soum (current administrative name, Burentogtokh Soum), Hovsgol Province in Mongolia (Schmid 1970). *Apataniana impexa* Schmid, 1968, has been reported from Russia (Ivanov 2011) and China (Yang et al. 2016). *Limnephilus hovsgolicus* Morse, 1999, is endemic to Lake Hovsgol (Morse 2021). Also, *Agrypnia hayfordae* Morse & Chuluunbat, 2007, has not yet been reported from other countries; it inhabits lakes and the type locality is Nuuriin Khooloi Lake, Thenkher Soum, Arkhangai Province in Mongolia. This species was collected also from Lake Terkhiin Tsagaan, Tariat Soum,

Arkhangai Province, by colleagues in 2018. In conclusion, only three of the above species, i.e., *Hydroptila pectinifera*, *Limnephilus hovsgolicus*, and *Agrypnia hayfordae*, are the known caddisfly endemics for Mongolia (Appendix).

Distribution and diversity of Mongolian caddisflies are usually reported in the literature for the three main basins and administrative provinces or rivers rather than the ten sub-basins discussed here. Higher richness of caddisfly species was observed in the Arctic Ocean Basin (AOB) than in the other two basins by Dulmaa and Nansalma (1970). Our results reflect the same observation due to the fact that the same literature sources were used and higher sampling efforts (sites) by our own surveys occurred in the AOB than in the CAIB and POB. Strangely, higher species richness was observed in areas with a high density of water networks of rivers and lakes. The AOB and CAIB have a greater density of surface water networks than the POB, and a higher percentage (over 40%) of Mongolia's geological formations including mountainous areas (Yembuu 2020) and isolated drainages. The AOB has higher stream connectivity than the CAIB, and the connectivity allows it to share similar species in the connected waterways, which tends to make the AOB to have lower species richness than the CAIB (Maasri et al. 2018). Despite this trend, the greater sampling effort of our surveys in the AOB has resulted in a higher species richness in the AOB than in the CAIB.

The highest species number was found in the family Limnephilidae, especially the genus *Limnephilus*. The genus *Limnephilus* is one of the largest genera with at least 185 species (unpublished data), inhabiting primarily cold water in northern latitudes and often found at higher altitudes (Ruiter 1995). These case-making caddisflies are known to be highly diverse and occur throughout the Holarctic Region (Morse 2016). Indeed, most of the species observed in Mongolia are case-making caddisflies (Apataniidae, Brachycentridae, Glossosomatidae, Goeridae, Hydroptilidae, Limnephilidae, Lepidostomatidae, Leptoceridae, Molannidae, and Phryganeidae). The elevated landscape of central and western Mongolian is especially suitable habitat for case-making and cold-water-dwelling caddisflies.

Among all types of habitats that were sampled, most of the species were observed in streams/rivers. The immature stages of most caddisflies can inhabit many available substrates in running water and are generally most diverse in streams and rivers (Resh and Rosenberg 1984); however, they are rare in springs (Thorp and Rogers 2011). The number of species occurring in lakes is relatively higher than those in ponds and springs; the 108 species observed from 48 lake sites indicate that lake-inhabiting Trichoptera have been investigated well in Mongolia.

The Mongolian Great Gobi Desert appears to represent an enormous barrier to distribution of caddisflies to and from the south. This pattern suggests a reason for the higher species richness observed in northern sub-basins (Selenge, Shishkhed, Bulgan, Tes, Depression of Great Lakes, Valley of Lakes, Kherlen, Onon and Khalkh Gol) than the Gobi sub-basin. Also, this might be the reason that caddisfly assemblages of Mongolia are more dissimilar to those in Chinese regions than to those in the Russian and Kazakh regions selected for comparison in this study. These results corroborate research indicating that more Mongolian caddisfly species are shared with Russia (Ivanov 2011) than with China (Yang et al. 2016). The composition of Mongolian caddisfly species and the low level of endemism we report here appear to be explained by similar biogeo-

graphic and meteorologic conditions in these and neighboring eastern, northern and western regions and the relatively dry, mostly inhospitable Gobi in southern Mongolia and northern China, resulting in a formidable isolation for aquatic insects (and possibly all freshwater biota) from the south for over 70 million years (Dashzeveg et al. 2005).

The similarity in the caddisfly species composition among the three main basins was not as different as we expected. The caddisfly assemblages in sub-basins of AOB and POB were different, but the CAIB was divided into two sub-basins more similar to either AOB or POB. This is probably due to the fact that the CAIB covers a large area from west to east in Mongolia. The faunas of the Depression of Great Lakes and Tes sub-basins of the CAIB in the northwest are more similar to those of the AOB, while the faunas of the Valley of Lakes and Gobi sub-basins of the CAIB in the south are more similar to those of the POB in eastern Mongolia, suggesting that Mongolian caddisfly species might be distributed differently than the faunas that were the basis of the current basin classification. In conclusion, the caddisfly fauna of Mongolia was investigated thoroughly, from the view of the distribution of species in different spatial scales with documented and estimated richness. Most of the species distributed in Mongolia are characteristic of the Palearctic Region. The caddisfly fauna of Mongolia was similar to Russia's closest bordering regions of Altay and Sayan Mountains, Pribaikalie, and Kazakhstan's Irtysh Basin, but different from that of China's bordering regions due to the lack of connections of the surface water network and the presence of the Mongolian Gobi Desert. Sampling effort results in higher richness; thus, further sampling in the sub-basins especially in the Gobi may yield more species. Knowing the species richness in the basins, and sub-basins allow us to manage and protect aquatic systems better and provide necessary knowledge for future freshwater biomonitoring.

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Appendix

Table A1. Compiled caddisfly species list from our own data and taxonomic literature, and their distribution in basins and sub-basins of Mongolia. Key: 0 = not reported, 1 = reported. Females of some species (sp.) could be identified only to genus. * = new records for the country, ** = endemic species. Biogeographic regions: EP = East Palearctic, HL = Holarctic (EP+NA+WP), NA = Nearctic, OL = Oriental, WP = West Palearctic.

[illegible]

Lepidostomatidae

61	<i>Lepidostoma albardanum</i> (Ulmer, 1906)	EP	1	0	0	0	1	0	0	0	0	0	2	74
62	<i>Lepidostoma hirtum</i> (Fabricius, 1775)	EP+WP	1	0	0	0	1	0	0	1	0	0	3	91
63	<i>Lepidostoma penicillatum</i> (McLachlan, 1875)	EP+WP	0	0	1	0	0	0	0	1	0	0	2	50
64	<i>Lepidostoma chaldyrense</i> (Martynov, 1909)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
65	<i>Lepidostoma stubbei</i> (Mey, 1980)	EP	0	0	0	0	0	0	0	1	0	0	1	1

Leptoceridae

66	<i>Ceraclea albimacula</i> (Rambur, 1842)	EP+WP	1	0	0	0	0	0	0	1	0	0	2	29
67	<i>Ceraclea annulicornis</i> (Stephens, 1836)	HL	1	0	1	1	0	1	0	1	0	0	5	217
68	<i>Ceraclea excisa</i> (Morton, 1904)	HL	1	1	0	0	1	0	1	1	0	0	5	292
69	<i>Ceraclea fulva</i> (Rambur, 1842)	EP+WP	1	0	0	0	0	0	1	0	0	0	2	98
70	<i>Ceraclea globosa</i> Yang & Morse, 1988	EP	1	0	0	0	0	0	0	0	0	0	1	3
71	<i>Ceraclea hastata</i> (Botosaneanu, 1970)	EP	1	0	0	0	0	0	0	0	0	0	1	1
72	<i>Ceraclea lobulata</i> (Martynov, 1935)	EP	1	0	0	1	0	0	0	1	0	0	3	94
73	<i>Ceraclea nigronevosa</i> (Retzius, 1783)	HL	1	1	1	0	0	0	0	1	0	0	4	140
74	<i>Ceraclea shuotsuensis</i> (Tsuda, 1942)	EP	1	0	0	0	0	0	0	1	0	0	2	115
75	<i>Ceraclea sibirica</i> (Ulmer, 1906)	EP	1	0	1	1	1	0	0	0	0	0	4	139
76	<i>Ceraclea trilobulata</i> Morse, Yang, & Levanidova, 1997	EP	1	0	0	0	0	0	0	0	0	0	1	1
77	<i>Erotesia baltica</i> McLachlan, 1877	EP	0	0	0	0	0	0	1	0	0	0	1	1
78	<i>Mystacides bifidus</i> Martynov, 1924	EP	1	0	0	0	0	0	0	0	0	0	1	1
79	<i>Mystacides interjectus</i> (Banks, 1914)	EP+NA	1	0	0	0	0	0	0	0	0	0	1	1
80	<i>Mystacides longicornis</i> (Linnaeus, 1758)	EP+WP	1	0	0	1	0	0	0	1	0	0	3	518
81	<i>Mystacides sepulchralis</i> (Walker, 1852)	EP+NA	1	1	0	0	0	0	0	0	0	0	2	70
82	<i>Mystacides sibiricus</i> Martynov, 1935	EP+OL	0	0	0	0	0	0	1	0	0	0	1	1
83	<i>Oecetis furva</i> (Rambur, 1842)	EP+WP	0	0	0	0	1	0	1	1	0	0	3	76
84	<i>Oecetis intima</i> McLachlan, 1877	EP+WP	1	0	0	1	0	0	0	1	0	0	3	43
85	<i>Oecetis lacustris</i> (Pictet, 1834)	HL	1	1	0	0	0	0	1	1	0	0	4	38
86	<i>*Oecetis nigropunctata</i> Ulmer, 1908	EP+OL	0	0	0	1	0	0	0	0	0	0	1	5
87	<i>Oecetis ochracea</i> (Curtis, 1825)	HL	1	1	0	1	0	1	1	1	1	1	8	258
88	<i>Parasetodes aquilonius</i> Yang & Morse, 1997	EP	1	0	0	1	0	0	0	0	0	0	2	4
89	<i>Parasetodes respersellus</i> (Rambur, 1842)	HL	0	0	0	0	0	1	0	0	0	0	1	2
90	<i>Setodes furcatulus</i> Martynov, 1935	EP	0	0	0	0	1	0	0	0	0	0	1	1
91	<i>Setodes punctatus</i> (Fabricius, 1793)	EP+WP	1	0	0	1	0	0	0	1	0	0	3	345
92	<i>Triadenodes fulvus</i> Navas, 1931	EP+OL	1	0	0	0	0	0	0	0	0	0	1	1
93	<i>Triadenodes internus</i> McLachlan, 1875	EP+WP	1	0	1	1	0	0	1	1	0	0	5	100
94	<i>Triadenodes jakutianus</i> Martynov, 1910	EP+NA	0	0	0	1	0	0	0	1	0	0	2	3
95	<i>Triadenodes levanidovae</i> (Morse & Vshivkova, 1997)	EP	1	0	0	1	1	0	1	0	0	0	4	187
96	<i>Triadenodes reuteri</i> McLachlan, 1880	EP+WP	1	1	1	1	0	1	1	1	0	0	7	138
97	<i>Triadenodes simulans</i> Tjeder, 1929	EP+WP	1	0	0	1	1	0	0	0	0	0	3	123

Limnephilidae

98	<i>Anabolia appendix</i> (Ulmer, 1905)	EP	1	0	1	0	1	0	0	1	1	0	5	119
99	<i>Anabolia servata</i> (McLachlan, 1880)	EP	1	0	0	1	0	0	0	0	0	0	2	2
100	<i>Anisogamodes flavipunctatus</i> (Martynov, 1914)	EP	1	0	0	0	1	0	1	1	0	0	4	93
101	<i>Annitella obscurata</i> (McLachlan, 1876)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	3
102	<i>Arctopora trimaculata</i> (Zetterstedt, 1840)	HL	1	0	0	0	0	0	0	1	0	0	2	9
103	<i>Asynarchus amurensis</i> (Ulmer, 1905)	EP+WP	1	0	0	1	1	0	0	1	0	0	4	7
104	<i>Asynarchus iteratus</i> McLachlan, 1880	EP+NA	1	1	0	0	0	0	0	1	0	0	3	658
105	<i>Asynarchus lapponicus</i> (Zetterstedt, 1840)	HL	1	1	0	0	0	0	0	1	0	0	3	19
106	<i>*Asynarchus sachalinensis</i> Martynov, 1914	EP	1	0	0	0	0	0	0	0	0	0	1	1
107	<i>Asynarchus thedenii</i> (Wallengren, 1879)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	2
108	<i>Brachypsyche rara</i> (Martynov, 1914)	EP	1	0	0	0	0	0	0	0	0	0	1	2
109	<i>Chaetopteryx sahlbergi</i> McLachlan, 1876	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
110	<i>Clostoea</i> sp	EP+NA	1	0	0	0	0	0	0	0	0	0	1	1
111	<i>Colpotaulus incisus</i> (Curtis, 1834)	EP+WP	1	1	0	1	0	1	1	1	0	1	7	86
112	<i>Dicosmoecus palatus</i> (McLachlan, 1872)	EP+WP	1	1	1	1	0	0	1	1	0	0	6	298
113	<i>*Drusus</i> sp	EP+WP	0	0	1	0	0	0	0	1	0	0	2	98
114	<i>Ecclisomyia digitata</i> (Martynov, 1929)	EP	1	1	0	0	0	0	1	1	0	0	4	69
115	<i>Ecclisomyia kamshtatica</i> (Martynov, 1914)	EP	1	0	0	0	0	0	0	0	0	0	1	16
116	<i>Grammotaulius sibiricus</i> McLachlan, 1874	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
117	<i>Grammotaulius signatipennis</i> McLachlan, 1876	HL	0	0	0	0	0	0	0	1	0	0	1	11

118	<i>Halesus sachalinensis</i> Martynov, 1914	EP	1	0	0	0	0	0	0	1	0	0	2	6
119	<i>Halesus tessellatus</i> (Rambur, 1842)	EP+WP	0	0	0	0	0	0	1	0	0	0	1	1
120	<i>Hydatophylax grammicus</i> (McLachlan, 1880)	EP+WP	1	1	1	0	0	0	0	0	0	0	3	25
121	<i>Hydatophylax festivus</i> (Navas, 1920)	EP	1	0	0	0	0	0	0	0	0	0	1	1
122	<i>Hydatophylax nigrovittatus</i> (McLachlan, 1872)	EP	1	1	0	0	0	0	0	0	0	0	2	57
123	<i>Hydatophylax soldatovi</i> (Martynov, 1914)	EP	1	0	0	0	0	0	0	0	0	0	1	10
124	<i>Hydatophylax variabilis</i> (Martynov, 1910)	HL	1	0	0	0	0	0	0	0	0	0	1	1
125	<i>Lenarchus productus</i> (Morton, 1896)	EP+WP	0	1	0	0	0	0	0	0	0	0	1	2
126	<i>Lepnevaina signata</i> Wiggins, 1897	EP	0	0	0	0	0	0	0	1	0	0	1	1
127	<i>Limnephilus abstrusus</i> McLachlan, 1872	EP	1	0	0	1	0	0	1	0	0	0	3	7
128	<i>Limnephilus alaicus</i> (Martynov, 1915)	EP+WP	0	0	0	0	0	0	1	1	1	0	3	12
129	<i>Limnephilus algosus</i> (McLachlan, 1868)	HL	1	0	0	0	0	0	1	1	0	1	4	122
130	<i>Limnephilus asiaticus</i> (McLachlan, 1874)	HL	1	0	0	0	0	0	1	1	0	0	3	8
131	<i>Limnephilus bulgani</i> Mey, 1991	EP	1	0	0	0	0	0	0	0	0	0	1	1
132	<i>Limnephilus correptus</i> McLachlan, 1880	EP	1	0	0	0	0	0	0	0	0	0	1	1
133	<i>Limnephilus diphys</i> McLachlan, 1880	HL	1	0	0	0	0	0	0	0	0	0	1	1
134	<i>Limnephilus dispar</i> McLachlan, 1875	HL	1	0	0	0	0	0	0	0	0	0	1	7
135	<i>Limnephilus fuxicatus</i> McLachlan, 1865	EP+WP	1	1	0	0	0	0	1	0	0	0	3	40
136	<i>Limnephilus flavicornis</i> (Fabricius, 1787)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
137	<i>Limnephilus fenestratus</i> (Zetterstedt, 1840)	HL	1	0	0	0	0	0	0	1	0	0	2	7
138	<i>Limnephilus fuscinervis</i> (Zetterstedt, 1840)	EP+WP	0	0	1	0	0	0	0	0	0	0	1	1
139	<i>Limnephilus fuscovittatus</i> Matsumura, 1904	EP+OL	1	1	0	0	0	0	1	1	0	0	4	55
140	** <i>Limnephilus bovsgolicus</i> Morse, 1999	EP	1	0	0	0	0	0	0	0	0	0	1	42
141	<i>Limnephilus major</i> (Martynov, 1909)	HL	1	0	0	0	0	0	1	1	0	0	3	11
142	<i>Limnephilus picturatus</i> McLachlan, 1875	HL	1	1	0	0	0	0	0	1	0	0	3	8
143	<i>Limnephilus politus</i> McLachlan, 1865	EP+WP	1	1	0	0	0	0	0	0	0	0	2	2
144	<i>Limnephilus primoryensis</i> Nimmo, 1995	EP	0	0	0	0	0	0	1	0	0	1	2	35
145	<i>Limnephilus quadratus</i> Martynov, 1914	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
146	<i>Limnephilus rhombicus</i> (Linnaeus, 1758)	HL	1	1	0	1	1	0	1	0	0	0	5	98
147	<i>Limnephilus samoedus</i> (McLachlan, 1880)	HL	0	0	1	0	0	0	0	1	0	0	2	8
148	<i>Limnephilus sparsus</i> Curtis, 1834	EP+WP	0	1	0	0	0	0	1	0	0	1	3	113
149	<i>Limnephilus stigma</i> Curtis, 1834	HL	1	1	0	0	0	0	0	1	0	0	3	44
150	<i>Limnephilus subnitidus</i> McLachlan, 1875	EP+WP	1	0	0	0	0	0	0	1	0	0	2	98
151	<i>Limnephilus vittatus</i> (Fabricius, 1798)	EP+WP	0	1	0	0	0	0	0	0	0	0	1	1
152	<i>Micropterna sequax</i> McLachlan, 1875	EP+WP	1	0	0	0	0	0	0	0	0	0	1	2
153	<i>Nemotaulius admorsus</i> (McLachlan, 1866)	EP	1	0	0	0	0	0	0	0	0	0	1	4
154	<i>Nemotaulius amurensis</i> Nimmo, 1995	EP	1	1	0	0	0	0	0	0	0	0	2	19
155	<i>Nemotaulius mutatus</i> (McLachlan, 1872)	HL	1	0	0	0	0	0	0	0	0	0	1	1
156	<i>Philartetus bergrothi</i> McLachlan, 1880	HL	1	1	0	0	0	1	0	1	0	0	4	109
157	<i>Philartetus rhomboidalis</i> Martynov, 1924	EP+WP	1	0	0	0	1	0	0	1	0	0	3	3
158	<i>Potamophylax</i> sp	EP+WP	1	0	0	0	0	0	0	0	0	0	1	2
159	<i>Pseudostenophylax</i> sp	HL	1	0	0	0	0	0	0	0	0	0	1	3
Molannidae														
160	<i>Molanna albicans</i> (Zetterstedt, 1840)	EP+WP	0	0	0	0	0	0	0	1	0	0	1	200
161	<i>Molanna moesta</i> Banks, 1906	EP+OL	0	0	0	0	1	0	0	0	0	0	1	1
162	<i>Molanna submarginalis</i> McLachlan, 1872	EP+WP	1	1	0	0	0	0	0	0	0	0	2	15
163	<i>Molannodes tinctus</i> (Zetterstedt, 1840)	HL	1	0	0	0	1	0	1	1	0	0	4	79
Phryganeidae														
164	<i>Agrypnia colorata</i> Hagen, 1873	HL	1	0	0	1	0	0	0	1	0	0	3	19
165	<i>Agrypnia crassicornis</i> (McLachlan, 1876)	EP+WP	1	0	0	0	0	0	1	1	0	0	3	19
166	<i>Agrypnia czerskyi</i> (Martynov, 1924)	EP+WP	1	0	0	1	1	0	1	0	0	0	4	32
167	** <i>Agrypnia hayfordae</i> Morse & Chuluunbat, 2007	EP	1	0	0	0	0	0	0	0	0	0	1	339
168	<i>Agrypnia obsoleta</i> (Hagen, 1864)	HL	1	1	1	1	0	0	0	1	0	0	5	345
169	<i>Agrypnia pagetana</i> Curtis, 1835	HL	1	1	1	0	0	0	1	1	0	0	5	12
170	<i>Agrypnia picta</i> Kolenati, 1848	EP+WP	1	1	0	1	0	1	1	0	0	0	5	40
171	<i>Hagenella</i> sp	HL	1	0	0	0	0	0	0	0	0	0	1	1
172	<i>Oligotricha hybridoides</i> Wiggins & Kuwayama, 1971	EP	1	0	0	0	0	0	0	0	0	0	1	1
173	<i>Oligotricha lapponica</i> (Hagen, 1864)	HL	1	1	0	0	0	0	0	0	0	0	2	7
174	<i>Oligotricha striata</i> (Linnaeus, 1758)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
175	<i>Phryganea bipunctata</i> Retzius, 1783	EP+WP	1	1	0	0	1	0	0	1	0	0	4	5

176	<i>Phryganea grandis</i> Linnaeus, 1758	EP+WP	1	1	0	0	0	0	1	1	0	0	4	25
177	<i>Semblis atrata</i> (Gmelin, 1789)	EP+WP	1	0	0	0	0	0	0	1	0	0	2	192
178	<i>Semblis phalaenoides</i> (Linnaeus, 1758)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
Polycentropodidae														
179	<i>Cyrnus</i> sp	EP+WP	0	0	0	0	0	0	1	0	0	0	1	1
180	<i>Holocentropus picicornis</i> (Stephens, 1836)	HL	1	0	0	0	0	0	0	0	0	0	1	2
181	<i>Neucentropus mandjuricus</i> (Martynov, 1907)	EP+OL	0	0	0	0	0	1	0	0	0	0	1	1
182	<i>Neureclipsis bimaculata</i> (Linnaeus, 1758)	HL	0	1	0	0	0	0	0	1	0	0	2	31
183	<i>*Nyctiophylax</i> sp	HL	0	0	0	0	0	0	1	0	0	0	1	1
184	<i>Plectrocnemia kusnezovi</i> Martynov, 1934	EP	1	0	0	0	0	0	0	0	0	0	1	1
185	<i>Polycentropus flavomaculatus</i> (Pictet, 1834)	EP+WP	0	0	0	0	0	0	0	1	0	0	1	2
Psychomyiidae														
186	<i>Psychomyia flavida</i> Hagen, 1861	EP+NA	1	0	1	1	1	1	1	1	1	0	8	7739
187	<i>Psychomyia minima</i> (Martynov, 1910)	EP	1	0	1	0	1	0	0	1	1	0	5	1565
188	<i>Psychomyia pusilla</i> (Fabricius, 1781)	EP+WP	1	0	0	0	0	0	0	0	0	0	1	1
Rhyacophilidae														
189	<i>Himalopsyche</i> sp	EP+NA+OL	1	0	0	0	0	0	0	0	0	0	1	1
190	<i>Rhyacophila angulata</i> Martynov, 1910	EP+OL	1	0	1	0	1	0	0	1	0	0	4	329
191	<i>Rhyacophila depressa</i> Martynov, 1910	EP	1	0	0	0	1	0	0	0	0	0	2	23
192	<i>Rhyacophila egijica</i> Schmid, 1968	EP	1	1	1	1	1	0	1	1	1	0	8	3349
193	<i>Rhyacophila impar</i> Martynov, 1914	EP	1	0	0	0	1	0	0	1	0	0	3	7
194	<i>Rhyacophila lata</i> Martynov, 1918	EP	1	0	0	0	0	0	0	0	0	0	1	76
195	<i>Rhyacophila mongolica</i> Levanidova, 1993	EP	1	1	0	0	0	0	0	0	0	0	2	77
196	<i>Rhyacophila nana</i> Levanidova, 1993	EP	1	0	0	0	0	0	0	0	0	0	1	8
197	<i>Rhyacophila nipponica</i> Navas, 1933	EP	1	0	0	0	0	0	0	0	0	0	1	1
198	<i>Rhyacophila retracta</i> Martynov, 1914	EP	1	0	0	0	0	0	0	0	0	0	1	11
199	<i>Rhyacophila sibirica</i> McLachlan, 1879	EP	1	1	1	1	0	0	1	1	0	0	6	411
Stenopsychidae														
200	<i>Stenopsyche griseipennis</i> McLachlan, 1866	EP+OL	0	0	1	0	0	1	0	0	0	0	2	14
Thremmatidae														
201	<i>Neophylax</i> sp	EP+NA+OL	1	0	0	0	0	0	0	0	0	0	1	1
TOTAL			159	51	39	38	34	17	52	87	15	7	499	47939

Comparison of caddisfly (Insecta, Trichoptera) assemblages from lake and river habitats of the Huron Mountains of Michigan (USA)

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Abstract

The caddisfly assemblages of six lakes and 12 1st–4th order streams of the Huron Mountains of northern Upper Michigan (USA) were sampled monthly with ultraviolet lights during June–September 2019. A total of 169 species representing 63 genera and 19 families was collected, including five species not found elsewhere in Michigan and two species endemic to the state. Species assemblages between lotic and lentic habitats were distinct from each other, with 11 species indicating lakes and 23 indicating rivers. Despite the taxonomic differences, biomass of functional feeding groups (FFGs) was similar between lakes and rivers, except for higher biomass of predators in the former and higher biomass of filtering collectors in the latter. The FFG biomass of both habitat types was dominated (50–70%) by shredders. Considering the undisturbed condition of the habitats, the caddisfly assemblages and FFG biomass of the Huron Mountains can serve as regional biological monitoring reference conditions.

Keywords

Functional feeding group, lakes, Michigan, streams, Trichoptera

Introduction

Due to the high degradation rates of freshwater habitats, knowledge on the original characteristic assemblages of such habitats is lacking (Ricciardi and Rasmussen 1999;

Master et al. 2000; Strayer 2006). Many recent studies have suggested large-scale declines in aquatic insect species (DeWalt et al. 2005; Houghton and Holzenthal 2010; Hawkins and Yuan 2016; Sánchez-Bayo and Wyckhuys 2019; Rhodes 2019; Houghton and DeWalt 2021) or fundamental changes to their community ecology (Baranov et al. 2020; van Klink et al. 2020). Without truly undisturbed reference sites for comparison, however, it is difficult to accurately evaluate current species composition or ecological functioning of freshwater ecosystems. This problem is especially true for lake ecosystems, as research on the biotic assemblages and potential for anthropogenic disturbance of such habitats has lagged far behind that of river habitats (Peck et al. 2020; Fergus et al. 2021). Thus, quantifying assemblages of ecologically important aquatic insect taxa within undisturbed reference sites, especially those of lakes, should be a scientific priority.

The caddisflies (Trichoptera) constitute a particularly important group of organisms for biological monitoring due to their high species richness, ecological diversity, and differing sensitivities to various anthropogenic disturbance (Barbour et al. 1999; Dohet 2002; Houghton 2008; Houghton et al. 2011; Morse et al. 2019a). Although the caddisflies of Michigan are generally well known (Houghton et al. 2018), new species and state records continue to be found in under-collected regions (Houghton 2020). Moreover, nearly all collections of the taxonomically important adult caddisflies in Michigan have consisted of a single sample from a collection site, usually an ultraviolet light trap deployed for a single evening. To accurately capture the characteristic species richness and ecological functioning of Michigan ecosystems, multiple samples would need to be taken from different seasons within a variety of habitats in an undisturbed region.

The Huron Mountain Club (HMC) is a ~ 6,000 ha private conservation reserve located in the Huron Mountains of Michigan (Fig. 1). The property is one of the last remaining old-growth mixed hemlock and hardwood forests in the northcentral US (Flader 1983; Yanoviak and McCafferty 1996). Other than some historical and contemporary logging, and a few cabins and small campgrounds, the entire region is undisturbed and has excellent water quality (Woodruff et al. 2010). The HMC contains the middle and lower reaches of the Pine and the Salmon Trout rivers as well as several lakes and smaller tributaries. Due to the undisturbed condition of its habitats, reference conditions have been established for many taxa that occur on the property (www.hmwf.org). When this study began, however, only 21 caddisfly species were known from the HMC (Woods 2011), mostly from Yanoviak and McCafferty's (1996) study of the benthic communities of the Pine River (Site 8), Mountain Stream (9), and the Salmon Trout River (17) (Fig. 1). The purpose of this study, therefore, was a thorough inventory of the caddisflies of the HMC property to establish reference conditions for species assemblages and ecological functioning within lakes and streams of the region.

Materials and methods

Six lakes and 12 stream sites were chosen for caddisfly sampling (Fig. 1, Tables 1, 2). Sites were chosen to reflect a variety of habitats (Fig. 2) that also had reasonable road

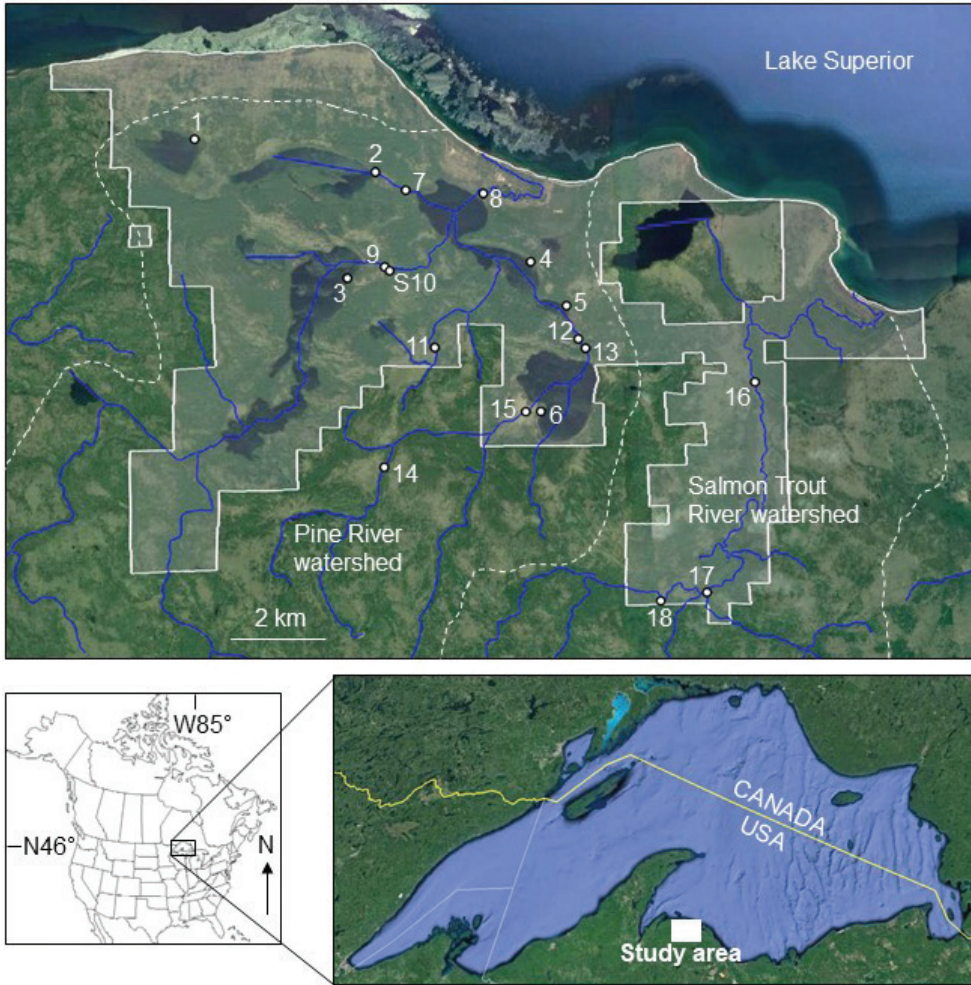


Figure 1. Location of the six lakes and 12 stream sites of the study. Solid white lines denote the approximate borders of the Huron Mountain Club property. Dashed white lines denote the approximate boundaries of the Pine River and Salmon Trout River watersheds. Site numbers correspond to Tables 1, 2. Base maps Google, National Oceanic and Atmospheric Administration, TerraMetrics.

access. Several rivers were sampled at more than one location. One site was just outside the HMC property. There were no dams or human settlements within the watersheds of any of the study sites.

In total, 23 environmental variables were measured at each site or obtained from other sources. Some variables applied only to streams, others only to lakes, and others to both habitat types (Table 2). Latitude, longitude, and elevation were determined using Google Earth Pro (GE), as was width at each stream site. Stream sinuosity was determined in GE by tracing the stream for ~ 2 km upstream of each sampling site and dividing by the straight line distance between the beginning and end of the trace (Gordon 2004). Some smaller tributaries necessitated traces < 2 km. Physicochemical stream vari-

Table 1. The 18 sites sampled during this study with the total number of caddisfly species caught at each site. Site numbers correspond to Fig. 1 and Table 2. All sites were sampled once during June, July, August, and September 2019. Mean species richness was the same in rivers as in lakes based on a non-parametric Mann-Whitney *U*-test between the habitat types ($P = 0.065$).

Site	Location	Latitude / Longitude	Elevation (m)	species
1	Howe Lake, northeast boathouse	46.8932°, -87.9436°	211	41
2	Rush Lake, east boathouse	46.8869°, -87.8967°	195	55
3	Mountain Lake, east boathouse	46.8681°, -87.9043°	258	48
4	Second Pine Lake, east boathouse	46.8705°, -87.8567°	185	42
5	Third Pine Lake, eastern picnic area	46.8626°, -87.8475°	186	44
6	Ives Lake, west side, at Stonehouse,	46.8439°, -87.8547°	232	53
				Mean of lakes 47 (±3.4)
7	Rush Creek, Mountain Lake Road	46.8836°, -87.8889°	187	70
8	Pine River, main entrance road	46.8828°, -87.8687°	184	71
9	Mountain Stream, at bridge	46.8699°, -87.8946°	227	48
10	Mountain Stream, below waterfall	46.8692°, -87.8933°	216	41
11	Fisher Creek, Loop Road	46.8555°, -87.8819°	250	44
12	River Styx, entrance foot bridge	46.8567°, -87.8446°	187	65
13	River Styx, base of cascade	46.8550°, -87.8428°	205	55
14	North Fork, Elm Creek, Loop Road	46.8377°, -87.8975°	248	64
15	Elm Creek, near Stonehouse	46.8439°, -87.8586°	233	52
16	Salmon Trout River, entrance bridge	46.8485°, -87.7989°	192	57
17	Salmon Trout River, Middle Falls	46.8100°, -87.8245°	223	50
18	Salmon Trout River, Lower Dam	46.8114°, -87.8125°	218	79
				Mean of rivers 58 (±2.4)

ables were measured during a 4-day period during August 2019. This period was chosen to maximize leaf abundance on trees while minimizing stream flow variation. No rain events occurred during the 4-day period. Twelve measurements of specific conductance (ECTestr Low, www.eutechinst.com), pH (AccuMetAP61, www.fishersci.com), flow velocity (Flowwatch, www.jdc.ch), and dissolved oxygen (YSI-55, OH, www.ysi.com) were taken near each sampling site within a 10-min period and the mean value was recorded. Measurements were taken for all sites within 2 h. This procedure was repeated over the subsequent 3 days, and a global mean was determined for each variable. Total area, total shoreline perimeter, maximum depth, and mean depth were determined for each lake from an internal bathymetry report of the property (www.hmwf.org).

Several other site variables were determined using the USEPA StreamCat database (<https://watersgeo.epa.gov/watershedreport>), accessed November 2020 (Hill et al. 2016). These variables included: percentage of base flow relative to total flow, distance from stream bottom to bedrock, distance from stream bottom to water table, percentage of organic matter by volume in the soil, soil permeability, mean composite topographic index (CTI), percentage of impervious surface, density of roads, percentage of plant cover not native to the region, and overall percentage of undisturbed (forest or wetland) land cover. All of these variables were at the local (HUC-12) catchment level. In addition, mean summer stream temperature was determined for each specific site, also from the StreamCat database.

Sampling for caddisfly adults occurred during 2019. An ultraviolet blacklight sample was collected from each site in June, July, August, and September, for a total of four

Table 2. Physicochemical data for the 18 sites of this study. Site numbers correspond to Table 1 and Fig. 1. See Materials and methods for further explanation of how data were obtained.

Parameter	Lake sites						River sites											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
pH	8.4	8.4	8.4	8.0	8.2	8.4	8.5	8.0	8.3	8.3	8.6	8.4	8.4	8.3	8.1	8.0	8.1	8.1
DO (mg/L)	7.4	8.1	7.9	7.2	7.4	7.9	8.9	8.2	8.4	8.4	8.6	7.2	7.6	9.0	7.2	8.5	9.1	9.1
K ($\mu\text{C}/\text{cm}^2$)	40	70	100	80	80	60	60	80	100	100	90	60	60	90	100	110	120	120
Stream temperature ($^{\circ}\text{C}$)			N/A				14.8	17.2	16.1	16.1	14.5	15.2	15.2	14.5	14.8	16.9	15.7	15.7
Width (m)			N/A			2	15	8	8	3	6	3	3	6	11	7	7	
Area (ha)	68	125	332	71	23	191						N/A						
Shoreline (km)	3.8	8.7	16.3	4.9	2.4	6.1						N/A						
Maximum depth (m)	15	90	20	14	5	34						N/A						
Mean depth (m)	5	22	6	3	1.5	9.4						N/A						
Velocity (m/s)			N/A				0.7	0.4	3.2	0.7	0.3	0.2	0.6	0.6	0.2	0.3	2.5	2.3
Sinuosity			N/A				1.16	1.84	1.15	1.15	1.58	1.24	1.18	1.75	1.83	1.47	1.24	1.25
Percent intact habitat	95	94	94	95	95	95	93	97	94	94	97	98	98	93	78	96	95	95
Percent exotic plants	0.1	0.1	4.9	0.0	0.0	5.4	1.9	8.2	4.8	3.0	3.0	4.2	4.2	3.5	4.4	4.3	6.8	6.8
Percent base flow	61	61	61	62	62	62	62	61	61	61	61	62	62	61	62	62	62	62
Distance to bedrock (cm)	89	89	130	89	89	138	89	89	130	130	130	138	138	130	130	140	130	130
CTI	587	587	851	653	653	932	460	645	387	387	395	470	470	419	799	448	355	355
Distance to H ₂ O table (cm)	178	178	181	157	157	142	157	157	181	181	181	142	142	182	182	152	182	182
Percent impervious surface	0.04	0.04	0.03	0.03	0.03	0.26	0.08	0.38	0.04	0.04	0.02	0.02	0.02	0.14	0.17	0.05	0.03	0.03
Percent soil organic matter	1.5	1.5	0.5	0.8	0.8	0.5	3.5	3.5	0.5	0.5	0.5	3.0	3.0	0.5	0.5	2.7	0.5	0.5
Soil permeability (cm/h)	12	12	32	12	12	23	12	12	32	32	32	23	23	32	32	26	32	32
Roads (km/km ²)	0.7	0.7	0.4	0.6	0.6	0.6	1.5	3.1	0.7	0.7	0.8	0.6	0.6	1.1	1.6	0.9	0.9	0.9

samples from each site. Each sample consisted of a 10-watt portable ultraviolet LED light placed over a white pan filled with 80% ethanol (Zemel and Houghton 2017). Lights were placed ~ 1 m from each site, turned on at dusk, and collected ~ 1 h after dusk (Wright et al. 2013). Samples were collected only if the peak daytime temperature was > 25° C, dusk temperature was > 18° C, and there was no noticeable wind or precipitation at dusk (Houghton 2004). Each set of monthly samples was taken within four days of each other. Since aquatic insects collected within 40 m of a habitat accurately reflect the assemblage of that habitat (Sode and Wiberg-Larson 1993; Peterson et al. 1999; Sommerhäuser et al. 1999; Brakel et al. 2015), dispersals of adults between sites, while certainly possible, were considered unimportant.

Specimens were identified using Houghton's (2012) treatment of the Minnesota caddisflies or with more specific taxonomic treatments as needed. Specimens were coded with their affinity for one of six different functional feeding groups (FFGs) based on Morse et al. (2019b) and some unpublished gut content analyses: algal piercers, filtering collectors, gathering collectors, predators, scrapers, and shredders. Codes consisted of '0' for no affinity for a FFG, '1' low affinity, '2' moderate affinity, '3' high affinity, and '4' near exclusive affinity (Chevenet et al. 1994) (Table 3). These codes were converted to proportions: 0 = 0.0, 1 = 0.25, 2 = 0.50, 3 = 0.75, and 4 = 1.0, to multiply by the determined biomass for each genus (Beauchard et al. 2017). This approach more accurately reflected the feeding plasticity of aquatic insects than pure categorization (Dolédéc et al. 2000; Gayraud et al. 2003; Tomanova et al. 2007).

Ash-free dry mass (AFDM) values for each species were taken from Houghton and Lardner's (2020) determination of 63 common caddisflies of the north-central US. Species without a determined value were assigned the value of a congener of similar size. While this approach did not reflect differences in body size due to differences in sexual dimorphism, specific habitat, larval food quality, or emergence timing, among other differences (Svensson 1975; Wagner 2002; Wagner 2005), it still allowed for a more precise determination of FFG differences between sites than simply counting specimens and treating them as ecologically equivalent, while also preserving the vast majority as vouchers. All specimens have been deposited in the Hillsdale College Insect Collection (HCIC).

To delineate differences between caddisfly assemblages of lake and river habitats, specimens were examined with a non-metric multidimensional scaling (NMDS) ordination using the program PC-ORD v.7 for Windows (Peck 2016). The data matrix consisted of $\log_{10}(x + 1)$ transformed specimen counts per site for each species for each of the monthly samples. The mean of these four values was then determined for each site for each species. All species were weighted equally. The NMDS ordination was conducted using the default program settings, 250 randomized runs, and a Bray-Curtis distance measure. A Monte Carlo test was conducted on each determined axis to assess its difference from a random ordination structure (Dexter et al. 2018). Since several important stream variables (e.g., width) are not appropriate for analyzing lakes, and others (e.g., flow velocity) may lead to artificial continua from lakes to slow-moving rivers, no secondary matrix

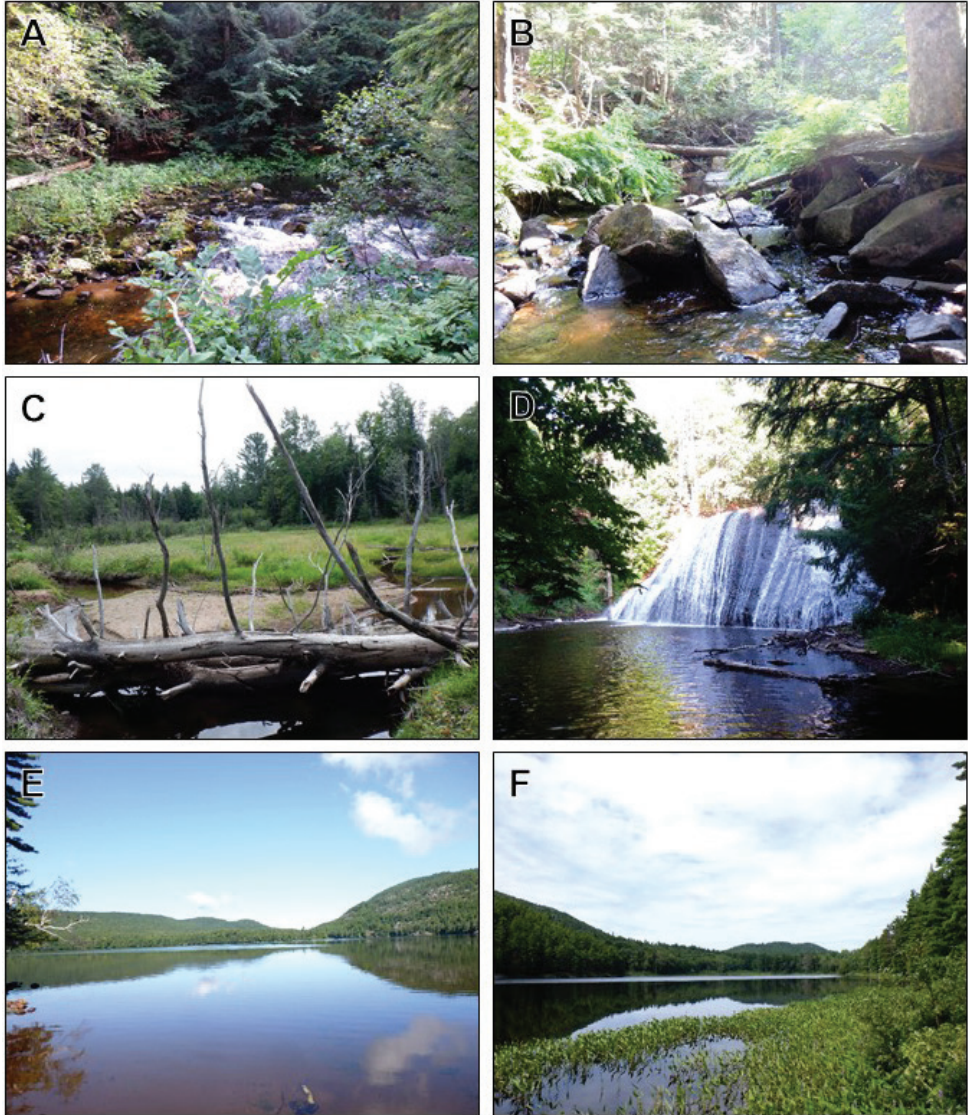


Figure 2. Representative habitats of the Huron Mountains **A** Middle Rapids of the Salmon Trout River (Site 17) **B** River Styx, below the cascade (13) **C** multiple braided channels of the North Fork of Elm Creek (14) **D** pool below the falls of Mountain Stream (10) **E** Mountain Lake (3) **F** Third Pine Lake (5). Site numbers correspond to Fig. 1 and Tables 1, 2. Photographs taken August 2019.

of environmental variables was correlated with the primary matrix. Differences in mean biomass for each FFG between lakes and streams were determined using non-parametric Mann-Whitney *U*-tests.

Species important for indicating lake or river habitats were determined with Dufrêne and Legendre's (1997) indicator species technique, also using PC-ORD. This

method determines a species' indicator value based on a combination of the percentage of habitats that contain a particular species, and the average abundance of that species within each habitat type divided by the average abundance of that species in all habitat types. Thus, in order to be a significant indicator of either lakes or rivers, a species needed to be common and abundant in the respective habitat type only.

Results

A total of 21,235 specimens were collected and identified, representing 169 species within 63 genera and 19 families (Table 3). Hydroptilidae (37), Leptoceridae (34), and Limnephilidae (29) were the most species-rich families. *Hydroptila* (15), *Ceraclea* (10), and *Limnephilus* (10) were the most species-rich genera.

Pycnopsyche guttifera (Walker) (Limnephilidae) (2392 mg) had the highest overall AFDM, followed by *Oecetis inconspicua* (Walker) (Leptoceridae) (1524), *Lepidostoma togatum* (Hagen) (Lepidostomatidae) (861), and *Onoconsmoecus unicolor* (Banks) (Limnephilidae) (685) (Table 3). Over half of the AFDM of the entire assemblage was represented collectively by the species of *Pycnopsyche* (28%), *Oecetis* (13%), *Lepidostoma* (7%), and *Ptilostomis* (7%). *Banksiola crotchii* Banks (Phryganeidae) and *Oecetis inconspicua* were found at all 18 sites; *Ptilostomis semifasciata* (Say) (Phryganeidae) and *Pycnopsyche guttifera* were found at 17 sites. Thirty-one species were found at only a single site.

An NMDS ordination of species assemblages for all sampling sites produced a two-dimensional solution explaining almost 90% of the variation in the data set (Fig. 3). Lake and river sampling sites were distinct from each other with no overlap. Mean species richness was similar in river (58) and lake (47) habitats (Table 1). Mean biomass was not different between lake and river sites for any FFG, except for higher filtering collectors in rivers and higher predators in lakes (Fig. 4). Eleven species indicated lakes and 23 indicated rivers (Table 3).

Nearly all sampling sites had local (HUC-12) catchment habitat composed of 93–98% native plant communities (Table 2), primarily eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), and white pine (*Pinus strobus*), with occasional oaks (*Quercus* spp.) and maples (*Acer* spp.). Impervious surface was < 0.5% of all local catchment areas. Specific conductance ranged 40–100 $\mu\text{C}/\text{cm}^2$ in lakes and 60–120 in streams; pH ranged 8.0–8.4 and 8.0–8.6 respectively, and dissolved oxygen ranged 7.2–8.1 ppm and 7.2–9.1 ppm. Most landscape variables exhibited minimal difference between sites.

Discussion

Several unique species were collected during this study (Table 3). Specimens of *Cernotina pallida* (Banks) (Polycentropodidae), *Hydroptila fiskei* Blickle (Hydroptilidae), *Limnephilus femoralis* Kirby and *L. thorus* Ross (Limnephilidae), and *Triaenodes perna* Ross (Leptoceridae) represent the only known collections of these species within Michigan.

Table 3. The 169 caddisfly species collected during this study, showing total number of localities (#locs) and total number of specimens (#spcs), and mean ash-free dry mass (AFDM) (mg) from lakes and rivers. Species are organized alphabetically by family and genus. Asterisks denote significant affinity with lakes or rivers based on indicator species analysis. Functional feeding groups (FFGs) as follows: FC = filtering collector, GC = gathering collector, Pi = algal piercer, Pr = predator, Sc = scraper, Sh = shredder.

Taxon	FFG affinity coding								AFDM (lakes)	AFDM (rivers)
	FC	GC	Pi	Pr	Sc	Sh	# locs	#spcs		
BRACHYCENTRIDAE (2)										
<i>Brachycentrus americanus</i> (Banks, 1899)	3	0	0	0	0	1	4	29	0.000	1.801
<i>Micrasema wataga</i> Ross, 1938	1	1	0	0	0	2	6	103	0.016	0.801
DIPSEUDOPSIDAE (1)										
<i>Phyllocentropus placidus</i> (Banks, 1905)	4	0	0	0	0	0	11	136	2.579	3.450
GLOSSOSOMATIDAE (3)										
<i>Glossosoma intermedium</i> Klapálek, 1892	0	0	0	0	4	0	9	113	0.047	2.654*
<i>G. nigrior</i> Banks, 1911	0	0	0	0	4	0	8	549	0.000	13.009*
<i>Protoptila tenebrosa</i> (Walker, 1852)	0	0	0	0	4	0	1	4	0.000	0.010
GOERIDAE (1)										
<i>Goera stylata</i> Ross, 1938	0	0	0	0	4	0	3	109	0.000	4.495*
HELICOPSYCHIDAE (1)										
<i>Helicopsyche borealis</i> (Hagen, 1861)	0	0	0	0	4	0	12	773	12.629	8.041
HYDROPSYCHIDAE (15)										
<i>Arctopsyche ladogensis</i> (Kolenati, 1859)	3	0	0	0	0	1	2	101	0.000	1.608
<i>Cheumatopsyche analis</i> (Banks, 1908)	4	0	0	0	0	0	11	76	0.115	2.133*
<i>C. campyla</i> Ross 1938	4	0	0	0	0	0	11	484	3.401	12.249*
<i>C. gracilis</i> (Banks, 1899)	4	0	0	0	0	0	8	263	0.058	7.551*
<i>C. oxa</i> Ross, 1938	4	0	0	0	0	0	3	6	0.040	0.102
<i>Hydropsyche alhedra</i> (Ross, 1939)	4	0	0	0	0	0	2	39	0.000	1.273
<i>H. betteni</i> Ross, 1938	4	0	0	0	0	0	11	174	1.370	9.249*
<i>H. morosa</i> (Hagen, 1861)	4	0	0	0	0	0	10	357	0.196	11.557*
<i>H. slossonae</i> (Banks, 1905)	4	0	0	0	0	0	5	87	0.000	2.840*
<i>H. sparna</i> (Ross, 1938)	4	0	0	0	0	0	13	722	0.678	26.843*
<i>H. vexa</i> (Ross, 1938)	4	0	0	0	0	0	1	3	0.000	0.098
<i>H. walkeri</i> (Betten and Mosely, 1940)	4	0	0	0	0	0	4	22	0.000	0.719
<i>Macrostemum zebratum</i> (Hagen, 1861)	4	0	0	0	0	0	1	2	0.000	0.295
<i>Parapsyche apicalis</i> (Banks, 1908)	3	0	0	0	0	1	2	2	0.000	0.079
<i>Potamyia flava</i> (Hagen, 1861)	4	0	0	0	0	0	2	2	0.079	0.039
HYDROPTILIDAE (37)										
<i>Agraylea multipunctata</i> Curtis, 1834	0	2	2	0	0	0	9	24	0.025	0.047
<i>Hydroptila albicornis</i> Hagen, 1861	0	0	3	0	1	0	1	1	0.001	0.000
<i>H. amoena</i> Ross, 1938	0	0	3	0	1	0	7	17	0.003	0.022
<i>H. ampoda</i> Ross, 1941	0	0	3	0	1	0	4	17	0.003	0.022
<i>H. antennopedia</i> Sykora and Harris, 1994	0	0	3	0	1	0	1	1	0.000	0.001
<i>H. consimilis</i> Morton, 1905	0	0	3	0	1	0	4	10	0.000	0.014
<i>H. hamata</i> Morton, 1905	0	0	3	0	1	0	3	30	0.003	0.040
<i>H. fiskei</i> Blickle, 1963	0	0	3	0	1	0	4	8	0.002	0.009
<i>H. jackmanni</i> Blickle, 1963	0	0	3	0	1	0	6	103	0.003	0.141
<i>H. novicola</i> Blickle & Morse, 1954	0	0	3	0	1	0	1	1	0.000	0.001
<i>H. salmo</i> Ross, 1941	0	0	3	0	1	0	1	1	0.000	0.001
<i>H. tortosa</i> Ross, 1938	0	0	3	0	1	0	1	1	0.001	0.000
<i>H. valhallia</i> Denning, 1947	0	0	3	0	1	0	5	8	0.000	0.011
<i>H. waubesiana</i> Betten, 1934	0	0	3	0	1	0	1	1	0.003	0.000
<i>H. wyomia</i> Denning, 1948	0	0	3	0	1	0	1	2	0.000	0.003
<i>H. xera</i> Ross, 1938	0	0	3	0	1	0	7	41	0.000	0.057
<i>Ithytrichia clavata</i> Morton, 1905	0	0	1	0	3	0	4	8	0.000	0.011
<i>Leucotrichia pictipes</i> (Banks, 1911)	0	0	2	0	2	0	1	1	0.000	0.001
<i>Mayatrichia ayama</i> Mosely, 1905	0	0	1	0	3	0	2	2	0.003	0.001

Taxon	FFG affinity coding							# locs	#spcs	AFDM (lakes)	AFDM (rivers)
	FC	GC	Pi	Pr	Sc	Sh					
<i>Neotrichia halia</i> Denning, 1948	0	0	0	0	4	0	3	9	0.002	0.008	
<i>N. okopa</i> Ross, 1939	0	0	0	0	4	0	1	1	0.000	0.001	
<i>Ochrotrichia tarsalis</i> (Hagen, 1861)	0	1	3	0	0	0	1	1	0.000	0.001	
<i>Orthotrichia aegerfasciella</i> (Chambers, 1873)	0	0	4	0	0	0	3	21	0.007	0.014	
<i>O. balduffi</i> Kingsolver & Ross, 1961	0	0	4	0	0	0	3	7	0.000	0.007	
<i>O. cristata</i> Morton, 1905	0	0	4	0	0	0	4	23	0.040	0.002	
<i>O. curta</i> Kingsolver & Ross, 1961	0	0	4	0	0	0	4	19	0.015	0.011	
<i>Oxyethira araya</i> Ross, 1941	0	1	3	0	0	0	1	1	0.000	0.001	
<i>O. coercens</i> Morton, 1905	0	1	3	0	0	0	4	39	0.006	0.034	
<i>O. forcipata</i> Mosely, 1934	0	1	3	0	0	0	5	7	0.000	0.007	
<i>O. michiganensis</i> Mosely, 1934	0	1	3	0	0	0	8	48	0.000	0.046	
<i>O. obtatus</i> Denning, 1947	0	1	3	0	0	0	2	3	0.004	0.001	
<i>O. rivicola</i> Blickle & Morse, 1954	0	1	3	0	0	0	7	21	0.000	0.020	
<i>O. sida</i> Blickle & Morse, 1954	0	1	3	0	0	0	2	8	0.005	0.006	
<i>O. verna</i> Ross, 1938	0	1	3	0	0	0	1	1	0.000	0.001	
<i>O. zeronia</i> Ross, 1941	0	1	3	0	0	0	1	1	0.000	0.001	
<i>Stactobiella delira</i> (Ross, 1938)	0	1	3	0	0	0	1	1	0.000	0.001	
<i>S. palmata</i> (Ross, 1938)	0	1	3	0	0	0	1	3	0.003	0.000	
LEPIDOSTOMATIDAE (6)											
<i>Lepidostoma bryanti</i> (Banks, 1908)	0	1	0	0	0	3	15	536	1.055	19.662*	
<i>L. griseum</i> (Banks, 1911)	0	1	0	0	0	3	2	9	0.000	0.339	
<i>L. sackeni</i> (Banks, 1936)	0	1	0	0	0	3	2	2	0.000	0.078	
<i>L. togatum</i> (Hagen, 1861)	0	1	0	0	0	3	16	1835	21.261	61.087	
<i>L. unicolor</i> (Banks, 1911)	0	1	0	0	0	3	4	22	0.000	0.860	
<i>L. vernale</i> (Banks, 1897)	0	1	0	0	0	3	2	3	0.000	0.117	
LEPTOCERIDAE (34)											
<i>Ceraclea alagma</i> (Ross, 1938)	0	2	0	1	0	1	5	37	4.169*	0.058	
<i>C. ancylus</i> (Vorhies, 1909)	0	2	0	1	0	1	6	4	0.463	0.000	
<i>C. arielles</i> (Denning, 1942)	0	2	0	1	0	1	3	420	0.000	11.131*	
<i>C. cancellata</i> (Betten, 1942)	0	2	0	1	0	1	6	31	3.127	0.232	
<i>C. excisa</i> (Morton, 1904)	0	2	0	1	0	1	1	1	0.114	0.000	
<i>C. flava</i> (Ross, 1904)	0	2	0	1	0	1	1	1	0.000	0.057	
<i>C. maculata</i> (Banks, 1899)	0	2	0	1	0	1	1	16	1.817	0.000	
<i>C. resurgens</i> (Walker, 1852)	0	2	0	1	0	1	12	266	2.731	14.428	
<i>C. tarsipunctata</i> (Vorhies, 1909)	0	2	0	1	0	1	13	205	17.491*	2.896	
<i>C. transversa</i> (Hagen, 1861)	0	2	0	1	0	1	14	210	13.318	5.5009	
<i>Leptocerus americanus</i> (Banks, 1899)	0	1	0	0	0	3	4	5	0.156	0.020	
<i>Mystacides interjecta</i> (Banks, 1914)	0	3	0	0	0	1	4	72	3.745*	0.053	
<i>M. sepulchralis</i> (Walker, 1852)	0	3	0	0	0	1	9	88	3.638	0.535	
<i>Nectopsyche albida</i> (Walker, 1852)	0	1	0	0	0	3	2	24	2.277	0.049	
<i>N. exquisita</i> (Walker, 1852)	0	1	0	0	0	3	4	25	2.474	0.000	
<i>N. pavidia</i> (Hagen, 1861)	0	1	0	0	0	3	7	167	1.568	2.063	
<i>Oecetis avara</i> (Banks, 1895)	0	1	0	2	0	1	7	315	0.418	10.769*	
<i>O. cinerascens</i> (Hagen, 1861)	0	1	0	2	0	1	12	284	20.124*	0.641	
<i>O. immobilis</i> (Hagen, 1861)	0	1	0	2	0	1	2	2	0.151	0.000	
<i>O. inconspicua</i> (Walker, 1852)	0	1	0	2	0	1	18	3370	221.438*	16.280	
<i>O. nocturna</i> Ross, 1966	0	1	0	2	0	1	1	2	0.151	0.000	
<i>O. osteni</i> Milne, 1934	0	1	0	2	0	1	10	169	10.136	0.798	
<i>O. persimilis</i> (Banks, 1907)	0	1	0	2	0	1	10	205	3.332	5.450	
<i>O. sordida</i> (Blahnik and Holzenthal, 2014)	0	1	0	2	0	1	5	84	0.377	2.977	
<i>Setodes incertus</i> (Walker, 1852)	0	3	0	1	0	0	2	4	0.064	0.032	
<i>S. truncatus</i> Houghton, 2021	0	3	0	1	0	0	2	4	0.000	0.096	
<i>Trienodes abus</i> Milne, 1935	0	1	0	0	0	3	2	2	0.099	0.0460	
<i>T. baris</i> Ross, 1938	0	1	0	0	0	3	3	4	0.199	0.099	
<i>T. dipsius</i> Ross, 1938	0	1	0	0	0	3	5	12	0.694	0.248	
<i>T. ignitus</i> (Walker, 1852)	0	1	0	0	0	3	4	34	0.000	1.684	

Taxon	FFG affinity coding								AFDM (lakes)	AFDM (rivers)
	FC	GC	Pi	Pr	Sc	Sh	# locs	#spcs		
<i>T. injustus</i> (Hagen, 1861)	0	1	0	0	0	3	10	339	29.827*	1.883
<i>T. marginatus</i> Sibley, 1926	0	1	0	0	0	3	5	77	1.883	2.874
<i>T. perna</i> Ross, 1938	0	1	0	0	0	3	1	1	0.099	0.000
<i>T. tardus</i> Milne, 1934	0	1	0	0	0	3	8	12	0.396	0.396
LIMNEPHILIDAE (29)										
<i>Anabolia bimaculata</i> (Walker, 1852)	0	1	0	0	0	3	7	8	1.206	1.005
<i>A. consocia</i> (Walker, 1852)	0	1	0	0	0	3	5	5	0.308	0.616
<i>Asynarchus montanus</i> (Banks, 1907)	0	1	0	0	0	3	2	8	0.000	1.608
<i>A. rossi</i> Leonard & Leonard, 1949	0	1	0	0	0	3	1	5	0.000	1.005
<i>Hesperophylax designatus</i> (Walker, 1852)	0	1	0	0	0	3	2	2	0.000	0.662
<i>Hydatophylax argus</i> (Harris, 1869)	0	1	0	0	0	3	11	59	2.174	30.974*
<i>Ironoquia lyrata</i> (Ross, 1938)	0	0	0	0	0	4	2	2	0.000	0.266
<i>Lenarchus crassus</i> (Banks, 1920)	0	3	0	0	0	1	1	1	0.000	0.133
<i>Limnephilus argenteus</i> Banks, 1914	0	1	0	0	0	3	1	1	0.000	0.133
<i>L. indivisus</i> Walker, 1852	0	1	0	0	0	3	3	8	0.000	1.530
<i>L. infernalis</i> (Banks, 1914)	0	1	0	0	0	3	7	34	12.239*	0.382
<i>L. femoralis</i> Kirby, 1837	0	1	0	0	0	3	1	1	0.000	0.133
<i>L. moestus</i> Banks, 1908	0	1	0	0	0	3	15	89	3.356	9.809
<i>L. ornatus</i> Banks, 1907	0	1	0	0	0	3	10	36	1.549	3.872
<i>L. rhombicus</i> (L., 1758)	0	1	0	0	0	3	2	5	0.000	0.645
<i>L. sericeus</i> (Say, 1824)	0	1	0	0	0	3	9	28	2.323	2.452
<i>L. submonilifer</i> Walker, 1852	0	1	0	0	0	3	8	18	0.774	1.936
<i>L. thorus</i> Ross, 1938	0	1	0	0	0	3	1	1	0.000	0.129
<i>Nemotaulius hostilis</i> (Hagen, 1873)	0	0	0	0	0	4	1	1	0.000	0.460
<i>Onocosmoecus unicolor</i> (Banks, 1897)	0	0	0	0	0	4	10	290	1.182	56.503*
<i>Platycentropus radiatus</i> (Say, 1824)	0	0	0	0	0	4	14	55	11.258	12.582
<i>Pseudostenophylax sparsus</i> (Banks, 1908)	0	1	0	0	0	3	9	16	0.797	1.728
<i>Pycnopysche aglona</i> Ross 1941	0	0	0	0	1	3	4	99	2.93	16.677
<i>P. antica</i> (Walker, 1852)	0	0	0	0	1	3	12	267	1.181	51.975*
<i>P. circularis</i> (Provancher, 1877)	0	0	0	0	1	3	12	126	1.466	22.358*
<i>P. guttifera</i> (Walker, 1852)	0	0	0	0	1	3	17	1088	85.767	156.507
<i>P. lepida</i> (Hagen, 1861)	0	0	0	0	1	3	10	134	2.932	23.091
<i>P. limbata</i> (MacLachlan, 1871)	0	0	0	0	1	3	6	12	0.367	2.016
<i>P. subfasciata</i> (Say, 1828)	0	0	0	0	1	3	10	218	74.039*	2.932
MOLANNIDAE (4)										
<i>Molanna blenda</i> Sibley, 1926	0	1	0	1	2	0	8	69	0.000	3.943*
<i>M. flavicornis</i> Banks, 1914	0	1	0	1	2	0	2	4	0.358	0.056
<i>M. tryphena</i> Betten, 1934	0	1	0	1	2	0	7	75	0.000	4.472*
<i>M. uniophila</i> Vorhies, 1909	0	1	0	1	2	0	13	664	59.505*	9.838
ODONTOCERIDAE (1)										
<i>Psilotreta indecisa</i> (Walker, 1852)	0	1	0	0	3	0	2	103	0.000	6.193
PHILOPOTAMIDAE (4)										
<i>Chimarra feria</i> (Ross, 1941)	4	0	0	0	0	0	3	5	0.000	0.148
<i>C. obscura</i> (Walker, 1852)	4	0	0	0	0	0	7	51	0.236	1.387
<i>Dolophilodes distinctus</i> (Walker, 1852)	4	0	0	0	0	0	11	374	0.131	12.221*
<i>Wormaldia moesta</i> (Banks, 1914)	4	0	0	0	0	0	2	2	0.000	0.066
PHRYGANEIDAE (8)										
<i>Agrypnia improba</i> (Hagen, 1873)	0	0	0	0	0	4	6	22	0.510	5.353
<i>A. vestita</i> (Walker, 1852)	0	0	0	0	0	4	4	4	1.529	0.255
<i>Banksiola crotchii</i> Banks, 1844	0	0	0	1	0	3	18	370	22.162	31.187
<i>B. dossuaria</i> (Say, 1828)	0	0	0	1	0	3	3	12	0.735	1.103
<i>Hagenella canadensis</i> (Banks, 1907)	0	0	0	1	0	3	2	2	0.000	0.510
<i>Phryganea cinerea</i> Walker, 1852	0	0	0	1	0	3	14	55	25.101	18.826
<i>Prilostomis ocellifera</i> (Walker, 1852)	0	0	0	1	0	3	13	66	16.839	31.272
<i>P. semifasciata</i> (Say, 1828)	0	0	0	1	0	3	17	85	40.896	30.672
POLYCENTROPIDIDAE (15)										

Taxon	FFG affinity coding								AFDM (lakes)	AFDM (rivers)
	FC	GC	Pi	Pr	Sc	Sh	# locs	#spcs		
<i>Cernotina pallida</i> (Banks, 1904)	1	0	0	3	0	0	3	38	0.668*	0.000
<i>Holocentropus flavus</i> Banks, 1908	1	0	0	3	0	0	4	11	0.000	0.383
<i>H. interruptus</i> Banks, 1914	1	0	0	3	0	0	5	6	0.170	0.170
<i>Neureclipsis crepuscularis</i> (Walker, 1852)	2	0	0	1	0	1	9	116	0.824	1.721
<i>Nyctiophylax affinis</i> (Banks, 1897)	1	0	0	2	0	1	6	248	1.627	0.734
<i>N. moestus</i> Banks, 1911	1	0	0	2	0	1	9	57	0.631	1.678
<i>Plectrocnemia albipuncta</i> Banks, 1930	1	0	0	3	0	0	8	50	0.083	0.649
<i>P. cinerea</i> (Hagen, 1861)	1	0	0	3	0	0	11	103	2.016*	0.400
<i>P. clinei</i> Milne, 1936	1	0	0	3	0	0	3	5	0.000	0.069
<i>P. icula</i> (Ross, 1941)	1	0	0	3	0	0	4	33	0.000	0.456
<i>P. remota</i> (Banks, 1911)	1	0	0	3	0	0	6	8	0.000	0.278
<i>P. sabulosa</i> (Leonard & Leonard, 1949)	1	0	0	3	0	0	3	11	0.000	0.383
<i>Polycentropus centralis</i> Banks, 1914	1	0	0	3	0	0	1	5	0.000	0.069
<i>P. confusus</i> Hagen, 1861	1	0	0	3	0	0	16	336	0.387	4.446
<i>P. pentus</i> Ross, 1941	1	0	0	3	0	0	6	43	0.000	1.496
<i>P. timesis</i> (Denning, 1948)	1	0	0	3	0	0	1	1	0.000	0.035
PSYCHOMYIIDAE (2)										
<i>Lype diversa</i> (Banks, 1914)	0	2	0	0	2	0	15	420	0.096	1.298*
<i>Psychomyia flavida</i> Hagen, 1861	0	3	0	0	1	0	15	178	0.081	0.516
RHYACOPHILIDAE (2)										
<i>Rhyacophila brunnea</i> Banks, 1911	0	1	0	3	0	0	1	4	0.000	0.151
<i>R. fuscula</i> (Walker, 1852)	0	1	0	3	0	0	6	305	0.234	35.506*
SERICOSTOMATIDAE (1)										
<i>Agarodes distinctus</i> (Ulmer, 1905)	0	2	0	0	0	2	9	60	4.640	1.657
THREMMATIDAE (2)										
<i>Neophylax concinnus</i> McLachlan, 1871	0	0	0	0	0	4	4	14	0.055	0.356
<i>N. oligius</i> Ross, 1938	0	0	0	0	0	4	9	271	0.000	7.422*

Both known Michigan endemic species, *Plectrocnemia sabulosa* (Leonard and Leonard) and *Setodes truncatus* Houghton, were also found during this study. The latter species is currently known worldwide only from the Pine (site 8) and Salmon Trout (17) rivers.

The known species richness of the Huron Mountains habitats represents > 50% of all 305 species found in Michigan (Houghton et al 2018; Houghton 2020) and > 30% of all ~ 550 species found in the Upper Midwest region of the United States (Rasmussen and Morse 2018; Houghton et al. 2022). The Huron Mountains habitats contained ~ 1.5 × as many caddisfly species (114) as the Black River Ranch of northern Lower Michigan, ~ 2.5 × that of Indiana Dunes National Lakeshore (64), and ~ 3.5 × that of Isle Royale National Park (46), other fairly undisturbed areas of Michigan and northern Indiana sampled with a rigorous effort (DeWalt and South 2015; DeWalt et al. 2016; Houghton 2016). The fauna of the Huron Mountains was more similar to those of the Black River Ranch and Isle Royale than it was to Indiana Dunes, with 8, 5, and 20 species found in the respective areas not found in the Huron Mountains. This result is not surprising given the similar latitude and terrestrial habitat of the Huron Mountains, Black River Ranch, and Isle Royale.

Habitat and water physicochemical data supported the undisturbed nature of Huron Mountains habitats, with high levels of intact native terrestrial habitat, low impervious surface, no historical or contemporary dams or human settlements, and low specific conductance values. Specific conductance is a general indicator of nutrient, sediment, and organic matter concentrations (Allan 2004). The values of HMC rivers were ~ 1/6 that of

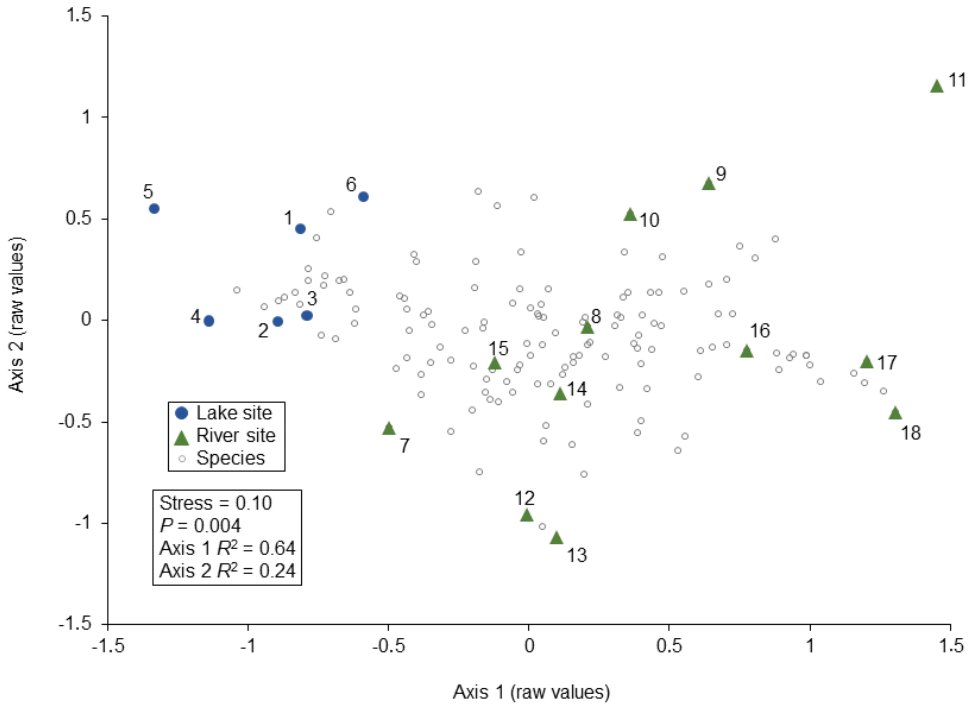


Figure 3. NMDS ordination of the 18 sampling sites based on caddisfly \log_{10} specimen abundance per species per site, and reflecting the combined four samples for each site. P -values from a Monte Carlo test of non-random ordination structure. Site numbers correspond to Fig. 1 and Tables 1, 2. Species labels omitted for clarity.

Michigan agricultural rivers (Castillo et al. 2000; Bernot et al. 2006; Arango et al. 2007; Houghton et al. 2011) and $\sim 1/3$ that of other undisturbed Michigan rivers (Houghton et al. 2018), suggesting very low anthropogenic seston enrichment. Yanoviak and McCafferty (1996) found similar low specific conductance values when they sampled the Pine River, Mountain Stream, and the Salmon Trout River ~ 27 years ago. The only stream site with $< 93\%$ intact native terrestrial habitat, Elm Creek (#15), had cattle grazing in its lower reaches > 100 years ago; such reaches were subsequently replanted with a wildflower meadow. While it is unlikely that any ecosystem in the contiguous 48 states of the US is in truly pristine condition, the habitats of the HMC probably represent some of the closest available to the original terrestrial and aquatic habitat conditions within the northcentral US (Flader 1983; Simpson et al. 1990) and are, thus, appropriate for determining reference conditions and differences in faunal assemblages between ecosystem types.

The separation of caddisfly species assemblages between lakes and streams despite their close geographic proximity supports the distinctness of lotic and lentic habitats. Of the 11 species that indicated lakes, over half were in the Leptoceridae, a family typically associated with lakes and slow-moving rivers (Wiggins 2004). Conversely, most of the species that indicated rivers were known rheophilic hydropsychids, glossosomatids, or rhyacophilids. Few previous studies (e.g., Kimura et al. 2006) have attempted

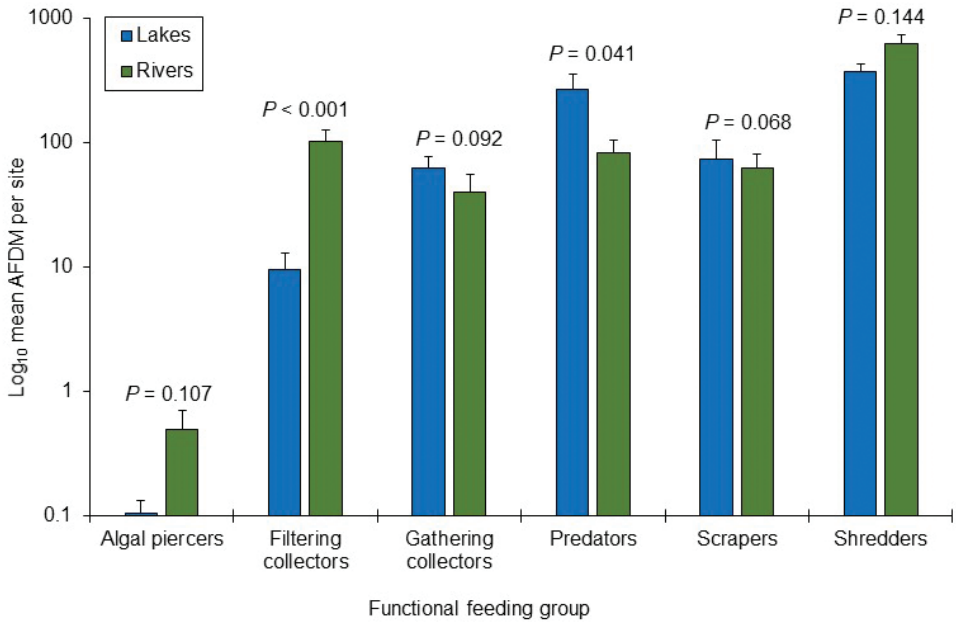


Figure 4. Log₁₀ mean (+SE) total AFDM for caddisfly FFGs between lakes and rivers of the Huron Mountains. *P*-values based on nonparametric Mann-Whitney *U*-tests of the mean biomass for each FFG between lake and river habitats. *N* = six for lakes and 12 for rivers.

to establish characteristic species assemblages or indicator species for lakes, and none has directly compared these assemblages to nearby rivers.

Despite the taxonomic differences between lakes and rivers, both total biomass and that of most individual FFGs were similar between the two habitat types. The higher biomass of filtering collectors in rivers was probably due to the flow velocity needed to inflate their capture nets (Wiggins 2004). The higher biomass of predators in lakes was greatly influenced by the predator *Oecetis inconspicua*, a highly abundant lentic species. Whereas riverine systems have had several models proposed that predict changes in FFG ecology based on stream size and other factors (Vannote et al. 1980; Thorp et al. 2006; Maasri et al. 2021), lake environments have received much less attention. Some previous studies have proposed that lakes, particularly eutrophic lakes, are primarily autochthonous (Francis et al. 2011; Galloway et al. 2014; Lau et al. 2014), while others have confirmed the importance of allochthonous carbon in supporting lentic food webs (Pace et al. 2004; Tanentzap et al. 2017). All such studies, however, focused on zooplankton instead of benthic insects. The high relative biomass of shredders (~ 50%) relative to scrapers (< 10%) in lakes of the Huron Mountains demonstrated the importance of coarse allochthonous input to lake food webs. While only caddisflies were sampled in this study, several other studies have demonstrated that trends in caddisfly FFG ecology usually reflect those of the overall insect assemblage (Mackay and Wiggins 1979; Dohet 2002; Houghton et al. 2011; Houghton et al. 2018; Morse et al. 2019a; Houghton 2021).

Due to the close proximity of sites in this study, it is likely that some specimens were sampled by a light trap of a different natural habitat. While this problem can never be completely eliminated, several studies suggest that the low vagility of caddisflies promotes minimal specimen 'leakage' between sampling sites (Sode and Wiberg-Larson 1993; Peterson et al. 1999; Sommerhäuser et al. 1999). Brakel et al. (2015), in particular, found a forest and meadow site of a Michigan stream separated by ~ 100 m had very little overlap in their adult caddisfly assemblages when sampled using ultraviolet lights. Further, the indicator species analysis (Dufrêne and Legendre 1997) employed in this study is negligibly influenced by occasional specimens. Thus, abundant riverine species such as *Cheumatopsyche campyla* Ross, *Hydropsyche betteni* Ross, or *H. morosa* Hagen constituted river indicator species, even though they occasionally were sampled at a lake.

Future research should include sampling caddisflies and other aquatic insects in remaining undisturbed habitats throughout the northcentral US and elsewhere. Observed differences of caddisflies between lakes and rivers would increase in value if also observed with other aquatic insect orders within other regions. Further sampling of lake habitats is particularly important so that models can be generated to predict changes in aquatic insect assemblages relative to specific lake variables.

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Checklist of the caddisflies (Insecta, Trichoptera) of the Upper Midwest region of the United States

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Abstract

Five hundred and fifty-two caddisfly species are reported from the Upper Midwest region of the United States, an area that includes 13 states and ~ 2 million km². Of these, 62 species are reported for the first time from the state of Iowa, 25 from Wisconsin, 18 from South Dakota, 12 from Illinois, five from Indiana, four from North Dakota, four from Minnesota, and one from Nebraska. The Upper Midwest fauna contains nearly 40% of all species known from the United States and Canada, as well as 22 species endemic to the region. Overall species richness was highest in Michigan (319 species), Kentucky (296), Minnesota (292), and Wisconsin (284). Differences in state species assemblages within the region largely followed a geographic pattern, with species richness declining in the western prairie states. There are almost certainly further species remaining to be found in this large region.

Keywords

Caddisfly, checklist, diversity, Midwest, Trichoptera, USA

Introduction

The Upper Midwest region of the United States (Fig. 1) encompasses 13 states and over 2 million km² and is derived based on membership in the Midwest Association of Wildlife and Fisheries Agencies (MAFWA 2021). The region has a > 70-year caddisfly research history. Many of the first investigations were by Ross (1938, 1944) on the species of Illinois. Subsequent checklists on the faunas of Indiana (Waltz and McCafferty 1983), Kansas (Hamilton et al. 1983), Kentucky (Resh 1975), Michigan (Leonard and Leonard 1949), Minnesota (Etnier 1965; Houghton et al. 2001), North Dakota (Harris et al. 1980), and Wisconsin (Longridge and Hilsenhoff 1973) followed thereafter. More recently, discoveries of new records, updated checklists, and more comprehensive faunal studies have occurred in Indiana (DeWalt et al. 2016; Bolton et al. 2019), Kentucky (Floyd et al. 2012; Evans et al. 2017), Michigan (DeWalt and South 2015; Houghton 2016, 2020; Houghton et al. 2018), Minnesota (Houghton 2012), Missouri (Moulton and Stewart 1996), Ohio (Armitage et al. 2011; Bolton et al. 2019), and Wisconsin (Hilsenhoff 1995). Conversely, the caddisflies of Iowa, Nebraska, and South Dakota are known only from regional studies (Blinn et al. 2009; Zuellig et al. 2012) and piecemeal collections. Despite the extensive collecting history, new records continue to be found in the region, even in well-collected states like Michigan (Houghton 2020). The purpose of this paper was to combine historical records and our own unpublished data into a checklist of the entire Upper Midwest region, focusing on new state records and species endemic to the region.

Materials and methods

We have been investigating the caddisflies of the Upper Midwest for ~ 20 years (Fig. 1). Collecting methods for adults have included sweep netting, malaise trapping, and ultraviolet light trapping. Most adult collecting took place during June and July, the peak emergence period of caddisflies in the region (Houghton 2018). Additional collections of adults were made during May, August, and September to obtain early and late emerging species. Larval collecting methods have included dip-netting, Hess sampling, Surber sampling, Hester-Dandy artificial substrate sampling, and hand collecting of specimens. We also accessed and confirmed specimens from the extensive Iowa (<https://programs.iowadnr.gov/bionet/>) and Wisconsin (<https://dnr.wisconsin.gov/topic/SurfaceWater/SWIMS>) Departments of Natural Resources larval macroinvertebrate databases.

Adult specimens were identified using Ross (1944), Houghton (2012), or more specific taxonomic treatments as necessary. Larvae were identified to the genus level using Morse et al. (2019 or earlier editions) and more specific species treatments as needed. Specimens collected by the authors are primarily deposited in the Hillsdale College Insect Collection, the Illinois Natural History Survey, the University of Iowa State Hygienic lab, and the University of Minnesota Insect Collection.

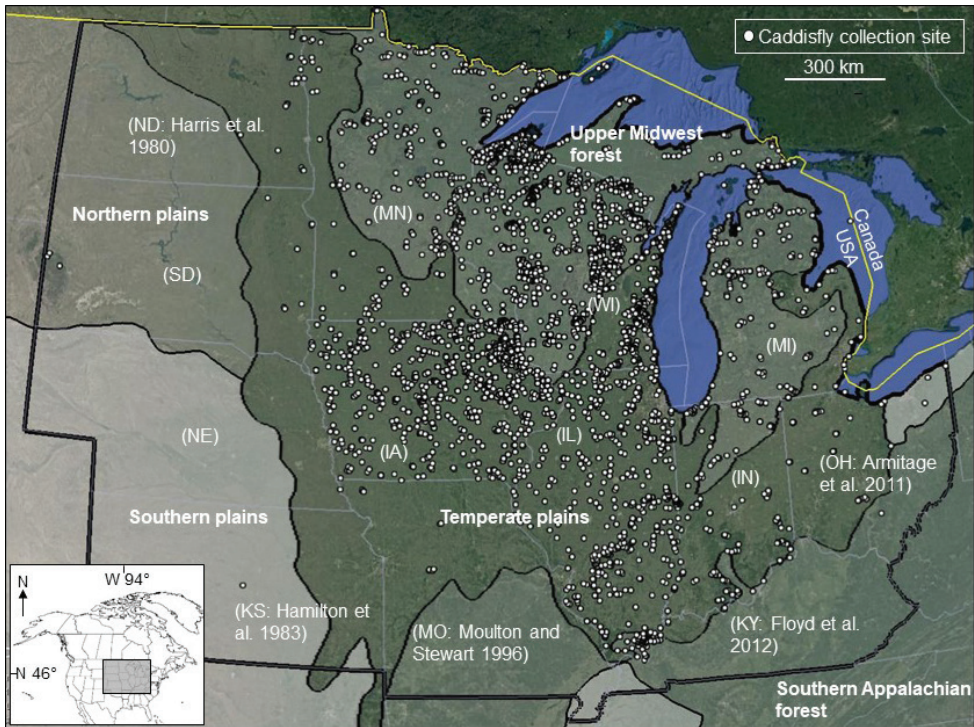


Figure 1. The 13 states and primary ecoregions of the Upper Midwest region, showing collecting localities within the last ~20 years by the authors or their colleagues. Citations are the most comprehensive taxonomic works for states where our collecting effort was low. State abbreviations, IA: Iowa, IL: Illinois, IN: Indiana, KS: Kansas, KY: Kentucky, MI: Michigan, MN: Minnesota, MO: Missouri, NE: Nebraska, ND: North Dakota, OH: Ohio, SD: South Dakota, WI: Wisconsin.

We also utilized the distributional checklist of Rasmussen and Morse (2020) as a starting point to investigate the presence of species that we did not personally identify. We generally accepted literature records, although we scrutinized each record for dubious assertions due to suspected misidentifications, misinterpretations of cited records, and an inability to locate the confirming specimen. Since a large portion of the Upper Midwest caddisfly checklist can already be found in Rasmussen and Morse (2020) or elsewhere, we do not recreate the entire list in this paper, but instead provide it as a supplementary data file. Nomenclature follows that of Rasmussen and Morse (2020).

Differences in caddisfly assemblages relative to geography were examined with a non-metric multidimensional scaling (NMDS) ordination using the program PC-ORD v. 7 for Windows (Peck 2016). The data matrix consisted of presence ('1') or absence ('0') values for each species for each state. All species were weighted equally. The NMDS ordination was conducted using the default program settings, 250 randomized runs, and a Jaccard distance measure. A Monte Carlo test was conducted on each determined axis to assess its difference from a random ordination structure (Dexter et al. 2018).

Results

Based on examination of ~ 750,000 larval and adult specimens from nearly 4,000 collecting localities (Fig. 1) and a synthesis of the literature, we report 552 caddisfly species from the Upper Midwest, representing 21 families and 97 genera (Suppl. material 1). Of these, 131 species are reported for the first time from one or more states of the region (Table 1), including 62 from Iowa, 25 from Wisconsin, 18 from South Dakota, 12 from Illinois, five from Indiana, four from North Dakota, four from Minnesota, and one from Nebraska. More detailed collecting data about these species records are available in Suppl. material 2.

Michigan (319) had the greatest species richness, followed by Kentucky (296), Minnesota (292), and Wisconsin (284) (Fig. 2). Only 13 species (2%) were found in all Upper Midwest states, whereas 144 species (26%) were found in a single state (Suppl. material 1). Of these single-state species, 53 (37%) were found exclusively in Kentucky and 21 (15%) in Missouri. A total of 22 species are reported as regional endemics (Table 2).

The NMDS ordination of species presence or absence per state produced a two-dimensional solution (Fig. 2). The two axes reflected > 90% of variation within the dataset. Distribution of the 13 states in ordination space had a high congruence with states in geographic space.

Hydroptilidae (117 species) was the most species rich family, followed by Limnephilidae (82), and Leptoceridae (76) (Fig. 3). Those families, plus the Hydropsychidae and the Polycentropodidae collectively represented nearly 75% of all species richness. The most species rich genera were *Hydroptila* (56 species), *Hydropsyche* (35), and *Limnephilus* (31) (Suppl. material 1).

Table 1. The 131 new state species records reported herein. Species organized by family and genus. More detailed collecting data are available in Suppl. material 2.

Taxon	IA	IL	IN	MN	ND	NE	SD	WI
BRACHYCENTRIDAE								
<i>Brachycentrus fuliginosus</i> Walker, 1852	–	–	–	–	–	–	–	X
<i>B. lateralis</i> (Say, 1823)	X	–	–	–	–	–	–	–
<i>B. numerosus</i> (Say, 1823)	X	–	–	–	–	–	–	–
GLOSSOSOMATIDAE								
<i>Agapetus tomus</i> Ross, 1941	–	–	–	–	–	–	–	X
<i>Glossoma parvulum</i> Banks, 1904	–	–	–	–	–	–	X	–
<i>Protoptila erotica</i> Ross, 1938	X	–	–	–	–	–	–	–
HELICOPSYCHIDAE								
<i>Helicopsyche borealis</i> (Hagen, 1861)	X	–	–	–	–	–	–	–
HYDROPSYCHIDAE								
<i>Cheumatopsyche aphanota</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>C. campyla</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>C. halima</i> Denning, 1948	X	–	–	–	–	–	–	–
<i>C. lasia</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>C. minuscula</i> (Banks, 1907)	–	X	–	–	–	–	–	–
<i>C. oxa</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>C. pasella</i> Ross, 1941	X	–	–	–	–	–	–	–
<i>Diplectrona modesta</i> Banks, 1908	X	–	–	–	–	–	–	–

Taxon	IA	IL	IN	MN	ND	NE	SD	WI
<i>Homoplectra doringa</i> (Milne, 1936)	–	X	–	–	–	–	–	–
<i>Hydropsyche aerata</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>H. alternans</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>H. arinale</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>H. betteni</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>H. dicantha</i> Ross, 1938	X	X	–	–	–	–	–	–
<i>H. hageni</i> Banks, 1905	X	–	–	–	–	–	–	–
<i>H. morosa</i> Hagen, 1861	–	–	–	–	–	–	X	–
<i>H. phalerata</i> Hagen, 1861	–	–	–	–	X	–	–	–
<i>H. scalaris</i> Hagen, 1861	X	–	–	–	–	–	–	–
<i>H. slossonae</i> Banks, 1905	X	–	–	–	–	–	–	–
<i>H. sparna</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>Macrostemum carolina</i> (Banks, 1909)	X	–	–	–	–	–	–	–
<i>Parapsyche apicalis</i> (Banks, 1908)	X	–	–	–	–	–	–	–
HYDROPTILIDAE								
<i>Agraylea multipunctata</i> Curtis, 1834	X	–	–	–	–	–	–	–
<i>Hydoptila ajax</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>H. albicornis</i> Hagen, 1861	X	–	–	–	–	–	–	–
<i>H. ampoda</i> Ross, 1941	–	–	–	–	–	–	–	X
<i>H. angusta</i> Ross, 1938	–	–	–	–	X	–	X	X
<i>H. arctia</i> Ross, 1938	–	–	–	–	–	–	X	–
<i>H. consimilis</i> Morton, 1905	–	–	–	–	–	–	X	–
<i>H. delineata</i> Morton, 1905	–	–	–	–	–	–	–	X
<i>H. grandiosa</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>H. gunda</i> Milne, 1936	–	X	–	–	–	–	–	–
<i>H. metoeca</i> Blickle & Morse, 1954	–	–	–	–	–	–	–	X
<i>H. perdita</i> Morton, 1905	X	–	–	–	–	–	–	–
<i>H. quinola</i> Ross, 1947	–	–	–	–	–	–	–	X
<i>H. scolops</i> Ross, 1938	–	–	X	–	–	–	–	–
<i>H. tusculum</i> Ross, 1947	–	–	–	–	–	–	–	X
<i>H. xera</i> Ross, 1938	–	–	–	–	–	–	–	X
<i>Neotrichia minutisimella</i> (Chambers, 1873)	X	–	–	–	–	–	–	–
<i>N. vibrans</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>Ochrotrichia alsea</i> Denning & Blickle, 1972	–	–	–	–	–	–	X	–
<i>O. arva</i> (Ross, 1941)	–	–	–	–	–	–	–	X
<i>O. riesi</i> Ross, 1944	–	–	–	–	–	–	–	X
<i>Orthotrichia cristata</i> Morton, 1905	X	–	–	–	–	–	–	–
<i>O. curta</i> Kingsolver & Ross, 1961	–	–	–	–	–	–	–	X
<i>Oxyethira forcipata</i> Mosely, 1934	X	–	–	–	–	–	–	–
<i>O. novasota</i> Ross, 1944	–	X	–	–	–	–	–	–
LEPIDOSTOMATIDAE								
<i>Lepidostoma griseum</i> (Banks, 1911)	–	X	–	–	–	–	–	–
<i>L. liba</i> Ross, 1941	X	–	–	–	–	–	–	–
<i>L. sommermanae</i> Ross, 1946	–	X	–	–	–	–	–	–
<i>L. togatum</i> (Hagen, 1861)	X	–	X	–	–	–	–	–
LEPTOCERIDAE								
<i>Ceraclea alagma</i> (Ross, 1938)	X	–	–	–	–	–	–	–
<i>C. alces</i> (Ross, 1941)	X	–	–	–	–	–	–	–
<i>C. ancylus</i> (Vorhies, 1909)	X	–	–	–	–	–	X	–
<i>C. cancellata</i> (Betten, 1934)	X	–	–	–	–	–	X	–
<i>C. enodis</i> Whitlock & Morse, 1994	X	–	–	–	–	–	–	–
<i>C. erratica</i> (Milne, 1936)	–	–	–	X	–	–	–	–
<i>C. maculata</i> (Banks, 1899)	–	–	–	–	–	–	X	–
<i>C. neffi</i> (Resh, 1974)	X	–	–	–	–	–	–	–
<i>C. nepha</i> (Ross, 1944)	X	–	–	–	–	–	–	–
<i>C. ophioderus</i> (Ross, 1938)	–	–	–	–	–	–	–	X
<i>C. resurgens</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>C. spongillovorax</i> (Resh, 1974)	X	–	–	–	–	–	–	–

Taxon	IA	IL	IN	MN	ND	NE	SD	WI
<i>C. transversa</i> (Hagen, 1861)	X	–	–	–	–	–	–	–
<i>Leptocerus americanus</i> (Banks, 1899)	–	–	–	–	–	X	X	–
<i>Mystacides interjectus</i> (Banks, 1914)	X	–	–	–	–	–	–	–
<i>Nectopsyche diarina</i> (Ross, 1944)	X	–	–	–	–	–	–	–
<i>N. exquisita</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>N. pavidata</i> (Hagen, 1861)	X	–	–	–	–	–	–	–
<i>Oecetis avara</i> (Banks, 1905)	–	–	–	–	–	–	X	–
<i>O. ditissa</i> Ross, 1966	–	–	–	–	–	–	–	X
<i>O. immobilis</i> (Hagen, 1861)	X	–	–	–	–	–	–	–
<i>O. nocturna</i> Ross, 1966	–	–	–	–	X	–	–	X
<i>O. ochracea</i> Curtis, 1825	X	–	–	–	–	–	–	–
<i>Trienodes aba</i> Milne, 1935	X	–	–	–	–	–	–	–
<i>T. baris</i> Ross, 1938	X	–	–	–	–	–	–	–
<i>T. cumberlandensis</i> Etnier & Way, 1973	–	X	–	–	–	–	–	–
<i>T. ignitus</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>T. marginatus</i> Sibley, 1926	X	–	–	–	–	–	–	–
<i>T. melaca</i> Ross, 1947	X	–	–	–	–	–	–	X
LIMNephilidae								
<i>Asynarchus mutatus</i> (Hagen, 1861)	–	–	–	–	–	–	–	X
<i>Chilostigmodes aeroelatus</i> (Walker, 1852)	–	–	–	X	–	–	–	–
<i>Hydatophylax argus</i> (Harris, 1869)	X	–	–	–	–	–	–	–
<i>Ironoquia punctatissima</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>Limnephilus castor</i> Ross & Merkle, 1952	–	–	–	–	–	–	X	–
<i>L. femoralis</i> Kirby, 1837	–	–	–	–	–	–	–	X
<i>Platycentropus amicus</i> (Hagen, 1861)	X	–	–	–	–	–	–	–
<i>Pseudostenophylax uniformis</i> (Betten, 1934)	X	–	–	–	–	–	–	–
<i>Psychoglypha subborealis</i> (Banks, 1924)	–	–	–	X	–	–	–	–
<i>Pycnopsyche guttifera</i> (Walker, 1852)	X	–	–	–	–	–	–	–
PHILOPOTAMIDAE								
<i>Chimarra aterrima</i> Hagen, 1861	X	–	–	–	–	–	–	–
<i>C. obscura</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>Dolophilodes distincta</i> (Walker, 1852)	–	X	–	–	–	–	–	–
<i>Wormaldia moesta</i> (Banks, 1914)	X	–	–	–	–	–	–	–
<i>W. shawnee</i> (Ross, 1938)	–	–	X	–	–	–	–	X
PHRYGANEIDAE								
<i>Agrypnia straminea</i> Hagen, 1873	–	–	X	–	–	–	–	–
<i>A. vestita</i> (Walker, 1852)	X	–	–	–	–	–	–	–
<i>Oligostomis pardalis</i> (Walker, 1852)	–	–	–	–	–	–	–	X
<i>Prilostomis angustipennis</i> (Hagen, 1873)	–	X	–	–	–	–	–	–
POLYCENTROPODIDAE								
<i>Cernotina spicata</i> Ross, 1938	–	–	–	X	–	–	–	X
<i>Holocentopus melanae</i> Ross, 1938	–	–	–	–	–	–	–	X
<i>H. picicornis</i> (Stephens, 1836)	–	–	–	–	X	–	–	–
<i>Neureclipsis piersoni</i> Frazer & Harris, 1991	–	X	X	–	–	–	–	–
<i>Nyctiophylax moestus</i> Banks, 1911	–	–	–	–	–	–	X	–
<i>Plectrocnemia albipuncta</i> Banks, 1930	–	–	–	–	–	–	–	X
<i>P. clinei</i> Milne, 1936	–	–	–	–	–	–	–	X
<i>P. icula</i> (Ross, 1941)	–	–	–	–	–	–	–	X
<i>Polycentropus centralis</i> Banks, 1914	X	–	–	–	–	–	–	–
<i>P. confusus</i> Hagen, 1861	X	–	–	–	–	–	–	–
PSYCHOMYIIDAE								
<i>Psychomyia flavida</i> Hagen, 1861	X	–	–	–	–	–	–	–
RHYACOPHILIDAE								
<i>Rhyacophila vibbox</i> Milne, 1936	X	–	–	–	–	–	–	–
THREMMATIDAE								
<i>Neophylax ayanus</i> Ross, 1938	–	X	–	–	–	–	–	–
Total	62	12	5	4	4	1	18	25

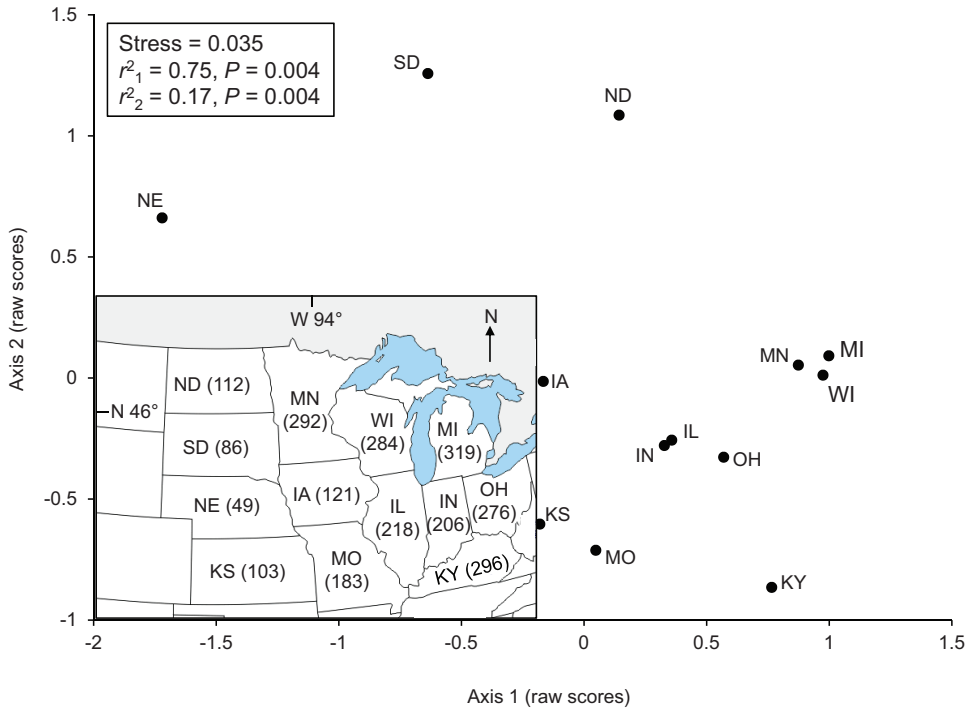


Figure 2. The 13 states of the Upper Midwest region delineated by location and by the results of an NMDS ordination of caddisfly species presence or absence per state. Total number of species for each state in parentheses. State abbreviations in Fig. 1.

Discussion

The majority of our reported new state records are species found in at least one other Upper Midwest state. Many of these species, such as *Ceraclea maculata* (Banks) (Leptoceridae) in South Dakota or *Psychomyia flavida* Hagen (Psychomyiidae) in Iowa, are common and widespread throughout the region. Thus, their recent discovery almost certainly reflects a lack of collecting in particular states.

Conversely, a few of our reported species represent some interesting range extensions. *Chilostigmodes aeroelatus* (Walker) (Limnephilidae) is known throughout Alaska and Canada (Rasmussen and Morse 2020), and our Minnesota collection represents the first record of the genus and species within the lower 48 states. *Limnephilus femoralis* Kirby (Limnephilidae) is a northern Holarctic species which has recently been collected in Michigan (Houghton 2020) and Wisconsin, in addition to the states of Maine and Washington (Rasmussen and Morse 2020). *Triaenodes cumberlandensis* Etnier and Way (Leptoceridae) was known only from the southeastern USA prior to our collection in Illinois. *Glossosoma parvulum* Banks (Glossosomatidae), *Ochrotrichia alsea* Denning & Blickle (Hydroptilidae), and *Limnephilus castor* Ross & Merkley (Limnephilidae) are all western species (Rasmussen and Morse 2020), and our records of them in western

Table 2. The 22 species that are global endemics to the Upper Midwestern region, organized by family and genus, and with known number of collection localities and recent collection year. Superscript references are after the table.

Taxon	IL	KY	MI	MN	MO	ND	NE	OH	No. localities	Collected
GLOSSOSOMATIDAE										
<i>Agapetus artesus</i> Ross, 1938	–	–	–	–	X	–	–	–	3	2017 ^a
<i>Proptoptila talola</i> Denning, 1948	–	–	–	X	–	–	–	–	1	1941 ^b
HYDROPTILIDAE										
<i>Hydroptila danieli</i> Harris & Armitage, 2011	–	–	–	–	–	–	–	X	6	1998 ^c
<i>H. howelli</i> Houp, Houp & Harris, 1998	–	X	–	–	–	–	–	–	3	1998 ^d
<i>H. kuehnei</i> Houp, Houp, & Harris, 1998	–	X	–	–	–	–	–	–	5	1998 ^d
<i>H. paraxella</i> Harris & Armitage, 2011	–	X	–	–	–	–	–	X	3	2008 ^c
<i>Neotrichia paraokopa</i> Keth, 2015	–	–	–	–	X	–	–	–	1	2013 ^d
<i>N. staufferi</i> Keth, 2015	X	–	–	–	–	–	–	–	1	2013 ^d
<i>Oxyethira itasca</i> Monson & Holzenthal, 1993	–	–	X	X	–	–	–	–	~20	2014 ^e
LEPTOCERIDAE										
<i>Ceraclea brevis</i> (Etnier, 1968)	–	–	–	X	–	–	–	–	1	1965 ^b
<i>C. erulla</i> (Ross, 1938)	–	–	–	–	–	–	–	X	1	1930s ^b
<i>C. maccalmonti</i> Moulton & Stewart, 1992	–	–	–	–	X	–	–	–	2	2002 ^f
<i>Setodes truncatus</i> Houghton 2021	–	–	X	–	–	–	–	–	2	2019 ^e
<i>Triaenodes phalacris</i> Ross, 1938	–	–	–	–	–	–	–	X	1	1930s ^b
LIMNephilidae										
<i>Chilostigma itasca</i> Wiggins 1975	–	–	–	X	–	–	–	–	4	2020 ^e
<i>Glyphopsyche missouri</i> Ross, 1944	–	–	–	–	X	–	–	–	2	2017 ^a
<i>Ironoquia plattensis</i> Alexander & Whiles, 2000	–	–	–	–	–	–	X	–	~25	2013 ^g
POLYCENTROPODIDAE										
<i>Cernotina ohio</i> Ross, 1939	–	–	–	–	–	–	–	X	1	1930s ^b
<i>Holocentropus chellus</i> (Denning, 1964)	–	–	–	–	–	X	–	–	1	1960s ^b
<i>H. milaca</i> (Etnier, 1968)	–	–	X	X	–	–	–	–	6	2021 ^e
<i>Plectrocnemia sabulosa</i> (Leonard & Leonard, 1949)	–	–	X	–	–	–	–	–	5	2019 ^e
<i>Polycentropus neiswanderi</i> Ross, 1947	X	X	–	–	–	–	–	X	4	1990s ^{c,d}

^aMabee et al. (2019), ^bknown only from holotype, ^cArmitage et al. (2011), ^dFloyd et al. (2012), ^eArmitage et al. (2015), ^fcollected by the authors, ^gFerro and Sites 2007, ^hVivian et al. 2013

South Dakota probably represent the eastern edge of their range. *Cernotina spicata* Ross (Polycentropodidae) was collected from both Wisconsin and Minnesota, thereby extending the known range of the species and the genus westward by nearly 800 km.

The 22 documented endemic species represent 4% of the total caddisfly fauna of the Upper Midwest. Not surprisingly, most of these species are rare and have been found at < 10 total localities throughout their ranges (Table 2). Most of the species have been collected within the last 10–20 years. The exceptions include *Ceraclea brevis* (Etnier), *C. erulla* (Ross), *Triaenodes phalacris* Ross (Leptoceridae), *Cernotina ohio* Ross, *Holocentropus chellus* (Denning) (Polycentropodidae), and *Proptoptila talola* Denning (Glossosomatidae), all of which are known only from their respective holotypes and have not been collected in > 50 years. *Ceraclea brevis* and *P. talola* are the subjects

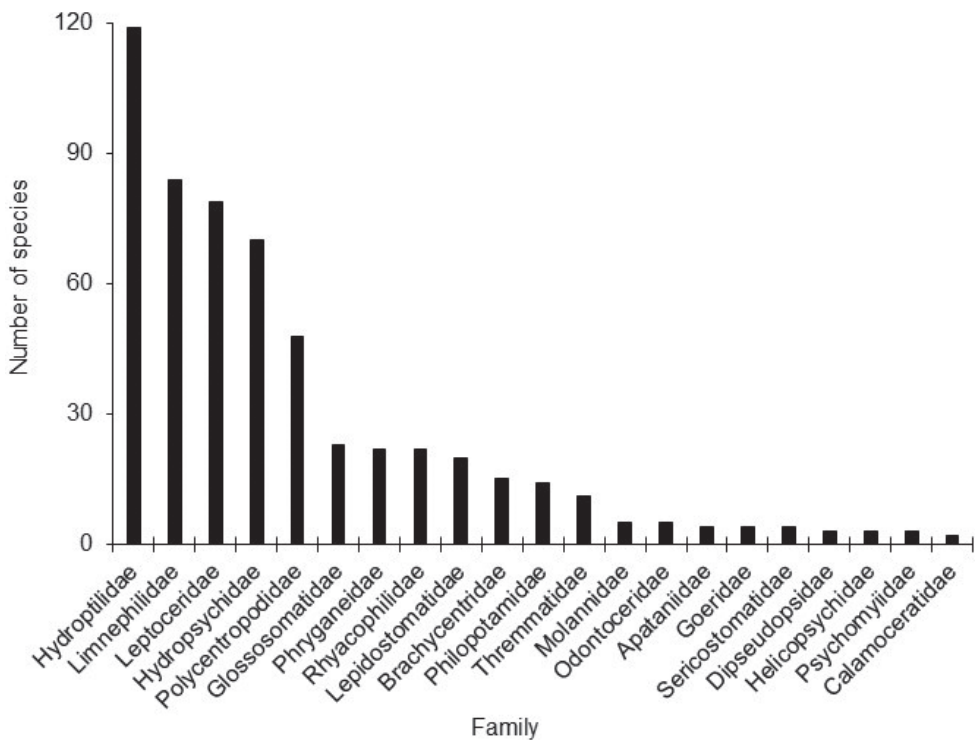


Figure 3. The total number of caddisfly species within each family known from the Upper Midwest region. $N = 552$ total species.

of taxonomic uncertainty due to the similarities of their holotypes to *C. tarsipunctata* (Vorhies) and *P. tenebrosa* (Walker), respectively (Houghton 2012). The uncertainty is compounded by the poor state of the holotype specimens. The holotype for *H. chellus* is in a similarly poor state (Nimmo 1986). *Ironoquia plattensis* Alexander & Whiles (Limnephilidae) is almost certainly the best studied of all Upper Midwest endemics. It is known from a series of locations within the Platte River drainage in Nebraska, where it appears to be decreasing in both prevalence and abundance due to drought, habitat loss, and cattle grazing (Harner and Geluso 2012; Vivian 2013).

The congruence of state species assemblages with geographic location was noteworthy and probably due to a combination of factors. Both latitude and longitude have been previously shown to affect caddisfly assemblages (Moulton and Stewart 1996; Houghton 2004; Blinn and Ruiter 2013; Shah et al. 2014). While some assemblage differences in our study certainly reflect species replacement over geographic distance, a large portion of the eastern-to-western gradient was probably also due to low species richness in the

western prairie states of the region, namely Kansas, Nebraska, North Dakota, and South Dakota (Fig. 2). Indeed, Nebraska has fewer known total caddisfly species (49) than what was frequently collected from a single blacklight trap in northern Minnesota, Michigan, or Wisconsin. This lower richness is probably due to a combination of the naturally arid environment of the western states (McNeely 2003), a high level of habitat degradation due primarily to agriculture (Houghton 2021), and a lack of sampling effort. Even basic species checklists have yet to be compiled for Nebraska and South Dakota. Iowa, similarly, had limited sampling effort prior to this study, and the known species richness of the state more than doubled based on the new records reported herein. Further sampling effort in the western portion of the Upper Midwest region will be needed to clarify the actual caddisfly assemblages and their correspondence with geographic location.

The total determined caddisfly species richness of the Upper Midwest region currently represents 37% of all described species from the United States and Canada, as well as 63% of genera and 81% of families (Rasmussen and Morse 2020). It is likely that many new caddisfly species remain to be discovered in the region. For example, Illinois is one of the best-collected states in both the Upper Midwest region and in the entire USA (Ross 1938; Ross 1944), and yet we found 12 new species records from the state. Future research should focus on states with minimal collecting effort, such as Nebraska and South Dakota, since these states undoubtedly still contain undiscovered caddisfly records.

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Google Earth base maps were used following permission guidelines (<https://www.google.com/permissions/geoguidelines/attr-guide/>). The valuable comments of Desiree Robertson and Paul Frandsen improved earlier version of the manuscript. This is paper #30 of the G.H. Gordon BioStation Research Series.

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Supplementary material 1

Current checklist of 552 caddisfly species known from the Upper Midwest region

Authors: David C. Houghton, R. Edward DeWalt, Todd Hubbard, Kurt L. Schmude, Jeffrey J. Dimick, Ralph W. Holzenthal, Roger J. Blahnik, James L. Snitgen

Data type: species data

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Link: <https://doi.org/10.3897/zookeys.1111.72345.suppl1>

Supplementary material 2

Collection data for the 131 new state species records

Authors: David C. Houghton, R. Edward DeWalt, Todd Hubbard, Kurt L. Schmude, Jeffrey J. Dimick, Ralph W. Holzenthal, Roger J. Blahnik, James L. Snitgen

Data type: species data

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Link: <https://doi.org/10.3897/zookeys.1111.72345.suppl2>

Aquatic beetle diversity from Volcán Tacaná, Mexico: altitudinal distribution pattern and biogeographical affinity of the fauna

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Abstract

Results of an aquatic beetle survey at Volcán Tacaná, Mexico, are presented with five altitudinal levels in a monthly sampling regime, aiming to estimate both diversity and altitudinal distribution patterns of the aquatic beetle fauna. The first list of aquatic beetle species from this mountain is presented, comprising 40 species in 32 genera and nine families, with four species recorded for the first time from Mexico and six recorded for the first time from Chiapas. The aquatic beetle fauna is characterized by Elmidae with 20 species, Dytiscidae with eleven species, Dryopidae with three, and Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae with one species each. The species composition through the sampled altitudinal gradient (670–1,776 m) was not homogeneous, with the elmid genera *Macrelmis*, *Heterelmis*, *Microcylloepus*, and *Austrolimnius* present at all levels, while *Hexanchorus*, *Neoelmis*, and *Onychelmis* were present at levels 1–3 (673–1,214 m); dytiscids were mostly present at levels 4 and 5 (1,619–1,776 m), and dryopids were present only at levels 1–3. A Parsimony Analysis of Endemicity supports a general partition between altitudinal levels 1–3 and levels 4 + 5.

Keywords

Aquatic Coleoptera, Central American Nucleus, Chiapas, faunistics, PAE

Introduction

Among the aquatic insects, aquatic beetles (Coleoptera) are one of the largest groups, with ca. 13,000 described species distributed in 30 families in three of the four coleopterian suborders (Short 2017). Within this insect group, the families Dytiscidae and Hydrophilidae are the largest, with ca. 4,300 and 2,900 species, respectively (Szczepański et al. 2018; Nilsson and Hákej 2020). Aquatic beetles are considered to have a great potential for biodiversity and conservation assessment of water habitats, besides their use as water quality indicators (Samir 2017). They have been recorded in all continents, except Antarctica, and inhabit almost all kinds of aquatic habitats from the smallest phytotelmata to large lakes and rivers (Bilton et al. 2019). Their distribution is determined by different ecological factors, including altitude, which plays an important role in aquatic beetle assemblage composition (Pérez-Bilbao et al. 2014).

Previous studies in the Neotropics have found that altitude may have a significant influence on the composition and structure of an aquatic insect community, as some genera may show a wide range of distribution, while others are characteristic of a particular altitudinal level (e.g., Arias 2004; Henriques-Oliveira and Nessimian 2010, in Brazil; González-Córdoba et al. 2015, 2016, 2020; Mosquera-Murillo and Sánchez-Vázquez 2018, in Colombia; Huanachin-Quispe and Huamantico-Araujo 2018, in Peru).

Approximately 583 species of aquatic Coleoptera are known from Mexico (Santiago-Fragoso and Spangler 1995; Arce-Pérez and Roughley 1999), although the actual number is probably greater. Several studies about local aquatic beetle diversity have taken place in Mexico, often aimed to evaluate the ecological condition of riparian systems, yet providing information on a still fragmentary view of this group's biodiversity (e.g., Arce-Pérez and Novelo-Gutiérrez 1990, 1991, 2015; Arce-Pérez 1995; Arce-Pérez and Roughley 1999; Santiago-Fragoso and Sandoval-Manrique 2001; Arce-Pérez et al. 2002; Gómez-Anaya et al. 2004; Navarrete-Heredia and Zaragoza-Caballero 2006; Campbell et al. 2008; Arce-Pérez and Morón 2011; Torres-García and Pérez-Munguía 2013).

The Tacaná volcano, in the southern Mexican state of Chiapas and bordering Guatemala, is a key element of Volcán Tacaná Biosphere Reserve, a protected area relevant for its rich biotic, cultural, and economic value. This reserve is at the northernmost range of the Central American Nucleus or Central American Volcanic Arc and lies within the Mesoamerican Biological Corridor (CONANP 2013), a dynamic biogeographical area resulting from the assembly of biotas of Nearctic and Neotropical origin. Understanding the geographical distribution and the local diversity of aquatic insects is important to assess the patterns and processes of biological diversification (Benzina et al. 2019). This study aims to record the aquatic beetle diversity from Volcán Tacaná as well as to assess their altitudinal distribution patterns and the biogeographic affinities of the fauna to aid our understanding of biological diversification in the region.

Aquatic entomology, taxonomy, biodiversity, and tropical ecosystems might be a few defining keywords in Ralph Holzenthal's philosophy as an academic advisor. These are relevant themes of encouragement for descriptive taxonomy and biodiversity exploration through several years of competing fields of knowledge, such as morphological and molecular approaches to systematics, which in the end are sides of the same disciplinary coin. This contribution is proudly dedicated by ACR, after 25 years of graduation, to Ralph's bright academic career, in the company of young colleagues and AMLL, currently a graduate student and future academic grandchild.

Materials and methods

Study area

The Tacaná volcano, with its summit at 4,092 m asl, is located in southeastern Chiapas state, Mexico, 30 km NE of Tapachula, with its NE half lying in Guatemala. It is part of the Sierra Madre de Chiapas and lies within the Volcán Tacaná Biosphere Reserve, recognized by UNESCO since 2006. This reserve is located in the Chiapas coast hydrological region (RH-23), on the Pacific slope, and includes the basins of the Suchiate, Coatán, Cahoacán, and Cosalapa rivers (CONANP 2013). The reserve exhibits the following climates: humid temperate (higher portions of the volcano at $\geq 2,000$ m; mean annual $T = 15.3^\circ\text{C}$), humid semi-warm (mid portions of the volcano ca. 1,300–2,000 m; mean annual $T = 20.7^\circ\text{C}$), and humid warm (lower portions of the volcano at $\leq 1,300$ m; mean annual $T = 24.3^\circ\text{C}$), all with abundant summer rains (mean annual rainfall = 4,438.28 mm).

Sampling procedures

Five sampling localities were established, each at an altitude level along the volcano (levels 1–5; Figs 1, 2; Table 1), in order to estimate an altitudinal distribution pattern of species. Besides single sampling sites at each level (locality), levels 3–5 each had a second sampling site (i.e., there was a total of eight sampling sites; Fig. 1, Table 1). Water body and level selection essentially followed availability of lotic systems, as lentic systems are generally missing except for a crater lake at the top of the volcano; absence of permanent streams at higher elevations precluded sampling at uniformly separated levels, particularly between levels 4 and 5.

Level 1. Finca Alianza, municipality of Cacahoatán. The vegetation is evergreen tropical forest. The Cahoacán river (R1) belongs to the Cahoacán basin. The sampling site ($15^\circ02.429'\text{N}$, $92^\circ10.199'\text{W}$) is located at 673 m asl.

Level 2. Finca Monte Perla, municipality of Unión Juárez. The vegetation is cloud forest. The river Cascada Monte Perla (R1) belongs to the Suchiate basin. The sampling site ($15^\circ02.870'\text{N}$, $92^\circ05.305'\text{W}$) is located at 998 m asl.

Level 3. Ejido El Águila, municipality of Cacahoatán. The vegetation is cloud forest. On this locality, two rivers were sampled. The first river, La Resbaladilla (R1), belongs to the Cahotán basin, and the sampling site ($15^\circ05.564'\text{N}$, $92^\circ10.849'\text{W}$) is at 1,214 m asl.

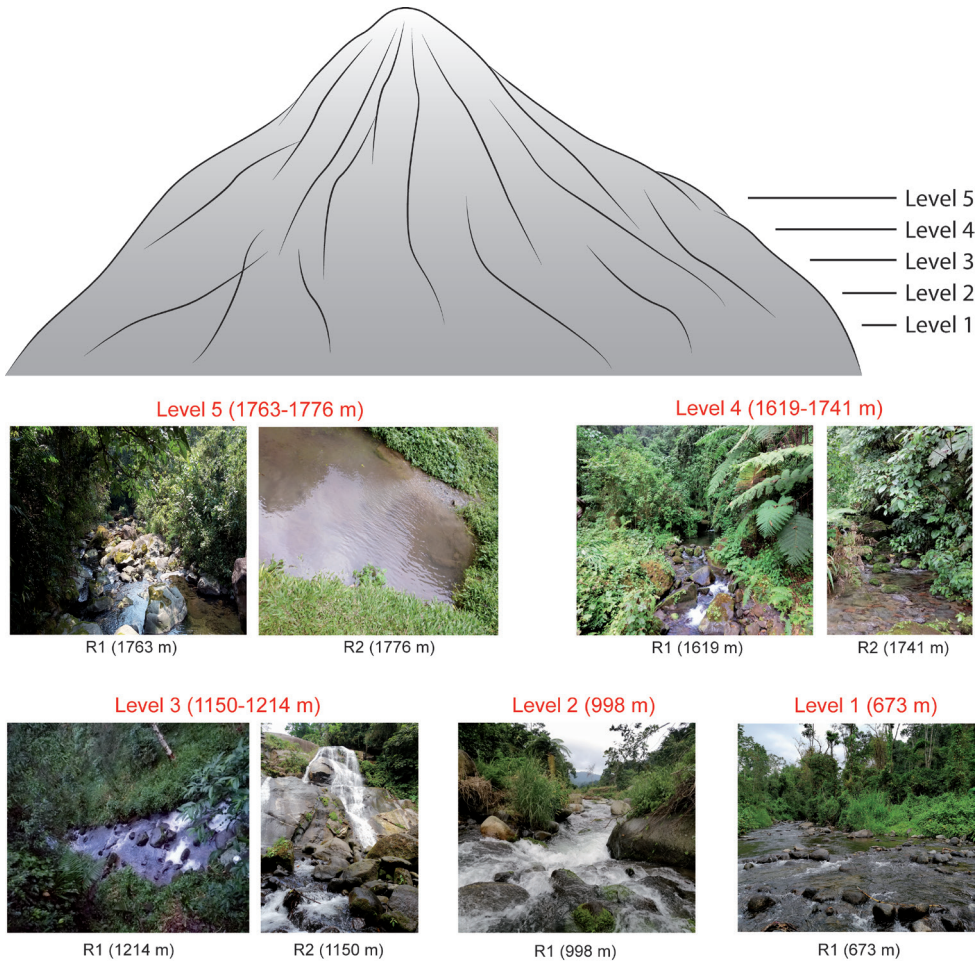


Figure 1. Levels and sampling sites for the aquatic beetle survey along an altitudinal gradient at Volcán Tacaná, Chiapas, Mexico, with habitat examples.

The second river, Cascada La Sirena (R2), belongs to the Coatán basin, and the sampling site ($15^{\circ}06.160'N$, $92^{\circ}11.001'W$) is located at 1,150 m asl.

Level 4. Ejido Benito Juárez El Plan, municipality of Cacahoatán. The vegetation is cloud forest. On this locality, two rivers were sampled, both belong to the Cahoacán basin. The first river, El Arroyo (R1), has its sampling site ($15^{\circ}05.946'N$, $92^{\circ}08.540'W$) at 1,619 m asl. The second river, La Cascada (R2), has its sampling site ($15^{\circ}05.911'N$, $92^{\circ}08.396'W$) at 1,741 m asl.

Level 5. Cantón San Isidro, municipality of Unión Juárez. The vegetation is pine forest. Two rivers were surveyed, both belong to the Suchiate basin. The first river (R1) has its sampling site ($15^{\circ}05.611'N$, $92^{\circ}05.644'W$) at an altitude of 1,763 m asl. The second river (R2) has its sampling site ($15^{\circ}05.588'N$, $92^{\circ}05.537'W$) at 1,776 m asl.

The aquatic beetles were sampled monthly over a year (February 2018–February 2019). In each water body (sampling site) three points were selected, separated by 30 m

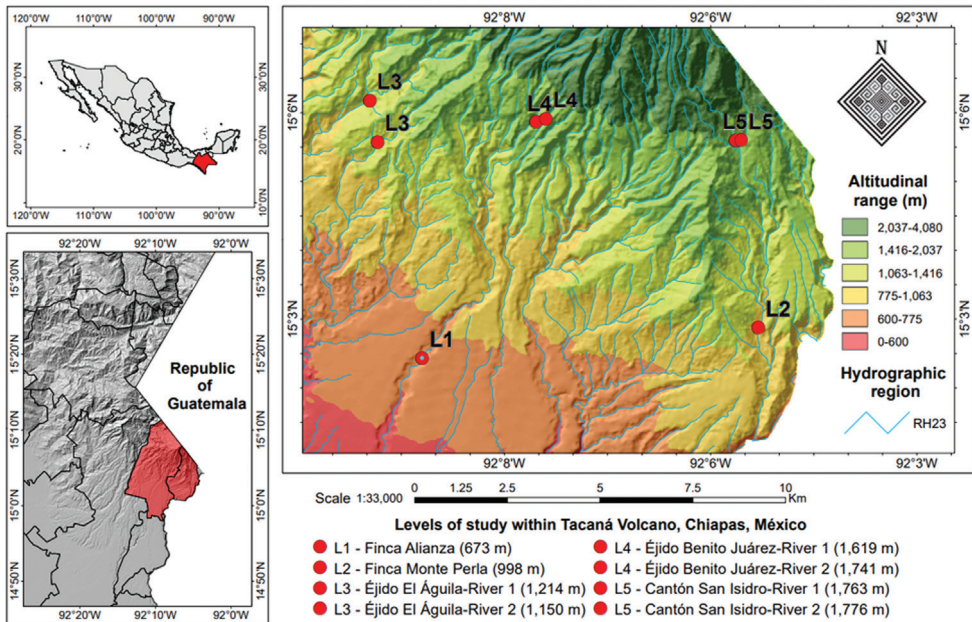


Figure 2. Distribution map of the five sampling levels and for the aquatic beetle survey along an altitudinal gradient at Volcán Tacaná, Chiapas, México.

from each other. Samples were obtained using a D-type benthos net (500 μ m mesh), with a dimension of 30.5 cm wide \times 53.3 cm long). A second trapping technique, a bucket black-light trap, was used for 3 hours at each sampling site. Captured specimens with organic matter surplus were stored in zippered plastic bags with 80% ethyl alcohol, which was replaced with clean alcohol after 24 hours; aquatic beetles were then sorted from other insect groups in the laboratory using a dissecting microscope, and subsequently identified.

Taxonomic identification

The aquatic beetle specimens were dissected and identified to species using features of the genitalic structures; individual genitalia were extracted and stored in microvials with glycerin. Specimens were mounted on entomological pins, together with their associated labels and genitalia; specimens smaller than 12 mm were placed in paper cartons (points).

Identification was performed through introductory genus-level keys (White and Roughley 2008; Archangelsky et al. 2009; Miller and Bergsten 2016; Benetti et al. 2018; Passos et al. 2018), and subsequently with specialized revisions and original species descriptions.

All the material examined was deposited in the Colección Nacional de Insectos (CNIN) of the Instituto de Biología, Universidad Nacional Autónoma de México.

Parsimony Analysis of Endemicity (PAE)

To aid unravel a general distribution pattern of the aquatic beetle fauna along the altitudinal gradient in the volcano, we performed a Parsimony Analysis of Endemicity (PAE).

Table 1. Distribution of aquatic beetle species (Coleoptera) in the sampling levels and sites of Volcán Tacaná, Chiapas, Mexico. 0 = absent; 1 = present. Nea = Neartic; Neo = Neotropical.

FAMILY	SPECIES	SAMPLING POINTS								BIOG. RE- GIONS
		Lv1	Lv2	Lv3		Lv4		Lv5		
		R1	R1	R1	R2	R1	R2	R1	R2	
Dryopidae	1. <i>Dryops mexicanus</i>	1	1	1	1	0	0	0	0	Neo.
	2. <i>Elmoparnus pandus</i>	1	0	0	0	0	0	0	0	Neo.
	3. <i>Helichus suturalis</i>	1	1	1	1	0	0	0	0	Nea.; Neo.
Dytiscidae	4. <i>Bidessonotus championi</i>	0	0	0	0	0	1	0	0	Neo.
	5. <i>Clarkhydrus</i> sp.	0	0	0	0	1	1	1	0	Neo
	6. <i>Copelatus distinctus</i>	0	0	1	1	1	1	1	1	Nea.; Neo.
	7. <i>Ilybiosoma flobrianum</i>	0	0	0	0	0	1	0	1	Neo.
	8. <i>Laccophilus proximus</i>	0	0	0	0	1	0	1	0	Nea.; Neo.
	9. <i>Liodesus affinis</i>	0	0	0	0	1	0	0	0	Nea.; Neo.
	10. <i>Neoclypeodytes fryii</i>	0	0	0	0	1	1	0	0	Nea.; Neo.
	11. <i>Platambus americanus</i>	0	0	0	0	1	1	1	1	Neo.
	12. <i>Rhantus gutticollis</i>	0	0	0	0	0	0	0	1	Nea.; Neo.
	13. <i>Thermonectus nigrofasciatus</i>	0	0	0	0	0	0	0	1	Nea.; Neo.
	14. <i>Uvarus subornatus</i>	0	0	0	0	0	1	0	0	Neo.
Elmidae	15. <i>Austrolimnius formosus</i>	1	1	1	1	1	1	1	1	Neo.
	16. <i>Austrolimnius sulcicollis</i>	1	1	1	1	1	1	1	1	Neo.
	17. <i>Cylloepus atys</i>	1	1	1	0	0	1	1	1	Neo.
	18. <i>Heterelmis glabra</i>	1	1	1	1	1	1	1	1	Nea.; Neo.
	19. <i>Heterelmis obesa</i>	1	1	1	1	1	1	1	1	Nea.; Neo.
	20. <i>Heterelmis obscura</i>	1	1	1	1	1	1	1	1	Nea.; Neo.
	21. <i>Heterelmis simplex</i>	1	1	1	0	0	1	1	1	Neo.
	22. <i>Hexacylloepus metapa</i>	1	1	1	1	0	1	1	1	Neo.
	23. <i>Hexanchorus usitatus</i>	1	1	1	1	0	0	0	0	Neo.
	24. <i>Huleechius spinipes</i>	1	1	1	1	0	1	1	1	Nea.; Neo.
	25. <i>Macrelmis graniger</i>	1	1	1	1	1	1	1	1	Neo.
	26. <i>Macrelmis leonilae</i>	1	1	1	1	1	1	1	1	Neo.
	27. <i>Macrelmis</i> sp.	0	0	0	0	0	0	0	1	Neo.
	28. <i>Microcyllloepus inaequalis</i>	1	1	1	1	1	1	1	1	Neo.
	29. <i>Microcyllloepus troilus</i>	1	1	1	1	0	1	0	1	Neo.
	30. <i>Microcyllloepus</i> sp.	1	1	1	1	1	1	1	1	Neo.
	31. <i>Neelmis apicalis</i>	1	1	1	1	0	0	0	0	Nea.; Neo.
	32. <i>Onychelmis longicollis</i>	1	1	1	1	0	0	0	0	Neo.
	33. <i>Phanocerus clavicornis</i>	1	0	1	1	1	1	0	0	Nea.; Neo.
	34. <i>Xenelmis bufo</i>	1	1	1	1	1	1	1	1	Neo.
Epimetopidae	35. <i>Epimetopus thermarum</i>	1	0	0	0	0	0	0	0	Nea.; Neo.
Gyrinidae	36. <i>Gyretes boucardi</i>	1	0	0	0	0	0	0	0	Neo.
Hydraenidae	37. <i>Hydraena</i> sp.	1	1	1	1	1	1	1	1	Neo.
Hydrophilidae	38. <i>Tropisternus fuscitarsis</i>	0	1	0	0	0	0	0	0	Nea.; Neo.
Luthrochidae	39. <i>Lutrochus</i> sp.	1	0	0	0	0	0	0	0	Neo.
Noteridae	40. <i>Notomicrus sharpi</i>	0	0	0	0	0	1	0	0	Nea.; Neo.

According to Morrone (2009) “...PAE constructs cladograms based on the cladistic analysis of presence-absence data matrices of species and supraspecific taxa”. A matrix was built with distributional units (i.e., sampling sites) used as “terminals” and species serving as “characters”, aiming to obtain a hierarchical structure in the resulting most parsimonious cladograms. Because PAE has been applied to discern a biogeographical signal, such as delimiting areas of endemism or historical relationship between preexisting areas of endemism (Crisci et al. 2003), our assumption is that even a general pattern between altitudinal levels may be informative of a faunistic differentiation along the gradient.

Two analyses were applied: one with the main five levels of sampling (localities) as terminals (i.e., levels 3–5 had sites fused in a single unit), and a second with all eight sampling sites as distribution units or terminals (Table 1). Aquatic beetle species were used as characters, codified as present (1) or absent (0) at each of the distributional units (sampling sites or terminals). A hypothetical distributional unit with all species absent (zero vector) was used to root the trees.

The matrices (Table 1) were built with WinClada (Nixon 2002), then exported as a Nexus file to perform a parsimony analysis in TNT (Tree Analysis using New Technology, version 1.5) (Goloboff and Catalano 2016). The most parsimonious cladogram was obtained through a heuristic algorithm with parameters: random seed = 0, hold = 3000, hold / = 50 in a TBR (tree bisection and reconnection technique) of 60 replicates. The most parsimonious topology was exported to Adobe Illustrator CS5 software to be edited.

Distribution maps

Mapping of the study site with the sampling sites was done with ArcGIS version 10.2. 2. Layers of states and municipalities were obtained from the National Institute of Statistics and Geography (INEGI), with information on a 1:50,000 scale. Projection of localities with geographical coordinates was carried out with Universal Transverse Mercator (UTM). The raster of the CEM model of the Chiapas area was obtained, a cut of municipalities within the study area was made, with the help of a vector layer of municipal boundaries. The elevation model was adjusted with a reclassification of the z (altitude) values so altitude differences within our area of interest could be visualized. Seven intervals from 0 m to 4080 m were used for the reclassification. In addition, a shadow map (hillshade) was made to better visualize slopes of the terrain of the study area. Finally, layers of the watersheds are located on a scale of 1:50,000, which belongs to the Costa de Chiapas hydrographic region (key RH23).

Results

In total, 23,295 specimens of aquatic beetles of 40 species, distributed in 32 genera and nine families (Dryopidae, Dytiscidae, Elmidae, Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae), were collected (Appendix 1). Elmidae had the highest richness with 20 species (50% of total richness). The lowest richness was recorded in Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae, with only one species each (2.5% richness, respectively).

We record the following four species from Mexico for the first time (Appendix 1): the Elmidae *Cylloepus atys* Hinton, 1946, *Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020, *Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992, and the Dytiscidae *Bidessonotus championi* J. Balfour-Browne, 1947. Additionally, four species of Dytiscidae, *Ilybiosoma flobrianum* Sharp, 1887, *Liodes affinis* Say, 1823, *Neoclypeodytes friyii* Clark, 1862, *Platambus americanus* (Aubé, 1838), one species of

Elmidae, *Huleechius spinipes* (Hinton, 1934), and one of Noteridae, *Notomicrus sharpi* J. Balfour-Browne, 1939, were recorded for the first time from the state of Chiapas.

List of species of aquatic beetles (Coleoptera) from Volcán Tacaná, Mexico

Entries are arranged alphabetically by family and genus. Entries for genera include comments on number of species, and distribution. Species entries include the valid combination, distributional and altitudinal information, as well as type of substrate where they were collected. Altitude or elevation data are given in m above sea level.

Results

Family Dryopidae Billberg, 1820

Genus *Dryops* Olivier, 1791

Dryops mexicanus Sharp, 1882

Note. *Dryops* has a worldwide distribution and comprises 79 species (Shepard and Sites 2016), three of them are recorded from Mexico.

Distribution. Mexico (Chiapas, Morelos), Belize, Costa Rica (Burgos and Trejo-Loyo 2001; Shepard 2004; Barr and Shepard 2017; Zaragoza-Caballero et al. 2019). It has been recorded at an altitudinal range of 200 to 840 m (Barr and Shepard 2017); in this study *D. mexicanus* was collected at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates consisting of gravel, macrophytes, and leaf packs; found in all sampling months (February 2018 through February 2019, dry and rainy seasons); also collected with a bucket light trap.

Genus *Elmoparnus* Sharp, 1882

Note. This genus includes eight species recorded in the Neotropics (Kodada and Jäch 2005), two of them are recorded in Mexico.

Elmoparnus pandus Spangler & Perkins, 1977

Distribution. Mexico (Chiapas, Oaxaca), Belize, Guatemala, Honduras, Costa Rica, Panama (Spangler and Perkins 1977; Barr and Shepard 2017). The known altitudinal range of this species is 200 to 1,219 m (Spangler and Perkins 1977; Barr and Shepard 2017). In this study, it was collected at level 1 (670 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs (June 2018, rainy season).

Genus *Helichus* Erichson, 1847

Note. This genus is found throughout the Oriental, Nearctic, and Neotropical regions, with 32 species described (Kodada and Jäch 2005).

***Helichus suturalis* LeConte, 1852**

Distribution. United States, Mexico (Chiapas, Durango, Hidalgo), Guatemala, Paraguay (Brown 1972a; Arce-Pérez et al. 2010; Shepard and Aguilar-Julio 2010). The known altitude records of the species are 1,590 and 2,438 m (Brown 1972a; Arce-Pérez et al. 2010). Herein, specimens were found at levels 1 (670 m), 2 (934 m), and 3 (1126–1194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Family Dytiscidae Leach, 1815

Genus *Bidessonotus* Régimbart, 1895

Note. This is one of the largest dytiscid genera in the New World, comprising 36 species (Nilsson and Hájek 2020), with seven species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Bidessonotus championi* J. Balfour-Browne, 1947**

Distribution. Mexico (new country record, Chiapas), Guatemala, Honduras, Nicaragua, Costa Rica (Balfour-Browne 1947; Miller 2016; Nilsson and Hájek 2020). The species has been recorded from an altitude of ca. 122 m (Balfour-Browne 1947), herein we recorded the species at level 4 (1,619 m).

Comments. Collected on macrophytes (February 2018, dry season).

Genus *Clarkhydrus* Fery & Ribera, 2018

Note. This genus has a Nearctic and Neotropical distribution and comprises 10 species, seven of which have been recorded in Mexico (Nilsson and Hájek 2020).

***Clarkhydrus* sp.**

Comments. This species was collected at levels 4 (rivers 1 and 2, 1,448–1,619 m) and 5 (river 1, 1,763 m) on substrates of macrophytes and leaf packs, and was present throughout sampling months (February 2018 through February 2019, dry and rainy season). Specimens did not match known described species of the genus; however, they are close to *C. decemsignatus*, yet male genital morphology differs.

Genus *Copelatus* Erichson, 1832

Note. This genus has a cosmopolitan distribution and comprises 454 species (Nilsson and Hájek 2020), 14 of which have been recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Copelatus distinctus* Aubé, 1838**

Distribution. United States, Mexico (Baja California, Chiapas, Guanajuato, Jalisco, Morelos, Oaxaca, Puebla, Sonora), Guatemala (Young 1963; Arce-Pérez and Roughley 1999; Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). This species has been recorded from moderate elevations (Young 1963) and 1,706 m (Miller and Bergsten 2014), herein it was found at levels 3 (1,126–1,194 m), 4 (1,448–1,619 m), and 5 (1,126–1,776 m).

Comments. Collected on substrates of macrophytes and leaf packs, through all months of sampling (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Ilybiosoma* Crotch, 1873

Note. This is a cosmopolitan genus that includes 17 species (Nilsson and Hájek 2020), five of them recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Ilybiosoma flobrianum* (Sharp, 1887)**

Distribution. Mexico (Estado de México; Chiapas, new state record; Morelos) (Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). There are no published records of altitude for the species; herein, the species was found at levels 4 (1,619 m) and 5 (1,776 m).

Comments. Specimens were found on leaf packs (May 2018, rainy season).

Genus *Laccophilus* Leach, 1815

Note. This cosmopolitan genus is the largest of the subfamily Laccophilinae, with 285 species (Nilsson and Hájek 2020), 26 of which are recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Laccophilus proximus* Say, 1823**

Distribution. United States, Mexico (Campeche, Chiapas, Coahuila, Oaxaca, San Luis Potosí, Tabasco, Tamaulipas, Yucatán, Veracruz), Belize, Guatemala, Costa Rica, Bahamas, Cuba, Puerto Rico, Guadeloupe (Scheer and Thomaes 2018; Nilsson and Hájek 2020). It has been recorded at altitudes between 14 and 2,438 m (Scheer and Thomaes 2018). In this study, it was collected between 1,126 and 1,723 m.

Comments. Specimens were found on leaf packs (February and March 2018).

Genus *Liodessus* Guignot, 1939

Note. This genus is distributed in North and South America, Africa, and Fiji (Miller and Bergsten 2016) and comprises 40 species (Nilsson and Hájek 2020), with four species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Liodessus affinis* (Say, 1823)**

Distribution. Canada, United States, Mexico (Baja California; Estado de México; Chiapas, new state record) (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020). No specific data about altitudinal distribution were found, herein this species was collected at 1,448 m.

Comments. Collected on macrophytes and leaf packs (February and March 2018, dry season).

Genus *Neoclypeodytes* Young, 1967

Note. This genus is present from southwestern Canada south through western United States and Mexico, with a few species in Panama and one in Jamaica (Miller and Bergsten 2016; Nilsson and Hájek 2020). It comprises 27 species (Nilsson and Hájek 2020), 15 of which are present in Mexico (Arce-Pérez and Roughley 1999; Arce-Pérez and Novelo-Gutiérrez 2015; Nilsson and Hájek 2020).

***Neoclypeodytes fryii* (Clark, 1862)**

Distribution. United States, Mexico (Baja California; Chiapas, new state record; Guanajuato; Oaxaca), Guatemala (Miller 2001; Nilsson and Hájek 2020). This species was previously recorded at an altitudinal range between 853 and 1,524 m (Miller 2001). In this study, the species was collected at level 4 (rivers 1 and 2, 1,425–1,619 m).

Comments. Collected on macrophytes and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Genus *Platambus* Thomson, 1859

Note. This genus is distributed in the Nearctic, Neotropical, Palearctic, and Oriental regions, with 67 species (Miller and Bergsten 2016; Nilsson and Hájek 2020), six of which are recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Platambus americanus* (Aubé, 1838)**

Distribution. Mexico (Chiapas, new state record; Oaxaca), Guatemala, El Salvador (Arce-Pérez and Roughley 1999; Larson et al. 2000; Hendrich et al. 2018; Nilsson and Hájek 2020). Previous altitudinal records are between 1,950 and 2,743 m (Hendrich et al. 2018), while in the present study the species ranged from levels 4 (river 2, 1,619m) to 4 (river 2, 1,776 m).

Comments. Collected on macrophytes and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Rhantus* Dejean, 1833

Note. This is a cosmopolitan genus with 90 species (Nilsson and Hájek 2020), four of which are recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

***Rhantus gutticollis* (Say, 1830)**

Distribution. Canada, United States, Mexico (Baja California, Coahuila, Colima, Chiapas, Chihuahua, Ciudad de México, Durango, Estado de México, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas), Guatemala, Honduras, Nicaragua, Costa Rica (Blackwelder 1944; Zimmerman and Smith 1975; Balke 1992; Arce-Pérez and Roughley 1999; Larson et al. 2000; Zaragoza-Caballero et al. 2019;

Nilsson and Hájek 2020). This species has been previously recorded from 0 to 2,250 m (Blanco-Aller and Régil 2016), herein it was collected at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Genus *Thermonectus* Dejean, 1833

Note. This genus is distributed across the Americas and comprises 20 species and two subspecies (Nilsson and Hájek 2020), with eight species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Thermonectus nigrofasciatus (Aubé, 1838)

Distribution. Mexico (Ciudad de México, Chiapas, Durango, Estado de México, Guanajuato, Hidalgo, Morelos, Oaxaca, Puebla, San Luis Potosí) (Arce-Pérez and Roughley 1999; Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). This species was collected at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Genus *Uvarus* Guignot, 1939

Note. This genus is distributed worldwide and contains 65 species, nine of which are present in Mexico (Larson et al. 2000; Miller and Bergsten 2016; Nilsson and Hájek 2020).

Uvarus subornatus (Sharp, 1882)

Distribution. Mexico (Chiapas, Oaxaca), Guatemala (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020). No previous altitudinal records for this species were found. In the present study, this species was found only at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Family Elmidae Curtis, 1830

Genus *Austrolimnius* Carter & Zeck, 1929

Note. This genus occurs in the Australasian and Neotropical regions, with more than 100 described species (Manzo 2005, 2007; Jäch et al. 2016). Twenty species of this genus have been recorded in the Americas, from northern Mexico through southeastern Argentina (Hinton 1971; Manzo 2007), with four species recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Austrolimnius formosus* (Sharp, 1882)**

Distribution. Mexico (Chiapas, Morelos, Guerrero), Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru, Brazil, Argentina (Sharp 1882; Hinton 1940b, 1941, 1971; Blackwelder 1944; Shepard 2004; Manzo 2007; Passos et al. 2009; Manzo and Archangelsky 2012; Miranda et al. 2012; González-Córdoba et al. 2016, 2020). Previous altitudinal records of *A. formosus* are from 600 m and 2,438 m (Hinton 1940b). In this study, the species was present in all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

***Austrolimnius sulcicollis* (Sharp, 1882)**

Distribution. Mexico (Chiapas, Guerrero), Guatemala, Costa Rica, Panama, Colombia, Venezuela, French Guiana, Ecuador, Peru (Sharp 1882; Hinton 1940b, 1941, 1971; Blackwelder 1944; González-Cordoba et al. 2020). *Austrolimnius sulcicollis* has been previously recorded from altitudes of 600 m and 2,438 m (Hinton 1940b). Herein, this species was collected in all sampling levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Genus *Cylloepus* Erichson, 1847

Note. This is the elmid genus with most species in the American continent, with 52 species and 2 subspecies currently known to this region (Segura et al. 2013; Jäch et al. 2016; Silva-Polizei and Barclay 2019), and eight species recorded in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Cylloepus atys* Hinton, 1946**

Distribution. Mexico (new country record, Chiapas), Peru (Hinton 1946). Previous altitudinal records are from approximately 500 m (Hinton 1940a). In this study, the species was collected at levels 1 (670 m), 2 (934 m), 3 (river 1, 1,126 m), 4 (river 2, 1,619 m), and 5 (rivers 1 and 2, 1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, through most of the sampling months (except March, July, and September 2018, dry and rainy season).

Genus *Heterelmis* Sharp, 1882

Note. This is a New World genus that comprises 22 species (Silva-Polizei 2018), seven of which are present in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Heterelmis glabra* (Horn, 1870)**

Distribution. Mexico (Chiapas, Estado de México, Hidalgo, Jalisco, Morelos, Nayarit, Oaxaca, Tamaulipas, Veracruz), Belize, Nicaragua, Costa Rica (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016). This species was previously recorded from 1,066 m and 1,219 m (Hinton 1940b). Herein, this species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, through all sampling months (February 2018 through February 2019, dry and rainy season).

***Heterelmis obesa* Sharp, 1882**

Distribution. Mexico (Chiapas, Durango, Estado de México, Hidalgo, Morelos, Oaxaca, Veracruz), Guatemala, Costa Rica, Nicaragua, Peru (Sharp 1882; Hinton 1940b; Blackwelder 1944; Spangler 1966; Brown 1972b; Jäch et al. 2016). This species was previously recorded from 1,463 m and 2,438 m (Hinton 1940b). In this study, the species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and litter, throughout all sampling months (February 2018 through February 2019, dry and rainy season).

***Heterelmis obscura* Sharp, 1882**

Distribution. Mexico (Chiapas, Colima, Estado de México, Morelos, Nuevo León, Oaxaca, San Luis Potosí, Veracruz), Guatemala, Costa Rica, Colombia, Peru, Brazil (Sharp 1882; Grouvelle 1889; Hinton 1940b; Blackwelder 1944; Brown 1972b; Santiago-Fragoso and Spangler 1995; Passos et al. 2009; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *H. obscura* are from 1,463 m and 2,438 m (Hinton 1940b). In this study, the species was found in all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

***Heterelmis simplex* Sharp, 1882**

Distribution. Mexico (Chiapas, Morelos), Guatemala, Costa Rica, Peru, Trinidad and Tobago (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al.

2016). No previous altitudinal records were found. This species was collected at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season).

Genus *Hexacylloepus* Hinton, 1940b

Note. This genus is distributed in the southwestern United States and the Neotropical region, with 25 described species (Jäch et al. 2016; Silva-Polizei et al. 2020), seven of which are recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016; Silva-Polizei et al. 2020).

***Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020**

Distribution. Mexico (new country record, Chiapas), Guatemala (Silva-Polizei et al. 2020). There are no previous records of altitude for *H. metapa*, herein the species was collected at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 to February 2019, dry and rainy season).

Genus *Hexanchorus* Sharp, 1882

Note. This is a New World genus and comprises 21 species, with three recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992**

Distribution. Mexico (new country record, Chiapas), Nicaragua, Costa Rica, Panama.

The known altitudinal record of *H. usitatus* was 1,075 m (Spangler and Santiago-Fragoso 1992). Herein, the species was found from levels 1 (670 m) through 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Huleechius* Brown, 1981

Note. This is a North American genus and includes three species (Jäch et al. 2016), with two recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Huleechius spinipes* (Hinton, 1934)**

Distribution. Mexico (Baja California; Chiapas, new state record; Coahuila; Estado de México; Guerrero; Jalisco; Nuevo León; Oaxaca; Tabasco; Veracruz) (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016). A previous altitudinal record of *H. spinipes* is from 1,524 m (Hinton 1940b). In this study, the species was found at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Genus *Macrelmis* Motschulsky, 1859

Note. This is a Nearctic and Neotropical genus, distributed from southern United States to South America, and comprises 49 species, 10 of which have been recorded from Mexico (Hinton 1940b; Passos et al. 2015; Jäch et al. 2016).

***Macrelmis graniger* (Sharp, 1882)**

Distribution. Mexico (Chiapas, Estado de México, Morelos, Oaxaca), Guatemala, Costa Rica, Nicaragua, Peru (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *M. graniger* are from 1,219 and 1,706 m (Hinton 1940b). Herein, this species was collected at level 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

***Macrelmis leonilae* Spangler & Santiago-Fragoso, 1986**

Distribution. Mexico (Chiapas, Guerrero, Morelos, Oaxaca, Veracruz), Guatemala, Honduras, Nicaragua, Costa Rica, Peru (Santiago-Fragoso and Spangler 1995; Segura et al. 2013). A previous altitudinal record of *M. leonilae* is 1,075 m (Spangler and Santiago-Fragoso 1986). Herein, this species was collected at level 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

***Macrelmis* sp.**

Comments. This species was collected at level 5 (river 2, 1,776 m) on substrates of macrophytes and leaf packs, and was present throughout sampling months (Feb-

ruary 2018 through February 2019, dry and rainy season). Specimens, including males, did not match known described species of the genus, although they are similar to *M. leonilae*. Male parameres of the specimens, in dorsal view, are slightly wider from the base to the apical portion, while in *M. leonilae* they are wider through the basal half.

Genus *Microcylloepus* Hinton, 1935

Note. *Microcylloepus* is widely distributed in the New World and comprises 30 species (Silva-Polizei 2018), five of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Microcylloepus inaequalis (Sharp, 1882)

Distribution. Mexico (Chiapas, Estado de Mexico, Morelos, Veracruz), Guatemala, Nicaragua, Costa Rica, Panama, Paraguay, Brazil (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *M. inaequalis* are at 1,463 m and 1,525 m (Hinton 1940c). Herein, this species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Microcylloepus troilus Hinton, 1940

Distribution. Mexico (Chiapas, Estado de Mexico). Previous altitudinal records of *M. troilus* are from 1,707 to 2,286 m (Hinton 1940b). In this study, *M. troilus* was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Microcylloepus sp.

Comments. This species was collected at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (river 2, 1,776 m) on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season). Specimens, including males, did not match exactly known described species of the genus, being close to *M. angustus*. Male genitalia of the specimens have the medium lobe slightly wider than *M. angustus*.

Genus *Neoelmis* Musgrave, 1935

Note. This genus is distributed across the American continent and has 50 described species (Jäch et al. 2016), five of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Neoelmis apicallis* (Sharp, 1882)**

Distribution. Mexico (Chiapas, Estado de México, Morelos, San Luis Potosí, Tamaulipas), Guatemala, Costa Rica (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records were at 137 m and 1,463 m (Hinton 1940b). In this study, the species was found at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, in about half of the sampling period (February to May, and August 2018, and February 2019, dry and rainy season).

Genus *Onychelmis* Hinton, 1941

Note. This genus is distributed in Central and South America, contains eight described species (Linský et al. 2021), and this study provides the northernmost point of its range.

***Onychelmis longicollis* (Sharp, 1882)**

Distribution. Mexico (new country record, Chiapas), Nicaragua, Panama, Colombia (González-Córdoba et al. 2016; Linský et al. 2021). Previous altitudinal records were from 1,219 to 1,828 m (González-Córdoba et al. 2016; Linský et al. 2021). In the present study, the species was found at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, during three months of the sampling period (February, April, and May 2018, dry and rainy season).

Genus *Phanocerus* Sharp, 1882

Note. This genus is distributed from North America through northern South America, with six described species (Jäch et al. 2016), one recorded in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

***Phanocerus clavicornis* Sharp, 1882**

Distribution. United States, Mexico (Chiapas, Colima, Guerrero, Hidalgo, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz), Belize, Guatemala, Honduras, Costa Rica, Panama, Venezuela, Brazil, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico (Spangler and Santiago-Fragoso 1992; Segura et al. 2013; Jäch et al. 2016). This species was previously recorded from an altitudinal range of 88–549 m (Hinton 1940b; Spangler and Santiago-Fragoso 1992). Herein, the species was found at levels 1 (670 m), 3 (1,126–1,194), and 4 (1,448–1,619 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs through four months of the sampling period (May, June, July, and August 2018, rainy season); also collected with a bucket light trap.

Genus *Xenelmis* Hinton, 1936

Note. This is a New World, mostly Neotropical genus with 11 described species (Jäch et al. 2016), two of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Sampaio et al. 2015; Jäch et al. 2016).

***Xenelmis bufo* (Sharp, 1882)**

Distribution. Mexico (Chiapas, Colima, Guerrero, Morelos), Belize, Panama, Venezuela (Segura et al. 2013; Jäch et al. 2016). A previous altitudinal record of *X. bufo* is from 1,219 m (Hinton 1940b). In this study, the species was found at all sampling levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season).

Family Epimetopidae Zaitzev, 1908**Genus *Epimetopus* Lacordaire, 1854**

Note. This genus is distributed across the Nearctic and Neotropical region, with 56 species described (Perkins 2012), eight of them recorded from Mexico (Arce-Pérez and Morón 2011; Perkins 2012).

***Epimetopus thermarum* Schwarz & Barber, 1917**

Distribution. United States, Mexico (Baja California Sur, Chiapas, Jalisco, Nayarit, Sinaloa, Sonora), Belize, Guatemala, Costa Rica, Panama, Venezuela (Perkins 2012).

This species was previously recorded at an altitudinal range of 5–914 m (Perkins 2012). In this study, the species was found in level 1 (670 m).

Comments. Collected with a bucket light trap (June 2018, rainy season).

Family Gyrinidae Latreille, 1810

Genus *Gyretes* Brullé, 1835

Note. This genus comprises 79 species worldwide (Oygur and Wolfe 1991; Babin and Alarie 2014), seven of them recorded from Mexico (Arce-Pérez and Roughley 1999).

Gyretes boucardi Sharp, 1882

Distribution. Mexico (Chiapas, Durango, Tabasco, Veracruz), Costa Rica (Arce-Pérez and Roughley 1999; Blanco-Aller 2014). Previous altitudinal records of *G. boucardi* are from 0–125 m (Blanco-Aller 2014). In this study, the species was found at level 1 (670 m).

Comments. Collected near substrate of macrophytes (October 2018, rainy season).

Family Hydraenidae Mulsant, 1844

Genus *Hydraena* Kugelann, 1794

Note. The genus occurs on all continents except Antarctica and comprises more than 990 species described (Trizzino et al. 2013), 36 of which are recorded from Mexico (Navarrete-Heredia and Quiroz-Rocha 2004).

Hydraena sp.

Comments. This species was collected at all sampled levels (670–1,776 m), on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season). Specimens were small and fragile, particularly males, and dissection was difficult, moreover genital morphology did not match species in keys, so genus-level identification was considered until further study; females were more abundant in collections.

Family Hydrophilidae Latreille, 1802

Genus *Tropisternus* Solier, 1834

Note. This is a New World genus distributed from northern Canada to southern South America, comprising 60 described species (Hansen 1999; Short and Hebauer 2006; Spangler and Short 2008), 19 of them recorded from Mexico (Arce-Pérez and Morón 2011).

***Tropisternus fuscitarsis* Sharp, 1882**

Distribution. Mexico (Chiapas, Colima, Distrito Federal, Jalisco, Estado de México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Veracruz) (Arce-Pérez and Morón 2011). Previous altitudinal records of *T. fuscitarsis* are from 0–125 m (Blanco-Aller 2014). Herein, the species was found in level 2 (934 m).

Comments. Collected with a bucket light trap (July and August 2018, rainy season).

Family Lutrochidae Kasap & Crowson, 1975**Genus *Lutrochus* Erichson, 1847**

Note. This genus comprises 29 species and is distributed across the Nearctic and Neotropical region (Maier and Short 2013, 2014; Maier 2016), with three species recorded from Mexico (Arce-Pérez et al. 2010; Maier 2016).

***Lutrochus* sp.**

Comments. This species was present at level 1 (670 m) and was collected on leaf packs (May 2018, rainy season). Specimens key out to an undescribed genus and species included in Maier (2016), an unpublished doctoral thesis, so a preliminary identification is maintained.

Family Noteridae Thomson, 1860**Genus *Notomicrus* Sharp, 1882**

Note. This genus comprises 15 species, 13 of them distributed in the New World (Baca et al. 2014; Guimarães and Ferreira 2019), and two of the latter species recorded from Mexico (Nilsson 2011).

***Notomicrus sharpi* J. Balfour-Browne, 1939**

Distribution. United States, Mexico (Chiapas, new state record; Oaxaca; San Luis Potosí; Tamaulipas), Guatemala, Costa Rica, Panama, Bahamas, Cuba, Jamaica, Dominican Republic, Puerto Rico, Virgin Islands, Guadeloupe (Arce-Pérez and Roughley 1999; Nilsson 2011; Manuel 2015). This species was previously recorded from 0–500 m (Blanco-Aller 2015; Manuel 2015). Herein, the species was found at level 4 (river 2, 1,619 m).

Comments. Collected on substrate of macrophytes (February 2018, dry season).

Altitudinal distribution of the aquatic beetle fauna

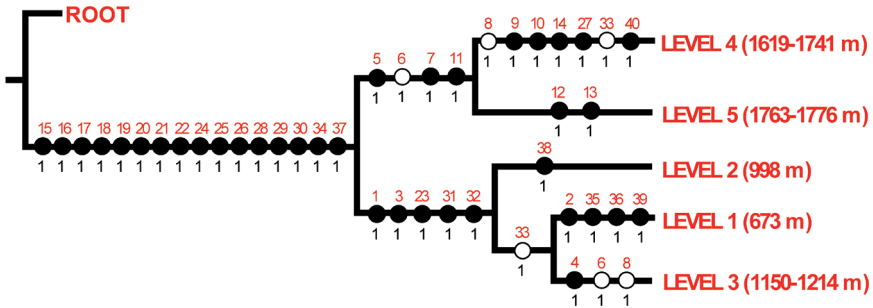
The aquatic beetle fauna from Volcán Tacaná is distributed throughout the sampled altitudinal gradient (670–1,776 m), however our initial hypothesis is that species distribution would not be homogeneous. We applied a Parsimony Analysis of Endemism (PAE) as a fast approach to detect a potential faunal partition, with a general finding of the three lower altitudinal levels grouping together (i.e., sharing similar species) and about 40% of the species with a widespread altitudinal distribution. A first PAE (Fig. 3A), including the five levels, each as a single unit, recovered a topology distinguishing two well-defined groups, one composed by the three lower levels (673, 998, and 1,150–1,214 m), and another composed by the two higher levels (1,619–1,741 m and 1,763–1,776 m). A second PAE (Fig. 3B), including each sampled river (i.e., rivers of levels 3–5 considered each as a unit) also recovered a group composed by the three lower levels (levels 1–3), nevertheless two rivers of levels 4 and 5 (i.e., R2 of levels 4 and 5, respectively) were recovered as closer to rivers from levels 1–3 than to other rivers of levels 4 and 5 (i.e., R1 of levels 4 and 5, respectively), yet support for the latter group (levels 1–3 + R2 of L4 and L5) is quite weak. This means that the next well supported group would be all rivers excluding river 1 of level 4.

The most diverse family was Elmidae (see some representatives on Fig. 4), with most species widespread along the five altitudinal levels, with the genera *Austrolimnius* (*A. formosus* and *A. sulcicollis*), *Xenelmis* (*X. bufo*), and *Heterelmis* (*H. glabra*, *H. obesa*, *H. obscura*, and *H. simplex*), occurring in all levels (except *H. simplex*, absent from R2 and R1 of levels 3 and 4, respectively). *Cylloepus atys* shares the same distribution pattern as *H. simplex*, while *Hexacylloepus metapa* and *Huleechius spinipes*, both occur in all altitudinal levels but are curiously absent from river 1 of level 4. *Macrelmis graniger* and *M. leonilae* are present in all rivers, while *Macrelmis* sp. is present only in river 2 of level 5. *Microcylloepus* (*M. inaequalis*, *M. troilus*, and *M. sp.*) are present in all altitudinal levels, however *M. troilus* is absent in river 1 of level 4 and river 1 of level 5. *Phanocerus clavicornis* has a fragmented distribution, occurring in levels 1, 3, and 4, while *Hexanchorus usitatus*, *Neelmis apicalis*, and *Onychelmis longicollis* are present in all rivers from levels 1–3.

Dytiscidae (see some representatives on Fig. 4), the second most diverse family, is characteristic of the higher levels (i.e., levels 4 and 5), with all genera represented by only one species. *Copelatus distinctus*, present in all rivers of levels 3–5, has the largest vertical distribution. *Platambus americanus*, *Ilyobiosoma flobrianum*, *Laccophilus proximus*, and *Clarkhydrus* sp. are present in levels 3 and 4, however only *P. americanus* is present in all four rivers of these levels. *Bidessonotus championi*, *Liodessus affinis*, *Uvarus subornatus*, and *Neochypeodytes fryii* are present in level 4, nevertheless only the latter species occurs in both sampled rivers. *Rhantus gutticollis* and *Thermonectus nigrofasciatus* are only present in river 2 of the highest level.

Dryopidae (see some representatives in Fig. 4) is present in the three lowest levels, with *Dryops mexicanus* and *Helichus suturalis* present in all rivers of such levels, while *Elmoparnus pandus* occurs only in level 1. *Epimetopus thermarum* (Epimetopidae),

(a)



(b)

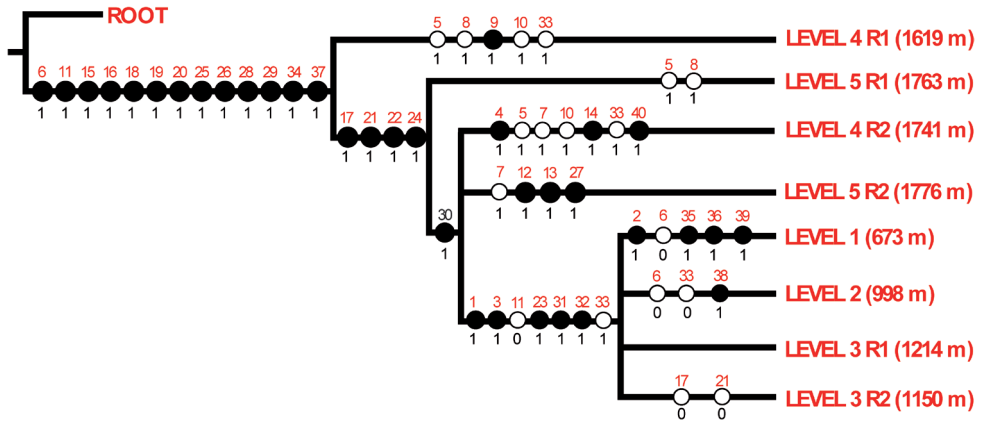


Figure 3. Parsimony Analysis of Endemicity (PAE) of the altitudinal levels and sites of the aquatic beetle fauna of Volcán Tacaná, Chiapas, Mexico **A** most parsimonious tree of the five sampling levels, with levels 3–5 considered each as a unit (number of steps = 43, consistency index (CI) = 93, retention index (RI) = 83) **B** strict consensus of the five most parsimonious trees of the five sampling levels, with levels 3–5 considered as two separate units each (number of steps = 53, consistency index (CI) = 75, retention index (RI) = 63). Red numbers = species (see Table 1); 1 = presence, 0 = absence, black circles = single event or first appearance, white circles = independent event or reversal (disappearance).

Gyretes boucardi (Gyrinidae), and *Lutrochus* sp. (Lutrochidae) occur only in level 1, while *Tropisternus fuscitarsis* (only recorded hydrophilid) is present in level 2, and *Notomicrus sharpi* (only noterid) occurs only in river 2 of level 4. Hydraenidae (*Hydraena* sp.) was present in all sampled rivers.

Biogeographical affinity of the aquatic beetle fauna

We attempt a general characterization of the fauna applying the criterion of Nearctic and Neotropical regions of Morrone (2006, 2017, 2019). Despite altitude of the

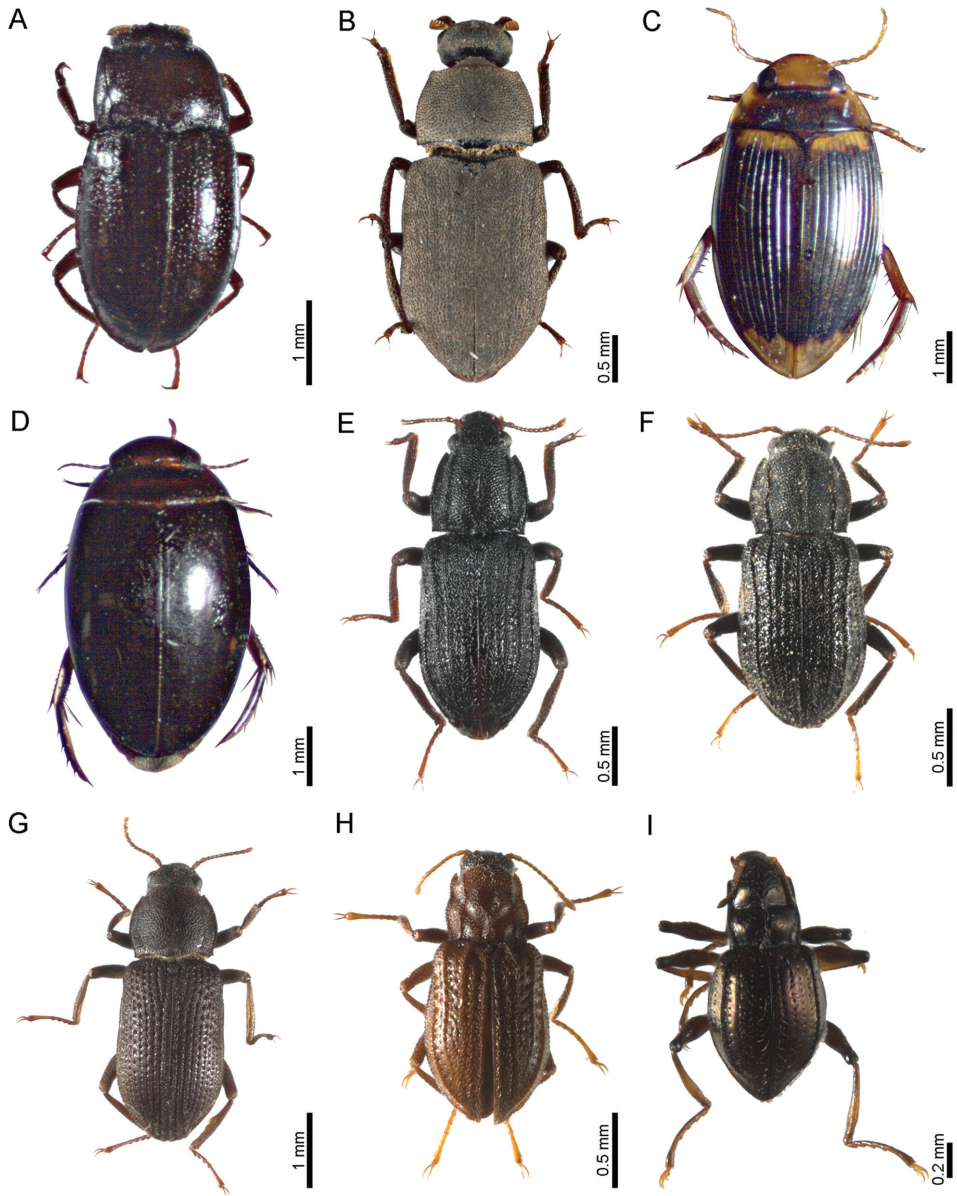


Figure 4. Habitus of representative species of the three most diverse aquatic beetle families from Volcán Tacaná, Chiapas, Mexico **A** *Elmoparnus pandus* Spangler & Perkins, 1977 (Dryopidae) **B** *Helichus suturalis* LeConte, 1852 (Dryopidae) **C** *Copelatus distinctus* Aubé, 1838 (Dytiscidae) **D** *Platambus americanus* (Aubé, 1838) (Dytiscidae) **E** *Cylloepus atys* Hinton, 1946 (Elmidae) **F** *Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020 (Elmidae) **G** *Macrelmis leonilae* Spangler & Santiago-Fragoso, 1986 (Elmidae) **H** *Microcylloepus Troilus* Hinton, 1940 (Elmidae) **I** *Onychelmis longicollis* (Sharp, 1882) (Elmidae).

sampled rivers, all species collected have distribution records within the Neotropical region (i.e., all levels present species of Neotropical affinity). About 60% of the species (24 out of 40) have a predominantly Neotropical distribution, while the remaining 40% (16 species) have a wide distribution in the New World, among which the elmids *Heterelmis glabra*, *H. obesa*, *H. obscura*, and *Huleechius spinipes* occur in all altitudinal levels (670–1,776 m); *Helichus suturalis* (Dryopidae), *Neoelmis apicalis* (Elmidae), and *Tropisternus fuscitarsis* (Hydrophilidae), *Epimetopus thermarum* (Epimetopidae) occur only in the two lowest levels (670 and 998 m); while *Notomicrus sharpi* (Noteridae) and the dytiscids *Laccophilus proximus*, *Liodes affinis*, *Neoclypeodytes fryii*, *Rhantus gutticollis*, and *Thermonectus nigrofasciatus* occur only in the two highest levels (1,610–1,776 m). Other two species with Neotropical and Nearctic records have a fragmented vertical distribution (the elmid *Phanocerus clavicornis*) or occur in the three highest levels (the dytiscid *Copelatus distinctus*).

Among the 20 species of Elmidae, 14 occur only in the Neotropical region, while the remaining six, particularly those of *Heterelmis*, have a wide distribution (i.e., they occur in the Nearctic and Neotropical regions). Most dytiscid species, six out of 11, have a wide distribution through the Nearctic and Neotropics, while the other five occur only in the Neotropical region. Elmidae and Dytiscidae have 80 and 50% of their distribution in the Brazilian subregions and the Mexican Transition Zone, respectively, with especial affinity to the Mesoamerican and Pacific domains. Dryopidae is represented by three species, two of them with records in the Neotropical region (Brazilian subregions and the Mexican Transition Zone) and one with Nearctic and Neotropical distribution. Gyrinidae (*Gyretes boucardi*), Hydraenidae (*Hydraena* sp.), and Lutrochidae (*Lutrochus* sp.), also have species with Neotropical affinity, whereas Epimetopidae (*Epimetopus thermarum*), Hydrophilidae (*Tropisternus fuscitarsis*), and Noteridae (*Notomicrus sharpi*) have species with a wide distribution in the New World. The latter six families also have an affinity to the Brazilian subregions, particularly to the Pacific and Mesoamerican domains.

Discussion

Aquatic beetles were present at the five sampling levels (L1, 673 m; L2, 998 m; L3, 1,150–1,214 m; L4, 1,619–1,741 m; and L5, 1,763–1,776m). This agrees with the widespread distribution of aquatic beetles, as well as their high capacity to inhabit different aquatic environments from sea level to mountains of 4,000 m high or more (Jäch and Balke 2008; White and Roughley 2008). Despite their broad presence in the volcano, aquatic beetle species were not distributed homogeneously along the altitudinal gradient, which is congruent with a high endemism in almost all families of this group, particularly those of lotic systems in warm climates (Jäch and Balke 2008).

Elmidae (riffle beetles) was the dominant group (20 spp.) and was present in all sampling levels. This coincides with previous findings in the Neotropics (e.g., Arias-Díaz et al. 2007; Huanachin-Quispe and Huamantico-Araujo 2018; Mosquera-Murillo and Sánchez-Vázquez 2018; Passos et al. 2018). General characteristics of the streams on a

volcanic bedrock with a variety of substrates, such as gravel, leaf litter, logs, and aquatic macrophytes, probably contributed to maintain a high diversity of elmids as reported by Elliot (2008) and Mosquera-Murillo and Sánchez-Vázquez (2018). Species of the New World genera *Heterelmis*, *Macrelmis*, and *Microcyllloepus*, and of the Neotropical *Austrolimnius* were present at all levels, while the Neotropical *Hexanchorus*, *Neoelmis*, and *Onychelmis* were restricted to levels 1–3.

Dytiscidae (predaceous diving beetles) was the second most diverse group (11 spp.) and was present mostly at levels 4 and 5, with only one species (*Copelatus distinctus*) at levels 3–5. Three species, *Bidessonotus championi*, *Ilybiosoma flobrianum*, and *Uvarus subornatus* were only observed at L4 (R2, 1,619 m), while *Rhantus gutticollis* and *Thermonectus nigrofasciatus* appeared only at L5 (R2, 1,776 m). This distribution may relate to the size of the streams at the higher levels, which were generally smaller and with weaker currents, so pools were more common, which appeared to be a suitable habitat for dytiscids; most collecting of dytiscids was at depositional zones of the stream. This agrees with a general preference of this family for lentic systems (Miller and Bergsten 2016; Benetti et al. 2018).

Dryopidae was the third family in species richness (3 spp.) and was present at lower elevations, with *Dryops mexicanus* and *Helichus suturalis* at levels 1–3, and *Elmoparnus pandus* only at level 1. This is a mostly tropical family, which appears to explain their presence at low elevations, although there are records at higher elevation in other areas (Huanachin-Quispe and Huamantico-Araujo 2018). This family includes species that may be observed in both lotic and lentic environments, however, many of the species may be present near the water margin or even outside (Jäch and Balke 2008), also their larvae are terrestrial. This particular biology may indirectly restrict the presence of adult dryopids at such lower elevation sites. During collecting, specimens were only found submerged associated to substrates.

The rest of the families were represented by one species each. Hydraenidae (*Hydraena* sp.) was observed at the five sampling levels, which agrees with the broad distribution of the group and that species of this genus occupy different types of habitats, from small streams to large rivers (Trizzino et al. 2013). Noteridae (*Notomicrus sharpi*) was only present at level 4 (river 2, 1,619 m), which is above the previous known altitudinal record; as dytiscids, noterids prefer environments with slow current and some depth (Megna and Deler 2006), which includes the small pond (with macrophytes) at one side of the main stream where the only specimen was captured. Epimetopidae (*Epimetopus thermarum*), Gyridae (*Gyretes boucardi*), and Lutrochidae (*Lutrochus* sp.) were only recorded at level 1 (693 m). It is known that *Epimetopus* is attracted to lights (Perkins 2012), this agrees with our findings as specimens were captured with a bucket light trap. *G. boucardi* was collected in October, agreeing with White and Roughley's (2008) time of emergence of late summer and early fall for the species; specimens were captured in an adjacent pool forming a large aggregation, *Lutrochus* sp. was only found at level 1, with specimens captured on macrophytes; this group is typically from lotic systems; however, it has been little studied in Mexico. Finally, Hydrophilidae (*Tropisternus fuscitarsis*) was only recorded at level 2; it is interesting this representative family was only present with one species, which was collected with bucket light trap, probably indicating a not very suitable habitat for the group in a volcanic-based ecosystem.

Species observed in levels 1–3 are usually of Neotropical affinity, while in levels 4 and 5 species with both Nearctic and Neotropical distribution increase. In general, most of the species are of Neotropical distribution with an affinity for the Pacific and Mesoamerican domains, which coincides with Morrone and Márquez (2001), who observed that the Coleoptera fauna of the Chiapas Highland province is related to the Veracruz and Pacific Lowlands provinces, which are part of the Mesoamerican domain. The relationship between the Chiapas Highland province and Veracruz and Pacific Lowlands provinces was confirmed by Morrone (2019). This general partition in two groups of altitudinal levels, 1–3 and 4 + 5, is supported by a PAE analysis, pointing out to a preliminary general pattern of altitudinal distribution for the aquatic beetle fauna of Volcán Tacaná.

Conclusions

The aquatic beetle fauna of Volcán Tacaná presents a high diversity, with Elmidae, Dytiscidae, and Dryopidae as the most species-rich families, being responsible for 85% of the species. Some families (e.g., Hydraenidae and Elmidae) are distributed along all the altitudinal range, while Dytiscidae is present particularly at the higher altitudinal levels (1,619–1,776 m); Noteridae is also present at high altitude, but only in a river located at 1,741 m. Remaining families, Dryopidae, Epimetopidae, Gyrinidae, Hydrophilidae, and Lutrochidae are present in lowlands (670–1,214 m). The aquatic beetle fauna of Volcán Tacaná presents a general partition in two well-defined groups: a lower altitude fauna (between 670, 934 and 1,150–1,214 m, levels 1–3) and a higher altitude fauna (between 1,619 and 1,776 m, levels 4 and 5). This fauna has an affinity to the Pacific and Mesoamerican biogeographic domains.

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Appendix I

Table A1. Collecting data of examined material of the new records of species for Mexico; all specimens are deposited at Colección Nacional de Insectos (CNIN), UNAM. LV1-LV5 = sampled levels; R1 and R2 = sampled rivers; m = male, f = female; * = specimens collected with bucket light trap (as explained in materials and methods).

Sample data (day/month/ year)	ELMIDAE				DYTISCIDAE
	<i>Cyloepus atys</i> Hinton, 1946	<i>Hexacyclopus metapa</i> Silva-Polizei, Barclay & Bispo, 2020	<i>Hexanchorus ustiatius</i> Spangler & Santiago-Fragoso, 1992	<i>Onychblemis longicollis</i> (Sharp, 1882)	<i>Bidessonotus championi</i> J. Balfour-Browne, 1947
10/02/2018	LV1R1 (2m)	LV1R1 (7m, 4f)			
11/02/2018	LV2R1 (1m)	LV2R1 (2f)			
13/02/2018				LV1R1 (1f)	
17/02/2018					LV4R2 (1m)
10/03/2018		LV1R1 (2m, 3f)	LV1R1 (10m, 8f); LV2R1 (1m, 2f)*		
09/04/2018			LV1R1 (10m, 14f)		
10/04/2018		LV2R1 (1m, 3f)			
11/04/2018				LV3R1 (1m); LV3R2 (2f)	
13/04/2018		LV3R2 (2m, 2f)			
20/04/2018	LV5R1 (1m, 1f)				
07/05/2018		LV1R1 (3m)	LV1R1 (44m, 58f); (59m, 76f)*		
09/05/2018	LV2R1 (1m, 1f)	LV2R1 (2m, 2f)		LV2R (1f)	
11/05/2018	LV3R1 (1f)	LV3R1 (1m, 2f)			
12/05/2018		LV3R2 (2m, 1f)	LV3R2 (28m, 26f); (2f)*		
08/06/2018	LV1R1 (1f)	LV1R1 (2m, 6f)			
09/06/2018		LV2R1 (4m, 9f)			
15/06/2018	LV4R2 (1m, 3f)				
22/06/2018	LV5 R1 (1m)				
08/07/2018		LV1R1 (3m, 5f)	LV1R1 (34m, 38f); (16m, 63f)*		
09/07/2018	LV1R1 (3m, 7f)	LV2R1 (45m, 31f)	LV2R1 (10m, 18f); (15m, 11f)*		
10/07/2018		LV3R2 (12m, 25f)	LV3R2 (17m, 24f)		
11/07/2018		LV3R1 (6m, 3f)	LV3R1 (32m, 25f)		
13/07/2018		LV4R2 (1m)			
14/07/2018	LV4R1 (1m); LV4R2 (1m)	LV4R2 (1f)			
20/07/2018	LV5R1 (1f)	LV5R1 (2m, 3f)			
07/08/2018	LV1R1 (2m, 1f)	LV1R1 (10m, 19f)	LV1R1 (1m); (1m, 2f)*		
08/08/2018	LV2R1 (1f)	LV2R1 (27m, 20f)			
10/08/2018	LV3R1 (1m)	LV3R1 (8m, 13f); LV3R2 (20m, 43f)	LV3R1 (1m)		

Sample data (day/month/ year)	ELMIDAE				DYTISCIDAE
	<i>Cyloepus atys</i> Hinton, 1946	<i>Hexacylloepus metapa</i> Silva- Polizei, Barclay & Bispo, 2020	<i>Hexanchorus ustitatus</i> Spangler & Santiago-Fragoso, 1992	<i>Onychlemis longicollis</i> (Sharp, 1882)	<i>Bidessonotus championi</i> J. Balfour-Browne, 1947
12/08/2018	LV4R2 (3m, 4f); LV4R2 (3m, 4f)				
13/08/2018		LV4R2 (1f)			
17/08/2018	LV5R2 (6m, 2f)				
04/09/2018		LV1R1 (10m, 3f)	LV1R1 (34m, 17f)		
05/09/2018		LV2R1 (1m)			
07/09/2018		LV3R1 (4m, 2f)			
03/10/18		LV1R1 (2m, 2f)	LV1R1 (11m, 26f)		
04/10/18			LV2R1 (6m, 13f)		
12/10/2018	LVR2 (2f); LV5R2 (1m, 1f)				
02/11/2018			LV1R1 (5m, 6f); LV2R1 (10m, 5f)		
07/11/2018		LV3R2 (1m, 2f)	LV3R2 (4m, 8f)		
23/11/2018	LV5R2 (2m)	LV5R1 (1f)			
03/12/2018		LV2R1 (2m, 3f)	LV2R1 (3m, 7f)		
04/12/2018	LV4R2 (2f)				
06/12/2018			LV3R2 (3m, 13f)		
09/12/2018		LV5R1 (2m)			
04/01/2019	LV2R1 (2f)		LV2R1 (7m, 15f)		
06/01/2019		LV3R2 (1m, 2f)	LV3R1 (2m, 2f)		
04/02/2019	LV1R1 (4f)	LV2R1 (1m, 3f)	LV1R1 (1m, 7f); LV2R1 (6m, 10f)		
05/02/2019			LV3R1 (12m, 19f)		

After a decade, a new Venezuelan species of *Corydalus* Latreille (Megaloptera, Corydalidae, Corydalinae) is discovered

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Abstract

A new species of dobsonfly from Venezuela, *Corydalus ralphi* Martins, Azevêdo, Hamada & Contreras, **sp. nov.**, was discovered a decade after the last description of a species of this genus in the country. The new species is morphologically similar to *C. wanningeri* Contreras-Ramos & von der Dunk, sharing a uniform reddish coloration of body and wings and similar male genitalic structures. Likewise, it shares this particular coloration with *C. neblinensis* Contreras-Ramos but the genitalic structure fits within the *C. crossi* Contreras-Ramos species group. Two specimens, one male and one female, were collected on Tarotá River, in the Gran Sabana region, Canaima National Park, in southern Venezuela. A key to identify males of the Venezuelan species of *Corydalus* is provided.

Keywords

Aquatic insects, biodiversity, Corydalinae, dobsonfly, Neotropics, taxonomy

Introduction

Corydalus Latreille is the most species rich genus of dobsonflies from the New World. This genus was revised 23 years ago by Contreras-Ramos (1998), and since then several more species have been described (Contreras-Ramos 2002; Contreras-Ramos and von der Dunk 2010; Ardila-Camacho 2014; Ardila-Camacho and Contreras-Ramos 2018) adding up to 39 extant valid species of *Corydalus*, plus one doubtful species that occurs in Indonesia: *Corydalus testaceus* Le Peletier de Saint Fargeau & Audinet-Serville in Latreille et al. 1828. Of the 39 valid species, 34 occur only in the Neotropical region, one species is restricted to the Nearctic region, and three species occur in both regions (Oswald 2021).

In total, 33 species of *Corydalus* occur in South America (Oswald 2021). Venezuela is the South American country with the greatest diversity of this genus, with 16 species described to date. Brazil is the second one with 13 species, followed by Colombia with 12 species. Recently, we studied specimens from Instituto Nacional de Pesquisas da Amazônia (INPA) which were temporarily on loan at Instituto de Biología-UNAM, and we found a couple of specimens from the Gran Sabana region, Canaima National Park Parque Nacional, Bolívar state, Venezuela that belong to an undescribed species, the 17th from this country.

Corydalus ralphi sp. nov. is superficially similar to *C. neblinensis* Contreras-Ramos (e.g., similar color of body and wings), yet it appears most closely related to *C. wanningeri* Contreras-Ramos & von der Dunk, both fitting within the *C. crossi* Contreras-Ramos species group. All these species are from Venezuela, the latter two described from Bolívar state. We are glad to make this contribution as part of a highly deserved homage to Prof. Ralph W. Holzenthal, who has studied Neotropical insect biodiversity, especially Trichoptera, and guided a large number of students for more than three decades.

Materials and methods

Several larvae of *Corydalus* were collected in Venezuela by Carlos Augusto Silva de Azevêdo and Neusa Hamada in the year 2007 by manual method; larvae were placed in containers with local ground substrate, so that several pupated and adults emerged, including two of the new species. This material was sent to ACR a few years ago, but was only recently examined. Specimens were collected on the Río Tarotá (Tarotá River), located on Canaima National Park, within the Gran Sabana region, Bolívar state, southern Venezuela. This region is composed by an upland savanna covering close to 18,000 km², with altitudes ranging from 750 to 1,450 m a.s.l., with a humid submontane climate, with average annual temperature ranging between 18 °C and 24 °C, and average annual rainfall between 2,000 and 3,000 mm (Huber 1995). This area is drained by tributaries of the Orinoco River, most of them black-water rivers, with very acidic and low mineral waters such as the Tarotá River (Huber 1995). To study genital structures, abdomen was cut between 7th and 8th segments, then cleared in 10% potassium hydroxide (KOH) overnight at room temperature, rinsed with

distilled water, observed in 80% ethyl alcohol, and posteriorly stored in microvials with glycerin, each pinned below the respective specimen. Observation of the genitalic morphology was made in Petri dishes below a Zeiss Discovery V8 stereomicroscope.

Drawings were made using a drawing tube attached to a stereomicroscope, and then they were vectorized using the program Adobe Illustrator CS6. Series of images of different focus were made using an Olympus TG-4 camera attached to a manual copy stand, posteriorly they were combined using the software HeliconFocus 6.7.1. Drawings and images were edited using the software Adobe Photoshop CS6. A distribution map was produced with the website <http://www.simplemappr.net>. Morphological terminology follows New and Theischinger (1993) for general morphology, Liu et al. (2016) for genital sclerites, and Breitkreuz et al. (2017) for wing venation. Specimens will be deposited at the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil.

Taxonomy

Corydalus ralphi Martins, Azevêdo, Hamada & Contreras, sp. nov.

<http://zoobank.org/5AFD72F9-1AB7-44B1-BB65-BABB9E1F2E1D>

Figures 1–7

Etymology. We are glad to name this new species after Prof. Ralph W. Holzenthal of the University of Minnesota, as homage to his bright career of research and teaching, motivating several generations of new insect biodiversity professionals.

Type material. *Holotype*, male, VENEZUELA: Bolívar, Parque Nacional Canaima, Gran Sabana, Río Tarotá, 5°49'15.0"N, 61°25'04.0"W, 1,324 m a.s.l., 14.iii.2007, leg. Azevedo, CAS; Hamada, N. (INPA). *Paratype*, female, same data as holotype (INPA).

Diagnosis. Head and pronotum pale reddish brown (Figs 1A, C, 2A, C), with yellowish elements on the head, especially on antennae and labrum. Body and wings generally pale reddish brown, wings unpatterned, thus resembling *C. neblinensis* Contreras-Ramos and *C. wanningeri* (Figs 1B, D, 2B, D). Male genitalia similar to *C. wanningeri*; however, in the new species the gonostylus 9 has a slightly projected and convex apex (Figs 5A, C, 6A), whereas *C. wanningeri* has a strongly extended and narrow apex (Figs 5B, D, 6B); *C. neblinensis* has a subclavate and unmodified gonostylus 9 (Contreras-Ramos 1998: fig. 26A, B). Shape of gonostyli 10 is also diagnostic. In the new species these are strongly sclerotized, almost parallel to each other, subtriangular, bluntly pointed, and caudally straight (Figs 5A, C, 6C); while they are strongly sclerotized, close to each other, convergent, and bluntly pointed in *C. wanningeri* (Figs 5B, D, 6D); and semi-membranous, widely separated, and papilliform in *C. neblinensis* (Contreras-Ramos 1998: fig. 26C). Gonostyli 10 of *C. ralphi* sp. nov. resemble those from *C. crossi*; however, the latter species is easily separated from the new one by its dark brown body and darkly patterned wings (Contreras-Ramos 2002: fig. 6). Females may be distinguished by the unpatterned pale reddish brown color (Figs 1C, 2C), and by the arrangements of the mandibular dentition (Fig. 3C), with the three basal teeth close to each other, and basal tooth smaller than the

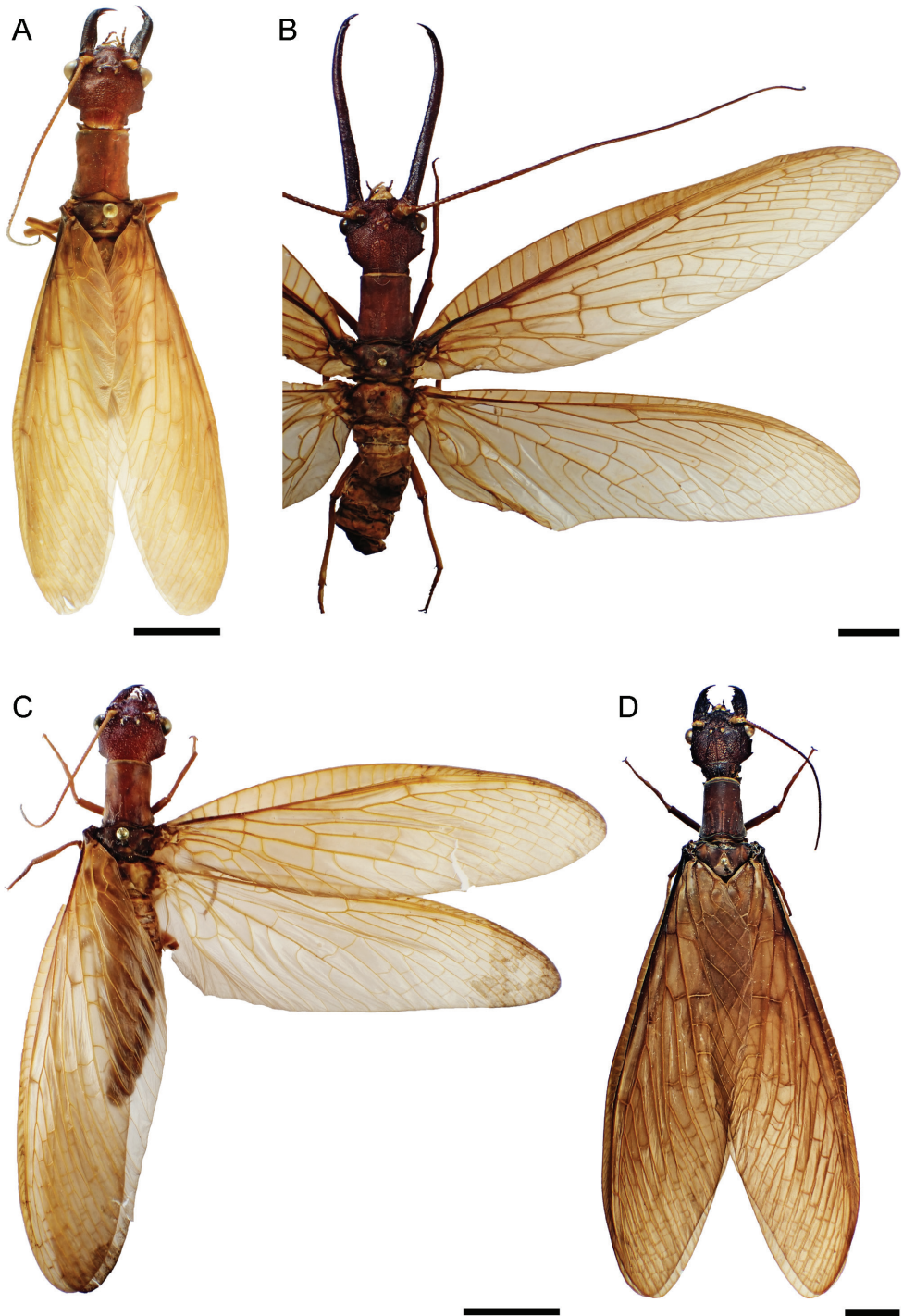


Figure 1. Dorsal habitus of *Corydalus* spp. **A** holotype of *C. ralphi* sp. nov., male **B** holotype of *C. wanningeri* Contreras-Ramos & von der Dunk, male **C** paratype of *C. ralphi* sp. nov., female **D** paratype of *C. wanningeri* Contreras-Ramos & von der Dunk, female. Scale bar: 1 cm.

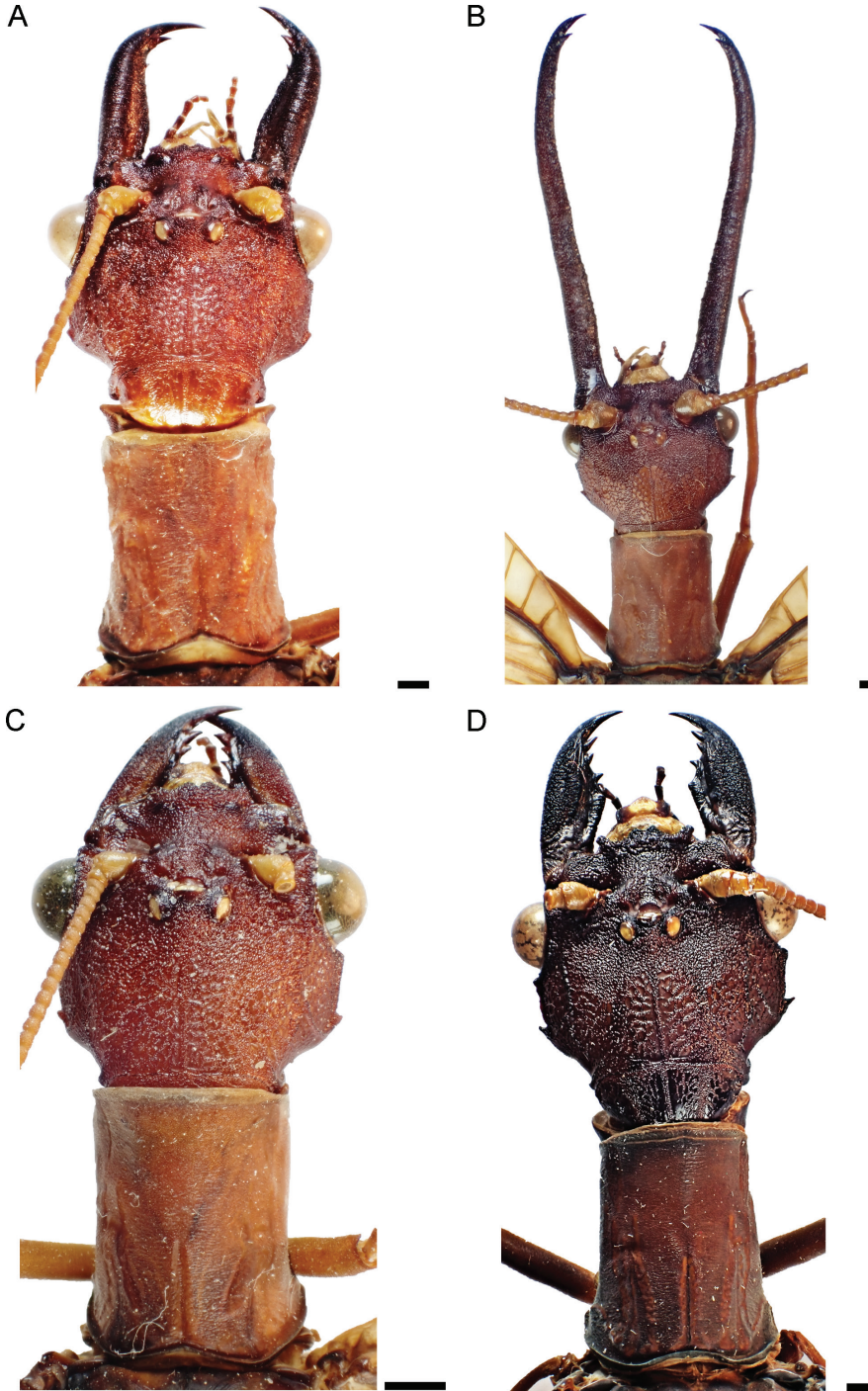


Figure 2. Head and pronotum of *Corydalus* spp., dorsal view. **A** holotype of *C. ralphi* sp. nov., male **B** holotype of *C. wanningeri* Contreras-Ramos & von der Dunk, male **C** paratype of *C. ralphi* sp. nov., female **D** paratype of *C. wanningeri* Contreras-Ramos & von der Dunk, female. Scale bar: 1 mm.

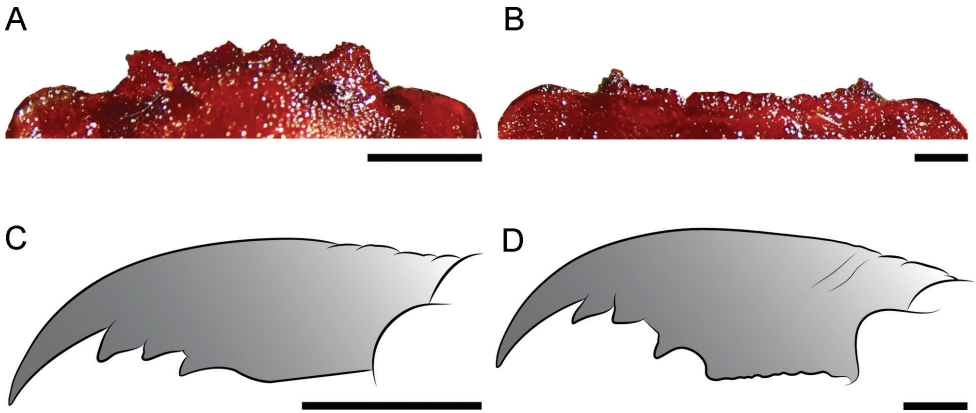


Figure 3. Head structures of *Corydalus* spp. **A** clypeal margin of holotype of *C. ralphi* sp. nov., male **B** clypeal margin of holotype of *C. wanningeri* Contreras-Ramos & von der Dunk, male **C** right mandible of paratype of *C. ralphi* sp. nov., female **D** right mandible of paratype of *C. wanningeri* Contreras-Ramos & von der Dunk, female. Scale bar: 1 mm.

second and third ones; also with an inner predental concavity and moderately separated first and second teeth in *C. wanningeri* (Fig. 3D), and with basal tooth larger than the second and third teeth in *C. neblinensis* (Contreras-Ramos 1998: fig. 26F).

Description. Male measurements: Head width 9.26 mm; mandible length 7.4 mm; antenna length 29.3 mm; forewing length 47.1 mm; hindwing length 40.2 mm; antenna length/forewing length 0.62. **Female measurements:** Head width 8.9 mm; mandible length 5.35 mm; antenna length 23.4 mm; forewing length 52.5 mm; hindwing length 47.7 mm; antenna length/forewing length 0.44. Body (Fig. 1A, C) pale reddish brown with yellowish elements, especially on head and thoracic pleura.

Head (Figs 2A, C, 3A, C). Pale reddish brown, unpatterned. Vertex infuscated, with three yellow ocelli each surrounded by darkish brown ring. Labrum yellow, with short yellow setae. Clypeal margin darkish brown, lateral projection well developed, subtriangular; medial projection well developed, deeply incised; lateral and median projection close to each other. Male mandible elongate, pale reddish brown with margins dark brown; median tooth longer than in female and narrow; apex curved inwards, bearing three teeth, basal preapical tooth small, subtriangular, and separated from the second preapical tooth, which is closely associated with a well-developed apical tooth. Female mandible same color as male, unmodified; basal preapical tooth small, close to second and third preapical teeth; second preapical tooth smaller than third, apical tooth well developed, darkish brown. Antenna 64–66-segmented, filiform; scape yellow, subquadrangular; pedicel yellow; flagellum yellow, with apical flagellomeres darkish brown. Maxilla darkish brown to yellow; maxillar palpi 5-segmented, palpomeres pale reddish brown with yellow apex. Labium darkish brown to yellow; labial palpi 3-segmented, darkish brown to yellow.

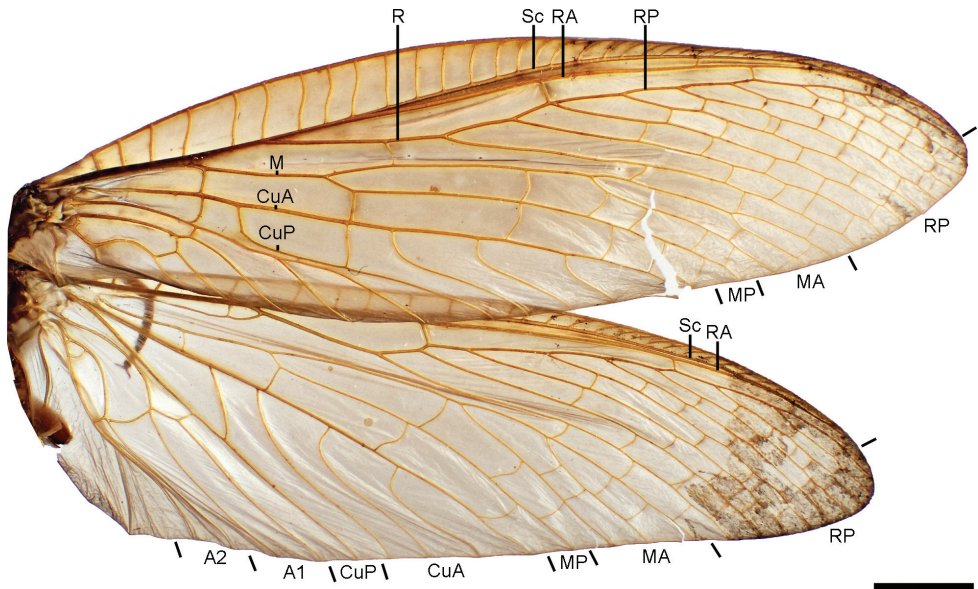


Figure 4. Wings of *Corydalus ralphi* sp. nov. Scale bar: 5 mm. Abbreviations: A, anal veins; CuA, cubitus anterior; CuP, cubitus posterior; MA, media anterior; MP, media posterior; RA, radius anterior; RP, radial posterior; and Sc, subcosta.

Thorax (Figs 1A, C, 2A, C). Pronotum rectangular, nearly 1.45 times longer than wide (length 7.9 mm/ width 5.4 mm), pale reddish brown, unpatterned; densely covered with minute pale brown setae. Mesonotum wider than long, pale reddish brown, unpatterned; densely covered with minute light brown setae. Metanotum similar to mesonotum, but slight narrower. Pteropleura yellow, with basal region of coxa darkish brown; covered with small yellow setae. Legs generally yellow, with small yellow setae, tarsal claws darkish brown.

Wings (Fig. 4). Forewing pale reddish brown, semitranslucent, unpatterned. Venation reddish brown, darker than membrane, densely covered with minute and fine reddish brown setae. Costal field wider at the base, with several simple costal crossvein; pterostigma indistinct. Sc running parallel to RA, and fusing with its apex. Radial field with four crossveins. RP with nine branches, several crossveins present between them. Radiomedial space with four crossveins. M forked bear $\frac{1}{4}$ of the wing length; MA forked in two main branches (MA_1 and MA_2), MA_1 forked near wing margin, MA_2 unforked; MP unforked; intramedial field with five crossveins. Mediocubital space with six crossveins. Cu forked basally to M fork; CuA with four branches; CuP unforked; intracubital field with one crossvein. Cubitoanal field with two crossveins. A_1 forked apically to Cu fork; field between A_1 and A_2 with one crossvein; A_2 forked basally to A_1 fork; field between A_2 and A_3 with one crossvein; A_3 simple. Hindwing with general aspect similar to forewing. Costal field wider at the base, with several simple costal crossvein; pterostigma indistinct. Sc running parallel to RA, and fusing with its apex. Radial field with three crossveins.

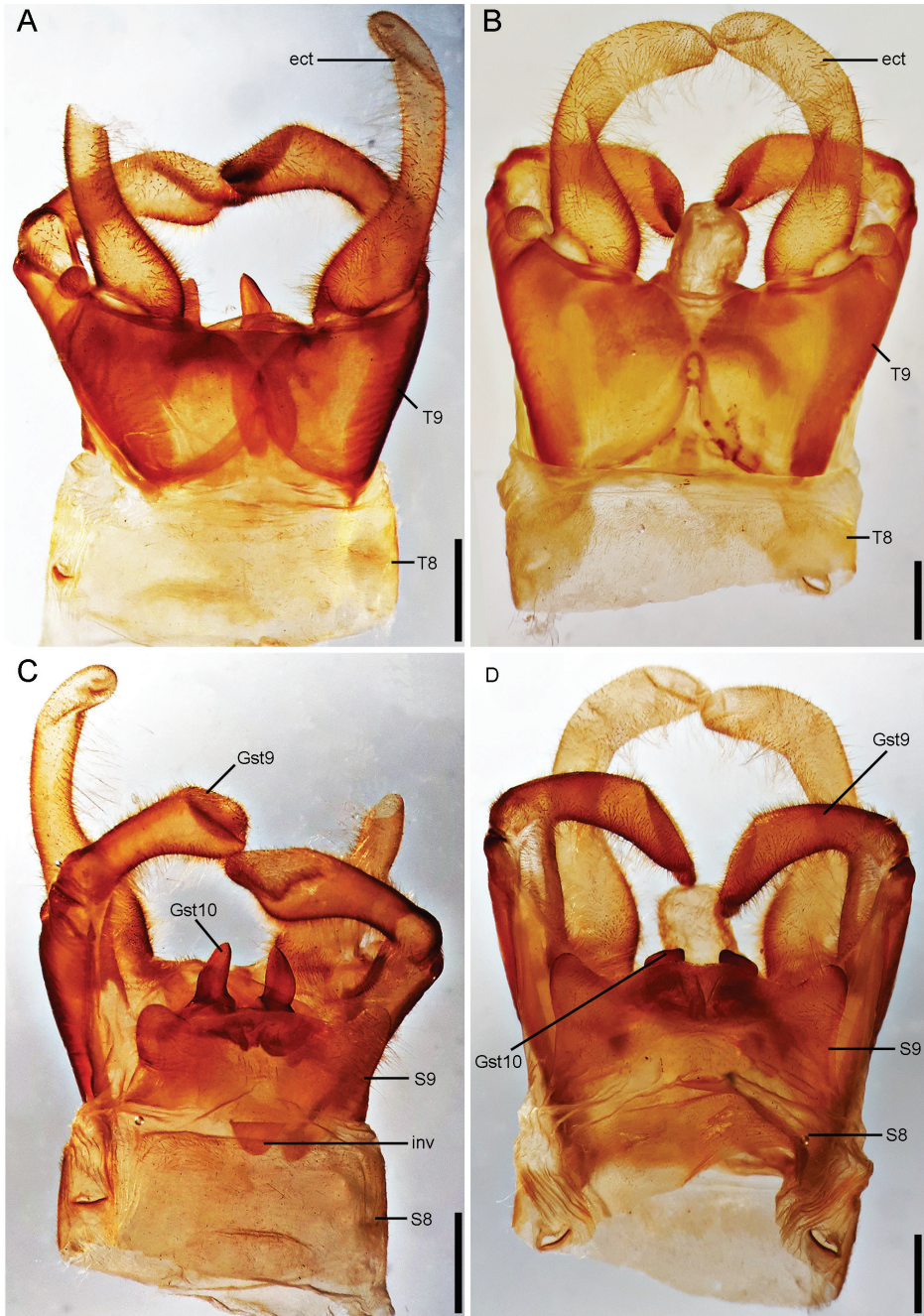


Figure 5. Male genitalia of *Corydalus* spp. **A** genitalia of holotype of *C. nalphi* sp. nov., dorsal view **B** genitalia of holotype of *C. wanningeri* Contreras-Ramos & von der Dunk, dorsal view **C** genitalia of holotype of *C. nalphi* sp. nov., ventral view **D** genitalia of holotype of *C. wanningeri* Contreras-Ramos & von der Dunk, ventral view. Scale bar: 1 mm. Abbreviations: ect, ectoproct; Gst 9, gonostylus 9; Gst 10, gonostylus 10; inv, invagination of membrane between segments 8 and 9; S8–9, sternites 8–9; T8–9, tergites 8–9.

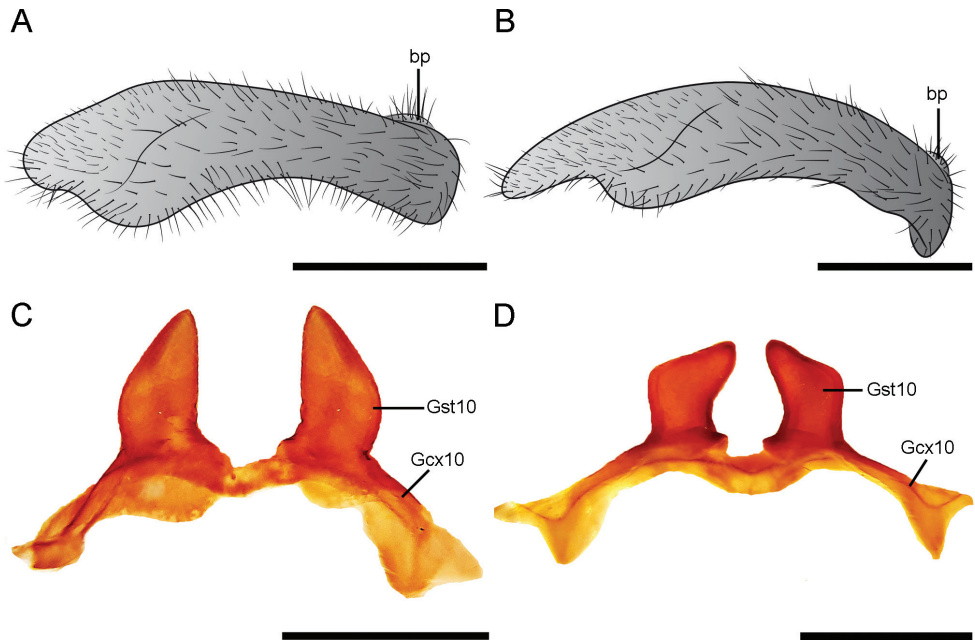


Figure 6. Structures of male genitalia of *Corydalus* spp. **A** gonostylus 9 of *C. ralphi* sp. nov., latero-caudal view **B** gonostylus 9 of *C. wanningeri* Contreras-Ramos & von der Dunk, latero-caudal view **C** gonocoxites and gonostyli 10 of *C. ralphi* sp. nov., ventral view **D** gonocoxites and gonostyli 10 of *C. wanningeri* Contreras-Ramos & von der Dunk, ventral view. Scale bar: 1 mm. Abbreviations: bp, basal projection of gonostylus 9; Gsx10, gonocoxite 10; Gst10, gonostylus 10.

RP with nine branches, several crossveins present between them. Radiomedial space with five crossveins, including the elongated, sigmoid 1r-m, with a veinlet linking it to R. M forked bear $\frac{1}{4}$ of the wing length; MA forked in two main branches (MA_1 and MA_2), MA_1 forked near wing margin, MA_2 unforked; MP unforked; intramedial field with three crossveins. Cu forked near the wing base; CuA with four branches; CuP unforked; intracubital field with one crossvein. Cubitoanal field with one crossvein. A_1 forked apically to Cu fork; field between A_1 and A_2 with one crossvein; A_2 forked near the same level of A_1 fork; field between A_2 and A_3 with one crossvein; A_3 simple.

Male genitalia (Figs 5, 6). Tergite 8 rectangular. Sternite 8 rectangular. Medial region of the membrane between sternites 8 and 9 presenting a large, well sclerotized, and subtriangular invagination, 1.5 times wider than long, bearing several minute setae inside and close its opening. Tergite 9 trapezoidal, cephalic V-shaped internal inflection reaching $\frac{2}{3}$ of the length of tergite; caudally V-shaped internal inflexion reaching $\frac{1}{3}$ of the tergite length. Anal tubercle inconspicuous. Sternite 9 subquadrate, semi-membranous, posterolateral lobes well developed. Gonostylus 9 subclavate, approximately as long as ectoproct, with apex composed by a slightly expanded and convex apex; basal protrusion present, poorly-developed. Gonocoxite 10 slightly convex, anterolateral projections well developed, wider than medial region, subtriangular;

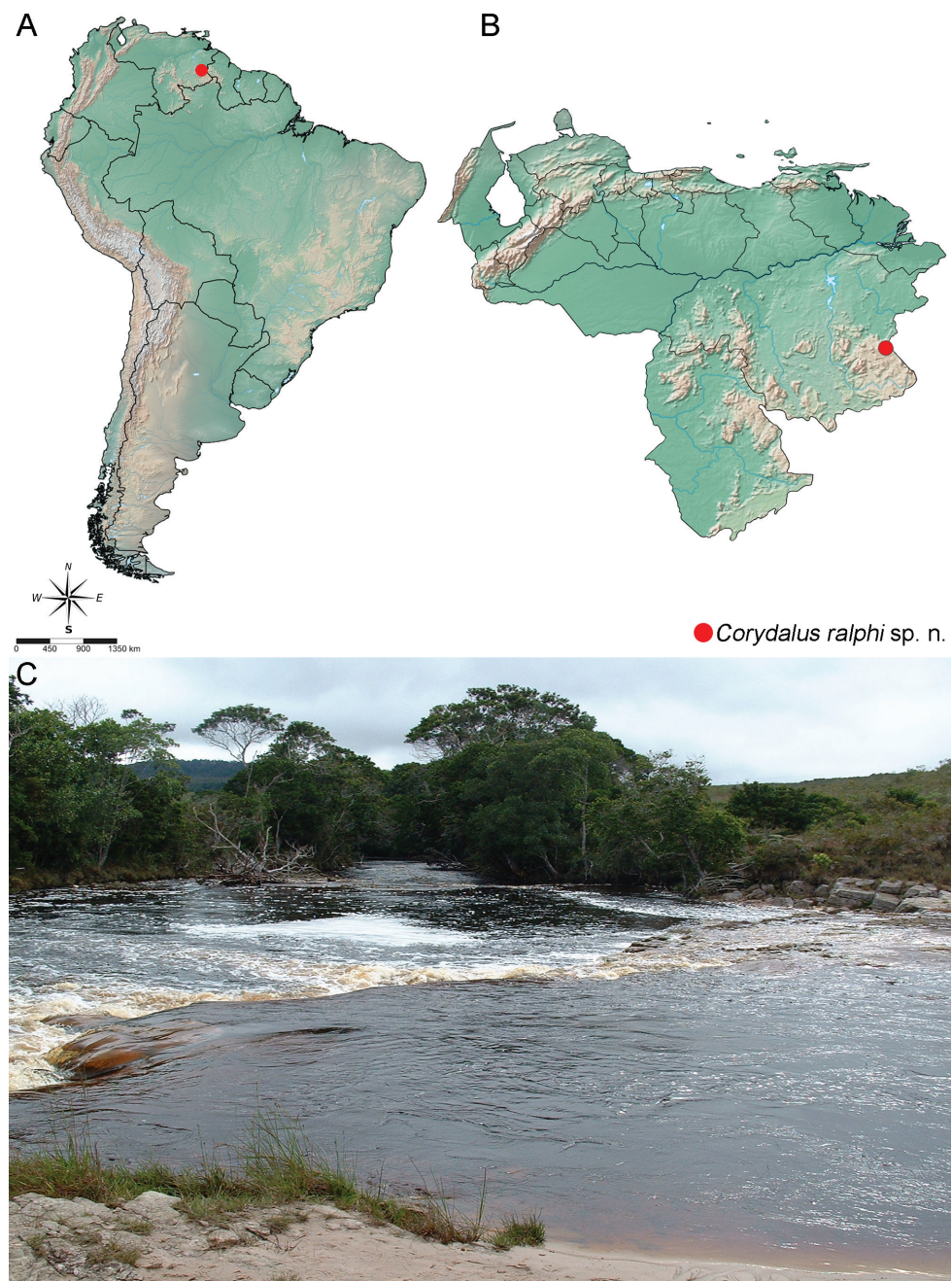


Figure 7. Habitat and distribution of *Corydalus ralphi* sp. nov. **A** South America **B** Venezuela **C** Tarotá River, Gran Sabana region, Bolívar state, Venezuela.

gonostylus 10 strongly sclerotized, subtriangular, almost parallel to each other, bluntly pointed, caudally straight. Ectoprocts as long as gonostylus 9, digitiform, basal 1/3 wide, roundly concave; apex slight curved inward. Pregenital sacs absent.

Female genitalia. Terminalia indistinct. Sternal pouch between abdominal segments 6 and 7, abdominal segments poorly developed. Gonocoxite 8 moderately sclerotized, discontinuous with pleural area, posterior margin mesally semi-membranous, concave. Gonocoxite 9 ovoid, uniformly setose; gonostylus 9 small, semicircular; ectoproct as a small ovoid sclerite, setose.

Distribution (Fig. 7A, B). Venezuela (Bolívar).

Habitat and bionomics (Fig. 7C). Larvae of the new species were collected under rocks near river banks and under the roots of aquatic Cyperaceae in the Tarotá River, Gran Sabana region in Bolívar state, southern Venezuela. Adults were obtained by rearing these larvae in laboratory conditions. Tarotá River has black water and is approximately 20 m wide, with sand bottom and scattered rock and boulders.

Comments. *Corydalus ralphi* sp. nov. is closely related to *C. wanningeri*, both from the state of Bolívar. The new species was collected in the plateau of the Gran Sabana region, inside the Canaima National Park, whereas *C. wanningeri* was collected adjacent to the NE limit of Canaima National Park, in a portion of winding road known as La Escalera, highway 10 (connecting Orinoco lowlands with the Gran Sabana plateau in the south), which is a humid slope covered with rain forest, with several brooks and waterfalls (Contreras-Ramos and von der Dunk 2010). It is unknown whether both species are parapatric, or actually sympatric. Both species share similar coloration of wings and body (Fig. 1), nevertheless males of each species may be differentiated by the shape of the gonostylus 9 apex, slightly expanded and convex in *C. ralphi* sp. nov. (Fig. 6A) and narrow and digitiform in *C. wanningeri* (Fig. 6B); gonostyli 10 are almost parallel to each other and caudally straight in *C. ralphi* sp. nov. (Fig. 6C), and apically convergent in *C. wanningeri* (Fig. 6D); anterior margin of clypeus has medial projection well developed and deeply incised in the new species (Fig. 3A), while it is flat to slightly concave, with shallow incision in *C. wanningeri* (Fig. 3B). Other characters that help differentiate males of both species are the length of the antennae, reaching 1/4 of the wing length in *C. ralphi* sp. nov. (Fig. 1A), and reaching 4/5 of the wing length in *C. wanningeri* (Fig. 1B); the new species has modified, yet short mandibles (Fig. 2A), while *C. wanningeri* has elongated mandibles (Fig. 2B); however, the variation in this trait is still unknown. Females may be separated by the dentition pattern. *Corydalus ralphi* sp. nov. lacks inner predental concavity, with first and second preapical teeth close to each other (Fig. 3C), while the inner predental concavity is evident in *C. wanningeri*, as well as the first and second preapical teeth are moderately separated (Fig. 3D).

Corydalus ralphi sp. nov. and *C. wanningeri* share a basal protrusion on male gonostylus 9 (Fig. 6A, B), as well as the general structure of gonocoxite and gonostylus 10 (Fig. 6C, D) with *C. crossi* (Contreras-Ramos 2002: figs 24, 25) (also recorded from Bolívar state), so these three species appear to be phylogenetically related. The latter species, however, may be easily separated from the former two by its darkly patterned wings.

Key to males of *Corydalus* species from Venezuela

Modified from Contreras-Ramos (1998; 2002), and Contreras-Ramos and von der Dunk (2010)

- 1 Abdomen: ectoproct short and broad (Contreras-Ramos 1998: fig. 5A), or tubular and sharply bent (Contreras-Ramos 2002: fig. 34); gonostylus 10 reduced, inconspicuous (Contreras-Ramos 1998: fig. 18C; Contreras-Ramos 2002: fig. 36) **2**
- Abdomen: ectoproct elongate, tubular (Fig. 5; Contreras-Ramos 2002: fig. 16); gonostylus 10 conspicuous, well developed (Fig. 6C, D; Contreras-Ramos 1998: fig. 4C) **5**
- 2 Head: strongly patterned with brownish and yellowish areas (Contreras-Ramos 2011: fig. 3C); Forewing: semitranslucent, conspicuously spotted (Contreras-Ramos 2011: fig. 3C); Abdomen: ectoproct broadly conical (Contreras-Ramos 1998: fig. 18A) ***C. flinti* Contreras-Ramos (Venezuela)**
- Head: unpatterned (Contreras-Ramos 2011: fig. 3B); Forewing: not so translucent, neither spotted (Contreras-Ramos 2011: fig. 3B); Abdomen: ectoproct shaped otherwise, flattened (Contreras-Ramos 1998: fig. 5A, E) or variously curved (Contreras-Ramos 2002: figs 28, 34) **3**
- 3 Head: postocular spine well developed (Contreras-Ramos 2011: fig. 3B); Abdomen: gonostylus 9 with apex narrow, directed dorsally, portion of internal apodeme as external outgrowth (Contreras-Ramos 1998: fig. 5A, E); ectoproct somewhat flattened, with dorsal elongate process (Contreras-Ramos 1998: fig. 5A, B) ***C. arpi* Navás (Brazil, Venezuela)**
- Head: postocular spine slightly developed (Contreras-Ramos 2002: figs 7, 8); Abdomen: gonostylus 9 with apex blunt or uniformly tubular (Contreras-Ramos 2002: figs 29, 35), outgrowth of apodeme absent; ectoproct with different shape **4**
- 4 Abdomen: gonostylus 9 subclavate (Contreras-Ramos 2002: figs 28, 29); sternite 9 with conspicuous sclerotized median projection (Contreras-Ramos 2002: fig. 29); ectoproct strongly curved, simple (Contreras-Ramos 2002: fig. 28) ***C. hayashii* Contreras-Ramos (Venezuela)**
- Abdomen: gonostylus 9 uniformly tubular (Contreras-Ramos 2002: figs 34, 35); sternite 9 with internal sclerotized ridge but lacking median projection (Contreras-Ramos 2002: fig. 35); ectoproct strongly curved (Contreras-Ramos 2002: fig. 34), with broad projection directed ventrally (Contreras-Ramos 2002: figs 35, 37) ***C. mayri* Contreras-Ramos (Venezuela)**
- 5 Abdomen: sternite 9 modified, with posteromedian projection (Contreras-Ramos 2002: fig. 17) or sub-attenuate and more sclerotized posteromedially (Contreras-Ramos 1998: fig. 27B) **6**
- Abdomen: sternite 9 unmodified, subquadrate (Fig. 5A, B; Contreras-Ramos 1998: figs 2B, 4B) **8**

- 6 Abdomen: sternite 9 sub-attenuate, noticeably more sclerotized posteromedially (Contreras-Ramos 1998: fig. 27B) ***C. nubilis* Erichson (Brazil, Colombia, French Guiana, Guyana, Venezuela)**
- Abdomen: sternite 9 with posteromedian projection (Contreras-Ramos 2002: fig. 17) **7**
- 7 Abdomen: posteromedian projection of sternite 9 large (nearly as long as sternum), thumblike (Contreras-Ramos 1998: fig. 31B); gonostylus 9 unguiform (Contreras-Ramos 1998: fig. 31B) ***C. tessellatus* Stitz (Colombia, Venezuela)**
- Abdomen: posteromedian projection of sternite 9 small (~ 1/2 as long as sternum), narrow (Contreras-Ramos 2002: fig. 17); gonostylus 9 tubular (Contreras-Ramos 2002: fig. 17) ***C. clavijoi* Contreras-Ramos (Venezuela)**
- 8 Abdomen: gonostylus 9 elongate, somewhat flattened or tubular (Contreras-Ramos 1998: figs 2B, 19B) **9**
- Abdomen: gonostylus 9 subclavate (Fig. 6A, B; Contreras-Ramos 1998: figs 4B, 7B, 17B) **11**
- 9 Abdomen: gonostylus 9 narrower and noticeably shorter than ectoproct (Contreras-Ramos 2002: fig. 23) ***C. crossi* Contreras-Ramos (Venezuela)**
- Abdomen: gonostylus 9 and ectoproct subequal in length and shape (Contreras-Ramos 1998: figs 2A, 19A) **10**
- 10 Abdomen: gonostylus 9 somewhat flattened (Contreras-Ramos 1998: fig. 2A, B), ectoproct base as wide as median region (Contreras-Ramos 1998: fig. 2A, B) ***C. affinis* Burmeister (Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Venezuela)**
- Abdomen: gonostylus 9 tubular (Contreras-Ramos 1998: fig. 19A, B); ectoproct base wider than median region (Contreras-Ramos 1998: fig. 19A, B) ***C. hecate* (McLachlan) (Brazil, Peru (?), Venezuela(?))**
- 11 Head: reddish brown (Fig. 2); Thorax: pronotum reddish brown (Fig. 2); Abdomen: ectoproct apex without incurvation (Fig. 5B, D; Contreras-Ramos and von der Dunk 2010: fig. 5) or slightly curved, although it may be enlarged (Fig. 5A, C; Contreras-Ramos 1998: figs 7F, 26E) **12**
- Head: yellowish to greenish brown; Thorax: pronotum yellowish to greenish brown; Abdomen: ectoproct apex with well-developed incurvation (Contreras-Ramos 1998: figs 4A, 17B) **15**
- 12 Forewing: contrastingly patterned (Contreras-Ramos 1998: fig. 58) ***C. batesii* McLachlan (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela)**
- Forewing: not so contrastingly patterned (Fig. 1) **13**
- 13 Forewing: pale, clear, nearly translucent, few subtle small white spots (Contreras-Ramos 1998: figs 124–126); Abdomen: gonostylus 9 unmodified (Contreras-Ramos 1998: fig. 26B; gonostylus 10 papilliform (Contreras-Ramos 1998: fig. 26C) ***C. neblinensis* Contreras-Ramos (Venezuela)**

- Forewing: rather opaque, uniformly pale reddish (Fig. 1; Contreras-Ramos and von der Dunk 2010: fig. 1); Abdomen: gonostylus 9 with expanded apex (Fig. 6A, B; Contreras-Ramos and von der Dunk 2010: figs 5, 6); gonostylus 10 elongate-trianguloid (Fig. 6C, D; Contreras-Ramos and von der Dunk 2010: figs 5, 6) 14
- 14 Head: anterior margin of clypeus with medial projection well developed and deeply incised (Fig. 3A); Abdomen: gonostylus 9 with slightly expanded and convex apex (Fig. 6A); gonostyli 10 almost parallel (Fig. 6C) ***C. ralphii* sp. nov. (Venezuela)**
- Head: anterior margin of clypeus with flat to slightly concave, with shallow incision (Fig. 3B); Abdomen: gonostylus 9 with strongly expanded and narrow apex (Fig. 6B); gonostyli 10 convergent (Fig. 6B)..... ***C. wanningeri* Contreras-Ramos & von der Dunk (Venezuela)**
- 15 Head: antenna conspicuously subserrate, sinuate (Contreras-Ramos 1998: fig. 17F); Abdomen: gonocoxites 10 with anteromedian projection (Contreras-Ramos 1998: fig. 17C)..... ***C. flavicornis* Stitz (Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Panama, Peru, Venezuela)**
- Head: antenna slightly subserrate; Abdomen: gonocoxites 10 without anteromedian projection (Contreras-Ramos 1998: fig. 4C) 16
- 16 Head: antenna, including scape and pedicel, pale to dark brown, apically infusate (Contreras-Ramos 1998: figs 43, 44, 48); Abdomen: gonostyli 10 lobes typically subequal in width and length, less than half length of lobe surpassing posterior edge of gonocoxites 10 (Contreras-Ramos 1998: fig. 4C); pregenital sacs well developed, conspicuous (Contreras-Ramos 1998: fig. 4F) ***C. armatus* Hagen (Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela)**
- Head: antenna, including scape and pedicel, yellow to yellowish green, up to distal 1/3 infusate (Contreras-Ramos 1998: figs 139–141); Abdomen: gonostyli 10 typically ~ 2× as long as wide, ~ 1/2× lobe surpassing posterior edge of gonocoxites 10 (Contreras-Ramos 1998: fig. 29C); pregenital sacs apparently absent, inconspicuous ***C. peruvianus* Davis (Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela)**

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Larval and female descriptions of *Mejicanotrichia* Harris & Holzenthal, 1997 (Trichoptera, Hydroptilidae, Leucotrichiinae) from Mexico

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Abstract

Mejicanotrichia Harris & Holzenthal, 1997 is a small genus of Hydroptilidae (Trichoptera), which consists of seven species, six of them distributed in Mexico, and one more in Guatemala. Larval descriptions of only two species (*M. blantoni* and *M. estaquilloso*) were previously known, as well as only females of three species (*M. blantoni*, *M. estaquilloso*, and *M. tamaza*) previously described. The present study provides descriptions of the larvae of *M. harrisi* and *M. tridentata*, as well as a description of the female of *M. harrisi*. Identification keys for adult males, known females, and known larvae are also provided. This work aims to incorporate more information into the taxonomy of the genus, its ecology, and facilitate additional characters of potential use in future phylogenetic studies.

Keywords

Biodiversity, caddisflies, immature stages, madicolous habitat, Neotropics, water quality

Introduction

Hydroptilidae represents the most diverse family of the order Trichoptera, currently with 2,570 species recorded worldwide (Morse et al. 2019) and 946 species distributed in the Neotropics (Holzenthal and Calor 2017). The genus *Mejicanotrichia* Harris & Holzenthal, 1997 was established to segregate species related to *Mejicanotrichia blantoni* (Flint, 1970), previously included in the genus *Alisotrichia* Flint, 1964. The genus contains seven recognized species, six of them distributed in Mexico, and one in Guatemala (Holzenthal and Calor 2017). The first larval description and illustration of *Mejicanotrichia* were provided by Wiggins (1996) within the genus *Alisotrichia*. Bowles et al. (1999) specified that the larva actually belonged to the genus *Mejicanotrichia*, in particular to *M. estaquillosa* Harris & Holzenthal, 1997; they also described the larva of *M. blantoni* and discussed the phylogenetic position of the genus within the subfamily Leucotrichiinae. Later, Santos et al. (2016) performed a phylogenetic analysis with morphological data that confirmed that *Mejicanotrichia* belongs to the monophyletic subfamily Leucotrichiinae and the tribe Alisotrichiini.

The larvae of this genus are characterized by having numerous, broad, and largely colorless setae on the dorsoventrally flattened body, with oval shaped sclerites on the prosternum and the divided meso- and metathorax. The body exhibits an ornamentation with pigmented points on the surface of the thorax and abdomen; the legs are of the same size and shape, with tarsal claws well developed, as well as anal prolegs prominent, square shaped, each with a simple large claw (Wiggins 1996; Bowles et al. 1999). A larval case is absent until the final instar; it resembles a seed and is attached to large, submerged rocks in madicolous habitats. The larvae inhabit running waters with high flow and are sometimes associated with waterfall systems (Harris and Holzenthal 1997; Bueno-Soria 2010). Adults are small (2–4 mm body length), the head bears three ocelli, antennae are simple; wings are narrowed and attenuated with a reduced venation; males present first wings modified with patches of scales except in *M. harrisi* Bueno-Soria & Barba-Álvarez, 1999 and *M. rara* Bueno-Soria & Barba-Álvarez, 1999 (Harris and Holzenthal 1997). The tibial spur formula is 0-2-4 (Flint 1970; Harris and Holzenthal 1997) and male sternite IX features a deep notch (Harris and Holzenthal 1997; Bueno-Soria and Barba-Álvarez 1999). Adult individuals are generally active during the day, found on vegetation and substrate along waterfalls or turbulent currents (Bueno-Soria 2010). Larvae of only two species, *M. blantoni* and *M. estaquillosa*, are known; similarly, females of only three species, *M. blantoni*, *M. estaquillosa*, and *M. tamaza* (Flint, 1970) have been described.

Thus, the aim of this study is to contribute to the knowledge of *Mejicanotrichia*, particularly larvae and females of the Mexican species, as well as to provide an environmental characterization of the larval habitat of the genus. We gladly dedicate this contribution to Dr. Ralph W. Holzenthal of the University of Minnesota, with our admiration as one of the main experts of Neotropical aquatic entomology, particularly in recognition to his dedication for the study of caddisfly biodiversity in Latin America.

Materials and methods

Specimens of *Mejicanotrichia harrisi* and *M. tridentata* (Bueno-Soria and Hamilton 1986) were collected in their type localities and its surroundings. Larvae and metamorphotypes (Milne 1938) were collected manually with thin entomological tweezers on large boulders. Adults were collected with an entomological aspirator during the day on boulders at the streams; likewise, the collections were made with an UV light trap. The specimens were preserved in absolute ethanol. Larvae were mounted with glycerin on temporary slides with concave depressions for observation. Drawings were performed under a Zeiss optical microscope using a clear-field camera with magnifications of 10×, 16×, and 40×. The pencil drawings were scanned and edited on Adobe Illustrator CC. In order to clear the genitalia and allow species level identification, adult entire specimens were placed in 10% potassium hydroxide (KOH) at room temperature for seven hours, then rinsed in a solution of acetic acid and distilled water to neutralize KOH. After clearing, specimens were stored in absolute ethanol. For observation of adults, the entire specimen was placed on a concave slide in pure glycerin. Several larval specimens were fixed in absolute ethanol and then coated with gold (Bozzola and Russell 1999) for scanning electron microscopy (JEOL JSM 6360-LV).

The morphological terminology used is based on Marshall (1979) for adult females and Wiggins (1996) for larvae. Taxonomic identification was based on Flint (1970), Bueno-Soria and Hamilton (1986), Harris and Holzenthal (1997), Bueno-Soria and Barba-Álvarez (1999), and Bueno-Soria (2010). The environmental parameters of the streams were evaluated in situ. Water temperature and dissolved oxygen (OD) were measured with an YSI model 54ARC oximeter; pH was evaluated with Tetra brand reactive strips; and total hardness was estimated by means of a Hach the titration kit (test 5B) given as calcium and magnesium carbonates (1 gpg = 17.1 mg CaCO₃/l).

Taxonomic descriptions

Larva

Mejicanotrichia harrisi Bueno-Soria & Barba-Álvarez, 1999

Figs 1A–C, 2A–D

Material examined. 25 larvae (IN-TR-00221). MEXICO, Guerrero, Tonalapa del Río, Tonalapa River, near the Atlmolonga “balneario” (780 m a.s.l., 18°20'57.05"N, 99°42'10.12"W), 25 January 2020; leg. M. Ramírez-Carmona and O. Lagunas-Calvo.

Diagnosis. Abdomen mainly membranous with presence of abdominal tergites and fine pigment spots (Fig. 1A). Propleural sclerite with irregular shape (Fig. 1B) compared to *M. tridentata*, also the abdomen is wider in appearance. The size of the mature larvae of *M. harrisi* (2.1 mm) is smaller compared to the other species of *Mejicanotrichia*. The propleural sclerite has the form of a “serrated tooth” unlike

the other species of the genus (Figs 1B, 4B; Bowles et al. 1999). Additionally, the abdominal dorsal tergites are wider and shorter than in *M. tridentata*, which exhibits a larger number of setae over the tergites than *M. harrisi*.

Description. Dorsoventrally depressed body, range length: 1.9–2.1 mm, covered extensively by colorless and thick setae (Fig. 1A). Dorsum covered almost entirely by fine pigments spots (ornamental) (Fig. 1C), which give it the appearance of “sandpaper” (Fig. 2A). Larval case absent until before pupation.

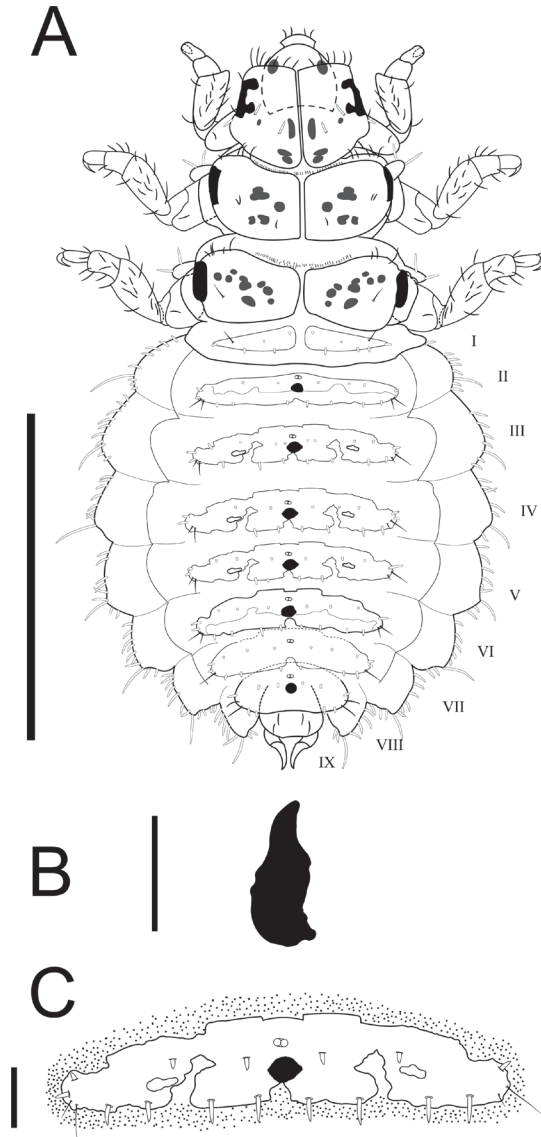


Figure 1. Larva of *Mejicanotrichia harrisi* Bueno-Soria & Barba-Álvarez, 1999 **A** habitus, dorsal **B** propleural sclerite **C** tergite of abdominal segment V, dorsal. Scale bars: 1 mm (**A**); 80 µm (**B**); 130 µm (**C**).

Head. Dark brown, prognathous, without visible ecdysial sutures. Antennae simple (Fig. 2B).

Thorax. Pro-, meso-, and metanotum divided by a median ecdysial line (Fig. 1A), with a lateral process with two thick and colorless setae except on pronotum. Pronotum anteriorly elongated, subsequently widened, longer than meso- and metanotum, covering much of the head; anterolateral corners folded towards the ventral region. The anterior pronotal margin with a row of thick and opaque setae. Propleural sclerite well developed and strongly dark, subtriangular (Fig. 1B). Prothorax with a pair of ventral sclerites, each with an oval to subrectangular shape. Meso- and metathorax covered with thick, short, colorless setae. Lateral margins thickly darkened, appearing with a longitudinal bar (Fig. 1A). Anterior margins of both nota with a row of opaque setae, in a smaller proportion than the pronotum. First pair of legs slightly shorter than the others. The three pairs of legs each with two rows of fine and moderately long setae on tibiae and tarsi, with well-developed tarsal claws.

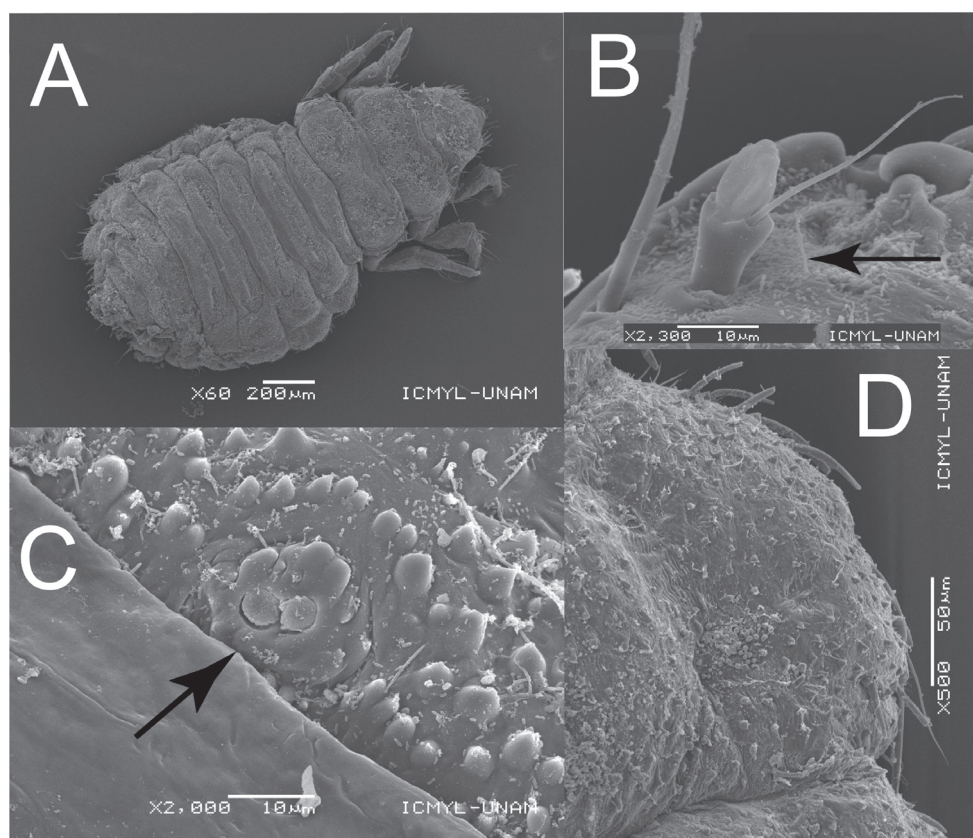


Figure 2. Scanning electron micrographs of larva of *Mejicanotrichia harrisi* Bueno-Soria & Barba-Álvarez, 1999 **A** habitus, dorsal **B** antenna **C** lacunae of abdominal segment V **D** lateral projection of abdominal segment V. Scale bars: 200 µm (**A**); 10 µm (**B**, **C**); 50 µm (**D**).

Abdomen. Long and wide, gradually tapering posteriorly. Venter with thick and extremely short setae irregularly distributed on surface. Segments I–VIII with well developed, short and wide tergites, covering much of each notum, those on segment I differing noticeably in size and shape from remainder. All tergites with thick and short colorless setae. Tergite I divided in two by a median line, with two thin and dark setae on the anterior margin. Tergites II–VII with medial lacunae and two fine and dark setae in the posterolateral margin (Figs 1A, C, 2C). Posterior and anterior margins of tergites with thick, short, and colorless setae, well distributed along both margins. Fine pigment spots more evident on integument around tergites (Fig. 1C). Middle of anterior margin of tergites III–VI, with two flattened projections. Lateral projections of abdomen without tergites, but lateral margins bear a continuous row of slightly thick, long, colorless setae (Fig. 2D); one seta noticeably longer than the others, arising at apex of each lateral projection. Segment IX strongly narrowed, posterior margin with four thick and opaque setae, two rows of thick setae in the middle. Anal prolegs prominent, cylindrical, projecting posteriorly, with well-developed anal claws curving ventrally (Fig. 1A).

Comments. The specimens were collected at a water temperature of 19 °C; with pH between 7.8–8.4; water presented a hardness of 171 mg CaCO₃/l; the dissolved oxygen was 7.6 mg/l and 89% of oxygen saturation.

Female

Mejicanotrichia harrisi Bueno-Soria & Barba-Álvarez, 1999

Fig. 3A–D

Material examined. 5 females (IN-TR-00220). MEXICO, Guerrero, Tonalapa del Río, Tonalapa River, near the Atlmolonga “balneario” (780 m a.s.l, 18°20'57.05"N, 99°42'10.12"W), 25 January 2020; leg. M. Ramírez-Carmona and O. Lagunas-Calvo.

Diagnosis. Unmodified antennae, hindwings lacking patches of scales, as in *M. rara*, with a body length of 2 mm. Abdominal segment VI without sternite process.

Description. Dark brown coloration (Fig. 3A). Body. Range length: 2.3–2.5 mm.

Head. Antennae simple, 17-segmented, scape slightly longer than flagellum; three ocelli present (Fig. 3B).

Thorax. Wings with reduced venation, mesoscutellum with a transverse line and subrectangular metascutellum. Tibial formula (0, 2, 4). Legs unmodified.

Abdomen. Segment VII elongated, without processes on sternite. Segment VIII short and ring-shaped, with a fringe of setae on posterior margin and a pair of apodemes extending anteriorly. Segment IX short, with pair of apodemes originating on posterolateral margin and extending anteriorly just before anterior margin of segment VII. Segment X rounded apically, with pair of lateral papillae (Fig. 3C). Bursa copulatrix mostly membranous, with pair of short and truncate lobes extended posteriorly; medially with keyhole-shaped opening and a shield-shaped sclerite (Fig. 3D).

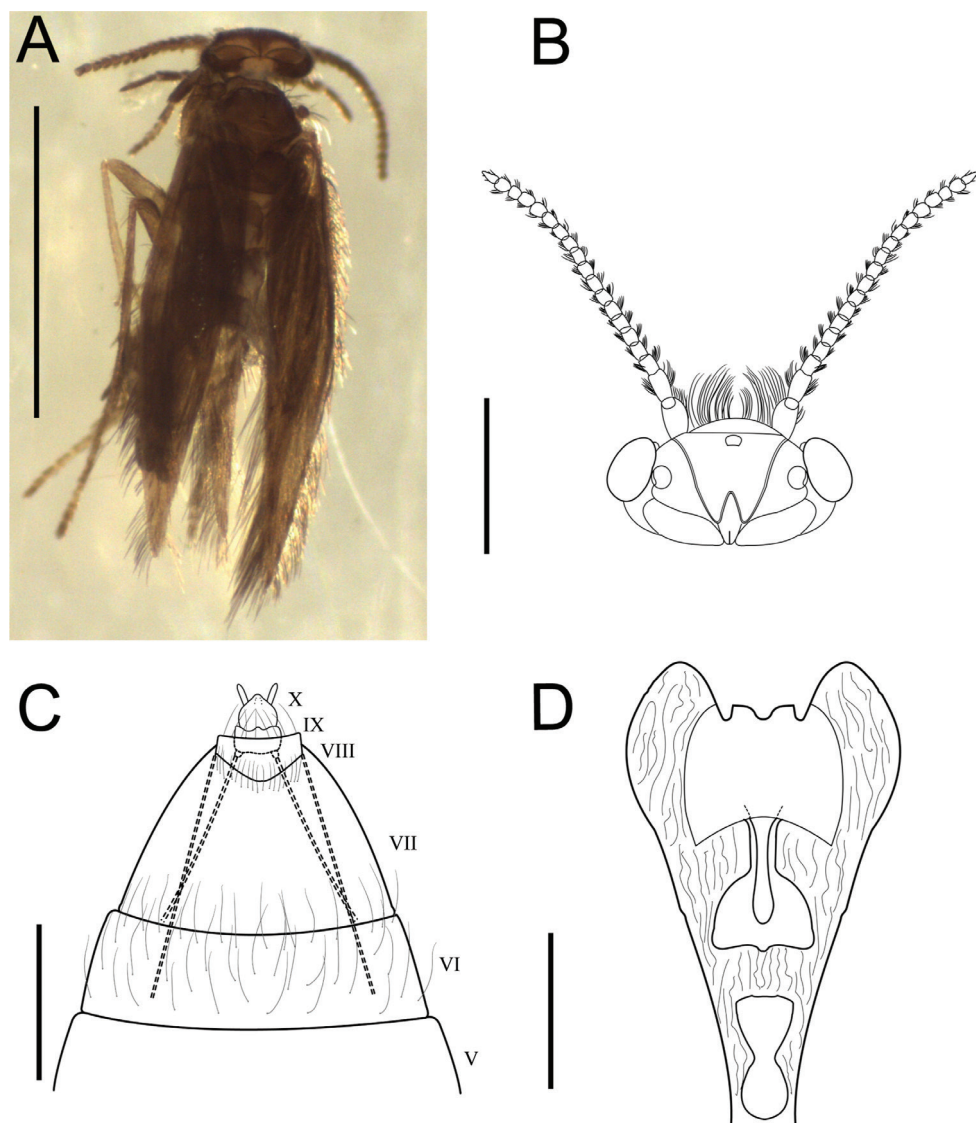


Figure 3. Female specimen of *Mejicanotrichia harrisi* Bueno-Soria & Barba-Álvarez, 1999 **A** habitus, dorsal **B** head, dorsal **C** segments VI-X of abdomen, ventral **D** bursa copulatrix ventral. Scale bars: 1 mm (**A**); 800 µm (**B**); 200 µm (**C**); 30 µm (**D**).

Comments. The specimens exhibit a keyhole-shaped opening in the bursa copulatrix, which occurs in the other species of the genus. On the other hand, females of *M. harrisi* differ from those of other species because of the presence of two short and membranous lobes that extend posteriorly, as well as for having a shield-shaped posterior sclerite (Fig. 3D).

Larva

Mejicanotrichia tridentata (Bueno-Soria & Hamilton, 1986)

Figures 4A–C, 5A–D

Material examined. 15 larvae (IN-TR-00222). MEXICO, Chiapas, Ixhuatán, 95 km 2.8 N Ixhuatán, tributary of the Teapa River (409 m a.s.l., 17°18'41.06"N, 93°0'17.78"W), 18 April 2019; leg. M. Ramírez-Carmona, O. Lagunas-Calvo and G. Rivas-Lechuga.

Diagnosis. Body mostly membranous ventrally. Thorax reddish-brown with dark spots dorsally. Abdominal tergites with dark and irregular spots (Fig. 4A). Conspicuous, dark, subtriangular sclerites on pleural area (Fig. 4B). A subtriangular and curved propleural sclerite is notoriously distinct from that of other species of the genus (Figs 1B, 4B; Bowles et al. 1999: figs 4–7). Abdominal dorsal tergites are long and narrow, with a larger number of setae than in *M. harrisi*. In addition, these tergites have a pigmentation pattern that is evenly distributed.

Description. Body dorsoventrally depressed, range length 2.0–2.3 mm, widely covered with thick, long, and colorless setae (Fig. 4A). Body mostly covered dorsally with fine pigments spots, appearing as “sandpaper” (Fig. 4C). Larval case absent until before pupation.

Head. Ocherous-brown, prognathous, without visible ecdysial sutures.

Thorax. Pro-, meso-, and metanotum divided longitudinally by a medial ecdysial line. Three thoracic nota each with two lateral processes, which have two thick and opaque setae. Pronotum widening posteriorly. Anterior margin of pronotum with a ridge of thick setae, anterolateral corners folding ventrally. Anterior portion of pronotum slightly covering back of the head (Figs 4A, 5A). First pair of legs slightly smaller, tibiae and tarsi of all legs each with two rows of fine setae on dorsal region (Fig. 5B). Two oval sclerites behind the insertion of the legs on each sternite. Anterior margin of meso- and metanotum with row of thick setae, separated at least twice the basal diameter of setae. Lateral margins short and darkened, appearing as longitudinal bars. Mesonotum covered extensively with thick and short setae.

Abdomen. Long and widened, narrowing posteriorly. Ventral region with irregularly distributed, thick, short setae. Segments I–VIII with dorsal tergites, largely covering dorsum of each segment; first sclerite divided longitudinally. Tergites II–VII with lacunae in middle and beyond posterior margin (Fig. 5C); with two fine and dark setae on posterolateral margins, and well-developed thick setae on anterior and posterior margins (Fig. 4C). Anterior margins of tergites II–VI each with a slight notch in the middle; fine pigment spots linearly grouped beyond posterior margin of tergites (Fig. 5D). Abdominal projections without tergites; lateral margins with row of thick and prominent setae, one of which noticeably longer than rest. Segment IX short and shield-shaped, with setae on posterior margin, as well as six setae medially on segment. Anal prolegs projected caudally, cylindrical, with well-developed claws.

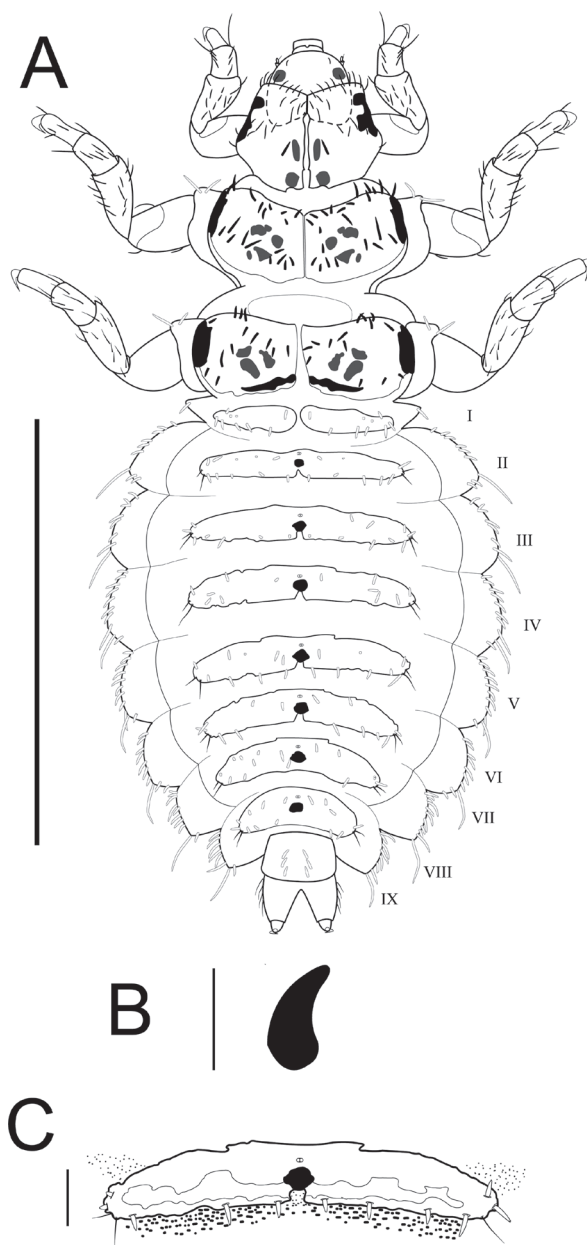


Figure 4. Larva of *Mejicanotrichia tridentata* (Bueno-Soria & Hamilton, 1986) **A** habitus, dorsal **B** propleural sclerite **C** tergite of abdominal segment V, dorsal. Scale bars: 1 mm (**A**); 65 μm (**B**); 80 μm (**C**).

Comments. The specimens were collected at a water temperature of 25 °C; with pH between 7.8–8.4; water presented a hardness of 136.8 mg CaCO_3/l ; the dissolved oxygen was 4.5 mg/l and 57% of oxygen saturation.

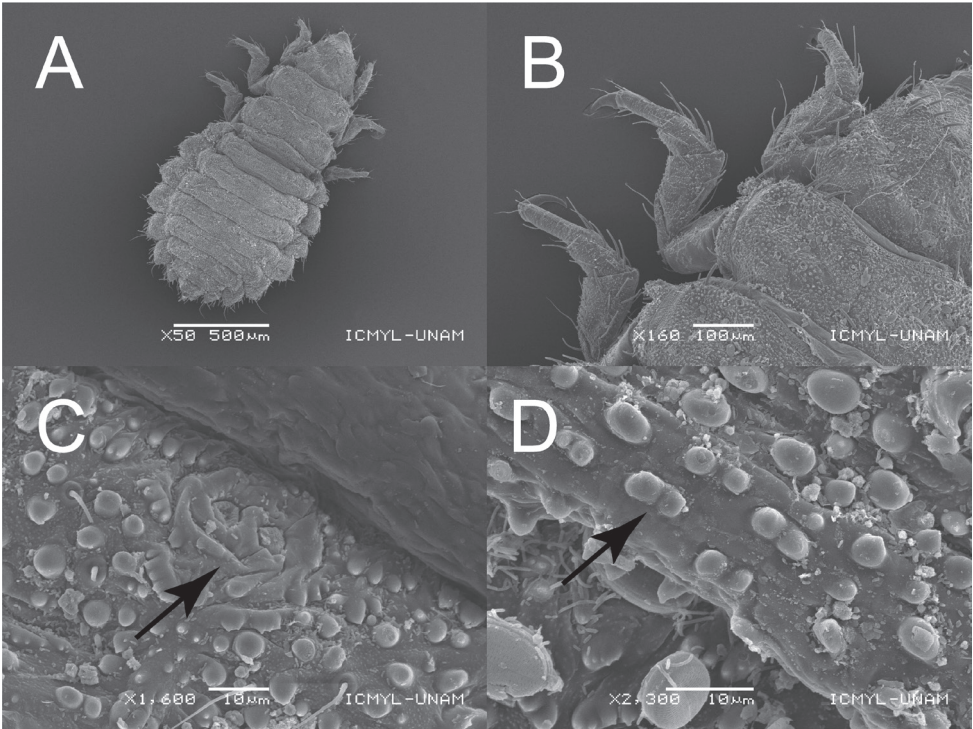


Figure 5. Scanning electron micrographs of larva of *Mejicanotrichia tridentata* (Bueno-Soria & Hamilton, 1986) **A** habitus, dorsal **B** left thoracic legs, dorsal **C** lacunae of abdominal segment V **D** dark ornamental pigments of abdominal tergites. Scale bars: 500 μm (**A**); B: 100 μm (**B**); C: 10 μm (**C**, **D**).

Identification keys

Key to adult males of *Mejicanotrichia* (after Bueno-Soria and Barba-Álvarez 1999)

- 1 Phallus with apical or subapical spines2
- Phallus without apical or subapical spines (Bueno-Soria and Barba-Álvarez 1999: fig. 8) *M. harrisi*
- 2 Phallus with three pairs of spines apically (Harris and Holzenthal 1997: fig. 10D, E) 3
- Phallus with two pairs or less of apical or subapical spines (Harris and Holzenthal 1997: fig. 8D, E) 4
- 3 Phallus apically with three pairs of elongate lateral spines and a central spine (Harris and Holzenthal 1997: fig. 10D, E) *M. estaquilloso*
- Phallus apically with three pairs of short spines and a pair of short lateral spines subapically (Harris and Holzenthal 1997: fig. 3D, E)
.....*M. blantoni*

- 4 Phallus apically with two pairs of elongate spines **5**
 – Phallus apically without spines (Harris and Holzenthal 1997: fig. 6D, E; Bueno-Soria and Barba-Álvarez 1999: fig. 8) **6**
 5 Phallus apically with a pair of elongate, weak spines laterally, pair of thin spines mesally and subapically with a pair of spicule bearing tergites (Harris and Holzenthal 1997: fig. 5D, E) ***M. tamaza***
 – Phallus apically with two pairs of elongate spines, without a subapical pair of spicules bearing tergites (Harris and Holzenthal 1997: fig. 8D, E)
 ***M. tridentata***
 6 Phallus subapically with a pair of lateral spines, with ejaculatory duct emerging between spines (Harris and Holzenthal 1997: fig. 6E) ***M. trifida***
 – Phallus subapically with a pair of thin, elongate spines laterally, without ejaculatory duct emerging between spines (Bueno-Soria and Barba-Álvarez 1999: fig. 4) ***M. rara***

Key to known females of *Mejicanotrichia*

- 1 Bursa copulatrix with two membranous lobes (Fig. 3D) **2**
 – Bursa copulatrix with one membranous lobe (Harris and Holzenthal 1997: fig. 4D) ***M. tamaza***
 2 Bursa copulatrix with keyhole-structure, with keyhole-shaped sclerite mesally (Fig. 3D) **3**
 – Bursa copulatrix without keyhole-structure, with oval sclerite mesally (Harris and Holzenthal 1997: fig. 4F) ***M. estaquilloso***
 3 Bursa copulatrix with shield-shaped sclerite (Fig. 3D) ***M. harrisi***
 – Bursa copulatrix without shield-shaped sclerite (Harris and Holzenthal 1997: fig. 4A) ***M. blantoni***

Key to known larvae of *Mejicanotrichia*

- 1 Fine pigments in posterior margin of abdominal tergites without pattern in pairs (Fig. 2C) **2**
 – Fine pigments in posterior margin of abdominal tergites with pattern in pairs (Figs 4C, 5D) ***M. tridentata***
 2 Propleural sclerite with rounded shape, claw-shaped or triangle-shaped (Bowles et al. 1999: figs 6, 7) **3**
 – Propleural sclerite not round-shaped, instead serrate tooth shaped (Fig. 1B)
 ***M. harrisi***
 3 Tergites without a blotched pattern over the body, propleural sclerite triangle-shaped (Bowles et al. 1999: fig. 6) ***M. blantoni***
 – Tergites with a blotched pattern over the body, propleural sclerite claw-shaped (Bowles et al. 1999: fig. 7) ***M. estaquilloso***

Discussion

The genus *Mejicanotrichia* is a Mesoamerican taxon with species distributed in a restricted fashion, both regarding a specific microhabitat, as well as a narrow geographical area. Knowledge of these species is practically limited to morphology of the adult males. The present work increases the knowledge of the larvae and we also contribute the description of the female of one species: *Mejicanotrichia harrisi* was originally described from the Temazcalapa River, in the state of Guerrero, with specimens collected between 1994 and 1995. We attempted to recover specimens from the original locality, but the stream was found to be completely dry. It was at a tributary of the Tonalapa River, 10 km away from the type locality, that adult (females and males) and larval specimens of *M. harrisi* were collected (Fig. 6A, B). In the case of *M. tridentata*, it was originally described within the genus *Alisotrichia* and collected in 1983 in Chiapas state; in the present study, we were able to recover immature stages at the type locality (Fig. 6C, D), thus allowing us to complete the taxonomic information of the species.

The larvae of *M. harrisi*, *M. tridentata*, and those described in previous studies differ from each other in the shape of the propleural sclerite (Figs 1B, 4B; Bowles et al. 1999), and by having different abdominal dorsal tergites, with *M. tridentata* having these longer and narrower than *M. harrisi*, as well as exhibiting a larger number of setae distributed on the tergites (Fig. 4A). Similarly, the fine pigment spots associated with the dorsal abdominal tergites present a group arrangement in the form of “horizontal bars” (Figs 4C, 5D). Although Bowles et al. (1999) do not mention abdominal dorsal tergites as distinctive characters between species (*M. blantoni* and *M. estaquillosa*), in the present work the dorsal sclerites on the abdomen were considered as distinctive characters between *Mejicanotrichia* species.

Species delimitation in Trichoptera is based entirely on primary characters presented by male genitalia, as these are conspicuous and complex (Holzenthal et al. 2007), whereas the female genitalia are much simpler, thus offering a smaller number of characters (Nielsen 1980; Holzenthal et al. 2007). However, the females of *M. harrisi* treated in the present study differ from those of the other species because they exhibit two short membranous lobes, which extend into the posterior region, as well as a posterior sclerite in form of a “shield” (Fig. 1D).

Some of the ecological affinities of the genus have resulted in morphological adaptations to the habitat, as referred to by Marshall (1979) and Bowles et al. (1999); some of the modifications resulted in a dorsoventrally flattened body, well-developed abdominal tergites and sturdy climbing legs. Larvae of *Mejicanotrichia* were found on the surface of large rocks, in high flowing environments and associated with river waterfalls (Bowles et al. 1999; Bueno-Soria 2010); and also in a madicolous habitat, referred to by Bowles et al. (1999) as the developmental environment for some hydroptilid larvae (Fig. 6B, D). In this habitat, coexistence with other genera associated with *Mejicanotrichia*, such as *Scelobotrichia*, *Leucotrichia*, and *Alisotrichia* (Santos et al. 2016), occurs.

Much of the flora of madicolous habitats is restricted to microalgae, which are mostly diatoms or patches of filamentous algae (Vaillant 1956; Sinclair and Marshall

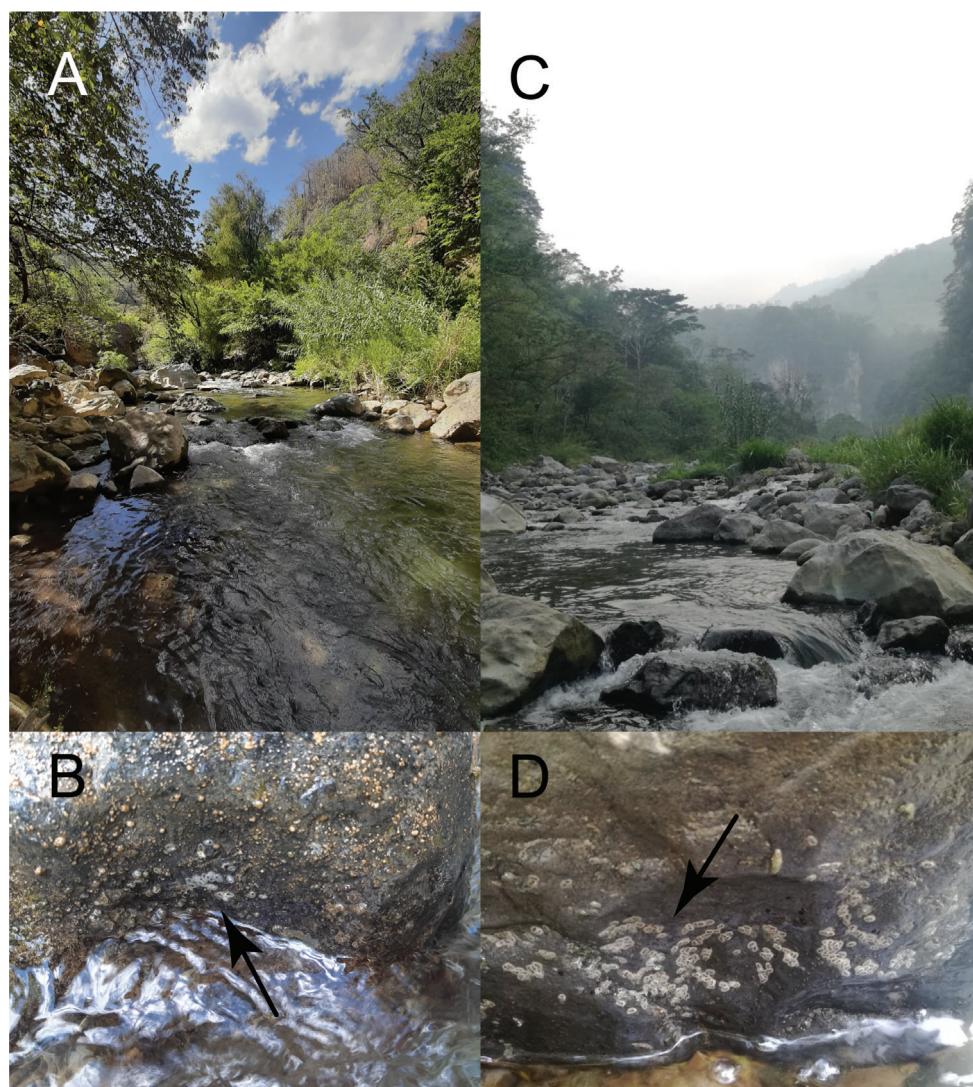


Figure 6. Collecting sites and cases of *Mejicanotrichia* in madicolous microenvironments **A** Tonalapa river, Guerrero **B** *M. harrisi*, pupal cases attached to rock, indicated by arrow **C** tributary of the Teapa river, Chiapas **D** *M. tridentata*, pupal cases attached to rock, indicated by arrow.

1986), so the larvae of *Mejicanotrichia* may belong to the “scraper” feeding group. On the other hand, the larvae of the genus do not present a case in the early stages, and it is not until the pupation stage that one is made. This case consists entirely of silk and resembles a seed attached to the surface of the rock (Wiggins 1996; Bowles et al. 1999; Bueno-Soria 2010). Otherwise, there are no studies (ecophysiological and ecological) that demonstrate the role played by hardness ($\text{mg CaCO}_3/\text{l}$) on trichopteran biology. Nevertheless, the data obtained in the field represent a clear example of the

overlap of distribution of *Mejicanotrichia harrisi* and *M. tridentata* with karst substrate in the country (Espinasa-Pereña 2007). In the two localities of study (Ixhuatán and Atlmolonga), the hardness estimates correspond to hard water (USGS scale), and in two of them hardness data were obtained at two different times, which reflected similar values, being slightly higher in the dry season. Therefore, this presupposes a possible relationship between water hardness and the presence of *Mejicanotrichia*.

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A new species of *Silvatares* (Trichoptera, Pisuliidae) from the Democratic Republic of the Congo

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Abstract

A new species of caddisfly in the family Pisuliidae from the Democratic Republic of the Congo is described and illustrated herein, *Silvatares holzenthali* **sp. nov.** Based on the presence of a pair of spines on the endotheca, this species belongs to the *thrymmifer* group. Additionally, *Silvatares laetae* is recorded for the first time from the D.R. Congo.

Keywords

Africa, new species, taxonomy, Trichoptera

Introduction

The caddisfly genus *Silvatares* Navás, 1931, along with *Pisulia* Marlier, 1943, belong to the African endemic family Pisuliidae. The species currently placed in *Silvatares* were originally included in the genus *Dyschimus* Barnard, 1934. Stoltze (1989) subsequently reviewed the family and included nine species in *Dyschimus*. Later, Prather and Holzenthal (2002) synonymized *Silvatares* and *Dyschimus*, thereby transferring all the species in the latter genus to *Silvatares* on the grounds that this name had precedence.

More recently, Ngrinshuti et al. (2019) described an additional species from Rwanda, raising the number of hitherto known species to eleven.

Species of *Silvatares* generally inhabit forested streams in sub-Saharan Africa (Table 1). The genus *Silvatares* is characterized in the adult stage by their larger size (vs. *Pisulia*), the shape of their maxillary palps, and a tibial spur formula of 2-4-4. The larvae are also large, have two or three accessory hooks on the anal claws, and the dorsal hump is absent on the first abdominal segment. A peculiarity of all Pisuliidae larvae are the cases. These are constructed from plant materials and are triangular in cross-section (Stoltze 1989; SUP, FNM, pers. obs.).

Stoltze (1989) informally subdivided the genus into three species groups: the *madagascariensis* group, characterized by the large internal lobes on the male tergum IX (including *S. madagascariensis*); the *ensifer* group, characterized by the presence of large lateral processes from the phallobase (including *S. collyrifer*, *S. ensifer*, *S. longinquus*, and *S. ornithocephalus*); and the *thrymmifer* group, characterized by the presence of a pair of apical spines on the endotheca (including *S. chitae*, *S. crassus*, *S. excelsus*, *S. furcifer*, *S. laetae*, and *S. thrymmifer*).

While identifying caddisfly material from our current survey of the fauna of the Democratic Republic of the Congo, we discovered a new country record and a new species of *Silvatares*. Herein we describe and illustrate this new species, based on a single male specimen.

Materials and methods

Study area

The Kahuzi-Biega National Park (KBNP: 1°36'S to 2°37'S, 27°33'E to 28°46'E) is a UNESCO World Heritage Site. It is located 20 km west of Bukavu, South Kivu Province, in the Democratic Republic of the Congo. The park was created in 1970 with 600 km² and was later extended to 6,000 km² in 1975 (Ngera et al. 2019). The park includes lowland and highland areas connected by a 7.4 km wide by 20 km long corridor. The KBNP is considered a biodiversity hotspot with a high rate of endemic species. Most studies carried out in the park have focused on mammals, birds, plants, and reptiles. Insects have rarely been studied in the area (Ngera et al. 2019).

The eastern part of the KBNP consists of high-elevation zones, ranging from 1800 m to 3308 m a.s.l. Bamboo forests, primary and secondary mountain forests, and swamp forests are the most common vegetation types in this area. Aquatic ecosystems include rivers, streams, and wetlands. The rivers and streams of the western flank of these mountains drain into the Lohoho and Luha rivers, both supplying water to one of the most important tributaries of the Congo River, the Lowa River (Ngera et al. 2019). Rivers and streams draining the eastern flanks flow into Lake Kivu, which is connected to Lake Tanganyika by the Ruzizi River. The soil is mostly of volcanic origin. Mean temperatures vary between 10.0 °C and 18.8 °C.

Table 1. Species of *Silvatares*, with their known distributions and life stages.

Species	Distribution	Known life stages
<i>Silvatares chitae</i> (Stoltze, 1989)	Tanzania	male, female
<i>Silvatares collyriifer</i> (Barnard, 1934)	South Africa	male, larva, pupa
<i>Silvatares crassus</i> (Stoltze, 1989)	Tanzania	male, female
<i>Silvatares ensifer</i> (Barnard, 1934)	South Africa	male, female
<i>Silvatares excelsus</i> Navás, 1931	Uganda, DRC	male
<i>Silvatares furcifer</i> (Marlier, 1953)	DRC	female, larva, pupa
<i>Silvatares holzenthali</i> sp. nov.	DRC	male
<i>Silvatares laetae</i> Ngirinshuti & Johanson, 2019	Rwanda, DRC*	male
<i>Silvatares longinquus</i> (Gibbs, 1973)	Ghana	male, female, larva**
<i>Silvatares madagascariensis</i> (Stoltze, 1989)	Madagascar	male
<i>Silvatares ornithocephalus</i> (Stoltze, 1989)	South Africa	male
<i>Silvatares thrymmifer</i> (Barnard, 1934)	South Africa	male, female, larva, pupa

* new country record.

** Gibbs did not formally describe the larva of *S. longinquus* but compared its appearance to *S. furcifer*.

Sampling site

The Lwiro River is located in the northeastern part of the KBNP. It originates in the Cigali swamp on the Kahuzi mountain, flows across a vast high-altitude forest (Tshibati) up to the border of the park. From there it flows through cultivated areas past several villages before draining into Lake Kivu. Within the park, it receives few first-order tributaries. Downstream of the park, several second-order streams flow into the Lwiro. The sampling site (Kakezi) is at 2,120 m a.s.l., ~ 2 km upstream of the Tshibati waterfall, and is dominated by natural forests. The water current averages 56.0 cm/s across lotic and lentic zones. The river is ~ 9.5 m wide with an average depth of ~ 40cm at the time of collection. Rocky substrates (boulders, stones, cobbles) dominate the riverbed, but organic substrates, especially logs and leaf packs also provide important habitat. Physical and chemical parameters showed slightly basic pH throughout the day (7.73 at 06:00 am to 7.8 at noon). Water temperature also increased during the day, measuring from 13.2 °C at 06:00 am to 15.0 °C at noon. Conductivity ranged from 60 to 62 µS/cm, total dissolved solids from 30 to 31 ppm, and dissolved oxygen was relatively low (5.1 mg/L, ~ 50% saturation).

The specimen of *Silvatares laetae* was collected from the vegetation at the Chashoga swamp (Tshibati sector, Kahuzi-Biega National Park) using a hand net. The elevation for this site is slightly lower than the other site (2,030 m a.s.l.).

Morphological methods

The specimen of *S. holzenthali* sp. nov. was collected using a UV light trap and fixed in 96% ethyl alcohol. Specimen preparation and observation was done following standard methods outlined in Blahník and Holzenthál (2004). The male

genitalia were prepared using 80% lactic acid at 90 °C for 1 h. The specimen was examined on an Olympus SZX10 stereoscope, and pencil sketches were made using a drawing tube attached to a Leitz Dialux 20 compound microscope. The pencil sketches were then scanned using a Konica Minolta bizhub C368 multifunction printer and imported into Adobe Illustrator CS6 to serve as a template for the digital illustration.

The distribution map (Fig. 1) was prepared in QGIS 3.22.4 Białowieża (QGIS Development Team, 2022). Vector and raster maps were prepared with Natural Earth (2018) and CIAT-CSI SRTM (Jarvis et al. 2008) data.

All specimens treated in this paper are stored in 96% ethyl alcohol and are deposited in the Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany (SMF).

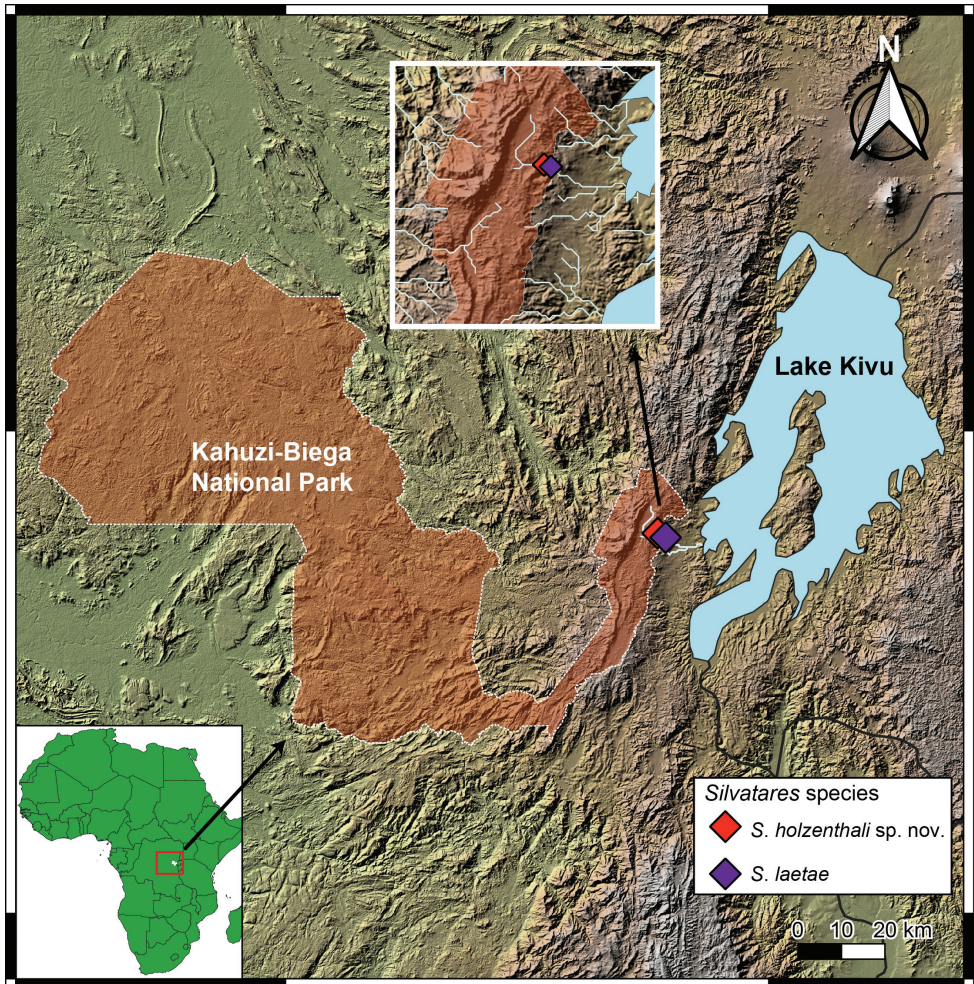


Figure 1. Distribution map of the *Silvatares* species treated in this paper.

Molecular methods

We removed a pair of legs of the new species and incubated the tissues in 60 µl TNES lysis buffer (100 mM Tris-HCl, 25 mM NaCl, 10 mM EDTA, 1% SDS) and 8 µl Proteinase K (20 mg/ml) overnight. For DNA binding and clean-up, we added 75 µl custom speed-bead suspension (Sera-Mag SpeedBeads Carboxylate, hydrophobic, Cytiva; see Rohland and Reich 2012, *Genome Res* 22: 939–946), incubated for 15 min on a nutating shaker, and washed the beads twice with 75% ethanol after the supernatant had been removed and discarded. The DNA was eluted from the air-dried beads with 1X TE.

DNA sequences were generated for the cytochrome-c-oxidase subunit I barcoding region (COI, 658 bp) using primers LCO1490-L and HCO2198-L (Nelson et al. 2007). Polymerase chain reactions (PCR) were run on a Mastercycler Pro S (Eppendorf, Hamburg, Germany) in reactions containing 1X MyTaq Reaction Buffer, 0.4 µM of each forward and reverse primer, 0.5 U MyTaq DNA Polymerase, 1 µl DNA and nuclease-free water to fill up to a 10 µl total volume. Reaction conditions were 1 min at 95 °C for initial denaturation followed by 35 cycles of 20 s at 95 °C (denaturation), 30 s at 45 °C (annealing) and 30 s at 72 °C (extension). The reaction ended with a final extension for 5 min at 72 °C. PCR products were visualized on agarose gels and purified using a modified ExoSAP protocol with Exonuclease I (20U/µl) and Fast AP Thermo Sensitive Alkaline Phosphatase (1U/µl; both ThermoFisher Scientific, Vilnius, Lithuania). DNA sequences were generated at the Laboratory Centre of the Senckenberg Biodiversity and Climate Research Centre using a 3730XL DNA Analyzer (Applied Biosystems).

The sequences were edited and aligned in Geneious Prime 2022.1 (Biomatters, New Zealand) and uploaded to BOLD Systems under accession number SPAFT001-22.

Results

Silvatares holzenthali sp. nov.

<http://zoobank.org/A8927970-7F34-49E0-B091-D11EC5BA79B4>

Figs 1–3

Holotype. DEMOCRATIC REPUBLIC OF THE CONGO • ♂; Sud-Kivu, Kahuzi-Biega National Park, Tshibati-Kakezi (up waterfalls); 2.21691°S, 28.77328°E, 2,120 m a.s.l.; 23 Aug. 2017; Mwangi leg (SMF) [SMFTRI00018633].0

Diagnosis. *Silvatares holzenthali* sp. nov. is a member of the *thrymmifer* group of Stoltze (1989) due to the presence of a pair of apical spines on the endotheca. The new species is closest to *S. excelsus* and *S. laetae* based on the presence of inferior appendages with a long, secondary basodorsal lobe. The apex of this lobe in *S. holzenthali* is slightly subtriangular in lateral view, while in *S. laetae* and *S. excelsus* it is slightly capitate. Additionally, tergum X in *S. holzenthali* is broad basally and tapers to a digitate apex while in *S. laetae* and *S. excelsus*, tergum X is broad throughout its length.

Description. Adult male. Overall color pale brown (in alcohol). Antennae pale brown with short, whitish setae; antennal segments cylindrical with secondary constriction subapically on each segment; antennae broken. Head and thorax with brown (especially dorsally) and pale brown setae, infraocular wart narrow and long with dark brown setae. Palpi pale brown with brown (especially on apical segment) and pale brown setae. Legs pale brown with short and long dark brown setae. Forewing length ~ 11.7 mm ($n = 1$; forewing apex damaged). Forewing membrane pale brown, except for a whitish mark on apicodorsal corner of thyridial cell, with short brown setae. Forewing (Fig. 2A) with forks I, II, and III present; discoidal cell closed; thyridium present; A_2 complete, reaching wing margin; A_3 incomplete and ending before reaching wing margin. Hindwing (Fig. 2B) with forks II and III present; discoidal cell closed; base of Cu_2 fused to base of A_1 . Segment V with elongate sternal glands, slightly broader apically, globose; segment VII with short ventromesal process.

Male genitalia. Segment IX (Fig. 3A) in lateral view widest midlaterally, anterior margin produced into broadly rounded lobe, posterior margin very slightly sinuous, dorsal margin longer than ventral margin, setae on ventral and posterodorsal surfaces. Segment IX (Fig. 3B) in dorsal view with posterior margin produced sublaterally and

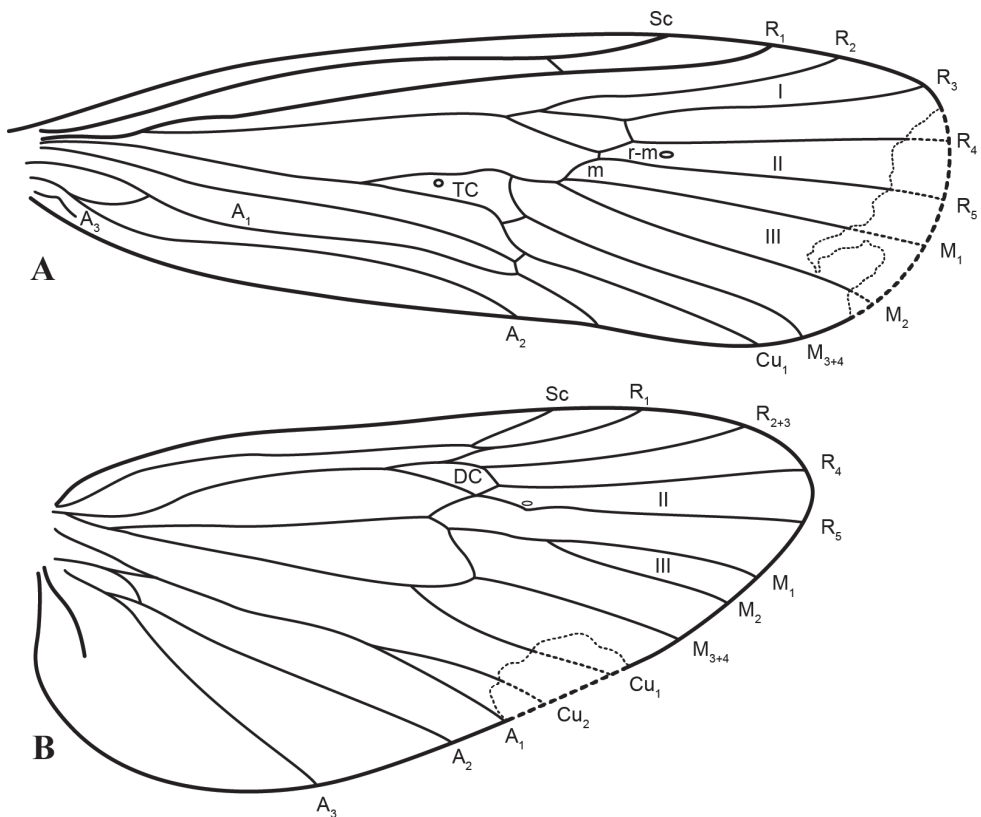


Figure 2. *Silvatares holzenthali*, new species, wing venation **A** forewing **B** hind wing.

concave mesally, anterior margin broadly concave; in ventral view (Fig. 3C), anterior and posterior margins broadly concave. Tergum X (Fig. 3A) in lateral view broad basally, tapering into digitate process, apex rounded, concave ventrally, down-turned; in dorsal view (Fig. 3B) divided by deep mesal cleft into two setose tergites, setae on lateral and apical margins; mesal margins angulate basally and subapically, lateral margins angulate mesally. Inferior appendages (Fig. 3A) with a dorsal lobe arising basally from dorsal surface. Basal segment long, ventral margin slightly concave basally, rounded apically. Dorsal segment longer than ventral segment, somewhat capitate apically. Phallic apparatus (Fig. 3D) short and stout, endothecal membrane expanded, with a pair of slender, sharply bent, acute endothecal spines apicodorsally, and a slender, Y-shaped sclerite apicoventrally (Fig. 3E; apex of phallic sclerite in dorsal view).

Female. Unknown.

Larva. Unknown.

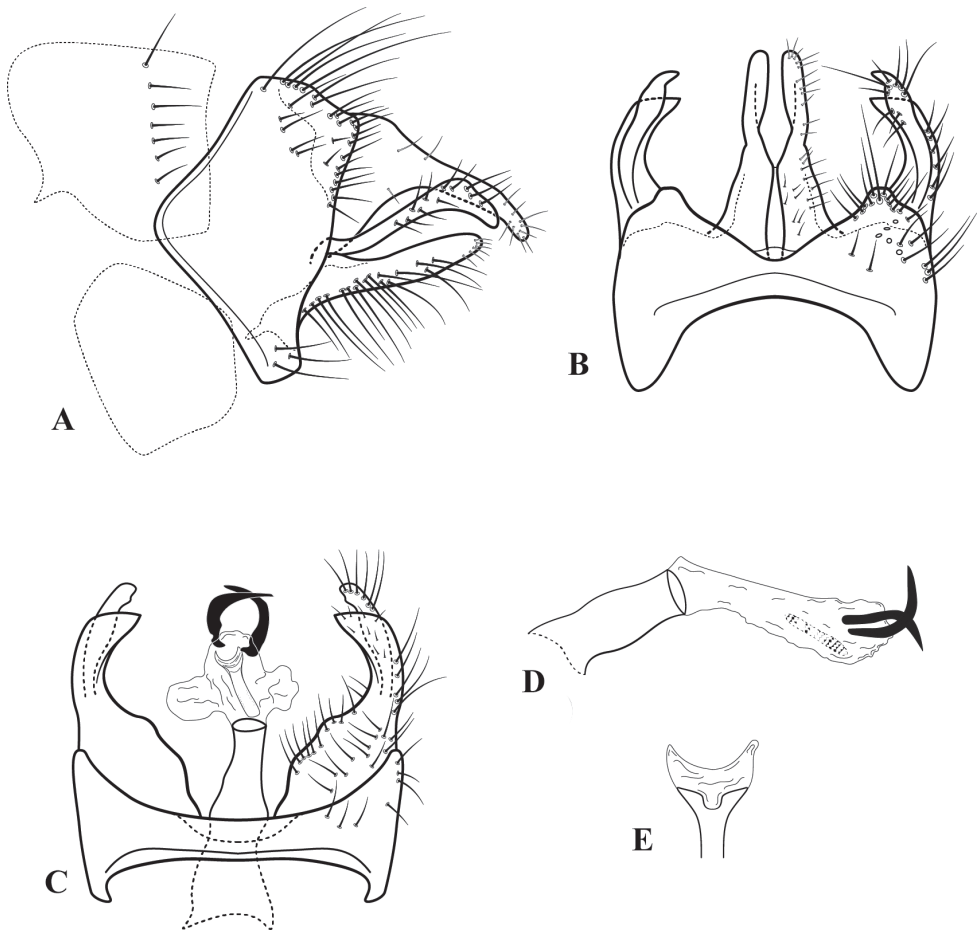


Figure 3. *Silvatares holzenthali*, new species, ♂ genitalia **A** lateral **B** dorsal **C** ventral **D** phallic apparatus, lateral **E** apex of phallic sclerite, dorsal.

Etymology. It is with great pleasure that we name this species after Dr. Ralph W. Holzenthal for his life-long contributions to Trichoptera taxonomy and systematics, especially in the Neotropics. Ralph has not only been an inspiration for Trichoptera researchers across the world but has been a very important mentor for the authors, and most importantly, a very dear friend, encouraging us throughout our careers. We thank Ralph for great craft beer tastings, memorable garden barbecues, fascinating field trips, and woodworking workshops.

Distribution. Democratic Republic of the Congo (Sud-Kivu Province) (Fig. 1).

Comments. The generated sequence was 658 bp in length and only had 0.2% of ambiguous sites. Using BOLD's tree-based identification tool, the sequence was sister to all available Pisuliidae sequences on the platform. Additionally, the sequence was most similar to an unidentified male adult from the Eastern Cape Province of South Africa, with an 89.14% similarity. However, the South African sequence was only 621 bp long.

Silvatares laetae Ngirinshuti & Johanson, 2019

Silvatares laetae Ngirinshuti & Johanson, 2019 [type locality: Rwanda: Wester Province: Nyamasheke District, Nyungwe National Park, Gisakura, Karamba River; NRS; ♂].

Material examined. DEMOCRATIC REPUBLIC OF THE CONGO • ♂; Sud-Kivu, Kahuzi-Biega National Park, Tshibati sector, Chashoga swamp; 2.21706°S, 28.7785°E, 2,030 m a.s.l.; 10 Jul. 2005; S. U. Pauls; collected from vegetation using a hand net (SMF). New country record.

Comments. This species has recently been described from the Nyungwe National Park in southwestern Rwanda, and it is one of the few species with broad distributions; however, this is a new distributional record. The male genitalia are identical to the illustrations provided in the original description.

Discussion

The Pisuliidae are a group of caddisflies with very interesting biogeography. Almost all species known to date are endemics from a single or very few sites in mountain ranges in Sub-Saharan Africa (Stoltze 1989). There are exceptions, however. For example, *S. crassus* is widespread in the mountains of South-Eastern Africa (Stoltze 1989), and *S. laetae* occurs in Rwanda and the eastern Democratic Republic of the Congo. In addition to this biogeographic pattern, their diversity is likely underestimated. For example, Gibon et al. (2001) estimated more than 20 still undescribed species in Madagascar.

Although *Silvatares* larvae often occur in large numbers, most species are known from very few adults (Stoltze 1989). For example, our new species is only known from a single specimen, as is the new country record of *S. laetae*. This might indicate that species of *Silvatares* are not crepuscular but active during the day, and using a

combination of collecting methods such as larval collections with subsequent adult/larval associations (e.g., Graf et al. 2005), Malaise traps and UV pan traps would be more appropriate to estimate their diversity and abundance better. *Silvatares laetae* from Chashoga swamp was, for example, also collected by day sweeping.

The new species *Silvatares holzenthali*, along with *S. excelsus*, *S. furcifer*, and *S. laetae*, is the fourth species of *Silvatares* recorded from the Democratic Republic of the Congo. Both species treated in this paper were collected in the Tshibati sector in the Kahuzi-Biega National Park. These species belong to the *thrymmifer* group, which is characterized by a pair of apical spines on the endotheca. While knowledge on their distributions is limited, it is interesting to note that the *thrymmifer* group is known from East and South Africa, while the *ensifer* group is known from West and South Africa. *Silvatares furcifer* is only known from females collected near the type locality of *S. excelsus*, and Prather and Holzenthal (2002) hypothesized that it is conspecific with *S. excelsus*, potentially reducing the number of known species from the D. R. of the Congo to three. However, the presence of additional potential sites for their occurrence (especially in central and south DRC), the distributional pattern of most species in the genus, and their daily activity patterns, additional undescribed *Silvatares* species might occur in the country.

Kahuzi-Biega National Park is listed as a threatened world heritage site, particularly for its high levels of biodiversity associated with the vast mountain and lowland rainforests. This status is based on the better known mammal, bird, and plant diversity. In contrast very little is known about the status of the insect fauna (e.g., Ngera et al. 2019). Considering that we know of only three (or four) species of the rare genus *Silvatares* in a very small section of the National Park suggests that more extensive surveys will likely reveal great caddisfly species diversity in these old rainforest habitats.

Acknowledgements

This study is an outcome of and was funded by the Deutsche Forschungsgemeinschaft (Project “Innovative integration of high-throughput DNA barcoding, transcriptome-based constrained phylogenetics, hyperspectral imaging, and morphology to assess and characterize a poorly known fauna”, PA1617/4-1). We also thank Bisimwa Bishweka and Burhalike Nyakaminika (Centre de Recherche en Sciences Naturelles, Lwiro, DRC) for their assistance in the field.

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Life history and secondary production of *Anomalocosmoecus illiesi* Marlier, 1962 (Trichoptera, Limnephilidae) in a small stream in the northern Ecuadorian Paramo

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Abstract

Life history of benthic faunas of tropical high-altitude cold environments are poorly studied. Here, monthly larval and adult data are presented for *Anomalocosmoecus illiesi* at Saltana Stream in Ecuador. In cold conditions throughout the year (6 °C), this species showed an asynchronous and continuous production. Larval density showed two peaks in August and April. All five larval instars were present in most months. Using the size-frequency method an annual rate of secondary production per biomass of 4.8 was calculated. The measured biomass was 785 mg/m².

Keywords

Andean Caddisflies, Limnephilidae, secondary production

Introduction

Anomalocosmoecus illiesi (Marlier, 1962) is the only species of the caddisfly family Limnephilidae found in Ecuador (Ríos-Touma et al. 2017). This species only inhabits streams and rivers located above 2,900 m a.s.l. (Jacobsen and Brodersen 2008), where water temperatures can be cold throughout the year. For example, Espinosa et al. (2020) found this species in streams with temperatures ranging from 1.5 to 11 °C.

In general, little is known about the life history (e.g., generation times, turnover, and secondary production) of tropical high-altitude insects (Jacobsen 2008). The few studies performed at high altitudes in Ecuador have shown that multiple size classes co-occur often and asynchrony in life cycles (Turcotte and Harper 1982; Jacobsen 2008; Studholme et al. 2017). In fact, *A. illiesi* larvae were studied by Turcotte and Harper (1982) in a small stream in southern Ecuador Paramo, where they found multiple size classes co-occurring throughout the year.

This species can be the dominant Trichoptera in some high-altitude streams in Ecuador. With this note on the life history and secondary production of *A. illiesi*, we aim to contribute to the knowledge of high-altitude tropical aquatic insects that remain understudied in taxonomy, ecology, and physiology.

Materials and methods

Study site

We conducted this study at the Saltana Creek (0°19'1.80"S, 78°13'8.8"W), a first-order stream of Esmeraldas River Basin that flows to the Pacific Ocean in Ecuador. This stream is located at 3,800 m a.s.l. The catchment area is covered by mixed Paramo vegetation and is protected in the Paluguillo Hydrological Protection Area. We visited the stream monthly from July 2009 to June 2010. Discharge was higher from June to August, while base flow conditions were found September–March. Temperature ranged from 5.5 to 10.6 °C, conductivity from 63 to 70 µS/cm, and pH from 6.5 to 7.8. Oxygen was close to saturation during the entire study period. More information about this stream can be found in Holzenthal and Ríos-Touma (2012) and Vimos et al. (2015).

Larval and adult sampling

Anomalocosmoecus illiesi larvae were obtained through 12 randomly taken monthly benthic Hess samples with an area of 0.02 m² and mesh of 250 µm. Also, a 2-minute kick-sample was collected every month covering all the habitats, including shoreline and aquatic vegetation. We fixed each sample with 5% formalin and preserved it in 90% ethanol. Head capsule width (**HCW**) and body length (**BL**) of all specimens were

recorded with an Olympus SZX 16 stereomicroscope calibrated for measuring with an ocular micrometer. The HCW was used since it is an accurate measurement to produce histograms and determine size classes (Komzák and Sedlák 2002; Brand and Miserendino 2012). Twenty random larvae of all size classes determined by the HCW were selected to determine dry mass and the relationship between body length and biomass. We also assessed the correlation between HCW and body length.

Adults were sampled using three amphibious emergence traps (Megaview Science, model BD5740A, Taiwan) ($1.1 \times 1.1 \times 1.1$ m) that were placed immediately above the stream covering the entire stream width from one side to the other and were operated for 24 h each month. Additionally, 12 flight-intercept traps (vertical, across the stream) and eight platform sticky traps (horizontal, placed above water level) were sampled monthly for 24 h. We used Tree Tanglefoot sticky compound on the acetate sheets (210×297 mm) of the traps and citric-based solvent to remove the specimens from the traps (following Encalada and Peckarsky 2007). All collected specimens were preserved in 96% ethanol.

Secondary production

We calculated secondary production following the size frequency method (Hamilton and Hynes 1969; Benke 1979; Benke and Huryn 2007). This non-cohort method assumes that mean size distribution from samples collected throughout a year is similar to a mortality curve for an average cohort (see details in Benke and Huryn 2007). We were able to catch a female and kept her alive in a vial with river water until she expelled the eggs into the water. We then refrigerated the eggs in the river water to 6 °C (similar to stream temperature) with 12 h of light. It took 12 weeks for the eggs to hatch. Unfortunately, we were not able to keep the larvae alive under laboratory conditions, but with this data we assumed a cohort production interval of six months, considering the constant cold temperatures of the stream. Our assumption of six months comes from our hatching data (three months for the egg to hatch in lab conditions), and from other studies in Limnephilids under similar temperatures (Gislason and Sigfusson 1987), where larval development and pupation took approximately 3–4 months, and where adults only lived a few days.

Results

Month larval density

Density ranged from 4.2 ind/m² in February to 37.5 ind/m² in April. Larvae were present in all months (Fig. 1).

Using the HCW, we were able to separate the five larval instars (Fig. 2). All instars were found in most months, showing an asynchronous and continuous pattern

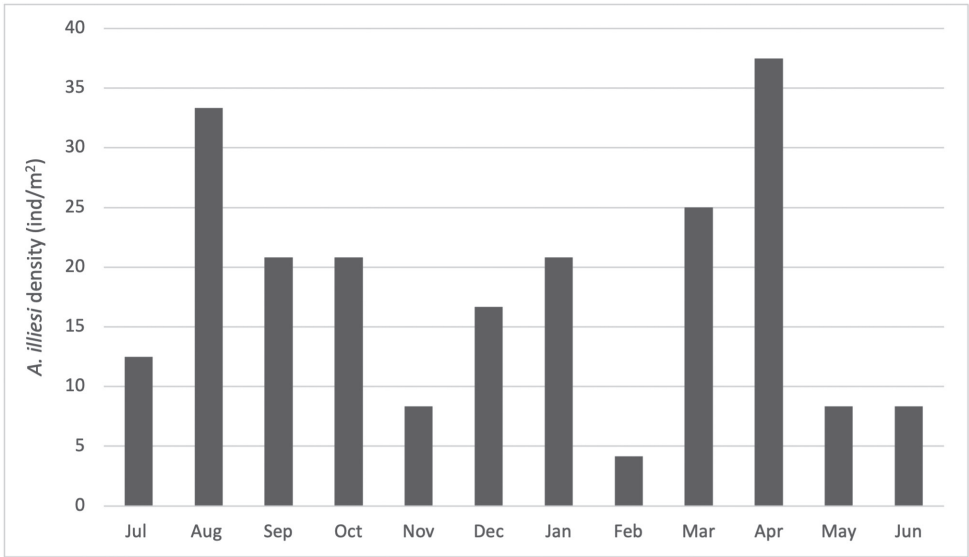


Figure 1. *Anomalocosmoecus illiesi* total monthly larval density (ind/m²) at Saltana stream, Ecuador from July 2009 to June 2010.

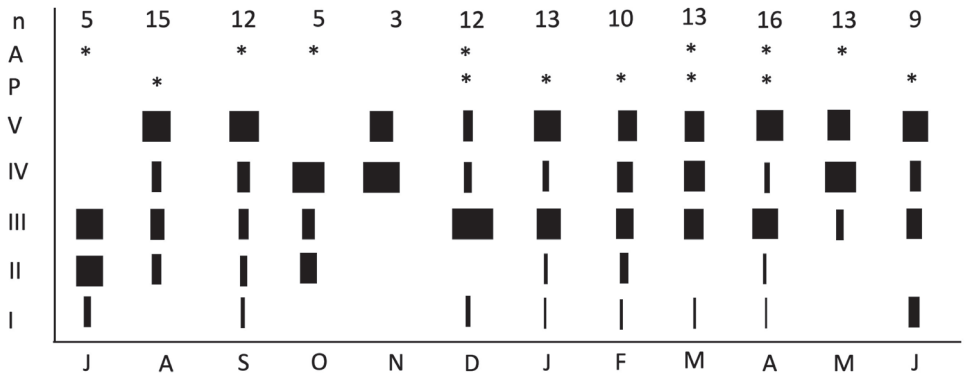


Figure 2. Size frequency of *Anomalocosmoecus illiesi* larval instars from July 2009 to June 2010 at Saltana Stream, Ecuador. The presence of pupae (P) and adults (A) are marked with asterisks, and the number of larvae taken into consideration (n) is marked for each month.

throughout the year. Pupae were found in August (3), December (1), January (1), February (1), March (2), and June (1).

Adults

Adults were found on our sticky traps in July (1), September (2), October (2), and December (1) of 2009 and from March to May in 2010 (3, one each month). Only four individuals were found in our emergence traps, three in September 2009 and one in May 2010.

Secondary production

Head capsule width (HCW) and body length (L) were highly correlated ($R^2 = 0.95$). With the weighed larvae and body length we calculated the biomass of the five instars in our monthly samples with the following equation: $W = 0.0072L^{2.5615}$.

Our data showed an annual biomass of 785 mg/m² (Table 1), with an annual production per biomass rate (P/B) of 4.8, considering all the instars and larvae found throughout the year and a Cohort P/B of 2.4, assuming two cohorts a year.

Table 1. Annual production of *Anomalocosmoecus illiesi* using the size frequency method, for monthly larval samples from Saltana stream, Ecuador. No. lost = individuals lost between instars; \hat{W} = mean individual mass between two instars; biomass lost = biomass lost between instars. Production (P) is the result of summing the biomass lost between each instar per the number of instars (stages, or size classes), calculated according to Benke and Huryn (2007). P/B is the production per biomass rate. CPI is the cohort production interval, which for *A. illiesi* we assumed was 6 months.

Instar	Density	Individual mass	(No./m ²)	Biomass	Mass at loss (mg)	Biomass lost	Times no. of size
	no./m ²	W (mg)	ΔN	(mg/m ²)	$\hat{W} = (W1 + W2)/2$	(mg/m ²)	classes (instars)
1	12.50	0.08	-70.83	1.00		-10.75	$\hat{W}\Delta N \times 5$
					0.15		-53.73
2	83.33	0.22	-104.17	18.61		-52.50	-262.48
					0.50		
3	187.50	0.78	20.83	147.12		27.32	136.61
					1.31		
4	166.67	1.84	41.67	306.46		90.32	451.58
					2.17		
5	125.00	2.50	125.00	312.01		312.01	1560.03
					2.50		
			Σ Biomass:	785.19		Production	1885.73
						(uncorrected)	
			P/B Cohort	2.40		Annual P	3771.47
			Annual P/B	4.80		CPI = 2	

Discussion

Continuous production and asynchronous life cycles have been previously reported for tropical taxa (Turcotte and Harper 1982; Jacobsen 2008; Studholme et al. 2017). However, data on tropical high-altitude cold streams are scarce. We assumed two generations a year based on hatching times from a single egg mass, the constant cold temperature of the stream, and information on other cold water-affiliated Limnephilidae species from Europe. This, however, is based on a single hatching observation and further studies must be done to test this assumption. Unfortunately, despite our efforts to maintain constant cold conditions in laboratory conditions, we were unable to keep additional larvae alive until emergence. Larvae in very cold environments, like in the boreal and subalpine zones in Sweden, showed similar patterns to those of milder climates, with growing periods when the temperatures were between 4 and 13 °C, but

some of them took 1–2 years to reach emergence (Ulfstrand 1968). The limnephilid *Apatania zonella* Zetterstedt, 1840 showed one generation per year in Iceland even though the spring-fed stream temperatures did not fluctuate much during the year (3–8 °C in summer and -1–4 °C in winter; Gislason and Sigfusson 1987). We believe that growth rates could be similarly slow for *A. illiesi*, but with continuous emergence.

The annual P/B found corresponds to the most frequent values worldwide (below 6), provided by Benke (1993), and is similar to other caddisflies from other parts of the world. Annual production and Annual P/B was in the same range found for caddisflies in Patagonia, and Ecuadorian Paramos (Brand and Miserendino 2012; Studholme et al. 2017). Jacobsen (2018) predicted that because of low temperatures and oxygen availability, production in Paramo stream insects will be lower compared to its lowland counterparts. We found values of annual production that are similar to the most productive tropical Trichoptera (Ramirez and Pringle 1998) including *Helicopsyche* in the southern Ecuadorian Paramo streams Studholme et al.(2017). To our knowledge, this is the first report of secondary production of a Limnephilid in South America.

Larval density could be related to flow, with lower densities at July and February, when spates occurred in the stream (Holzenthal and Ríos-Touma 2012; Vimos et al. 2015). Hydrology and temperature (Prat 1981; Wagner and Schmidt 2004; Armitage 2006) can strongly affect community composition and therefore the annual production of caddisflies. For example, Prat (1981) showed that lower temperatures due to hydrological changes in a reservoir in Spain caused a slower growth rate for *Psychomyia pusilla* Fabricius, 1781 and the production of a single generation, compared to two generations in the previous year. Wagner and Schmidt (2004) found that community diversity declined in years with random flows with effects also seen in the emergence of Ephemeroptera, Plecoptera and Trichoptera taxa. Also, work on other Paramo caddisflies has shown that, besides temperature, food availability such as periphyton density results in secondary production differences among streams with similar temperatures (Studholme et al. 2017). In our stream temperature was constant through the year and it was independent from hydrology. Therefore, we conclude that a main factor controlling density of this and other macroinvertebrates will be unpredictable spates that can occur in these as well as in other streams around the world (Wagner and Schmidt 2004; Ríos-Touma et al. 2011; Tonkin et al. 2017).

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Review and redescription of species in the *brasiliانا* group of *Smicridea* (*Rhyacophylax*) (Trichoptera, Hydropsychidae, Smicrideinae): exploration of the utility of geometric morphometrics as a method for delimitation and characterization of species in the genus

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Abstract

The *Smicridea brasiliانا* species group includes five species distributed in northeastern Argentina and Brazil: *Smicridea* (*Rhyacophylax*) *brasiliانا* (Ulmer), *S. (R.) weidneri* Flint, *S. (R.) vermiculata* Flint, *S. (R.) arobasis* Flint, and *S. (R.) nanda* Flint. The original descriptions of these species and their placement in the *brasiliانا* species group were mainly based on the morphology of the male genitalia. However, the fine structure of the internal sclerites of the phallus, which proved to be useful for species delimitation, was not analyzed at the time. In this contribution, we provide a detailed description of the male genitalia and the morphology of the head, and analyze the shape of the wings using geometric morphometrics. The analyzed species can be easily differentiated by the shape of the phallus, especially by the structure of the internal sclerites, the shape of the head in dorsal view, and the shape of the cephalic setose warts. Furthermore, the geometric morphometric approach allowed their separation through the wing shape. The preliminary analysis of these features suggests that the *brasiliانا* species group is not natural but its monophyly should be further tested within the framework of a phylogenetic analysis of all the species of the subgenus *Rhyacophylax*.

Keywords

Forewing shape, male genitalia, Neotropical, *Smicridea* (*Rhyacophylax*) *atrobasis*, *Smicridea* (*Rhyacophylax*) *nanda*, *Smicridea* (*Rhyacophylax*) *vermiculata*, *Smicridea* (*Rhyacophylax*) *weidneri*

Introduction

Smicridea is the only genus of Smicrideinae present in the Neotropical region (Scheft-er 1996; Flint et al. 1999). It is very diverse, represented by 255 described species grouped in two subgenera, *Smicridea* (*Smicridea*) McLachlan with 145 species and *Smicridea* (*Rhyacophylax*) Müller with 110 species (Holzenthall and Calor 2017; Alves et al. 2018; Mey and Ospina-Torres 2018; Sganga and Gibon 2018; Gibon and Sganga 2019; Rázuri-Gonzales and Armitage 2019; Vilarino et al. 2019; Desiderio et al. 2021; Queiroz et al. 2021; Santana et al. 2021). The taxonomy of *Smicridea* adult males has been studied extensively over the years, through the description of single species or the fauna of large geographic areas (e.g., Flint 1974). In the last decade approximately 74 new *Smicridea* species have been described (Albino et al. 2011; Rueda Martín and Sganga 2011; Oláh and Johanson 2012; Alves et al. 2018; Mey and Ospina-Torres 2018; Sganga and Gibon 2018; Gibon and Sganga 2019; Rázuri-Gonzales and Armitage 2019; Vilarino et al. 2019; Desiderio et al. 2021; Queiroz et al. 2021; Santana et al. 2021) but neither subgenus has been reviewed.

The *Smicridea* (*Rhyacophylax*) *brasiliiana* (Ulmer, 1905) species group currently contains five species: *S. brasiliiana*, *S. weidneri* Flint, 1972, *S. vermiculata* Flint, 1978, *S. atrobasis* Flint, 1983, and *S. nanda* Flint, 1983, that are distributed in northeastern Argentina and Brazil (Holzenthall and Calor 2017). This species group was established by Flint (1983) who did not provide a set of defining characters for the group but discussed the features that allowed the differentiation of these species (mainly the coloration, the presence of processes at the tip of the phallus, the shape of the internal sclerites, and the morphology of the tenth tergum and the inferior appendages). The relationships between these species were established by Flint in their original descriptions (Flint 1972, 1978, 1983). The identification of *Smicridea* species has long been based on the male genitalia, especially the structure of the tenth tergum and the phallus, allowing the delimitation of several species groups in both subgenera. These groups were never formally defined (following the principle of monophyly) but created to include species with similar characteristics. Because of this missing framework, several species in both subgenera were never placed in a species group. Oláh and Johanson (2012) summarized some of these groups, listed their defining characters, and the species included in them, in order to provide a framework to include their new species. However, a comprehensive work including a review and phylogenetic analysis of all *Smicridea* species, and a test of the validity of these species groups is lacking.

The morphology of the male genitalia has been extensively used for the delimitation of species in the order Trichoptera as a whole. Other characteristics of the adult morphology, such as the shape of the antennae and palps, the presence of ocelli, spur formula, shape and distribution of setose warts, and wing venation are usually used

to identify families and genera (Holzenthall et al. 2007). In the genus *Smicridea* the structure of the internal sclerites of the phallus has been proven to be useful for the differentiation of species in the subgenus *Rhyacophylax*, mainly in closely related ones (e.g., Rocha et al. 2016; Santana et al. 2021). Despite its importance, this character has not been analyzed in detail in the early descriptions of *Smicridea* species, which is the case for *S. brasiliiana*, *S. nanda*, and *S. weidneri*. A few authors have analyzed non-genital characters for the identification of *Smicridea* species. Oláh and Johanson (2012) and Sganga and Gibon (2018) used the maxillary palp formula to represent the length ratio of the 5 palp articles. More recently, Vilarino et al. (2019) explored the use of new characters to evaluate species delimitation such as the presence and shape of head setose warts and sutures, eye size, and forewing forks. All these features were variable among the species described and represent a source of characters for future phylogenetic analysis.

In recent decades, the number of geometric morphometric studies in insects has increased in the literature. This methodology became a powerful tool to detect minimal shape variations which often are undetectable by traditional morphological studies and emphasizes differences between groups (Villemant et al. 2007). It is usually applied to distinguish species (Baylac et al. 2003; Lorenz et al. 2017; Simões et al. 2020), identify population structure (Kiyoshi and Hikida 2012; Kamimura et al. 2020), sexual dimorphism (Gushki et al. 2018), study morphological evolution during ontogeny (Springolo et al. 2021), and map phylogenetic hypotheses (Huang et al. 2020), among others. Studies based on the taxonomic delimitation of species that are difficult to solve by traditional anatomical methods have been carried out in various insect taxa (Sábio et al. 2014), many of them based on wing geometry (Kiyoshi and Hikida 2012; Shimabukuro et al. 2016; Huang et al. 2020; Simões et al. 2020). The wings of the species of *Smicridea* (*Rhyacophylax*) are very conserved in the arrangement of their veins, which makes them an excellent material to investigate interspecific variations for the delimitation of species.

In the present work, we aimed to redescribe the species in the *Smicridea brasiliiana* group offering a detailed description of the genital segments, especially the phallus, and provide non-genital characters for their identification. Additionally, we tested the use of geometric morphometrics for species delimitation. Integrative taxonomic investigations, which include traditional tools together with modern methodologies, are increasingly being implemented to solve species delimitation problems (González et al. 2019). Geometric morphometrics techniques show high performance in this task (Mutanen and Pretorius 2007). This work represents the first study that incorporates the geometric morphometric approach to the taxonomy of the order Trichoptera, in particular the genus *Smicridea*.

Materials and methods

Specimens of *Smicridea brasiliiana*, *S. nanda* and *S. weidneri* housed in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM)

were examined. Those specimens were identified and loaned by Dr. Oliver Flint Jr. Additionally, we borrowed specimens of *S. atrobasis* and *S. (R.) vekona* from the Facultad de Humanidades y Ciencias, Universidad de la República (Uruguay, **FHCM**) and the Instituto de Biodiversidad Neotropical, CONICET-Universidad Nacional de Tucumán, (Argentina), respectively. Specimens of the other species treated herein were collected in Salto Encantado Provincial Park and Forest Refuge and research center Antonia Ramos (Misiones province, Argentina).

The samples were collected in December 2004 and November 2013 using light and Malaise traps. The specimens obtained were fixed and preserved in 80% EtOH. Voucher specimens were deposited at the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina).

For identification and illustration of the specimens the abdomen was cleared using a hot 10% NaOH solution. Then the cuticle was rinsed in distilled water, neutralized with acetic acid, and mounted in a dish with glycerin for observation. Line drawings of the genital structures were produced using a camera lucida attached to a microscope. Line illustrations of the heads were constructed using photographs as templates, which were obtained with a digital camera fixed to a stereomicroscope. All the images were digitalized with Adobe Illustrator (v. 15.0.0 Adobe Systems Inc.).

For the description of the heads the following distances were measured (Fig. 1):

IOD	interocular distance;
CSL	length of the coronal suture;
MEW	maximum eye width;
MHW	maximum head width.

All the measures were taken using a stereomicroscope with a graduated eyepiece. The terminology used by Albino et al. (2011) was followed for the description of the male genitalia, the one from Wells and Neboiss (2018) for the setose warts, and the one from Oláh and Johanson (2007) for the cranial areas.

For the morphometric analysis, all the species included in the *brasiliana* group were used along with five additional species from the same subgenus, in order to increase the discriminatory power of the methodology.

The left forewings of males ($n = 154$) of *Smicridea (Rhyacophylax) mesembrina* (Navás, 1918) ($n = 21$), *S. weidneri* ($n = 16$), *S. vermiculata* ($n = 22$), *S. (R.) spinulosa* Flint, 1972 ($n = 18$), *S. atrobasis* ($n = 18$), *S. (R.) vekona* Oláh & Johanson, 2012 ($n = 19$), *S. (R.) pampeana* Flint, 1980 ($n = 18$), *S. (R.) unguiculata* Flint, 1983 ($n = 20$), *S. nanda* ($n = 1$), and *S. brasiliana* ($n = 1$) were dissected. Then, the removed wings were extended and mounted on a slide, using alcohol as medium, and covered with a coverslip. The alcohol was left to evaporate before taking photographs with a digital camera fixed to a stereomicroscope (two photographs were taken of each wing). Cartesian coordinates of ten landmarks of each wing (Fig. 2) were digitized using tps-UTILS v. 1.38 (Rohlf 2006a) and tps-DIG v. 2.05 (Rohlf 2006b). The landmark configurations were scaled, translated and rotated using the GLS Procrustes superimposition method (Bookstein 1991) using the MorphoJ software v. 1.06d

(Klingenberg 2011) and subsequently a thin-plate spline analysis was performed allowing the visualization of shape differences as deformation.

Permutation tests for distances by species pairs (20,000 rounds of permutations) for the Mahalanobis (Table 1) and Procrustes distances were performed. Then the percentage of correct reclassification by pairs of species was calculated from the cross-validation procedure.

Canonical variate analysis (CVA) was performed on aligned landmark coordinates and the specimens were reclassified to each species (jackknife method) to evaluate the effectivity of the discriminant analysis for assigning them to their own group using the software Past v. 4.02 (Hammer et al. 2001).

The species *S. nanda* and *S. brasiliiana* were excluded from all the statistical tests mentioned above due to an insufficient number of specimens.

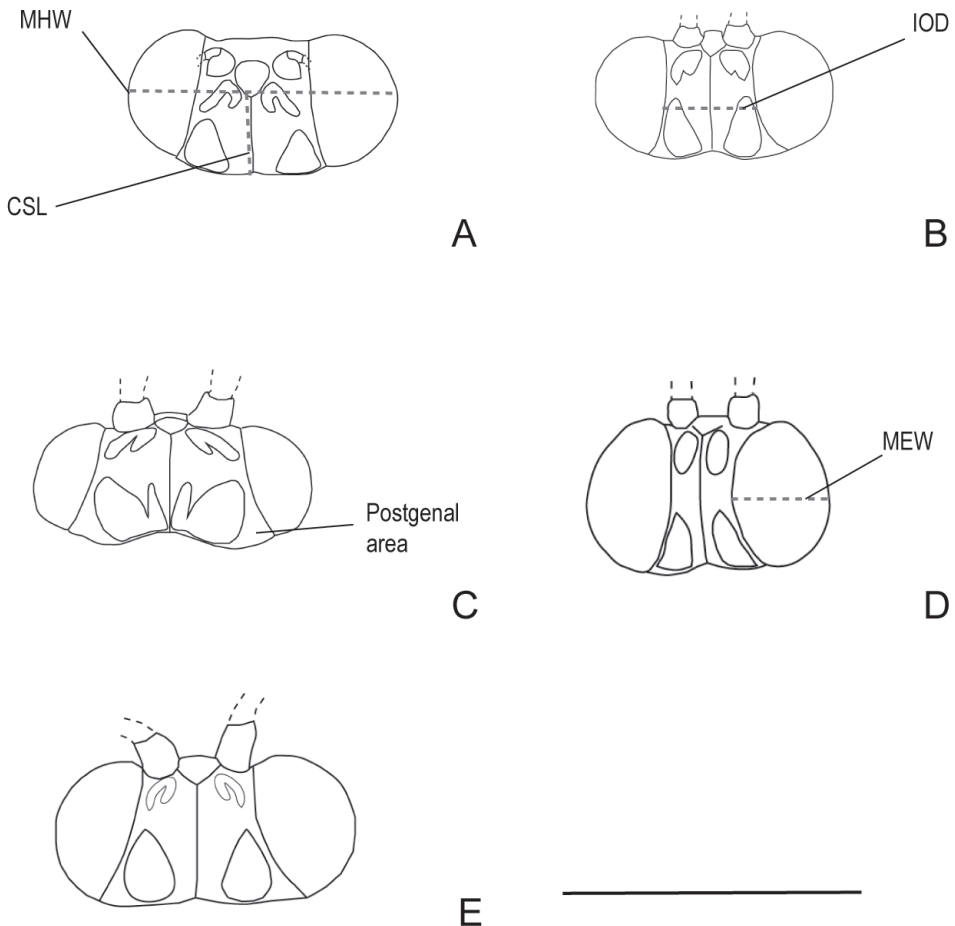


Figure 1. Heads in dorsal view of the species of the *brasiliiana* group **A** *Smicridea (Rhyacophylax) brasiliiana* **B** *S. (R.) weidneri* **C** *S. (R.) vermiculata* **D** *S. (R.) atrobasis* **E** *S. (R.) nanda*. Abbreviations: CSL length of the coronal suture, IOD interocular distance, MEW maximum eye width, MHW maximum head width. Scale bar: 1 mm.

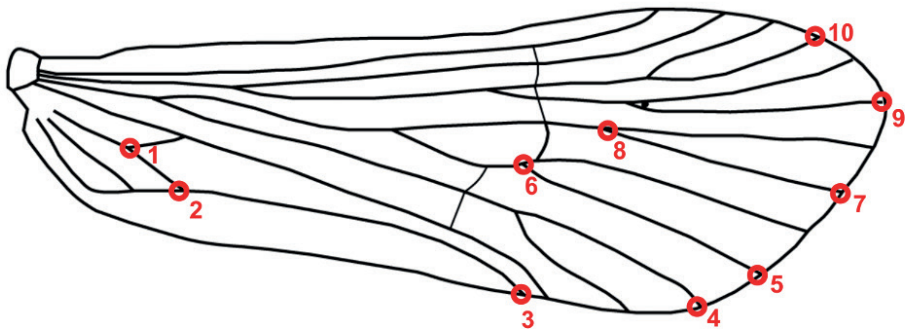


Figure 2. Forewing of *Smicridea* (*Rhyacophylax*) *mesembrina* showing the location of the selected landmarks (1–10).

Table 1. Canonical variate analysis of *Smicridea* species mean wing shape. Number of individuals used of each species are indicated in diagonal. The percentage of correct classification above the main diagonal and Mahalanobis distances are below. The P-values < 0.05 for permutation tests (2000 permutation runs) are marked with asterisks (*).

	<i>S. atrobasis</i>	<i>S. vekona</i>	<i>S. weidneri</i>	<i>S. spinulosa</i>	<i>S. unguiculata</i>	<i>S. vermiculata</i>	<i>S. mesembrina</i>	<i>S. pampeana</i>
<i>S. atrobasis</i>	18	100.00%	79.41%	100.00%	100.00%	100.00%	100.00%	100.00%
<i>S. vekona</i>	5.9096*	19	88.57%	86.48%	88.74%	97.56%	100.00%	91.89%
<i>S. weidneri</i>	4.0849*	4.9467*	16	100.00%	97.22%	100.00%	100.00%	97.05%
<i>S. spinulosa</i>	6.9183*	4.7454*	6.12*	18	92.10%	92.50%	100.00%	100.00%
<i>S. unguiculata</i>	6.1731*	5.1658*	6.2365*	2.8877*	20	92.85%	100.00%	92.10%
<i>S. vermiculata</i>	9.1635*	8.2066*	8.518*	4.5723*	4.3243*	22	100.00%	100.00%
<i>S. mesembrina</i>	9.1130*	9.3375*	10.8162*	8.0428*	7.1655*	9.1801*	21	97.44%
<i>S. pampeana</i>	5.1981*	5.1464*	6.3722*	5.3095*	4.6305*	7.9502*	6.4921*	18

A principal component analysis (PCA) with the consensus configurations of the species of the *brasiliiana* group (*S. brasiliiana*, *S. weidneri*, *S. vermiculata*, *S. atrobasis*, and *S. nanda*) was performed. In addition, the thin plate spline method was used to illustrate the transformations of the wing shapes compared to the consensus wing shape of the group. Mahalanobis distances between the mean shapes of each species of the *brasiliiana* group were used to construct a dendrogram using the Unweighted pair-group method with arithmetic mean (UPGMA) with the software Past v. 4.02 (Hammer et al. 2001).

For wing size analysis, centroid size (CS) was used as a measure of size and was computed as the square root of the sum of squared distances from all landmarks to the centroid of the landmarks configuration (Bookstein 1991). The CS variation for each species is shown with a violin-plot. Differences in CS among species were assessed through a Kruskal-Wallis test and a posteriori pairwise test. *Smicridea nanda* and *S. brasiliiana* were not included in this analysis due to insufficient number of specimens, but the CS of both species are shown in the plot.

Systematics

Family Hydropsychidae Curtis, 1835

Subfamily Smicrideinae Scheffer, 1996

Genus *Smicridea* McLachlan, 1871

Subgenus *Rhyacophylax* Müller, 1879

Smicridea (Rhyacophylax) brasiliiana (Ulmer, 1905)

Figs 1A, 3A–E

Smicridea (Rhyacophylax) brasiliiana (Ulmer), 1905: 107 [as *Rhyacophylax brasilianus*]. Weidner 1964: 97 [lectotype]. Flint 1966: 7 [invalid lectotype, misidentification]; 1972: 238 [discussion of lectotype]. Paprocki et al. 2004: 9 [checklist]; Paprocki and França 2014: 32 [checklist]. Holzenthal and Calor 2017: 165 [catalog].

Material examined. ARGENTINA • 1 male; Misiones, Río Iguazú, camp. Nandu; 25 Feb. 1973; OS Flint Jr. det.; USNM.

Flint (1972) examined the type series of this species from the Ulmer collection (housed at the Zoologisches Museum Hamburg) where he found two mixed species, *Smicridea (Rhyacophylax) brasiliiana* and another closely related species that he described as *S. (R.) weidneri*. The specimen we used for this redescription was collected in 1973 in Misiones province (Argentina) and identified by Dr. Flint. This specimen was borrowed from the USNM.

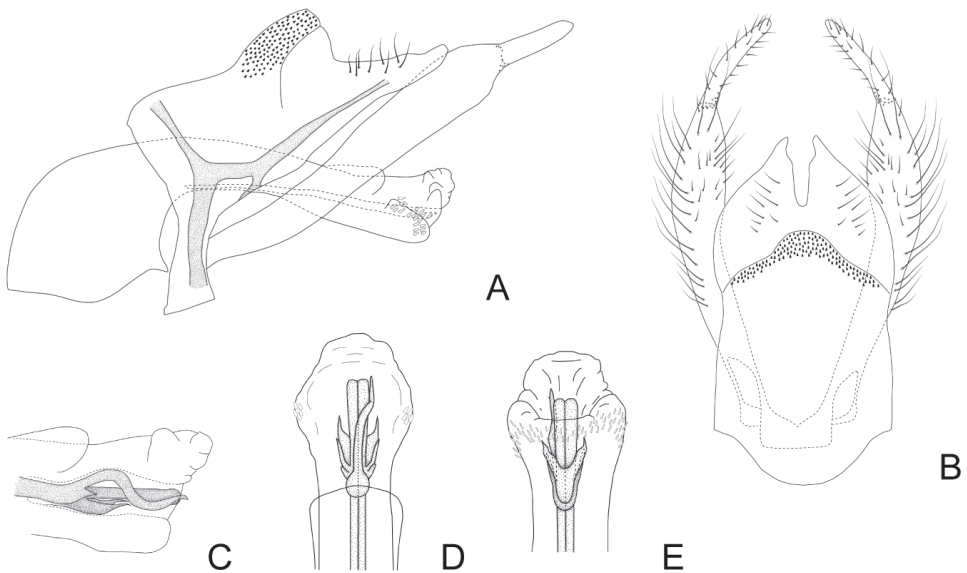


Figure 3. Male genitalia of *Smicridea (Rhyacophylax) brasiliiana* **A** segments IX, X, inferior appendages and phallus, lateral view **B** segments IX, X and inferior appendages, dorsal view **C** tip of the phallus, lateral view (lateral spines removed) **D** tip of the phallus, dorsal view **E** tip of the phallus, ventral view.

Description. Adult male. General color of the body light brown. Length of the forewings: 6.3 mm ($n = 1$). Coloration of the forewings similar to the body, with a subapical transverse, sinuous, white stripe, and a white, rectangular spot at midlength of the costal margin.

Head (Fig. 1A). In dorsal view rectangular, transverse. Mesal margins of the eyes, in dorsal view, parallel, postgenal areas reduced. Interocular area rectangular, wider than long. Interocular distance $2.2 \times$ shorter than MHW. Coronal suture $2/3 \times$ shorter than IOD. Eyes lightly produced anteriorly, maximum eye width $3.3 \times$ shorter than MHW. Anterolateral setose warts present, subtriangular, bifid posteriorly, mesal lobe shorter than the lateral. Posterior setose warts subtriangular. Maxillary palps missing.

Male genitalia. Anterolateral margin of segment IX rounded and produced (Fig. 3A). Tergum of segment X triangular in lateral view, apex rounded, dorsal and ventral margins straight, the ventral one with a sclerotized H-shaped area directed anteriorly through segment IX (Fig. 3A); in dorsal view divided mesally into two subtriangular hemitergites with apex subacute; internal margin of each hemitergite straight, with a concavity subapically (Fig. 3A, B). Inferior appendages with two articles, setose, curved mesally in dorsal view; basal article narrow for a short distance proximally, from where it widens to the apex; apical article narrow, short, with rounded apex (Fig. 3B). Phallus with long and tubular phallobase; basal portion broad, forming an angle of $\sim 90^\circ$ with distal part, which is slightly curved and with widened apex (Fig. 3A, C); dorsal periphallallic cap present subapically; apex of the phallus with a row of small spines extending from one side to the other ventrally, in dorsal view slightly produced laterally (Fig. 3A, C–E). Internal sclerotized section of ejaculatory duct long and straight in lateral view ($\sim 2/3$ the phallobase length), in dorsal view longitudinally divided in two (Fig. 3E); distal end with an elongate, pointed dorsal plate, that bends upwards, then ventrad to the left at mid-length and upwards again, ending slightly beyond the tip of the ejaculatory duct; basally this plate bears a lateral spine; ventrally to the ejaculatory duct there are two spine-like plates and two lateroventral subrectangular plates that narrow posteriorly ending in a point (Fig. 3C–E). Endotheca simple.

Systematic considerations. This species seems to be related to *S. weidneri* and *S. nanda*. Genitally, these species share the presence two pairs of elongate sclerites, dorsal and ventrad to the ejaculatory duct, which take different forms in the three species. Additionally, the morphology of the setose warts of the head of these species is similar, with the anterolateral setose warts bifid and the posterior ones triangular. *Smicridea brasiliiana* can be distinguished by the presence of the elongate, sinuous, and pointed dorsal plate at the distal end of the ejaculatory duct, absent in the other two species, and the shape of the ventral plates that are spine-like, and the lateroventral ones that are subrectangular and pointed. Also, *S. brasiliiana* has series of spines surrounding lateroventrally the end of the phallus, which are lacking in the other two species.

Distribution. Argentina (new record), Brazil.

***Smicridea (Rhyacophylax) weidneri* Flint, 1972**

Figs 1B, 4A–D

Smicridea (Rhyacophylax) weidneri Flint, 1972: 238; 1966:8 [as *brasilianus*, distribution]. Marinoni and de Almeida 2000: 286 [distribution; biology]. Paprocki et al. 2004: 9 [checklist]. Sganga 2006: 142 [distribution]. Paprocki and França 2014: 37 [checklist]. Manzo et al. 2014: 166 [distribution]. Holzenthal and Calor 2017: 187 [catalog].

Material examined. ARGENTINA • 1 male; Misiones, Capiovy; 5 Apr. 1971; CM & OS Flint Jr. col.; paratype; USNM • 15 males; Misiones, Oberá, Centro de Investigación y Refugio de Selva Antonia Ramos, A° Ramos; 17 Nov. 2013; JV Sganga col.; light trap.

Description. Adult male. Coloration of the body stramineous. Length of the forewings 4.5 mm ($n = 16$), coloration similar to that of the body, with two transverse, brown bands, one subapical, almost straight and the other sinuous, at midlength.

Head (Fig. 1B). In dorsal view rectangular, transverse. Mesal margins of the eyes, in dorsal view, concave, postgenal areas small, triangular. Interocular area rectangular, longer than wide. Interocular distance $2.75 \times$ shorter than MHW. Coronal suture $1.08 \times$ longer than IOD. Maximum eye width $3 \times$ shorter than MHW. Anterolateral setose warts present, oval, with a V-shaped notch posteriorly. Posterior setose warts subtriangular. Maxillary palp formula: I-II-IV-III-V.

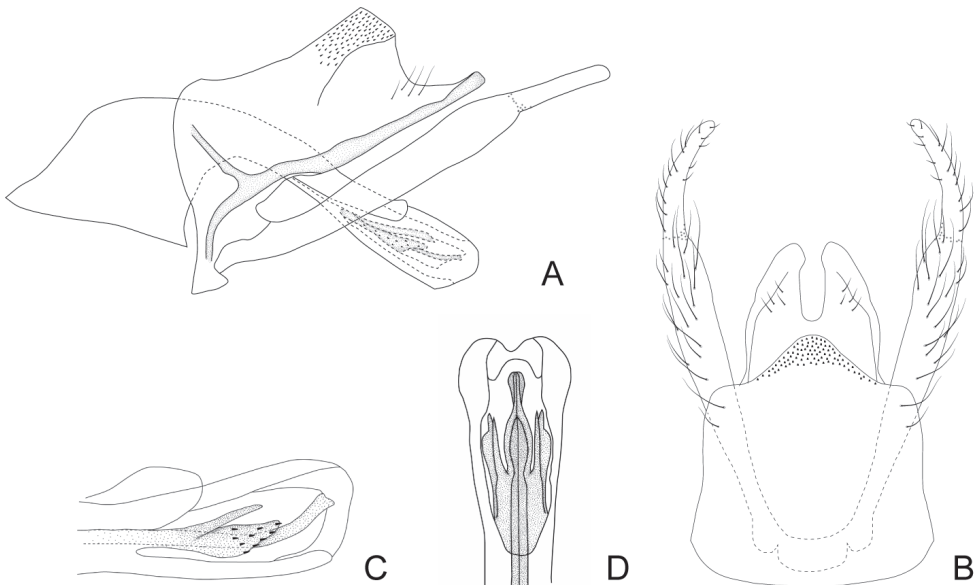


Figure 4. Male genitalia of *Smicridea (Rhyacophylax) weidneri* **A** segments IX, X, inferior appendages and phallus, lateral view **B** segments IX, X and inferior appendages, dorsal view **C** tip of the phallus, lateral view **D** tip of the phallus, dorsal view.

Male genitalia. Anterolateral margin of segment IX slightly rounded. Tergum of segment X triangular in lateral view, dorsal and ventral margins straight, the ventral one with a sclerotized Y-shaped area directed anteriorly through segment IX (Fig. 4A); in dorsal view divided mesally into two triangular hemitergites, with apex rounded and mesal margins concave (Fig. 4B). Inferior appendages with two articles, basal article slightly widened distally, apical one curved mesad in dorsal view, slightly narrowing towards the apex, which is rounded (Fig. 4A, B). Phallus long, with a tubular phallobase; basal portion broad, forming an angle of $\sim 90^\circ$ with distal part, that is straight and with apex somewhat widened; dorsal periphallalic cap present subapically (Fig. 4A). Internal sclerotized section of ejaculatory duct long and sinuous in lateral view ($\sim 2/3$ the phallobase length), distal end curved upwards (Fig. 4A, C); in dorsal view longitudinally divided in two, apex spindle-shaped (Fig. 4D); in lateral view with two rhomboidal dorsolateral plates in the posterior half of the ejaculatory duct, with ventral and posterior margins serrated and with small spines on its distal surface; dorsal to these plates there are two wide spine-like plates directed posteriorly (Fig. 4A, C, D). Endotheca simple.

Systematic considerations. This species seems to be closely related to *S. brasiliiana* and *S. nanda* (see Systematic considerations section for *S. brasiliiana*). *Smicridea weidneri* can be identified by the spindle-shaped distal end of the ejaculatory duct, that is simple in the other two species, and the shape of the two pairs of plates, two rhomboidal, with ventral and posterior margins serrated, and covered with small spines, and two spine-like, wide, directed posteriorly.

Distribution. Argentina, Brazil.

Smicridea (Rhyacophylax) vermiculata Flint, 1978

Figs 1C, 5A–D

Smicridea (Rhyacophylax) vermiculata Flint, 1978: 381. Marinoni and de Almeida 2000: 286 [distribution; biology]. Blahnik et al. 2004: 4 [distribution]. Paprocki et al. 2004: 9 [checklist]. Sganga 2006: 142 [distribution]. Calor 2011: 321 [checklist]. Paprocki and França 2014: 36 [checklist]. Holzenthal and Calor 2017: 186 [catalog].

Material examined. ARGENTINA • 27 males; Misiones, Oberá, Centro de Investigación y Refugio de Selva Antonia Ramos, A° Ramos; 17 Nov. 2013; JV Sganga col.; light trap.

Description. Adult male. General coloration of the body brown. Length of forewings 4.5 mm ($n = 22$), coloration similar to that of the body, with a distinct transverse, white band subapically.

Head (Fig. 1C). In dorsal view rectangular, transverse. Internal margins of the eyes, in dorsal view, convergent, postgenal areas triangular. Interocular area trapezoidal. Interocular distance $1.85 \times$ shorter than MHW. Coronal suture $1.47 \times$ shorter than IOD. Maximum eye width $4.35 \times$ shorter than MHW. Anterolateral setose warts present, oval, bifid posteriorly, with mesal lobe shorter than the lateral. Posterior setose warts subtriangular, with a digitate mesal lobe. Maxillary palp formula: I-II-IV-III-V.

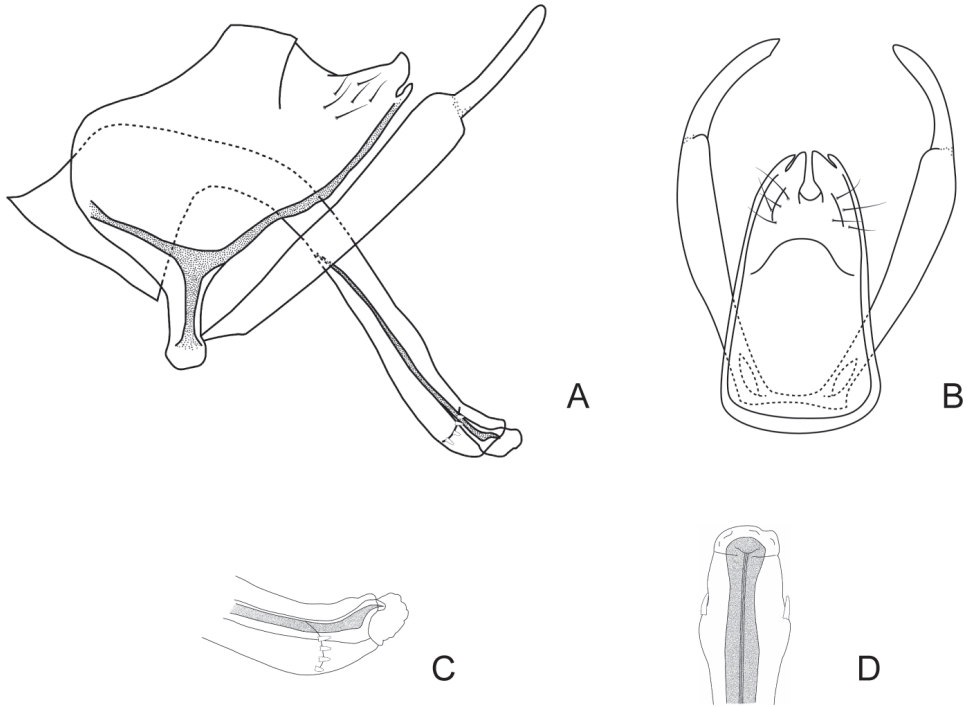


Figure 5. Male genitalia of *Smicridea (Rhyacophylax) vermiculata* **A** segments IX, X, inferior appendages and phallus, lateral view **B** segments IX, X and inferior appendages, dorsal view **C** tip of the phallus, lateral view **D** tip of the phallus, dorsal view.

Male genitalia. Anterolateral margin of segment IX rounded, produced. Tergum of segment X triangular in lateral view, dorsal margin straight, ventral slightly rounded, with a subapical lobe, and a sclerotized Y-shaped area directed anteriorly through segment IX (Fig. 5A); in dorsal view divided mesally into two triangular hemitergites, with apex rounded and bearing a lateral lobe, mesal margins straight, with an anterior notch (Fig. 5B). Inferior appendages with two articles, basal article slightly widened distally, apical one curved mesad in dorsal view, apex pointed (Fig. 5A, B). Phallus long, with a tubular phallobase; basal portion broad, forming an angle of $\sim 90^\circ$ with distal part, which is very long and with apex slightly upturned (Fig. 4A); phallus bears subapically four spines mesoventrally on each side, which are directed posteriorly (Fig. 5A, C, D). Internal sclerotized section of ejaculatory duct long ($\sim 1/2$ the phallobase length) and bent ventrad anteriorly in lateral view, distal end curved upwards and with a posterior concavity (Fig. 5A, C); in dorsal view longitudinally divided in two (Fig. 5D). Endotheca simple.

Systematic considerations. This species seems to be related to *S. (R.) dentifera* Flint, 1983 and *S. (R.) unguiculata*. The three species have simple ejaculatory ducts and lateroventral spines at the apex of the phallus. The features that allow the differentiation of *S. vermiculata* are the position of the spines of the phallus (it has 4 mesoventral

spines on each side directed posteriorly), the ejaculatory duct that is curved upwards and bears a posterior concavity, and the presence of the apicolateral lobe on tergum X.

Distribution. Argentina, Brazil, Paraguay.

***Smicridea (Rhyacophylax) atrobasis* Flint, 1983**

Figs 1D, 6A–D

Smicridea (Rhyacophylax) atrobasis Flint, 1983: 63. Paprocki et al. 2004: 9 [checklist]. Sganga 2006: 142 [distribution]. Sganga and Angrisano 2005: 132 [distribution]. Rueda Martín and Sganga 2011: 2225 [♂; distribution]. Paprocki and França 2014: 32 [checklist]. Isa Miranda and Rueda Martín 2014: 200 [distribution]. Holzenthal and Calor 2017: 163 [catalog].

Material examined. URUGUAY • 22 males; Salto, Salto Grande; 19 Nov. 1955; a la luz, en la cascada; FHCM • 1 male; Artigas, río Uruguay, barra Arroyo Guaviyú; 22 Nov. 1954; CS Carbonell leg. (OS Flint Jr. det.) • 1 male; San Gregorio; 29 Nov. 1959; Carbonell, Mesa, San Martín leg. (OS Flint Jr. det.).

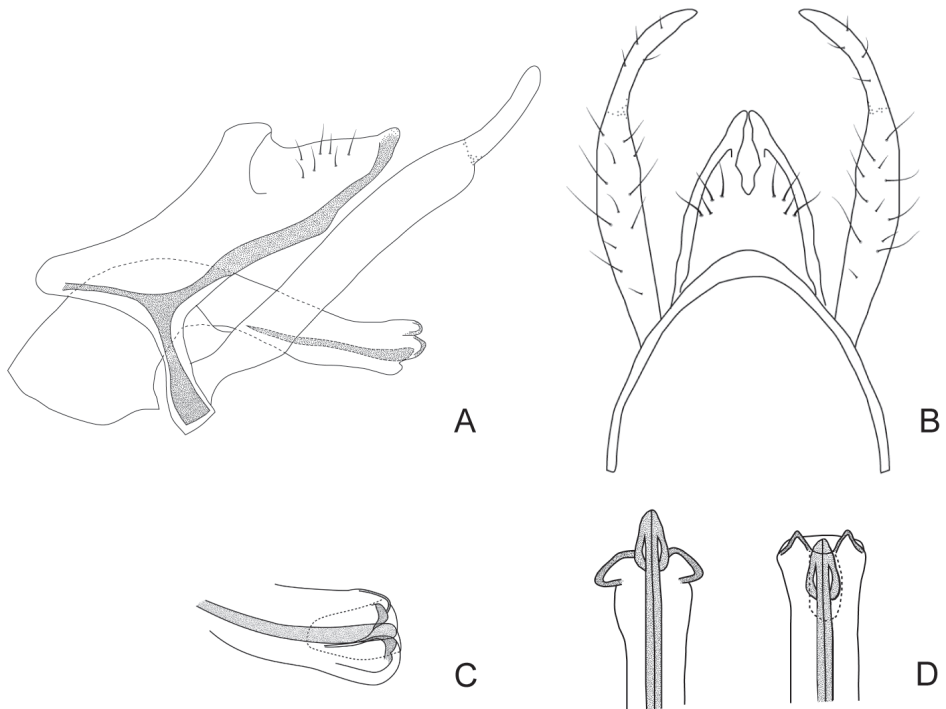


Figure 6. Male genitalia of *Smicridea (Rhyacophylax) atrobasis* **A** segments IX, X, inferior appendages and phallus, lateral view **B** segments IX, X and inferior appendages, dorsal view **C** tip of the phallus, lateral view **D** tip of the phallus, dorsal view (left evaginated, right invaginated).

Description. Adult male. Coloration of the body in alcohol stramineous. Length of forewings 5.4 mm ($n = 18$). We were not able to observe the coloration of the wings in the specimens preserved in alcohol due to discoloration of the cuticle through time, but Flint (1983) described it from dried specimens as follows: “forewings dark purplish black in basal quarter and in two transverse bands apical, otherwise covered with golden hair”.

Head (Fig. 1D). In dorsal view rectangular, transverse. Mesal margins of the eyes, in dorsal view, convex, postgenal areas reduced. Interocular area rectangular, narrow, longer than wide. Interocular distance $7.3 \times$ shorter than MHW. Coronal suture $2.2 \times$ longer than IOD. Eyes very prominent, maximum eye width $2.4 \times$ shorter than MHW. Anterolateral setose warts present, elongate, oval. Posterior setose warts subtriangular. Maxillary palp formula: I, II-III, IV-V.

Male genitalia. Anterolateral margin of segment IX sinuous. Tergum of segment X triangular in lateral view, dorsal and ventral margins rounded, with a ventral sclerotized Y-shaped area directed anteriorly through segment IX (Fig. 6A); in dorsal view divided mesally into two triangular hemitergites, with apex pointed, mesal margins concave (Fig. 6B). Inferior appendages with two articles, basal article slightly widened distally, apical one curved mesad in dorsal view, apex pointed (Fig. 6A, B). Phallus long, with a tubular phallobase; basal portion broad, forming an angle of $\sim 120^\circ$ with distal part; apex broadened, ending in two laterodorsal and two lateroventral lobes, that become directed basad as the endotheca is everted (Fig. 6A, C, D). Internal sclerotized section of ejaculatory duct $\sim 2/3$ the phallobase length, straight, slightly upturned apically in lateral view (Fig. 6A, C); in dorsal view longitudinally divided in two, apex shaped like an arrowhead (Fig. 6D). Endotheca simple.

Systematic considerations. This species seems to be closely related to *Smicridea mesembrina*. These two species bear apicolateral lobes on the phallus, but while the apex of the sclerotized section of the ejaculatory duct in *S. mesembrina* is simple, in *S. atrobasis* it is shaped like an arrowhead. Additionally, *S. atrobasis* has a very distinctive feature that is the prominent eyes and reduced interocular area.

Distribution. Argentina, Bolivia, Brazil, Uruguay.

Smicridea (Rhyacophylax) nanda Flint, 1983

Figs 1E, 7A–D

Smicridea (Rhyacophylax) nanda Flint, 1983:65. Sganga 2006: 142 [distribution]. Holzenthal and Calor 2017: 177 [catalog].

Material examined. ARGENTINA • 1 male; Misiones, Río Iguazú, camp. Nandu; 25 Feb. 1973; OS Flint Jr. col.; paratype; USNM.

Description. Adult male. General coloration of the body light brown. Length of forewings 6.8 mm ($n = 1$), coloration similar to that of the body, with a soft darkening on the crossveins and a pale, subapical, transverse band.

Head (Fig. 1D). In dorsal view rectangular. Internal margins of the eyes, in dorsal view, concave, postgenal areas small, triangular. Interocular area trapezoidal. Interocular distance $2.6 \times$ shorter than MHW. Coronal suture $1 \times$ the length of IOD. Eyes slightly produced anteriorly, maximum eye width $3.25 \times$ shorter than MHW. Anterolateral setose warts present, very subtle, oval, bifid posteriorly. Posterior setose warts subtriangular. Maxillary palp formula: I-II-III-IV-V.

Male genitalia. Anterolateral margin of segment IX slightly rounded on the dorsal half (Fig. 7A). Tergum of segment X subtriangular in lateral view, with rounded apex, dorsal and ventral margins straight, ventral one with a sclerotized H-shaped area directed anteriorly through segment IX; in dorsal view divided mesally into two subtriangular hemitergites with rounded apex and mesal margins straight (Fig. 7B). Inferior appendages with two articles, curved mesally in dorsal view, basal article slightly widened distally, apical article narrow, short, apex pointed (Fig. 7A, B). Phallus with long and tubular phallobase; basal portion slightly broad, bending ventrad mesally, distal part straight (Fig. 7A); basal and distal parts of the phallus forming an angle of $\sim 90^\circ$; dorsal periphallic cap present at midlength. Sclerotized part of ejaculatory duct curved dorsad at midlength; tip directed upwards in lateral view; with two dorsolateral elongated, oval plates in lateral view and two spine-like sclerites beneath them (Fig. 7A, C, D). Endotheca wrinkled (Fig. 7D).

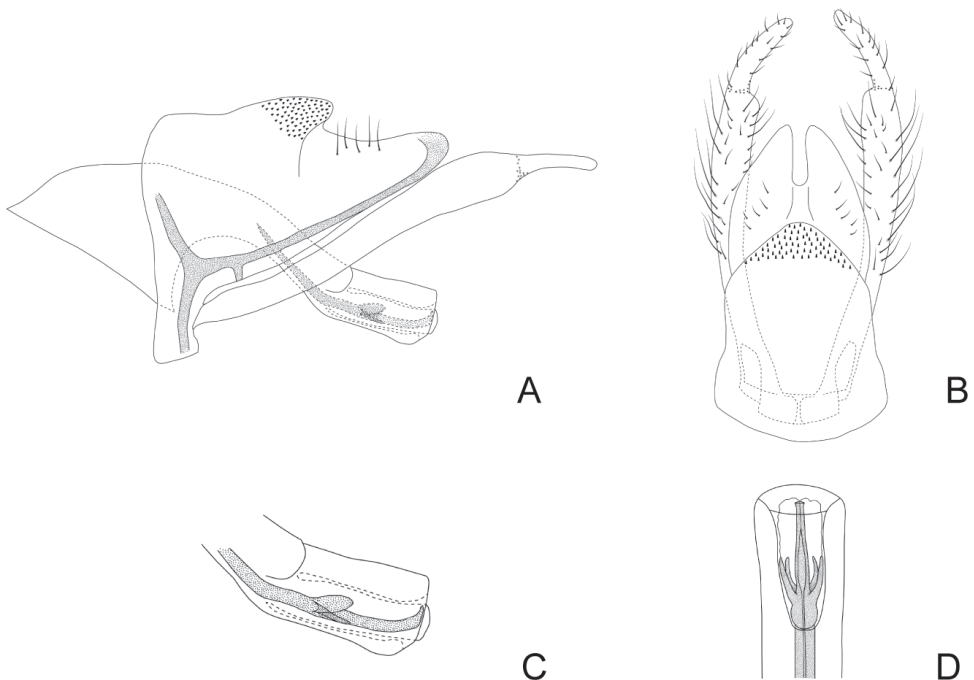


Figure 7. Male genitalia of *Smicridea* (*Rhyacophylax*) *nanda* **A** segments IX, X, inferior appendages and phallus, lateral view **B** segments IX, X and inferior appendages, dorsal view **C** tip of the phallus, lateral view **D** tip of the phallus, dorsal view.

Systematic considerations. This species seems to be related to *S. brasiliiana* and *S. weidneri* (see Systematic considerations section for *S. brasiliiana*). *Smicridea nanda* is characterized by the ejaculatory duct that is curved dorsad at midlength and distally upturned, and the shape of the two pairs of sclerotized plates: the dorsolateral ones elongated, oval in lateral view and the other two spine-like lying beneath them.

Distribution. Argentina.

Geometric morphometric analysis

This approach allowed the differentiation of the analyzed species based on their wing shape. In the CVA analysis, the first two axes explained 79.25% of the shape variance. The shape configurations of *S. mesembrina* and *S. weidneri* occupied extreme morphospaces in the CV1 axis, and *S. mesembrina* and *S. vermiculata* in the CV2 axis (Fig. 8A). The superposition of the mean configurations of these species associated with CV1 and CV2 (Fig. 8B, C) showed that the basal bifurcation of M_1 and M_2 (landmark 8) and the apex of the wing (landmarks 3–5, 7, 9, 10) were the most affected areas for *S. mesembrina* and *S. weidneri* (Fig. 8B) while the base of the anal area (landmarks 1, 2), the apices of Cu_{1a} and M_4 (landmarks 4, 5), the basal bifurcation of M_1 and M_2

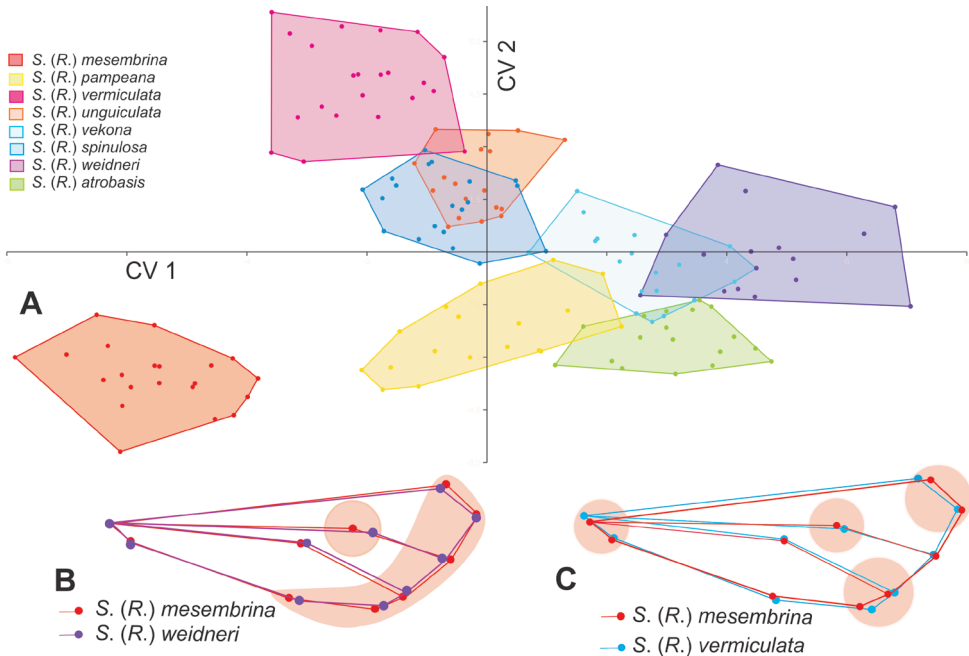


Figure 8. **A** Canonical Variate Analysis (CVA) scatter plot of the wing shape landmark data of eight *Smicridea* species **B, C** patterns of shape change along each axis by superposition of the mean configurations of the species located in extreme morphospaces of each axis **B** superposition of the mean (average) wings shape of *Smicridea* (*Rhyacophylax*) *mesembrina* - *S. (R.) weidneri* **C** superposition of the mean wings shape of *S. (R.) mesembrina* - *S. (R.) vermiculata*.

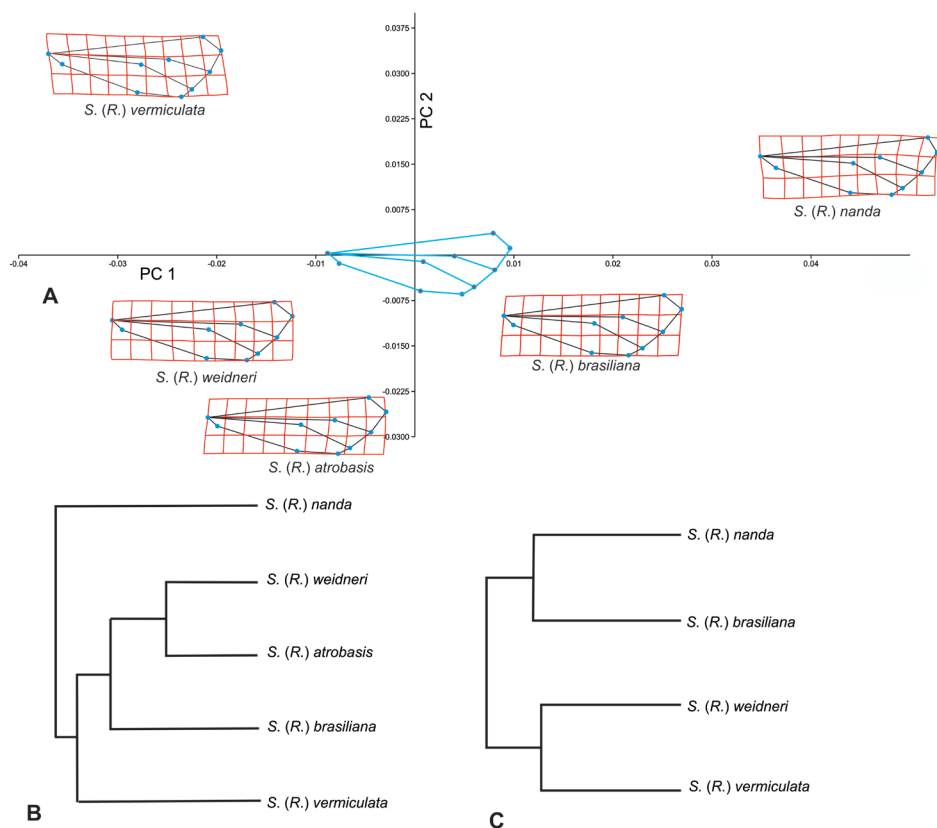


Figure 9. Principal Component Analysis (PCA) of the geometric landmark data of the wings of the *brasiliiana* species group **A** scatter plot showing the average configuration of the wing shape in the deformation grids of each species from consensus shape of species group (indicate in the center of the plot) in the first two CPs. The circles represent the locations of the reference points in the mean shape of each species **B** UPGMA. Dendrogram from Mahalanobis distance of *brasiliiana* species group and **C** without *Smicridea (Rhyacophylax) atrobasis*.

(landmark 8), and the apex of R_3 (landmark 10) were the most affected for *S. mesembrina* and *S. vermiculata* (Fig. 8C). CV1 was able to discriminate 4 groups: the first made up of *S. mesembrina*, the second by *S. pampeana* + *S. unguiculata* + *S. spinulosa*, the third by *S. vekona* + *S. atrobasis*, and finally *S. weidneri*. CV2 discriminated species that had not been separated by CV1. Although overlapping morphospaces were observed, the shape conformations were statistically different ($p < 0.05$) and a high percentage of correct reclassification of the specimens was obtained using the complete data set (83%), which increases if pairs of species are taken into consideration (Table 1).

The principal component analysis of the consensus shapes of the species included in the *brasiliiana* group revealed that *S. nanda* showed the furthest configuration and *S. (R.) brasiliiana* the closest from the consensus shape of the group (Fig. 9A). The morphospaces that the different average configurations occupy in the space of the PCA

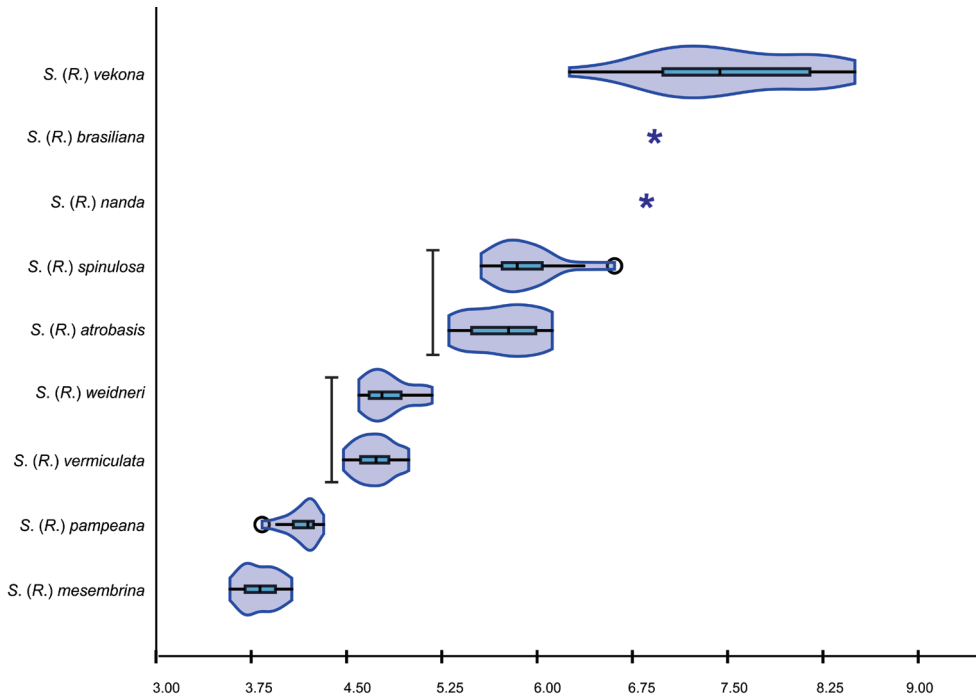


Figure 10. Violin plot of the centroid sizes (CS) of the wings of the ten *Smicridea* species analyzed. Bar: no significant differences between CSs ($p > 0.05$). *: $n = 1$.

plot can be visualized in Fig. 9A. *Smicridea weidneri* and *S. atrobasis* showed the most similar configurations, although statistically different ($p < 0.05$). This result was contradictory with the morphological analysis of the genitalia and head that suggested that *S. atrobasis* was not closely related with the rest of the species in the group. Therefore, we performed two UPGMA a posteriori, the first including all the species of the *brasiliiana* species group (Fig. 9B) and the second excluding *S. atrobasis*. In the latter UPGMA, both *S. weidneri* and *S. vermiculata* as well as *S. nanda* and *S. brasiliiana* were grouped together (Fig. 9C).

Wing size analysis

All species included in the analysis differed in CS ($p < 0.05$), except *S. (R.) spinulosa* with *S. (R.) atrobasis* ($p > 0.05$) and *S. (R.) vermiculata* with *S. (R.) weidneri* ($p > 0.05$) (Fig. 10).

Discussion

Based on the analysis of the fine structure of the genitalia of the species of the *brasiliiana* group we consider that the group is heterogeneous. *Smicridea brasiliiana*, *S. weidneri*, and *S. nanda* seem to be closely related species with complex phallic structures, including internal plates of different shapes associated with the distal end of the sclerotized

ejaculatory duct that are absent in *S. atrobasis* and *S. vermiculata*. In particular the genitalia of *S. vermiculata* is most similar to that of *S. dentifera* Flint and *S. unguiculata* Flint, which are unplaced to species groups, that have a simple ejaculatory duct and lateral subapical spines at the phallus. The analysis of the morphology of the heads of these species also supports a closer relationship between *S. brasiliiana*, *S. weidneri*, and *S. nanda*, with anterolateral setose warts bifid and posterior setose warts triangular. The head of *S. vermiculata* is more similar in shape to these species but differs in the structure of the posterior setose warts that bear internal lobes and the postgenal areas that are more developed. In contrast, the head of *S. atrobasis* is unique in the group, with a more quadrangular outline, very large eyes, a reduced interocular area, and oval anterolateral setose warts. The genitalia of this species is also different from the rest: the apex of the ejaculatory duct is shaped like an arrowhead in dorsal view and the phallus ends in two laterodorsal and two lateroventral lobes. The presence of apicolateral lobes on the phallus is also found in *S. (R.) mesembrina*, not placed in a species group. The relationships between *S. brasiliiana*, *S. weidneri*, and *S. nanda* are also strengthened by the configurations of the forewings, as was observed through the geometric morphometrics analysis.

The placement of *S. atrobasis* in the *brasiliiana* group is conflictive. As stated before, although the configuration of the forewing of this species is similar to that of *S. weidneri*, the genitalia and the morphology of the head of both species differ. The relationships of the forewing configurations in the *brasiliiana* species group were compared in the dendrogram, with and without *S. atrobasis*. The exclusion of this species from the analysis shows the same patterns that the ones observed using the morphology of the genitalia and features of the head. In this context, the similarities in the forewing configuration could be seen as a homoplasy rather than a homology, although further phylogenetic analyses are needed for confirmation.

The geometric morphometric analysis of wing shapes was useful for discriminating the species herein studied. This is the first study that uses this methodology in the order Trichoptera and needs to be examined in more species of *Smicridea*, and other caddisfly taxa as well, using not only wing shapes but other structures of the body. The larvae of *Smicridea* (*Rhyacophylax*) are good candidates to test this approach. In this subgenus the larvae are generally very similar, with no clear defining characters to separate them, but there are subtle interspecific differences in the shape of the head and the frontoclypeal apotome (JS pers. obs.). These differences in shape could be tested with this methodology. Taking into consideration that landmark configurations can be used in phylogenetic reconstructions (Catalano et al. 2010, 2015; Palci and Lee 2019), the exploration of this type of characters in the study of Trichoptera can be of great relevance.

Conclusions

In this study, we provided a new approach for the delimitation of species in the genus. The head morphology is somewhat overlooked in the descriptions of most Trichoptera

species. Here, we propose a more comprehensive approach including more detailed descriptions of relevant characters, besides the male genitalia, that would be useful for differentiating closely related species. Likewise, we demonstrated that the geometric morphometrics analysis of wing shapes can be used to discriminate the species of *Smicridea* (*Rhyacophylax*) herein studied. This fast, simple, and inexpensive method proved to be an efficient technique to confirm the identity of the specimens and could potentially be used to differentiate cryptic species, which were previously reported in *Smicridea* and other insect genera (Pauls et al. 2010; Chroni et al. 2018; Chatpiyaphat et al. 2021). Furthermore, it can also be a source of characters for phylogenetic analysis, not as a substitute for traditional morphological characters, but rather as a complementary descriptor of shape diversity (Palci and Lee 2019).

Even though the analyzed features indicate that the *brasiliiana* group might not be a natural group as informally defined, the relationships between these species and the rest of the species in the subgenus *Rhyacophylax* must be established by a phylogenetic analysis and the monophyly of all the current groups of species should be tested.

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***Notalina (Neonotalina) ralphi* sp. nov. (Trichoptera, Leptoceridae), a new long-horned caddisfly from the Cerrado biome of Brazil, with new records for *N. (Neonotalina) brasiliiana* Holzenthal, 1986 and an identification key**

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Abstract

The long-horned caddisfly genus *Notalina* Mosely, 1936 contains 27 species divided into two subgenera. The Neotropical *N. (Neonotalina)* Holzenthal, 1986 occurs exclusively in South America. Its species are organized into two species groups, *brasiliiana* and *roraima*. Nine species have been recorded so far in Brazil, mainly distributed in the Cerrado and Atlantic Forest biomes of Southeast Region, and only one species has been recorded from the Central-West and Northeast Regions. In this paper a new species of *N. (Neonotalina)* is described and illustrated based on adult males from two protected and preserved areas

in the Cerrado biome of Brazil. *Notalina* (*Neonotalina*) *ralphi* **sp. nov.** belongs to the *brasiliana* species group and can be recognized mainly by the morphology of the preanal appendages and segment X. New distributional records are provided for *N.* (*Neonotalina*) *brasiliana* Holzenthal, 1986. Additionally, a key to identify males of the ten species in the *brasiliana* species group is provided.

Keywords

Aquatic insects, geographic distribution, taxonomy, Triplectidinae

Introduction

Leptoceridae, or long-horned caddisflies, with ~2,200 species, is the second most species-rich trichopteran family (Morse et al. 2019). Based on the current classification of the family proposed by Malm and Johanson (2011), four subfamilies are recognized: Grumichellinae Morse, 1981, Leptocerinae Leach, 1815, Leptorussinae Morse, 1981, and Triplectidinae Ulmer, 1906.

Notalina Mosely, 1936 belongs to Triplectidinae and contains 27 species divided into two subgenera, the nominotypical *Notalina* (*Notalina*) (15 species) and *Notalina* (*Neonotalina*) Holzenthal, 1986 (12 species) restricted to the Australasian and Neotropical regions, respectively (Calor 2008; Holzenthal and Calor 2017; Henriques-Oliveira et al. 2018). *Notalina* species are easily distinguished in the adult stage, but not in the immature stages (Holzenthal 1986; Calor and Froehlich 2008). Two species groups (*brasiliana* and *roraïma*) were informally defined in the Neotropical subgenus *Neonotalina* by Holzenthal (1986) based mainly on characters of the male genitalia. Later, the monophyly of both the species groups and subgenera were supported by Calor et al. (2006). The *brasiliana* group is characterized by having a complex phallic apparatus with acuminate lateral flanges at the apex and a well-developed phallotremal sclerite, while in *roraïma* group, the phallic apparatus is simple with spatulate lateral flanges at the apex and a small phallotremal sclerite (Holzenthal 1986).

In the Neotropical region, *N.* (*Neonotalina*) occurs exclusively in South America. Its highest species diversity occurs in Brazil, with nine species described (*N. brasiliana* Holzenthal, 1986, *N. cipo* Holzenthal, 1986, *N. franciscana* Henriques-Oliveira, Rocha & Nessimian, 2018, *N. froehlichii* Calor & Holzenthal, 2006, *N. goianensis* Calor, 2008, *N. hamiltoni* Holzenthal, 1986, *N. jordanensis* Henriques-Oliveira, Spies & Dumas, 2012, *N. morsei* Holzenthal, 1986, and *N. paulista* Calor & Holzenthal, 2006), distributed mainly in the highlands of the Cerrado and Atlantic Forest biomes of Southeastern region of the country (Calor and Santos 2021).

In this study, we describe and illustrate a new species of *N.* (*Neonotalina*) based on adult males from two protected and preserved areas in the Cerrado biome of Central-west and North regions of Brazil, in Federal District and Tocantins states, respectively. We also provide new distributional records for *N. brasiliana*. In addition, a key is provided to identification of males of species in the *brasiliana* group.

Materials and methods

Specimens were collected mainly in streams of three conservation units of the Brazilian Cerrado biome. Two of them located in the Federal District, midwestern Brazil (Estação Ecológica de Águas Emendadas (ESECAE) in Planaltina and Parque Nacional de Brasília (PNB) in Brasília) and the third unit located in the Tocantins state, northern Brazil (Parque Estadual do Lajeado (PEJ)), located in the Palmas municipality). One additional specimen was collected in a river in the São Desidério municipality, west of Bahia state, northeast region. Adults were collected by Malaise trap (Gressitt and Gressitt 1962) and light traps positioned near and about the water. The specimens were preserved in 80% ethanol.

In order to observe male genital structures, the abdomen of each specimen was removed and diaphanized using heated 10% KOH as detailed by Blahnik and Holzenthal (2004). After diaphanization, the abdomen was mounted with glycerin on a temporary slide and was examined under a Leica DM5500 B compound microscope. After observation, the abdomen was permanently stored in glycerin in a microvial, together with the remainder of the respective specimen in a plastic vial with ethanol (Desiderio et al. 2021).

Photographs of the habitus, head and wings of adults were obtained using a Leica DFC420 video camera attached to a Leica M165C stereomicroscope and with a LED illumination dome (Kawada and Buffington 2016). Photographs of the male genitalia were taken with a Leica DFC295 video camera attached to a Leica DM5500B compound microscope. Stacks of images of each structure were then combined automatically into a single image using Helicon Focus Pro stacking software (version 7.6.4). Stacked images of the genitalia were used as templates in Adobe Illustrator for vector illustrations. All photographs and illustrations were assembled into plates using Adobe Photoshop.

The distribution map was prepared using QGIS Las Palmas 2.18.10 software (QGIS Development Team 2016). Vector and raster maps used IBGE (2019) and Natural Earth (2020) data. Morphological terminology follows Holzenthal (1986) and Calor et al. (2006) for the male genitalia with modifications. The species description and identification key were constructed using the DELTA software (Description Language for Taxonomy) (Dallwitz et al. 1993, 2016). Lists of material examined were prepared using the AUTOMATEX macro in Microsoft Excel (Brown 2013).

Types and other material examined are deposited in the following collections: Coleção de Invertebrados, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil (**INPA**), Museu de Zoologia da Universidade Federal da Bahia, Salvador, Brazil (**UFBA**), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (**MZUSP**), University of Minnesota Insect Collection, St. Paul, Minnesota, USA (**UMSP**), Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (**DZRJ**), and Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (**DZUP**).

Taxonomy

Notalina (Neonotalina) ralphi sp. nov.

<http://zoobank.org/F6A903EA-547F-4D59-9BE2-EC6232601A22>

Figs 1, 2

Diagnosis. This new species can be easily recognized by the absence of processes on the median portion of tergum X, inferior appendages with ventromesal process indistinct laterally and distinct ventrally with subtruncated apex, and Y-shaped phallotremal sclerite in lateral view. *Notalina ralphi* sp. nov. is morphologically similar to *N. franciscana* based on the subtruncate mesoventral process of the inferior appendages in ventral view. However, *N. ralphi* sp. nov. has the acuminate preanal appendages, which in *N. franciscana* are clavate. In addition, in the new species the ventrolateral margin of the segment X has stout, short setae, whereas *N. franciscana* has these setae only in the apex of the tergum.

Description. Male. Head brown (in alcohol) (Fig. 1B); maxillary and labial palps brown; antennae pale brown (Fig. 1A). Thorax brown; pleuron pale brown (Fig. 1C). Forewing brown, with small hyaline spot at thyridial cell; forewing length 7.8 mm ($n = 4$), forks I and V present (Fig. 1D); hind wing length 6 mm ($n = 4$), forks I, III, and V present, fork I very narrow and fork III with very short petiole (Fig. 1E). Legs pale brown; tibial spur formula 2, 2, 4 (Fig. 1A). Segment IX, in lateral view, broadest ventrolaterally, anterior margin slightly sinuous (Fig. 2A); apicodorsal area with paired, poorly developed, distantly situated protuberance; posterolateral margin bearing setae. Preanal appendages setose, long, and slender, $\sim 2/3$ length of segment X (Fig. 2A, B); in dorsal view, apex acuminate towards inner margin, bearing long setae (Fig. 2B). Segment X, in lateral view, saddle-shaped; anterodorsal area slightly convex; mid-dorsal area without lateral protuberance; distal area without dorsomesal and dorsolateral processes; apicolateral processes rounded, bearing short stout setae (Fig. 2A); in dorsal view, V-shaped apicomeres extending anteriorly $\sim 1/3$ length of segment X; with a row of 5–7 short stout setae subapically. Inferior appendage, in lateral view, with broad basal portion, apical portion elongate, digitate, setose; basodorsal process rounded, smaller than basoventral process; dorsomesal process long and broad, apex acute, directed apicodorsad (Fig. 2A); in ventral view, basoventral process well developed, slightly asymmetrical, rounded, apex directed mesad (Fig. 2C); ventromesal process, in lateral view, indistinct (Fig. 2A); in ventral view, distinct with subtruncated apex (Fig. 2C). Phallic apparatus with a pair of strongly sclerotized, acuminate phallobase flanges, apex directed dorsad (Fig. 2D); phallotremal sclerite well developed, roughly Y-shaped in lateral view (Fig. 2D), with an anteriorly directed projection when viewed ventrally (Fig. 2E).

Type material. Holotype BRAZIL • ♂; Federal District, Planaltina, Estação Ecológica de Águas Emendadas, Córrego Tabatinga; 15.545361°S, 47.566222°W, 1047 m, 04–24 Apr. 2018, G.R. Desidério, C.A. Campos, F. Camelo legs.; Malaise trap; INPA.

Paratypes BRAZIL • 3 ♂♂; same data as for holotype (UMSP) • 4 ♂♂; Federal District, Planaltina, Estação Ecológica de Águas Emendadas, Córrego Tabatinga; 15.545361°S, 47.566222°W; 1047 m a.s.l.; 07–24 Apr. 2018; G.R. Desidério, C.A. Campos, F. Camelo legs.; INPA; • 4 ♂♂; same collection data as for preced-

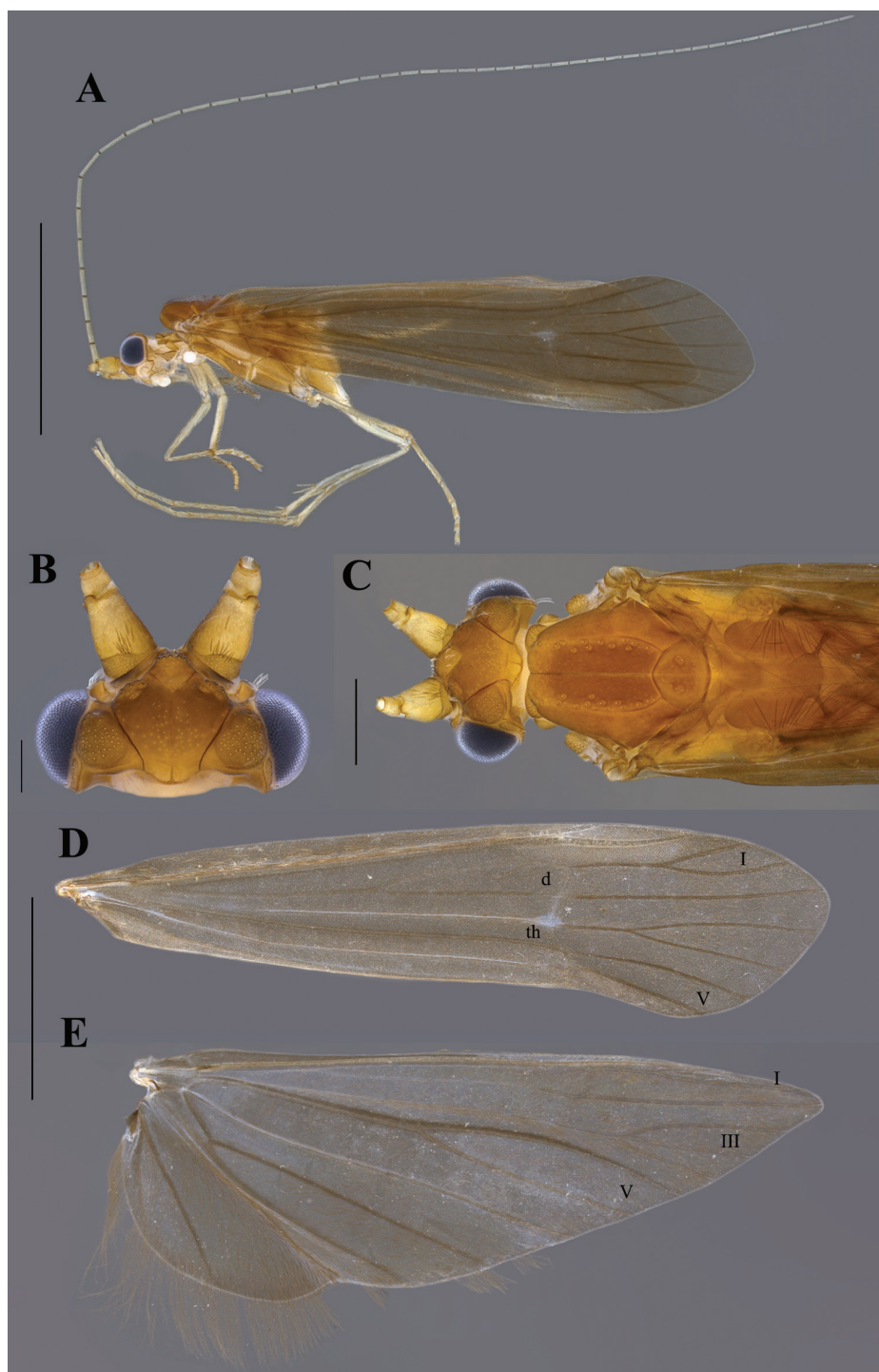


Figure 1. *Notalina* (*Neonotalina*) *ralphi* sp. nov., holotype, ♂ (INPA) **A** lateral habitus **B** head, dorsal view **C** head and thorax, dorsal view **D** forewing, right dorsal view **E** hind wing, right dorsal view. Scale bars: 0.2 mm (**B**); 0.5 mm (**C**); 2 mm (**A, D, E**).

ing; 24 Apr. – 07 May. 2018; UFBA; • 1 ♂; same collection data as for preceding; MZUSP; • 10 ♂♂; Tocantins, Palmas, Parque Estadual do Lajeado, Igarapé da Onça; 10.112361°S, 48.258639°W; 596 m a.s.l.; 06–11 May. 2017; N. Hamada, G. Amora legs; INPA; • 20 ♂♂; same collection data as for preceding; 19 Dec. 2017; INPA; •

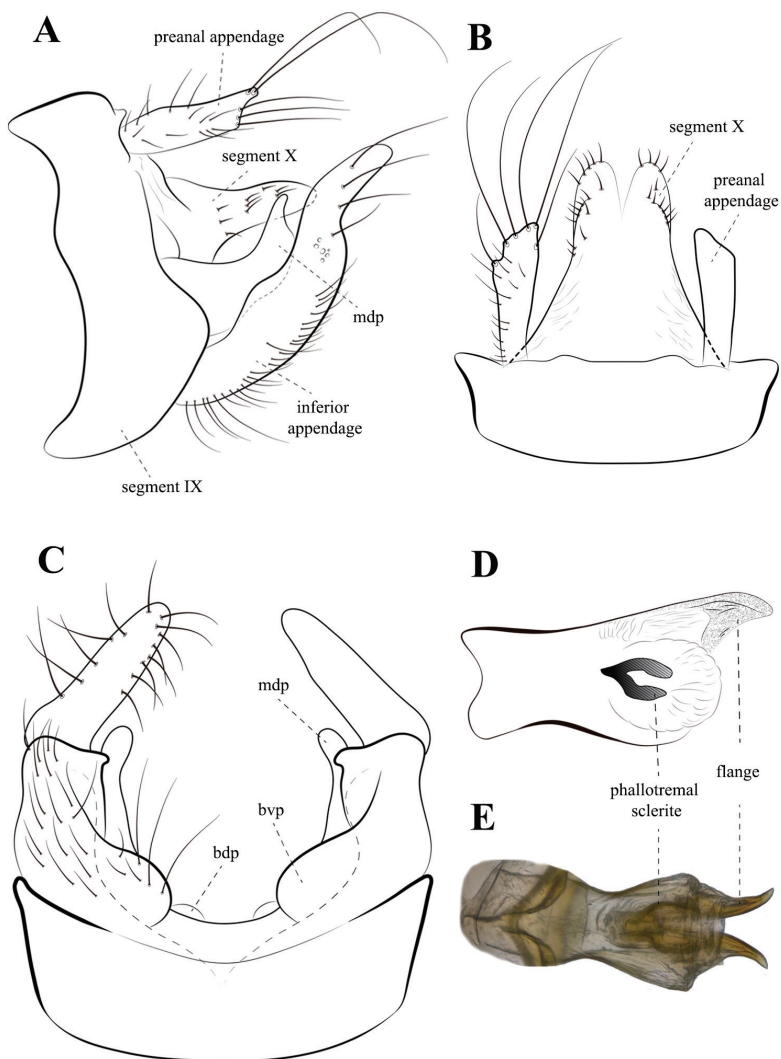


Figure 2. *Notalina (Neonotalina) ralphi* sp. nov., male genitalia, holotype **A** lateral view **B** dorsal view **C** ventral view **D** phallic apparatus, lateral view **E** phallic apparatus, ventral view. Abbreviations: bdp, basodorsal process; bvp, basoventral process; mdp, mesodorsal process.

16 ♂♂; same collection data as for preceding; UFBA; • 5 ♂♂; same collection data as for preceding; DZRJ; • 5 ♂♂; MZUSP; • 7 ♂♂; same collection data as for preceding; 18 Jan. 2018; DZUP.

Etymology. The new species is named in honor of Dr. Ralph W. Holzenthal (University of Minnesota, USA) in recognition of his efforts to the advancement of the knowledge on Neotropical caddisflies and his contributions in supervising new entomologists.

Distribution. BRAZIL: Cerrado biome (Federal District and Tocantins states) (Fig. 3).

New distribution record

Notalina (*Neonotalina*) *brasiliانا* Holzenthal, 1986

Notalina (*Neonotalina*) *brasiliانا* Holzenthal, 1986: 63 [type locality: Brazil, Minas Gerais, Serra do Caraça; MZUSP; ♂; ♀]; Paprocki et al. 2004: 13 [checklist]; Calor et al. 2006: 41 [distribution]; Paprocki and França 2014: 60 [checklist].

Material examined. BRAZIL – **Bahia** • 1 ♂; São Desidério, Rio das Fêmeas, BR-020, ponte (#02); 12.466667°S, 45.854583°W; 744 m a.s.l.; 23 Oct. 2008; N. Hamada, G. Fleck, C.A.S. Azevêdo, R. Kikuchi legs; INPA; – **Distrito Federal** • 1 ♂; Planaltina, Estação Ecológica de Águas Emendadas, Córrego Brejinho; 15.592583°S, 47.637333°W; 983 m a.s.l.; 04 Apr. – 24 May. 2018; G.R. Desidério, C.A. Campos, F. Camelo legs; INPA; • 4 ♂♂; Brasília, Parque Nacional de Brasília, Córrego Milho Cozido; 15.662500°S, 48.016556°W; 1076 m a.s.l.; 09 Apr. – 04 Jul. 2018; G.R. Desidério, C.A. Campos, F. Camelo legs; INPA.

Distribution. BRAZIL: *Cerrado* (Bahia [new record], Distrito Federal [new record] and Minas Gerais States) (Fig. 3).

Key to males of *Notalina* (*Neonotalina*) *brasiliانا* species group

- 1 Preanal appendage long, ~ 2/3 length of segment X (Holzenthal 1986: fig. 3B) **2**
- Preanal appendage short, ~ 1/2 length of segment X (Holzenthal 1986: figs 5B, 7B) **6**
- 2 Apicolateral processes of segment X mound-like, broad (Fig. 2B) **3**
- Apicolateral processes of segment X digitate, slender (Calor 2008: fig. 2E) ... **5**
- 3 Basal portion of inferior appendage slender in lateral view (Henriques-Oliveira et al. 2018: fig. 2A), ventromesal process roughly triangulate in lateral view (Henriques-Oliveira et al. 2018: fig. 2E) ***N. franciscana***
- Basal portion of inferior appendage broad in lateral view (Fig. 2A), ventromesal process rounded or inconspicuous in lateral view (Fig. 2D) **4**

- 4 Preanal appendages acuminate (Fig. 2B); segment IX broadest ventrolaterally (Fig. 2A); submedian area of segment X without lateral protuberance, distal area without dorsomesal processes (Fig. 2B); dorsomesal process of inferior appendage broad (Fig. 2A) ***N. ralphi* sp. nov.**
- Preanal appendages digitate (Henriques-Oliveira et al. 2012: fig. 3); segment IX broadest laterally (Henriques-Oliveira et al. 2012: fig. 2); submedian area of segment X with lateral protuberance, distal area with dorsomesal processes (Henriques-Oliveira et al. 2012: figs 2, 3); dorsomesal process of inferior appendage slender (Henriques-Oliveira et al. 2012: fig. 2) ***N. jordanensis***
- 5 Dorsomesal processes of segment X short, 1/2 the length of the ventrolateral processes (Calor 2008: fig. 2E); apical portion of inferior appendage ca. the same length as basal portion (Calor 2008: fig. 2A); ventromesal process roughly triangulate in lateral view (Calor 2008: fig. 2A); apex of phallotremal sclerite single-pointed (Calor 2008: fig. 2D) ***N. goianensis***
- Dorsomesal processes of segment X long, 1/3 longer than the ventrolateral processes (Holzenthal 1986: fig. 3B); apical portion of inferior appendage longer than basal portion (Holzenthal 1986: fig. 3A); ventromesal process blade-like in lateral view (Holzenthal 1986: fig. 3A); apex of phallotremal sclerite bi-pointed (Holzenthal 1986: fig. 3E) ***N. brasiliiana***
- 6 Apicodorsal area of segment IX with single or paired protuberances (Holzenthal 1986: fig. 8B; Calor et al. 2006: figs 1C, 2C); apicolateral processes of segment X digitate, slender (Calor et al. 2006: figs 1C, 2C) **7**
- Apicodorsal area of segment IX without protuberances; apicolateral processes of segment X mound-like, broad (Holzenthal 1986: figs 5B, 7B) **9**
- 7 Distal area of segment X with dorsomesal processes (Calor et al. 2006: fig. 1A, C); basal portion of inferior appendage slender (Calor et al. 2006: fig. 1A); basoventral process symmetrical, triangulate (Calor et al. 2006: fig. 1B); phallobase with basodorsal process (Calor et al. 2006: fig. 1D) ***N. froehlichii***
- Distal area of segment X without dorsomesal processes (Holzenthal 1986: fig. 8B); basal portion of inferior appendage broad (Holzenthal 1986, fig. 8A; Calor et al. 2006: fig. 2A), basoventral process asymmetrical, somewhat truncate (Holzenthal 1986: fig. 8C; Calor et al. 2006: fig. 2B); phallobase without basodorsal process **8**
- 8 Apicodorsal area of segment IX with single protuberance (Holzenthal 1986: fig. 8B); segment IX broadest laterally (Holzenthal 1986: fig. 8A); distal area of segment X without dorsolateral processes (Holzenthal 1986: fig. 8A, B); apical portion of inferior appendage shorter than basal portion in lateral view (Holzenthal 1986: fig. 8A); phallotremal sclerite slender, single-pointed (Holzenthal 1986: fig. 8E) ***N. hamiltoni***
- Apicodorsal area of segment IX with paired protuberances (Calor et al. 2006: fig. 2B); segment IX broadest ventrolaterally (Calor et al. 2006: fig. 2A); distal area of segment X with dorsolateral processes (Calor et al. 2006: fig. 2A, C); apical portion of inferior appendage longer than basal portion in lateral

- view (Calor et al. 2006: fig. 2A); phallotremal sclerite broad, bipointed (Calor et al. 2006: fig. 2E) *N. paulista*
- 9 Distal area of segment X with dorsolateral processes; without dorsomesal processes (Holzenthal 1986: fig. 7A, B); basal portion of inferior appendage broad, with ridge (Holzenthal 1986: fig. 7A), basoventral process symmetrical (Holzenthal 1986: fig. 7C); apex of phallotremal sclerite directed ventrally (Holzenthal 1986: fig. 7D) *N. cipo*
- Distal area of segment X without dorsolateral processes; with dorsomesal processes (Holzenthal 1986: fig. 5A, B); basal portion of inferior appendage slender, without ridge (Holzenthal 1986: fig. 5A), basoventral process asymmetrical (Holzenthal 1986: fig. 5C); apex of phallotremal sclerite directed dorsally (Holzenthal 1986: fig. 5D) *N. morsei*

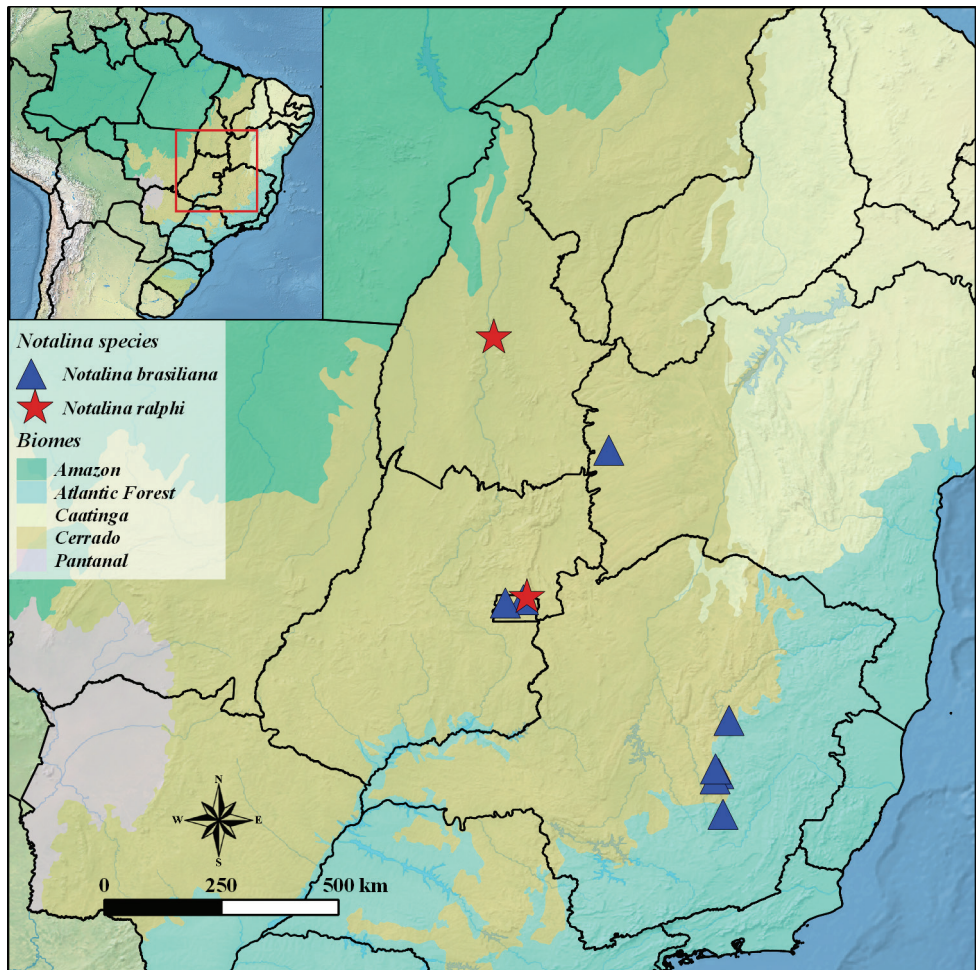


Figure 3. Geographical distribution map of *Notalina* (*Neonotalina*) *brasiliana* Holzenthal, 1986 and *Notalina* (*Neonotalina*) *ralphi* sp. nov.

Discussion

The species diversity of *N. (Neonotalina)* in Brazil is concentrated in the Atlantic Forest and Cerrado biomes of Southeastern region with eight species (*N. brasiliانا*, *N. cipo*, *N. franciscana*, *N. froehlichii*, *N. hamiltoni*, *N. jordanensis*, *N. morsei* and *N. paulista*). So far, only one species of *N. (Neonotalina)* has been recorded from the Central-West (*N. goianensis*) and Northeast (*N. cipo*) regions (Calor 2008; Dias et al. 2015). However, with the discovery of *N. ralphi* sp. nov. described here and the new records of *N. brasiliانا*, the number of *N. (Neonotalina)* species recorded from the Central-West and Northeast regions is increased to two species each, bringing the total number of species of the subgenus for Brazilian Cerrado biome to eight (Table 1).

The occurrence of *N. (Neonotalina)* species in the Federal District represents the first record of Integripalpia for the federative unit. Previously, only seven species of Anulipalpia were known (Santos et al. 2021). In addition, the record of *N. ralphi* sp. nov. in Tocantins state is the northernmost record of the *brasiliانا* species group, previously established by *N. goianensis* from the Chapada dos Veadeiros, Goiás state (Calor 2008). *Notalina (Neonotalina) brasiliانا* was previously known only from the Serra do Caraça and Serra do Cipó (Holzenthal 1986), two mountainous regions located in the southern portion of the Espinhaço mountain range, in the Minas Gerais state. Calor et al. (2006) reported this species for other mountains of Minas Gerais state, also in Cerrado biome (Parque Estadual do Rio Preto and Serra do Abreu). Here, the distribution range of this species is extended to Cerrado biome in the Bahia state and Federal District, representing the first records for Northeast and Central-West regions of Brazil, respectively.

Notalina (Neonotalina) ralphi sp. nov. has strong affinity to the *brasiliانا* species group of Holzenthal (1986) and can be considered a member of this group based on the characteristics of the phallic apparatus. Although its morphological similarities and differences are assessed for the adult stage with *N. franciscana*, the phylogenetic relationships with other species in the *brasiliانا* species group should be evaluated under a combined morphological/molecular phylogenetic approach.

Table 1. Distribution of *Notalina (Neonotalina)* species recorded from Brazil. Abbreviations for Brazilian states: BA = Bahia; Federal District = DF; ES = Espírito Santo; Goiás = GO; MG = Minas Gerais; RJ = Rio de Janeiro; SP = São Paulo; Tocantins = TO.

Species	Region (state)	Biome
<i>N. brasiliانا</i> Holzenthal, 1986	Southeast (MG); Central-West (DF); Northeast (BA)	Cerrado
<i>N. cipo</i> Holzenthal, 1986	Southeast (MG); Northeast (BA)	Atlantic Forest; Cerrado
<i>N. franciscana</i> Henriques-Oliveira, Rocha & Nessimian, 2018	Southeast (MG)	Cerrado
<i>N. froehlichii</i> Calor & Holzenthal, 2006	Southeast (MG)	Cerrado
<i>N. goianensis</i> Calor, 2008	Central-West (GO)	Cerrado
<i>N. hamiltoni</i> Holzenthal, 1986	Southeast (SP)	Atlantic Forest
<i>N. jordanensis</i> Henriques-Oliveira, Spies & Dumas, 2012	Southeast (SP)	Atlantic Forest
<i>N. morsei</i> Holzenthal, 1986	Southeast (ES, MG, RJ, SP)	Atlantic Forest; Cerrado
<i>N. paulista</i> Calor & Holzenthal, 2006	Southeast (MG, SP)	Atlantic Forest; Cerrado
<i>N. ralphi</i> sp. nov.	Central-West (DF); North (TO)	Cerrado

Therefore, this study highlights the need for more taxonomic studies focused on *N.* (*Neonotalina*) in Brazil, especially in the poorly sampled Amazon, Caatinga, Pampas, and Pantanal biomes, as well as an updated phylogenetic study including species newly described, morphological characters of immature stages, and multi-locus molecular sequence data.

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The Trichoptera of Panama. XIX. Additions to and a review of the genus *Leucotrichia* (Trichoptera, Hydroptilidae) in Panama

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Abstract

Prior to 2016, three species of caddisflies in the genus *Leucotrichia* (Trichoptera: Hydroptilidae) were known from Panama. Subsequently, one new species and four new country records were added to Panama's fauna. Herein, four new species are described (*Leucotrichia cortadera* **sp. nov.**, *L. holzenthali* **sp. nov.**, *L. luma* **sp. nov.**, *L. ruiteri* **sp. nov.**) and two new country records added for Panama (*L. botosaneanui* Flint, 1996, *L. hispida* Thomson & Holzenthal, 2015). The resulting total of 14 species makes Panama the most species-rich country for this genus. Panama's species assemblage is most similar to Costa Rica and Mexico. However, the similarities among faunas in all these countries is very low (< 35%). Thus, more new country records are possible with additional collecting. Recent collections (2015–2021) of new caddisfly species and country records in this genus were effected primarily by use of Malaise traps. Our collections also evidenced multiple species from the same collecting site, with seven species each found in both lowland and mid-altitude sites. Investigation of the distribution of *Leucotrichia* species with altitude reveals a preference by several species for higher altitude locations. Additional Malaise trap collections over extended time periods are needed to verify the validity of all observations and preliminary conclusions made to date.

Keywords

Caddisflies, collection methods, Leucotrichiinae, new species, species coexistence

Introduction

The genus *Leucotrichia* Mosely, 1934 is in the microcaddisfly family Hydroptilidae and subfamily Leucotrichiinae. Known only in the New World, species of this genus are found throughout the continental United States, Central America, South America, and much of the Caribbean (Thomson and Holzenthal 2015). The background and development of *Leucotrichia* as a genus, its relationships with other Leucotrichiinae genera, and the composition and relationships within the genus can best be understood by referencing Flint (1970), Marshall (1979), Olah and Johanson (2011), Thomson and Holzenthal (2012, 2015), Santos et al. (2016), and Holzenthal and Calor (2017). The latter publication lists 44 extant species and one fossil species, *Leucotrichia adela* Wells & Wichard, 1989 from Dominican amber. Since then, one new species has been added to the genus (Thomson and Armitage 2021).

The larval stages are dorsoventrally depressed and occupy lotic-erosional habitats. The first four instars are free-living, with these stages completed fairly rapidly (less than two weeks). This is followed by a fifth instar that builds an elliptical, flattened case, usually found firmly affixed to large rocks and boulders (Wiggins 1996a). These silken cases are purse-like and have round openings at either end. During pupation, the openings are sealed, with one subsequently cut open for egress by the pharate adult. Often cases are repaired and reused by subsequent generations (Wiggins 1996b). The larval diet of *Leucotrichia* species consist of periphyton and fine particulate organic matter, and they have been categorized as both scrapers and collector-gatherers. Adults can be collected in UV light traps or, more commonly, by sweeping streamside vegetation (Holzenthal and Calor 2017). We have found Malaise traps to be most productive.

Leucotrichia viridis Flint, 1967 was the first species of this genus recorded from Panama (Flint 1970). In that same publication, *L. chiriquiensis* Flint, 1970 and *L. fairchildi* Flint, 1970 became the first two species originally described from Panama. These three species remained the extent of our knowledge for this genus in Panama until Armitage et al. (2016) added *L. melleopicta* Mosely, 1934, the nominate species for the genus, which was described from Mexico. Subsequently, new additions were made: *L. extraordinaria* Bueno-Soria, Santiago-Fragoso & Barba-Álvarez, 2001 and *L. mutica* Flint, 1991 by Armitage et al. (2018); *L. rhomba* Thomson & Holzenthal, 2015 by Harris and Armitage (2019); and, recently a new species, *L. cultrata* Thomson & Armitage, 2021. Herein, we add four new species and two new country records, bringing the total number of species known from Panama to 14. Further, based on our discoveries for this genus in Panama, we have amassed sufficient data to discuss and perhaps speculate on the topics of potential diversity, coexistence, altitudinal distribution, and geographical affinities.

Materials and methods

Single, overnight collections were made using UV light traps (Calor and Mariano 2012). Multiple-day collections were made employing Malaise traps over four or more 24-hour periods. Collection locations are presented in Fig. 17.

Morphological terminology used for male genitalia generally follows that of Marshall (1979), as mirrored by Thomson and Holzenthal (2015). For simplicity, paired structures are discussed in the singular. Procedures for specimen preparation followed those explained in detail by Blahnik et al. (2007). For specimen examination and illustration, cleared genitalia were placed in a watch glass with glycerin and cotton. Genitalia were examined with an Olympus BX43 compound microscope at 250–500 × magnification. Structures were traced in pencil with the use of a camera lucida (drawing tube) mounted on the microscope. Pencil sketches were scanned (Fujitsu ScanScap S1500M scanner) and were then edited and digitally inked in Adobe Photoshop and Illustrator (CS5.1). Electronic “drawing” was completed with the aid of a graphics tablet (Bamboo Pen, Wacom Co., Ltd.). Species descriptions were constructed using the program DELTA (Dallwitz et al. 2016).

All specimens included in this publication are stored in 80% alcohol. Holotypes of the species described are deposited in the Universidad de Panamá Museo de Invertebrados (**MIUP**). Other specimens are deposited in the University of Minnesota Insect Collection (**UMSP**), the Museo de Peces de Agua Dulce e Invertebrados (**MUPADI**) of the Universidad Autónoma de Chiriquí (**UNACHI**), or the Colección Zoológica Dr. Eustorgio Méndez (**COZEM**) of the Instituto Conmemorativo Gorgas de Estudios de la Salud (Gorgas Institute).

Results

The distribution of species among the 19 unique locations within Panama wherein the genus *Leucotrichia* has been collected to date is presented in Table 1, which complements Fig. 17. We have sampled, to varying degrees, 16 of the 52 major cuencas (watersheds) in Panama and found species of *Leucotrichia* in eight of these (Fig. 17; Table 2). In addition, we have found them in all five of the administrative units (of a total of 14: 10 provinces and four comarcas) which have been sampled to date.

In Table 2, we provide additional information about the major watersheds (cuencas) in which *Leucotrichia* has been collected in Panama. The number of unique locations in which each species has been found to date is presented in Table 3. In Table 4, we present the species which potentially could be found in Panama as new country records. These species were selected by targeting countries in which shared species currently occur. The distribution by altitude for each species known from Panama is presented in Fig. 18. Whereas, most species have been collected in a somewhat broad spectrum of altitudes, particularly in the low to mid-altitude range, at least a few appear to be restricted to higher altitudes. We should note that Fig. 18 was constructed from unique records, single records from each sample location/stream, and does not reflect multiple records from the same sites over a single or multiple year period.

A perusal of the country distributions in the species accounts given below is not overly informative. Only one species, *L. fairchildi*, is somewhat widespread.

Table 1. Species associated with each collected stream. See Fig. 17 for locations and Table 2 for watershed (cuenca) information.

Label	Cuenca	Stream	Species
1	102	Rio Candela-Finca Felix	<i>Leucotrichia chirquiensis</i> <i>Leucotrichia hispida</i> <i>Leucotrichia ruiteri</i>
2	102	Quebrada Norte	<i>Leucotrichia chirquiensis</i> <i>Leucotrichia cultrata</i>
3	102	Afl. Rio Chiriqui Viejo	<i>Leucotrichia hispida</i>
4	102	Rio Chiriqui Viejo	<i>Leucotrichia hispida</i>
5	106	Rio Chirigagua	<i>Leucotrichia extraordinaria</i>
6	108	Quebrada del Guayabo	<i>Leucotrichia hispida</i>
7	108	Quebrada Grande	<i>Leucotrichia extraordinaria</i> <i>Leucotrichia mutica</i>
8	108	Quebrada Jaramillo	<i>Leucotrichia botosaneanui</i> <i>Leucotrichia cortadera</i> <i>Leucotrichia cultrata</i> <i>Leucotrichia extraordinaria</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia rhomba</i> <i>Leucotrichia ruiteri</i>
9	108	Rio Majagua	<i>Leucotrichia cortadera</i> <i>Leucotrichia cultrata</i> <i>Leucotrichia extraordinaria</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia rhomba</i> <i>Leucotrichia viridis</i>
10	93	Quebrada Martinez	<i>Leucotrichia fairchildi</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia mutica</i>
11	93	Quebrada Rambala	<i>Leucotrichia cultrata</i> <i>Leucotrichia extraordinaria</i> <i>Leucotrichia fairchildi</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia mutica</i> <i>Leucotrichia rhomba</i> <i>Leucotrichia viridis</i>
12	97	Rio Llanito	<i>Leucotrichia melleopicta</i>
13	97	Rio Piedra de Moler	<i>Leucotrichia extraordinaria</i> <i>Leucotrichia fairchildi</i> <i>Leucotrichia holzenthali</i> <i>Leucotrichia melleopicta</i>
14	97	Rio Calovebora	<i>Leucotrichia cultrata</i> <i>Leucotrichia extraordinaria</i>
15	97	afl. Rio Calovebora	<i>Leucotrichia extraordinaria</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia mutica</i>
16	132	Rio Mulaba, 2do Brazo	<i>Leucotrichia extraordinaria</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia rhomba</i> <i>Leucotrichia ruiteri</i>

Label	Cuenca	Stream	Species
17	132	Rio Mulaba, afl. 1er Brazo	<i>Leucotrichia cultrata</i> <i>Leucotrichia melleopicta</i> <i>Leucotrichia viridis</i>
18	115	Rio Chileno	<i>Leucotrichia cultrata</i> <i>Leucotrichia luma</i>
19	138	Rio Sajalice	<i>Leucotrichia luma</i>

Table 2. Major watersheds in which *Leucotrichia* species have been collected.

Cuenca No.	Major River	Drainage Area (km ²)	Receiving Body
93	Guariviara	2121	Caribbean Sea
97	Calovébora	485	Caribbean Sea
102	Chiriqui Viejo	1376	Pacific Ocean
106	Chico	593	Pacific Ocean
108	Chiriqui	1905	Pacific Ocean
115	Chagres	3338	Caribbean Sea
132	Santa Maria	3326	Pacific Ocean
138	Chame	1476	Pacific Ocean

Table 3. Number of unique streams (*max* = 19) in which each *Leucotrichia* species was found.

Species	No. of Streams
<i>Leucotrichia extraordinaria</i>	9
<i>Leucotrichia melleopicta</i>	9
<i>Leucotrichia cultrata</i>	7
<i>Leucotrichia hispida</i>	4
<i>Leucotrichia mutica</i>	4
<i>Leucotrichia rhomba</i>	4
<i>Leucotrichia fairchildi</i>	3
<i>Leucotrichia ruiteri</i>	3
<i>Leucotrichia viridis</i>	3
<i>Leucotrichia chirquiensis</i>	2
<i>Leucotrichia cortadera</i>	2
<i>Leucotrichia luma</i>	2
<i>Leucotrichia botosaneanui</i>	1
<i>Leucotrichia holzenthali</i>	1
Means:	2.84 species stream ⁻¹ 3.86 streams species ⁻¹

Six species occupy portions of a distributional axis from Mexico southeast to northern South America (Colombia, Venezuela). Two other species have a distribution which involves (*L. botosaneanui*) or includes (*L. fairchildi*) Trinidad and Panama, which is orthogonal to this more common northwest/southeast axis. Six *Leucotrichia* species currently are endemic to Panama, including the four species described herein.

Table 4. Species of *Leucotrichia* which could potentially be found in Panama, based on the current range distributions of its species.

Species	Current distribution
<i>L. melleopicta</i> group	
<i>Leucotrichia angelinae</i> Thomson & Holzenthal, 2015	Venezuela
<i>Leucotrichia ayura</i> Flint, 1991	Colombia
<i>Leucotrichia brochophora</i> Flint, 1991	Colombia
<i>Leucotrichia denticulata</i> Thomson & Holzenthal, 2015	Mexico
<i>Leucotrichia dianeae</i> Thomson & Holzenthal, 2015	Costa Rica
<i>Leucotrichia dinamica</i> Bueno-Soria, 2010	Mexico
<i>Leucotrichia forrota</i> Oláh & Johanson, 2011	Ecuador, Peru
<i>Leucotrichia fulminea</i> Thomson & Holzenthal, 2015	Ecuador
<i>Leucotrichia inflaticornis</i> Botosaneanu, in Botosaneanu and Alkins-Koo 1993	Trinidad
<i>Leucotrichia inops</i> Flint, 1991	Colombia, Ecuador
<i>Leucotrichia interrupta</i> Flint, 1991	Colombia
<i>Leucotrichia kateae</i> Thomson & Holzenthal, 2015	Venezuela
<i>Leucotrichia limpia</i> Ross, 1944	Costa Rica, Mexico, U.S.A.
<i>Leucotrichia padera</i> Flint, 1991	Colombia
<i>Leucotrichia pectinata</i> Thomson & Holzenthal, 2015	Ecuador
<i>Leucotrichia repanda</i> Thomson & Holzenthal, 2015	Venezuela
<i>Leucotrichia riostoumae</i> Thomson & Holzenthal, 2015	Ecuador
<i>Leucotrichia sidneyi</i> Thomson & Holzenthal, 2015	Venezuela
<i>Leucotrichia tapantia</i> Thomson & Holzenthal, 2015	Costa Rica
<i>Leucotrichia termitiformis</i> Botosaneanu, in Botosaneanu and Alkins-Koo 1993	Trinidad
<i>Leucotrichia tritoven</i> Flint, 1996	Guyana, Tobago, Trinidad, Venezuela
<i>Leucotrichia zopilote</i> (Holzenthal & Harris, 1999)	Costa Rica
<i>L. pictipes</i> group	
<i>Leucotrichia pictipes</i> Banks, 1911	Mexico, U.S.A.
<i>Leucotrichia imitator</i> Flint, 1970	Costa Rica, Guatemala, Mexico
<i>Leucotrichia sarita</i> Ross, 1944	Costa Rica, El Salvador, Grenada, Guatemala, Mexico, Nicaragua, U.S.A.

Confining ourselves primarily to countries with four or more species, we calculated similarity values and constructed a cluster diagram to show the relative affinity among seven Latin American countries (Fig. 19). Brazil, with three species, was included because of its role (Santos et al. 2016) in the evolution of the subfamily, tribe, and perhaps genus over geologic time. First, as expanded upon below, Brazil shares no species with other countries for this genus. The second result of the analysis is that none of the affinities among countries reach the 50% level. Costa Rica and Mexico approached that value, but fell short. Panama, currently with the most species of any country, is only ~ 35% similar to the combined diversity of Costa Rica and Mexico, and even less with the other countries presented herein.

Taxonomy

Diagnosis of *Leucotrichia*

As expanded upon in the Discussion section, we think it is difficult at the present time to provide a definitive diagnosis for this genus based on adult characters. *Leucotrichia* is characterized by a prominent row of setae along the posterior margin of segment IX; a ventral process on abdominal segment VII in almost all species; inferior appendages simple, fused or not, bearing a dorsal spine in most species; and the subgenital plate with a ventral arm, accompanied by a dorsal arm in ca. half of the species.

With this equivocal diagnosis, we present fourteen species of *Leucotrichia* which we have found to date in Panama. Included are four new species to science and two first country records for Panama. Several of the species defined below bear morphological characters which are exceptions to those that served heretofore as diagnostic for this genus. Flint (1970), in his generic revision of this genus, identified characters which distinguish two species groups: *L. melleopicta* Group and *L. pictipes* Group. Our presentation of species below is organized within these two subgeneric groupings. Additional information about each species, including citations in which each species is referenced, can be found in Holzenthal and Calor (2017).

The plates for three species (*L. melleopicta*, *L. mutica*, and *L. rhomba*) were modified from Harris and Armitage (2019). We did this purposefully because these reflect study of numerous specimens from different parts of Panama, as well as exhibiting some small variations with those provided in Thomson and Holzenthal (2015). Drawings in the latter publication were sometimes based on a single individual, and not from Panama. We suggest researchers reference plates in both publications when identifying material from outside Panama. Further rationale and discussion of this subject is provided in the Remarks section under the species accounts below for the three taxa listed above.

General drawings for unmodified *Leucotrichia* body parts are given in Fig. 1. Examples of body parts which are modified in some species are presented in Fig. 2.

Leucotrichia melleopicta group

Leucotrichia botosaneanui Flint, 1996

Fig. 3

Diagnosis. This species is similar to *L. chiriquiensis*, *L. hispida* Thomson & Holzenthal, 2015, and *L. viridis*, three species that also occur in Panama. The phallus of all four species has a similar appearance, due to the elongate basal supports of the midlength complex and the small pair of membranous, apical lobes (Fig. 3E, F). *Leucotrichia botosaneanui* can be distinguished by the small, double-pointed mesoventral process on sternum VII, which is longer and much more prominent in the other species.

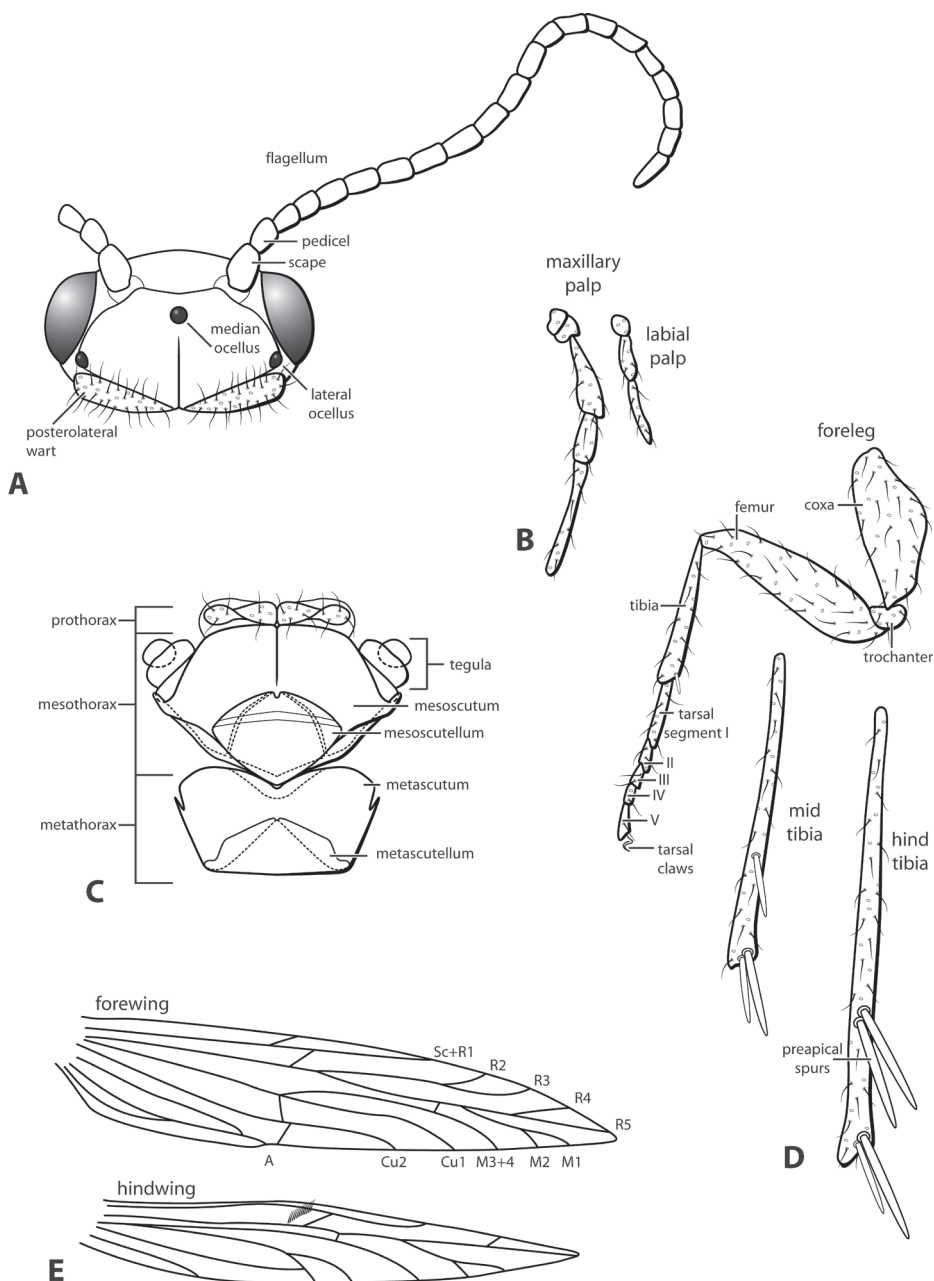


Figure 1. Unmodified *Leucotrichia* **A** head and antennae, dorsal **B** palps **C** thorax, dorsal **D** legs and spur formula (1, 3, 4) **E** wings. Modified from Thomson and Holzenthal (2015).

Material examined. PANAMA: Chiriqui Province • 1 male; Cuenca 108; Boquete District; Quebrada Jaramillo; Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.; 19–25 Apr. 2018; K. Collier, leg.; Malaise trap; in alcohol; MUPADI.

Distribution. Panama, Trinidad, Tobago.

***Leucotrichia chiriquiensis* Flint, 1970**

Figs 2B, 4

Diagnosis. *Leucotrichia chiriquiensis* is most similar to *L. botosaneanui*, *L. hispida*, and *L. viridis*, based on a similar appearance of the phallus, as discussed under *L. botosaneanui*. This species can most swiftly be identified as distinct from the others based on the structural modifications of the antennae and head.

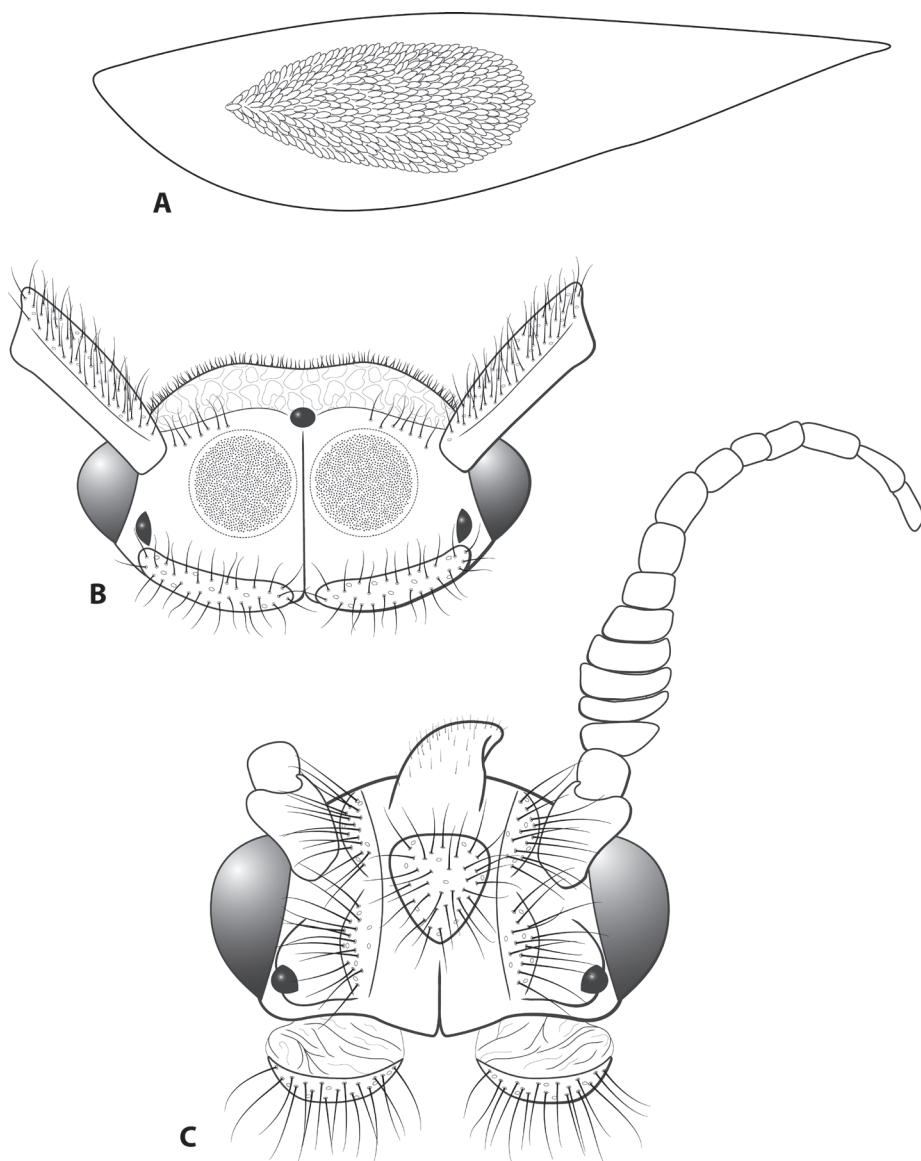


Figure 2. Modifications **A** Forewing, *Leucotrichia ruiteri* sp. nov. **B** head and scape, *Leucotrichia chiriquiensis* Flint, 1970 **C** head and antennae, *Leucotrichia fairchildi* Flint, 1970. Fig. 2B and 2C modified from Thomson and Holzenthal (2015).

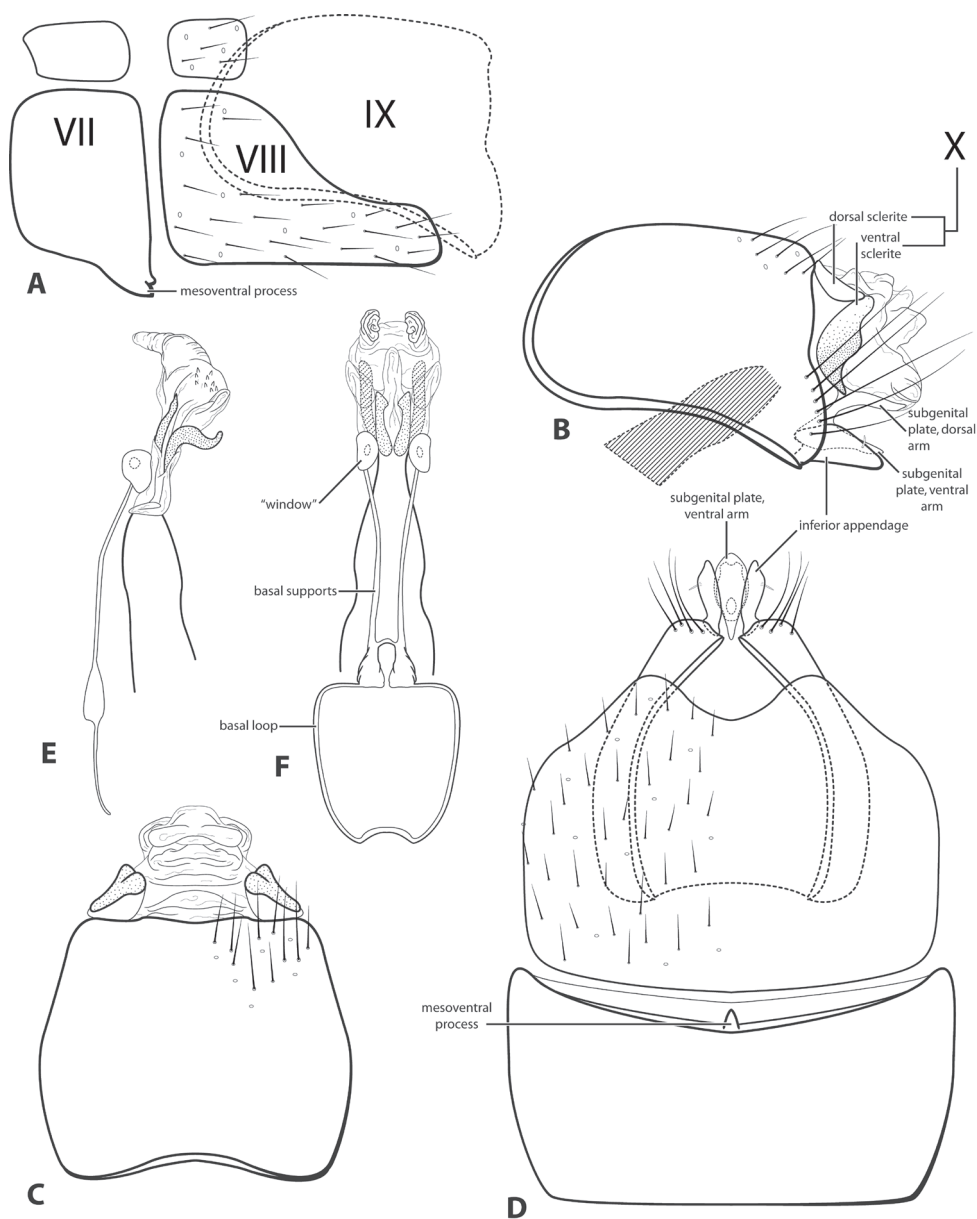


Figure 3. *Leucotrichia botosaneanui* Flint, 1996. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

Material examined. **PANAMA: Chiriqui Province** • 2 males; Cuenca 102; Renacimiento District; La Amistad International Park, Río Candela, Finca Felix, PSP-SCB-PILA-C102-2017-021; 8.890557°N, 82.61201°W; 2,128 m a.s.l.; 25 Jan. 2015; C. Nieto, E. Pérez, A. Cornejo, leg.; UV light trap; in alcohol; **COZEM** • *ibid.*, 2 males; Tierras Altas District; Mount Totumas Cloud Forest and Biological Reserve,

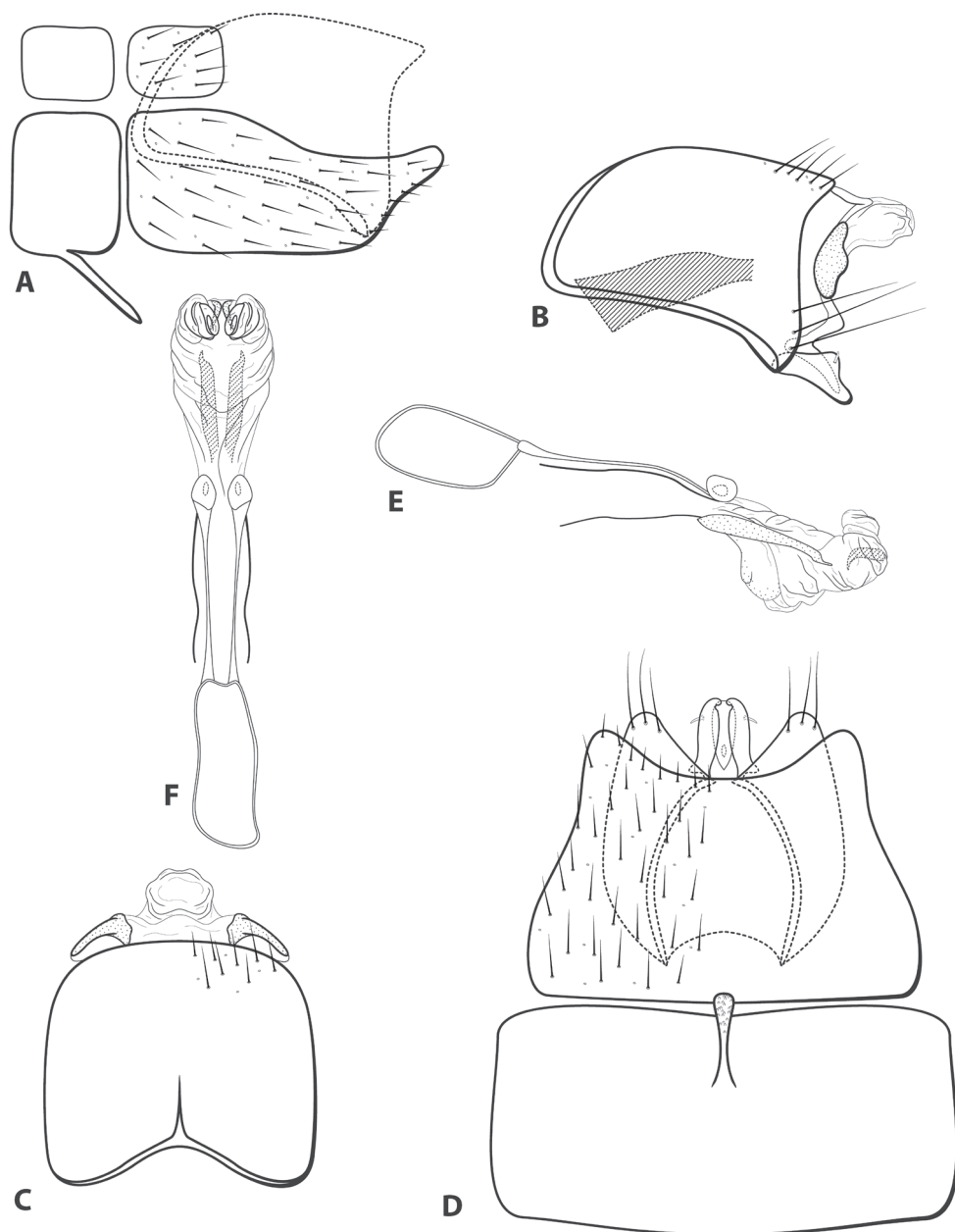


Figure 4. *Leucotrichia chiriquiensis* Flint, 1970. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

Quebrada Norte; 8.873613°N, 82.690512°W; 1,709 m a.s.l.; 26 Apr.–10 May 2015; B. Armitage, T. Arefina-Armitage, leg.; Malaise trap; MUPADI • *ibid.*, 5 males; 28 Jan.–2 Feb. 2018; J. Dietrich, leg.; Malaise trap; MUPADI • *ibid.*, 3 males; 16–20 Feb. 2018; MUPADI • *ibid.*, 1 male; 16–20 Mar. 2018; MUPADI • *ibid.*, 1 male; 10–15

Jul. 2018; MUPADI • *ibid.*, 2 males; 9–12 Sep. 2018; MUPADI • *ibid.*, 2 males; 8–11 Nov. 2018; UMSP.

Distribution. Panama.

***Leucotrichia cortadera* sp. nov.**

<http://zoobank.org/9EBB00CA-9C88-4BCC-9A07-8C5A250CF95E>

Fig. 5

Type locality. PANAMA: Chiriqui Province: Cuenca 108; Boquete District; Quebrada Jaramillo, Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.

Type material. Holotype: male, PANAMA: Chiriqui Province: Cuenca 108; Boquete District; Quebrada Jaramillo, Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.; 16–20 Jun. 2018, K. Collier, leg.; Malaise trap; in alcohol; MIUP-001-T-2021.

Paratype: PANAMA: Chiriqui Province: 1 male; Dolega District, Río Majagua, Banquito de Palmira, Potrerillos; 8.68093°N, 82.53276°W; 840 m a.s.l.; 19 Jul.–1 Aug. 2019, Y. Aguirre, T. Ríos, leg.; Malaise trap (M002); in alcohol; UMSP.

Diagnosis. *Leucotrichia cortadera* sp. nov. is similar to *L. fulminea* Thomson & Holzenthal, 2015, a species endemic to Ecuador. Both species bear a pair of large, distinct sclerotized plates on the phallus apex. *Leucotrichia cortadera* can be separated by the small spines present on the dorsolateral surface of the phallus apex, which are absent in *L. fulminea*. Additionally, the inferior appendages are separate in *L. fulminea*, while they are fused in *L. cortadera*.

Description. Male. Length of forewing 2.1 mm ($n = 2$). Wings unmodified. Head unmodified, with three ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown. **Genitalia.** Abdominal sternum VII mesoventral process with enlarged apex (Fig. 5A, D). Sternum VIII with rounded posteroventral production in lateral view (Fig. 5A); in ventral view, posterior margin concave with broadly rounded mesal projection (Fig. 5D). Segment IX anterolateral margin convex, posterolateral margin straight with slight irregularity (Fig. 5B); dorsally, anterior margin concave, posterior margin concave with broadly rounded mesal projection (Fig. 5C). Tergum X with dorsal sclerite small, irregular; ventral sclerite with upper half rounded and bent posteriad; membranous apex suborbicular (Fig. 5B, C). Subgenital plate with dorsal arm simple, extending dorsad, apex acute (Fig. 5B); ventral arm simple, apex with emargination, in ventral view slightly restricted mesally, apex with broad emargination (Fig. 5B, D). Inferior appendage narrow basally, broadest submesally, with single dorsal subapical spine (Fig. 5B); ventrally entirely fused, broadest mesally, apex rounded with small pointed mesal emargination (Fig. 5D). Phallus tubular basally, constricted at midlength with median complex bearing spherical “windows”; apex membranous and bearing pair of large, acute sclerotized plates and numerous small apical spines on dorsal and lateral surface (Fig. 5E, F).

Distribution. Panama.

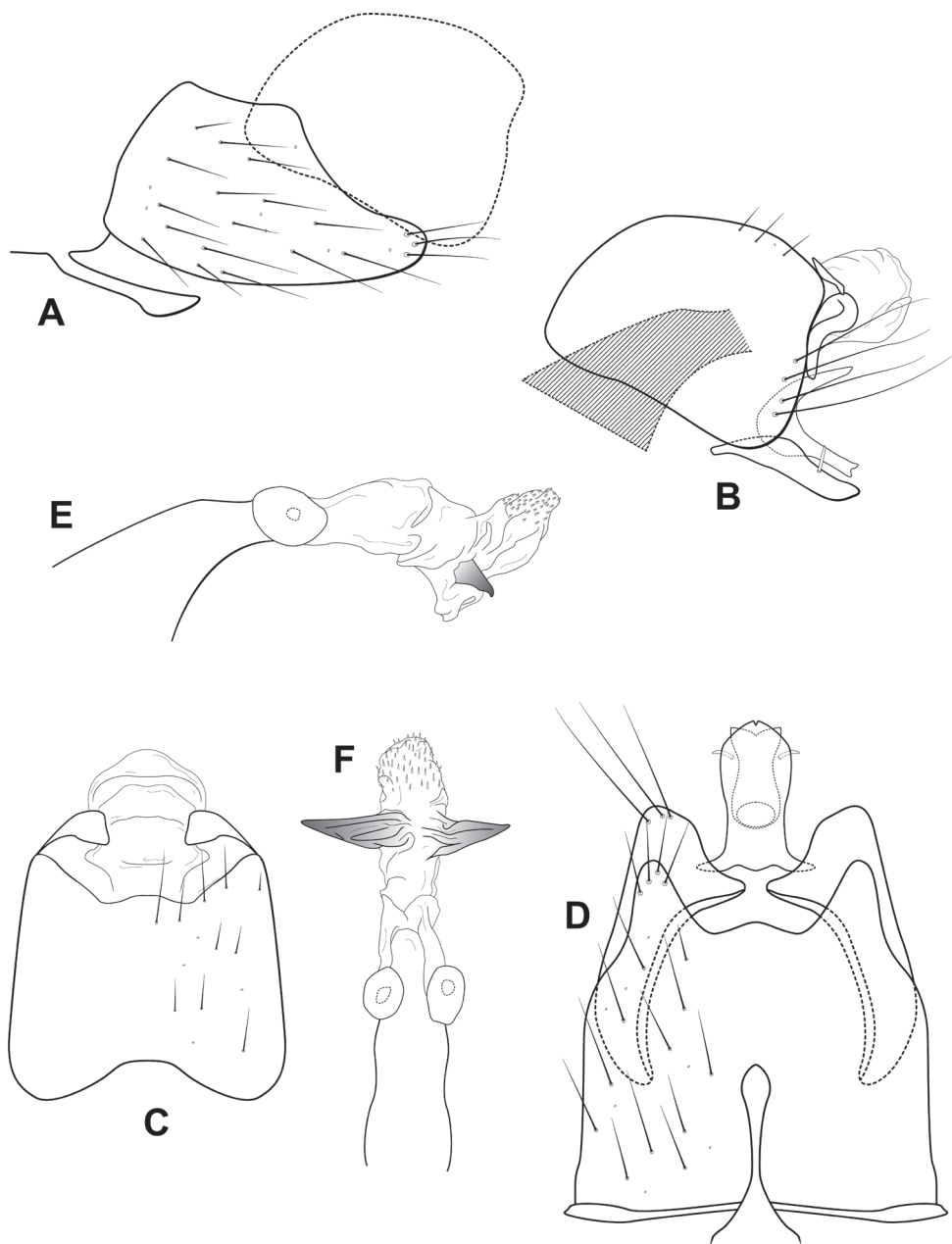


Figure 5. *Leucotrichia cortadera* sp. nov. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal.

Etymology. The specific epithet is derived from *cortadera*, Spanish for “knife, cutting instrument”, referring to the shape of the large sclerotized plates found on the phallus apex.

***Leucotrichia cultrata* Thomson & Armitage, 2021**

Fig. 6

Diagnosis. *Leucotrichia cultrata* is similar to *L. hispida* and *L. viridis*. The phallus of all three species shares a similar appearance with the basal loop of the median complex extended on basal supports and a ventral “bulge” to the membranous apex. The mesoventral process of sternum VII can be used to separate the three, being long and digitate in *L. cultrata*, bearing a tuft of prominent apical setae in *L. hispida*, and enlarged and apically blunt when viewed ventrally in *L. viridis*.

Material examined. **PANAMA: Bocas del Toro Province** • 2 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala, Rambala Jungle Lodge, 8.91627°N, 82.15469°W; 120 m a.s.l.; 9 Aug. 2014; E. Carlson, leg.; UV light trap; in alcohol; MUPADI • *ibid.*, 5 males; 28 Mar. 2015 • *ibid.*, 2 males; 31 Mar.–11 Apr. 2015; Malaise trap • *ibid.*, 17 males; 12–15 Nov. 2017. **Chiriqui Province** • 1 male; Cuenca 102; Tierras Altas District; Mount Totumas Cloud Forest and Biological Reserve, Quebrada Norte; 8.873613°N, 82.690512°W; 1,709 m a.s.l.; 10–15 Jul. 2018; J. Dietrich, leg.; Malaise trap; in alcohol; MIUP • *ibid.*, 2 males; 8–11 Nov. 2018; UMSP • *ibid.*, 1 male; Cuenca 108; Dolega District, Río Majagua, Banquito de Palmira, Potrerillos; 8.68083°N, 82.53250°W; 840 m a.s.l.; 28 Feb.–14 Mar. 2019, Y. Aguirre, T. Ríos, leg.; Malaise trap (M001); in alcohol; MUPADI • *ibid.*, 1 male; Quebrada Jaramillo, Finca Monterey; 8.76320°N, 82.41383°W; 1,214 m a.s.l.; 8–12 May 2018; B. Armitage, T. Arefina-Armitage, leg.; Malaise trap; in alcohol; MUPADI. **Panama Oeste Province** • 2 males; Cuenca 115; Altos de Campana National Park, Río Chileno, PSPSCB-PNAC-C115-2018-028; 8.71650°N, 80.00740°W; 497 m a.s.l.; 23–31 May 2018; T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; COZEM. **Veraguas Province** • 2 males; Cuenca 097; Santa Fe District; Santa Fe National Park; Río Calovébora, PSPSCB-PNSF-C097-2017-006; 8.55038°N, 81.16486°W; 461 m a.s.l.; 23–27 Apr. 2017, A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise Trap; in alcohol; COZEM • *ibid.*, 1 male; Cuenca 132; Río Mulaba, afl. 1er Brazo, PSPSCB-PNSF-C132-2017-008; 8.51706°N, 81.12140°W; 770 m a.s.l.; 19–23 Apr. 2017; T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise trap; in alcohol; COZEM.

Distribution. Panama.

***Leucotrichia extraordinaria* Bueno-Soria, Santiago-Fragoso & Barba-Álvarez, 2001**

Fig. 7

Diagnosis. This species is similar to *L. dianeae* Thomson & Holzenthal, 2015 and *L. tapantia* Thomson & Holzenthal, 2015, two species originally described from Costa Rica that could potentially be collected in Panama (Table 4). In all three species, the posterolateral margin of sternum VIII is notably produced. Additionally, all three share a similar shape to the phallus apex, with bears a pair of apical lobes and lacks any spines or externally sclerotized structures. *Leucotrichia extraordinaria* can be easily separated

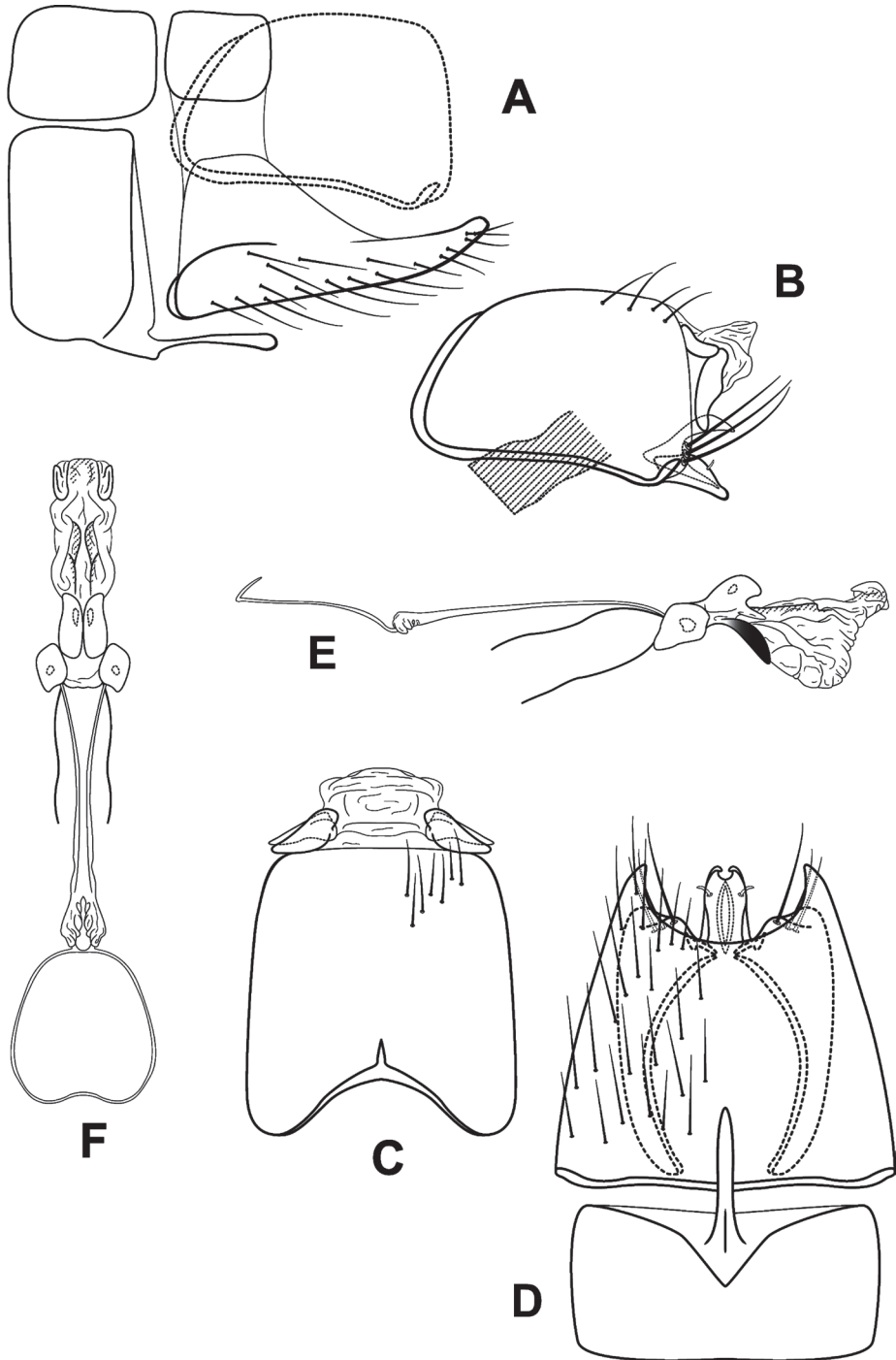


Figure 6. *Leucotrichia cultrata* Thomson & Armitage, 2021. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Armitage (2021).

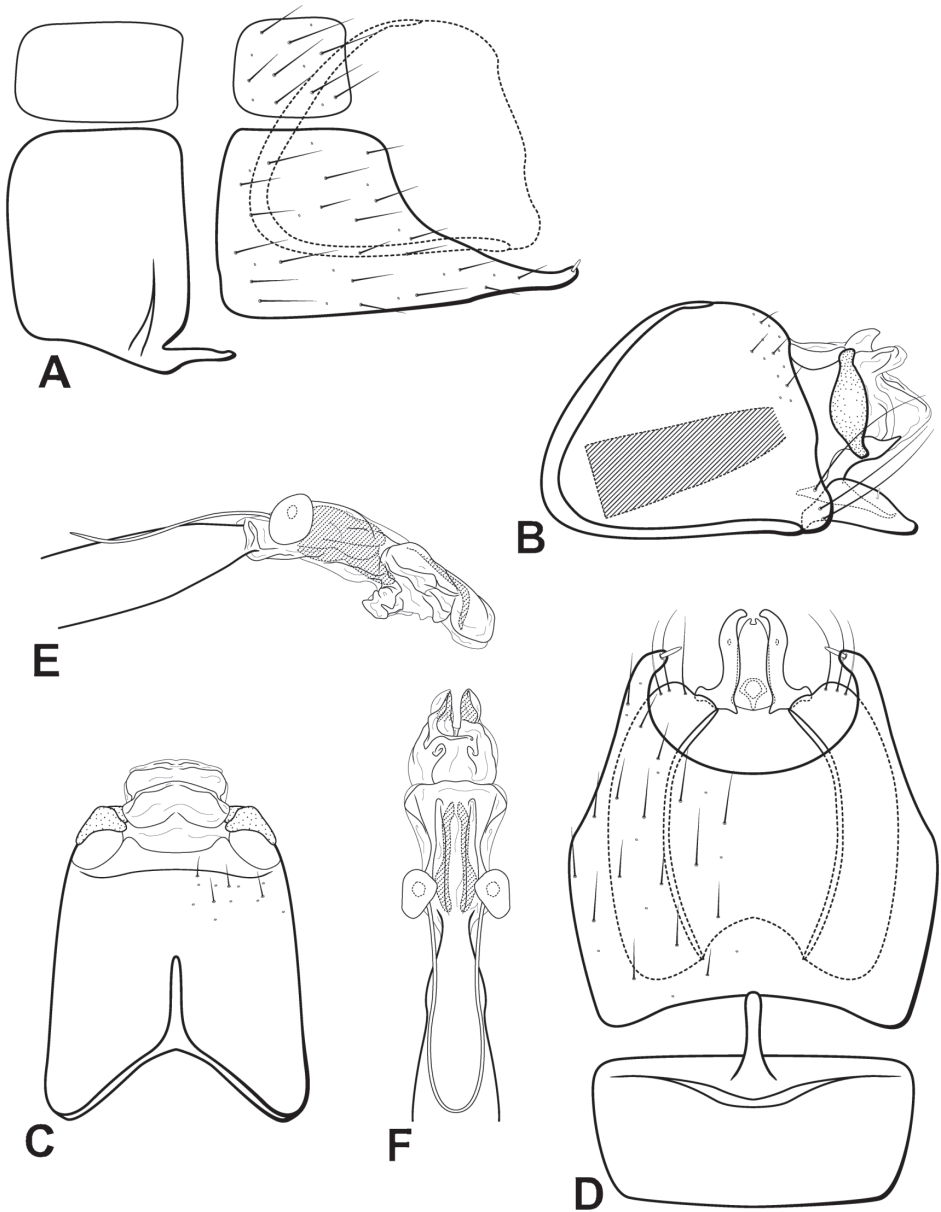


Figure 7. *Leucotrichia extraordinaria* Bueno-Soria, Santiago-Fragoso & Barba-Álvarez, 2001. Male genitalia: **A** segments VII–VIII and segment IX lateral, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal, **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

by the single peg-like apical seta on the posterolateral production of sternum VIII, a feature not shared with the other two species.

Material examined. PANAMA: Bocas del Toro Province • 59 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala; Rambala Jungle Lodge;

8.91627°N, 82.15469°W; 120 m a.s.l.; 7–9 Oct. 2016; E. Carlson, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 18 males; 15–20 Nov. 2016; MUPADI • *ibid.*, 13 males; 21–31 Dec. 2016; MUPADI; *ibid.*, 6 males; 6–12 Feb. 2017; MUPADI • *ibid.*, 18 males; 12–15 Jun. 2017; MUPADI • *ibid.* 3 males; 28–30 Jun. 2017; MUPADI. **Chiriqui Province** • 1 male; Cuenca 108; Boquete District; Quebrada Grande; Valle Escondido; 8.7797°N, 82.44016°W; 1,122 m a.s.l.; 29 Apr.–2 May 2018; B. Armitage, T. Arefina-Armitage, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 1 male; Quebrada Jaramillo, Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.; 12–19 Aug. 2018; K. Collier, leg.; Malaise trap; in alcohol; MIUP • *ibid.*, 2 males; 14–22 Oct. 2018 • *ibid.*, 3 males; Dolega District, Río Majagua, Potrerillos, Banquito de Palmira; 8.68083°N, 82.532528°W; 840 m a.s.l.; 28 Feb–14 Mar. 2019; T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; UMSP • *ibid.*, 3 males; Río Chirigagua, SSE Guayabal; 8.64102°N, 82.5578°W; 751 m a.s.l.; 19 Jun. 2015; C. Nieto, T. Abrego, E. Pérez, A. Tuñón, M. Molinar, A. Cornejo, leg.; UV light trap; in alcohol; COZEM. **Veraguas Province** • 2 males; Cuenca 097; Santa Fe District; Santa Fe National Park; afl. Río Calovébora; PSPSCB-NPSF-C-097-2017-005; 8.54318°N, 81.16398°W; 515 m a.s.l.; 19 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; UV light trap; in alcohol; COZEM • 1 male; Río Calovébora, PSPSCB-PNSF-C097-2017-006, 8.55038°N, 81.16486°W; 461 m a.s.l.; 23–27 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise Trap; in alcohol; COZEM • *ibid.*, 39 males; Cuenca 132, Río Mulaba, 2do Brazo, PSPSCB-NPSF-C-132-2017-007; 8.52577°N, 81.13045°W; 623 m a.s.l.; 19–23 Apr. 2017; Malaise trap; COZEM • *ibid.*, 7 males; Río Piedra de Moler; PSPSCB-NPSF-C-097-2017-011; 8.55343°N, 81.17675°W; 395 m a.s.l.; 20 Apr. 2017; COZEM.

Distribution. Mexico, Panama.

Leucotrichia hispida Thomson & Holzenthal, 2015

Fig. 8

Diagnosis. This species is similar to *L. botosaneanui*, *L. chiriquiensis*, and *L. viridis*, based on characteristics of the phallus, as discussed under *L. botosaneanui*. *Leucotrichia hispida* can be recognized using the tuft of setae on the posteroventral projection of sternum VIII and the lack of any external spines or sclerites on the apex of phallus.

Material examined. PANAMA: **Chiriqui Province** • 1 male; Cuenca 102; Renacimiento District; La Amistad International Park, Río Candela, Finca Felix, PSPSCB-PILA-C102-2017-021; 8.890557°N, 82.61201°W; 1,996 m a.s.l.; 25 Jan. 2015; C. Nieto, E. Pérez, A. Cornejo, leg.; UV light trap; in alcohol; COZEM • *ibid.*, 1 male; Río Chiriqui Viejo, PSPSCB-PNVB-C108-2017-016; 8.87550°N, 82.55336°W; 2,117 m a.s.l.; 5–8 Jun. 2017; E. Álvarez, T. Ríos, E. Pérez, leg.; Malaise trap; COZEM • *ibid.*, 2 males; afl. Río Chiriqui Viejo, PSPSCB-PILA-C102-2017-022; 8.90124°N, 82.61817°W; 2,354 m a.s.l.; 17–21 Jun. 2017; UMSP • *ibid.*, 2 males; Cuenca 108;

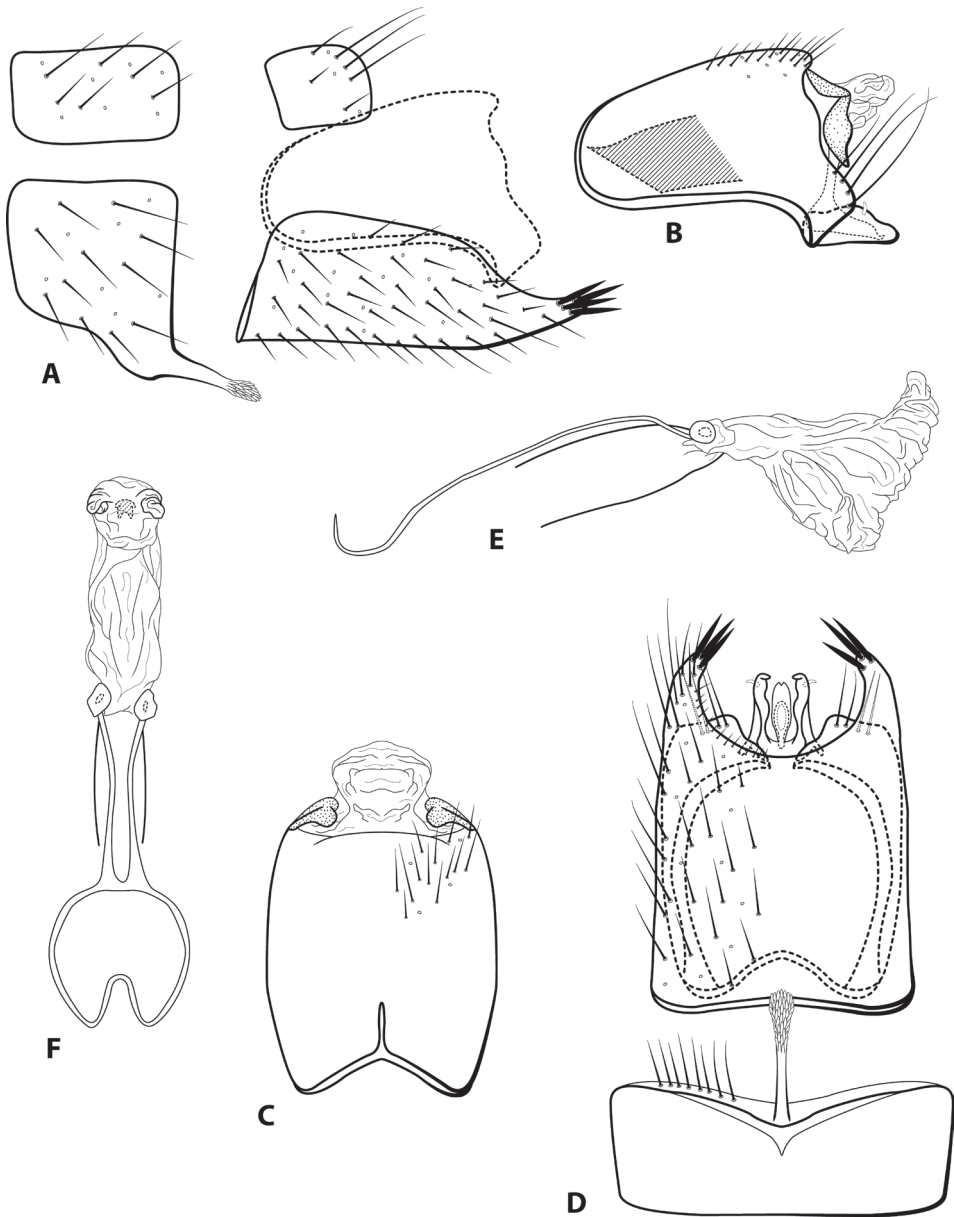


Figure 8. *Leucotrichia hispida* Thomson & Holzenthal, 2015. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

Quebrada del Guayabo, Volcan Baru National Park, PSPSCB-PNVB-C108-2017-018; 8.84939°N, 82.49349°W; 1,947 m a.s.l.; 5–8 Jun. 2017; E. Álvarez, E. Pérez, T. Ríos, leg.; Malaise trap; in alcohol; MUPADI.

Distribution. Costa Rica, Panama.

***Leucotrichia holzenthali* sp. nov.**

<http://zoobank.org/A5A3CC50-0E9D-490F-B042-EA3E3E4D7412>

Fig. 9

Type locality. PANAMA: Veraguas Province: Cuenca 097; Santa Fe District; Santa Fe National Park; Río Piedra de Moler; PSPSCB-PNSF-C097-2017-011; 8.55343°N, 81.17675°W; 395 m a.s.l.

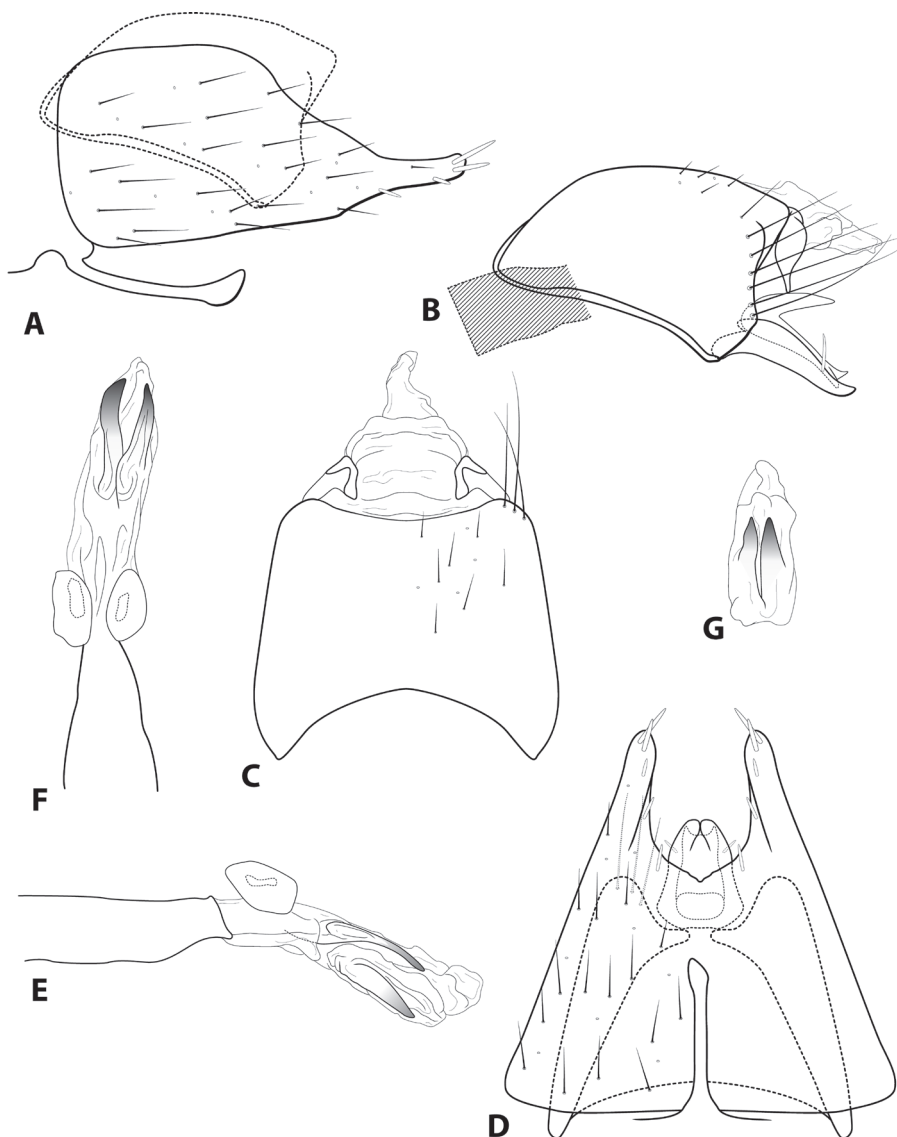


Figure 9. *Leucotrichia holzenthali* sp. nov. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal **G** phallus apex, ventral.

Type material. Holotype: male, **PANAMA: Veraguas Province:** Cuenca 097; Santa Fe District; Santa Fe National Park; Río Piedra de Moler; PSPSCB-PNSF-C097-2017-011; 8.55343°N, 81.17675°W; 395 m a.s.l.; 20 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; UV light trap; in alcohol; MIUP-002-T-2021. **Paratype:** same data as for holotype; 1 male; UMSP.

Diagnosis. *Leucotrichia holzenthali* sp. nov., is similar to *L. dinamica* Bueno-Soria, 2010, a species currently known only from Mexico. Both species bear a pair of large scissor-like sclerites on the apex of the phallus. *Leucotrichia holzenthali* can be distinguished by the additional pair of ventral sclerites on the phallus apex and the peg-like setae on abdominal sternum VIII, both characteristics that are absent on *L. dinamica*.

Description. Male. Length of forewing 1.7 mm ($n = 2$). Wings unmodified. Head unmodified, with three ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown. **Genitalia.** Abdominal sternum VII mesoventral process with enlarged apex (Fig. 9A, D). Sternum VIII with posteroventral production bearing prominent peg-like setae (Fig. 9A), in ventral view posterior margin concave (Fig. 9D). Segment IX anterolateral margin convex, posterolateral margin irregular (Fig. 9B); dorsally, anterior margin concave, posterior margin broadly concave (Fig. 9C). Tergum X with dorsal sclerite not apparent; ventral sclerite broadest mesally with slender ventral apex; membranous apex subtriangular in dorsal view (Fig. 9B, C). Subgenital plate with dorsal arm simple, extending posteriad, apex acute (Fig. 9B); ventral arm simple, apex with emargination, in ventral view with truncate base and rounded apical emargination (Fig. 9B, D). Inferior appendage broadest basally, with pointed basal emargination, prominent dorsal subapical seta, apex acute (Fig. 9B); ventrally broadly fused, broadest basally, apex rounded (Fig. 9D). Phallus tubular basally, constricted at midlength with median complex bearing spherical “windows”; apex membranous, bearing pair of large scissor-like apical sclerites dorsally and pair of large acute sclerites ventrally (Fig. 9E, F).

Distribution. Panama.

Etymology. Named in honor of Dr. Ralph W. Holzenthal, for a long and robust career in caddisfly taxonomy and systematics. Dr. Holzenthal has been a friend and colleague to each of the authors, and an invaluable mentor in particular to the first author.

Leucotrichia luma sp. nov.

<http://zoobank.org/C11BC765-4839-4131-8D82-04EFB0045C1A>

Fig. 10

Type locality. PANAMA: Panama Oeste Province: Cuenca 115; Altos de Campana National Park, Río Chileno, PSPSCB-PNAC-C115-2018-028; 8.716502°N, 80.00740°W; 497 m a.s.l.

Type material. Holotype: male, **PANAMA: Panama Oeste Province •** Cuenca 115; Altos de Campana National Park, Río Chileno, PSPSCB-PNAC-C115-2018-028; 8.716502°N, 80.00740°W; 497 m a.s.l.; 27–31 May 2018, T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; COZEM; MIUP-003-T-2021. **Paratypes:** ibid., 4 males; COZEM and UMSP • ibid., 12 males; Cuenca 138; Río Sajalice, PSPSCB-PNAC-

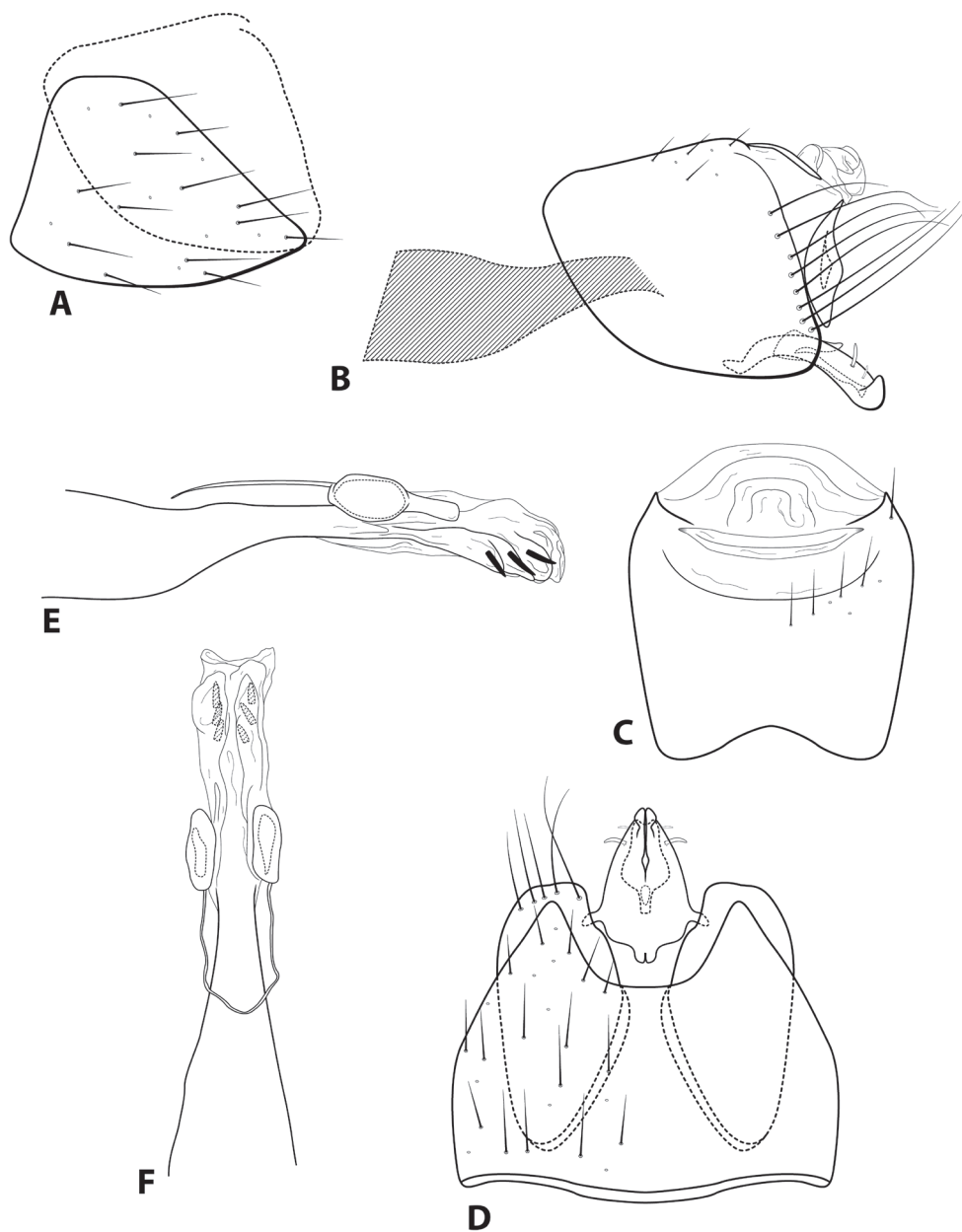


Figure 10. *Leucotrichia luma* sp. nov. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal.

C138-2018-030; 8.67625°N, 79.89748°W; 194 m a.s.l.; 27–31 May 2018; Malaise trap; in alcohol; COZEM and MUPADI.

Diagnosis. *Leucotrichia luma* is most similar to *L. inflaticornis*, a species currently known only from Trinidad. Certain characteristics found on the genitalia of these

species make them very similar, such as the symmetrical rows of spines on the phallus apex, a unique arrangement within the genus. Key differences, however, make it possible to separate the two. Inflated antennal segments, a key feature of *L. inflaticornis*, were not observed in any of the specimens collected in Panama and identified as *L. luma*. Additionally, *L. luma* specimens all present three pairs of spines on the phallus apex, while the original description of *L. inflaticornis* states that there should be four. The first author has observed the holotype specimen of *L. inflaticornis* and found that the abdomen, including the phallus, was missing and key features of the genitalia cannot be confirmed. Since specimens cannot be compared to the *L. inflaticornis* holotype, we compare these specimens to the original description and illustration and offer this new species description for the specimens from Panama.

Description. Male. Length of forewing 1.8–2.0 mm ($n = 17$). Wings unmodified. Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown. **Genitalia.** Abdominal sternum VII without apparent mesoventral process. Sternum VIII with acute posteroventral production, in ventral view posterior margin concave (Fig. 10A, D). Segment IX anterolateral margin convex, posterolateral margin straight (Fig. 10B); dorsally, anterior margin concave, posterior margin concave (Fig. 10C). Tergum X with dorsal sclerite simple, slender; ventral sclerite semi-elliptical with rounded emargination mesally on posterior margin; membranous apex small, suborbicular (Fig. 10B, C). Subgenital plate with dorsal arm digitate, approximately half the length of ventral arm (Fig. 10B); ventral arm slender, apex truncate, with irregular ventral margin, in ventral view broadest mesally with rounded apical emargination (Fig. 10B, D). Inferior appendage with base extending anteriorad, with two dorsal subapical spines, apex curved dorsad (Fig. 10B); in ventral view broadly fused, with digitate basal projections (Fig. 10D). Phallus tubular basally, constricted at midlength with median complex bearing basal loop and pair of spherical “windows”; apex membranous and bearing 3 sets of symmetrically arranged stout, dark spines (Fig. 10E, F).

Distribution. Panama.

Etymology. The specific epithet is derived from *luma*, Latin for “thorn”, referring to the spines found on the phallus apex.

Leucotrichia melleopicta Mosely, 1934

Fig. 11

Diagnosis. *Leucotrichia melleopicta* is most similar to *L. mutica*, also recorded from Panama. These species possess an inferior appendage with a similar shape, and the dorsal sclerite of the phallus of both bears a dorsal sclerite with a distinct apical emargination. *Leucotrichia melleopicta* can be distinguished by the elongate basal sclerite of the phallus and the poorly developed basal loop (Fig. 11E), and by the enlarged apex of the mesoventral process on segment VII (Fig. 11A).

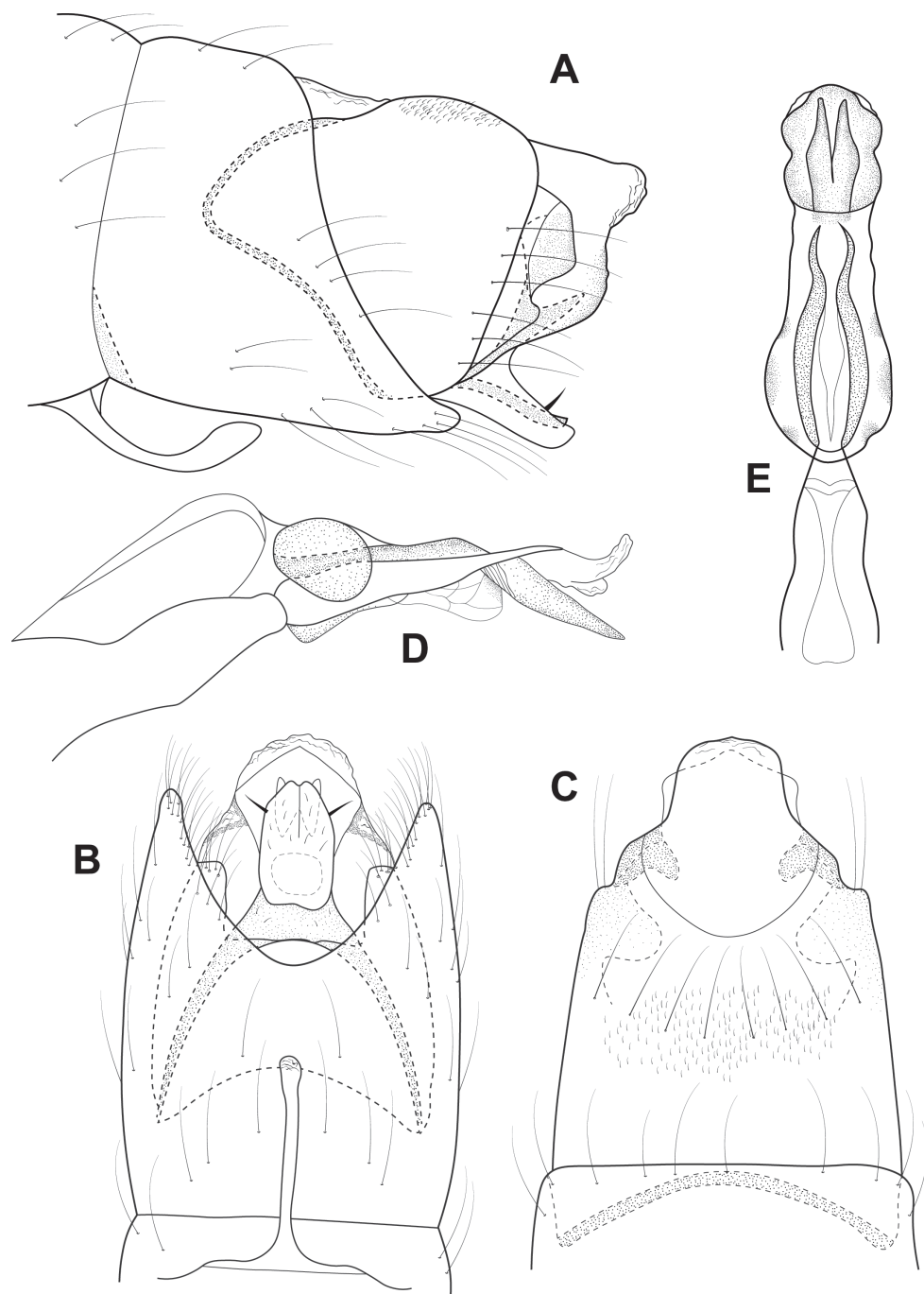


Figure 11. *Leucotrichia melleopicta* Mosely, 1934. Male genitalia: **A** segments VII–X, lateral **B** segments VIII–X, ventral **C** segments IX–X, dorsal **D** phallus, lateral **E** phallus dorsal. Modified from Harris and Armitage (2019).

Material examined. PANAMA: Bocas del Toro Province • 6 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala; Rambala Jungle Lodge; 8.91627°N, 82.15469°W; 120 m a.s.l.; 28 Mar. 2015; B. Armitage, T. Arefina- Armitage, leg.; UV light trap; in alcohol; MUPADI • *ibid.*, 68 males; 31 Mar.–11 Apr. 2015; E. Carlson, leg.; Malaise trap • *ibid.*, 38 males; 7–9 Oct. 2016 • *ibid.*, 36 males; 15–20 Nov. 2016 • *ibid.*, 66 males; 21–31 Dec. 2016 • *ibid.*, 55 males; 6–12 Feb. 2017 • *ibid.*, 32 males; 12–15 Jun. 2017 • *ibid.*, 17 males; 28–20 Jun. 2017. **Comarca Ngäbe Buglé** • 1 male; Cuenca 093; Palo Seco Forest Preserve; Quebrada Martinez; Alto de Valle, detrás de las caseta de MiAmbiente; 8.79484°N, 82.19047°W; 480 m a.s.l.; 5–19 May 2019; T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 4 males; 24 May–6 Jun. 2019 • *ibid.*, 5 males; 22 Sep.–11 Oct. 2019 • *ibid.*, 2 males; Willie Mazu, 8.79361°N, 82.19391°W, 538 m a.s.l.; 13–27 Sep. 2019 • *ibid.*, 1 male; 11–30 Oct. 2019. **Chiriqui Province** • 27 males; Cuenca 108, Boquete District; Quebrada Jaramillo; Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.; 19–25 Apr. 2018, K. Collier, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 41 males; 8–12 May 2018 • *ibid.*, 54 males; 16–20 Jun. 2018 • *ibid.*, 5 males; 12–19 Aug. 2018 • *ibid.*, 52 males; 14–22 Oct. 2018 • *ibid.*, 6 males; 15–22 Nov. 2018 • *ibid.*, 48 males; Dolega District, Río Majagua, Potrerillos, Banquito de Palmira; 8.68083°N, 82.532528°W; 840 m a.s.l.; 28 Feb–14 Mar. 2019; T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; UMSP. **Veraguas Province** • 2 males; Cuenca 097, Santa Fe District, Santa Fe National Park, afl. Río Calovébora; PSPSCB-NPSF-C-097-2017-005; 8.54318°N, 81.16398°W; 515 m a.s.l.; 19–23 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise trap; in alcohol; COZEM • *ibid.*, 1 male; Río Llanito, PSPSCB-NPSF-C-097-2017-012; 8.56553°N, 81.18817°W; 340 m a.s.l.; 21 Apr. 2017; UV light trap; COZEM • *ibid.*, 1 male; Río Pedra Moler; PSPSCB-NPSF-C-097-2017-011; 8.55343°N, 81.17675°W; 395 m a.s.l.; 20 Apr. 2017 • *ibid.*, 104 males; Cuenca 132, Río Mulaba, 2do Brazo, PSPSCB-NPSF-C-097-2017-007; 8.52577°N, 81.13045°W; 623 m a.s.l.; 19–23 Apr. 2017; Malaise trap; COZEM • *ibid.*, 41 males; Río Mulaba, afl. 1er Brazo; PSPSCB-NPSF-C-097-2017-008; 8.51706°N, 81.1214°W; 770 m a.s.l.; 19–23 Apr. 2017; COZEM.

Distribution. Mexico, Panama, Venezuela.

Remarks. In the paper Harris and Armitage (2019), *Leucotricha melleopicta* was redrawn to compare with *L. mutica* as both species were common throughout Panama. In Thomson and Holzenthal (2015) the drawings were prepared from material collected in Mexico and compared to that of Venezuela. There were no comparisons with specimens from Central America. The drawings of genitalic features in the two publications are very similar. However, in the material from Mexico there was a posterior cleft in the ventral arm of the subgenital plate, which was not observed in material from Panama. This is a small character to observe and it could be present but not seen with the arm slightly turned, or it could be absent. The phallus drawings are similar, but in Harris and Armitage the subapical rods are separate, while in Thomson & Holzenthal they are fused. However, the rods are not fixed in position and there is some lateral movement. This is based on the large

number of examined specimens from Panama. Likewise the phallic apical rods are fused basally in Harris and Armitage, while they are separate, but closely aligned in Thomson and Holzenthal. Both arrangements of the phallic rods were observed in the material from Panama.

***Leucotrichia mutica* Flint, 1991**

Fig. 12

Diagnosis. This species is similar to *L. melleopicta*; both species display ranges that include Panama. As discussed under *L. melleopicta*, these species share similarities in the dorsal sclerite of the phallus apex, although this sclerite is much smaller than that seen in *L. melleopicta* (Fig. 12E), and the general shape of the inferior appendage. *Leucotrichia mutica* can be recognized separately from *L. melleopicta* by the tapering mesoventral process on segment VII (Fig. 12A), and by the prominent basal loop of the phallus (Fig. 12D, E).

Material examined. **PANAMA: Bocas del Toro Province** • 17 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala; Rambala Jungle Lodge; 8.91627°N, 82.15469°W; 120 m a.s.l.; 7–9 Oct. 2016; E. Carlson, leg.; Malaise trap; in alcohol; MUPADI • ibid., 10 males; 15–20 Nov. 2016 • ibid., 6 males; 21–31 Dec. 2016 • ibid., 6 males; 6–12 Feb. 2017 • ibid., 14 males; 12–15 Jun. 2017 • ibid., 47 males; 28–30 Jun. 2017. **Comarca Ngäbe Buglé** • 1 male; Quebrada Martinez, Bosque Protector Palo Seco, Alto de Valle; detrás de las caseta de MiAmbiente, M0002; 8.79424°N, 82.1904724°W; 480 m a.s.l.; 24 May–6 Jun. 2018; Y. Aguirre, T. Ríos, leg.; Malaise trap; in alcohol; MUPADI. **Chiriqui Province** • 1 male; Cuenca 108; Boquete District; Quebrada Grande; Valle Escondido; 8.7797°N, 82.44016°W; 1,122 m a.s.l.; 11 Mar. 2018; T. Arefina-Armitage, leg.; UV light trap • 6 males; 29 Apr.–2 May 2018; Malaise trap • ibid., 1 male; 21 May 2018; UV light trap • ibid., 1 male; 8.783645°N, 82.444287°W; 1,147 m a.s.l.; 27–30 May 2018; Malaise trap • ibid., 1 male; 17–20 Jun. 2018 • 6 males; 23 Jul. 2018; UV light trap • ibid., 2 males; 10 Nov. 2018. **Verguñas Province** • 1 male; Cuenca 097; Santa Fe District; Santa Fe National Park; afl. Río Calovébora; PSPSCB-NPSF-C-097-2017-005; 8.54318°N, 81.16398°W; 515 m a.s.l.; 19–23 Apr. 2017; Malaise trap; in alcohol; COZEM.

Distribution. Colombia, Panama.

Remarks. *Leucotrichia mutica* in Thomson and Holzenthal (2015) was drawn from the holotype of the species from Colombia. This specimen had the lower half of the phallus missing from the medial ring-like structure downward, leaving only the apical portion. The species was fairly common in Panama, and we were able to identify it from the apical portion of the phallus, which in *Leucotrichia* is typically diagnostic, as well as the other genitalic features. Based on the fact that Thomson and Holzenthal's original description was based on this single specimen from Colombia, we redrew it in Harris and Armitage (2019) to better reflect variation in the species and to include the basal portion of the phallus. The latter can be very useful in the diagnosis of the species.

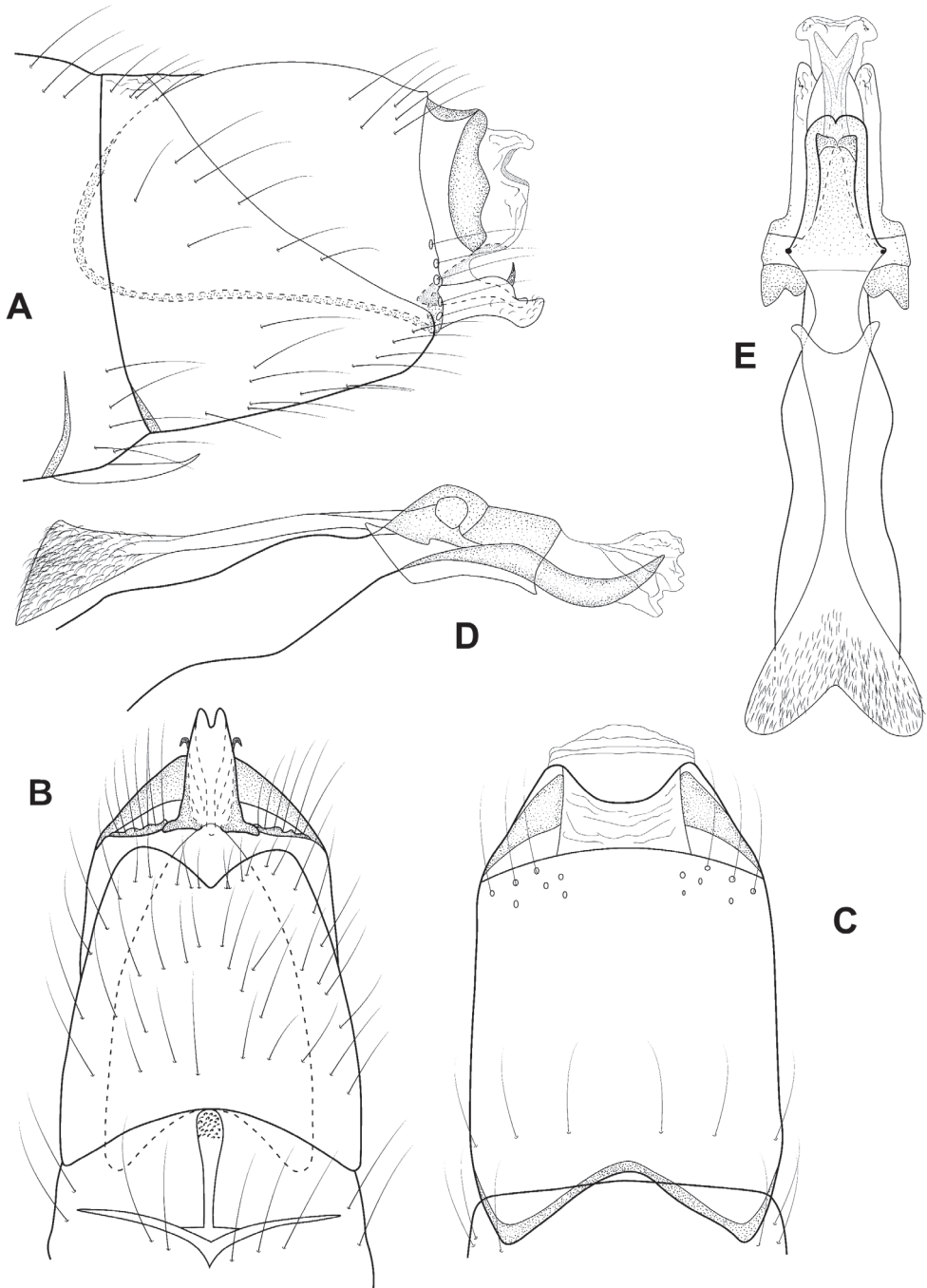


Figure 12. *Leucotrichia mutica* Flint, 1991. Male genitalia: **A** segments VII–X, lateral **B** segments VII–IX, ventral **C** segments IX–X, dorsal **D** phallus, lateral **E** phallus, dorsal. Modified from Harris and Armitage (2019).

***Leucotrichia rhomba* Thomson & Holzenthal, 2015**

Fig. 13

Diagnosis. *Leucotrichia rhomba* is similar to *L. brochophora* Flint, 1991 and *L. padera* Flint, 1991, two species recorded from Colombia, but not currently known from Panama. All three species share a similar appearance of the phallus apex, with no spines and either few or no externally sclerotized structures. The anterolateral margin of segment IX is also produced in all three species. *Leucotrichia rhomba* can be recognized by the elongate mesoventral process of segment VII, which is enlarged, rhomboid, and rugose in ventral view (Fig. 13A, B), and by the obovoid dorsal sclerite of the phallus apex (Fig. 13E).

Material examined. PANAMA: **Bocas del Toro Province** • 6 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala; Rambala Jungle Lodge; 8.91627°N, 82.15469°W; 120 m a.s.l.; 12–15 Jun. 2017; E. Carlson, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 1 male; 28–30 Jun. 2017 • *ibid.*, 2 males; 15–20 Nov. 2016. **Chiriqui Province** • 5 males; Cuenca 108; Boquete District; Quebrada Jaramillo; Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.; 16–20 Jun. 2017; K. Collier, leg.; Malaise trap • *ibid.*, 1 male; 14–22 Oct. 2018. • *ibid.*, 5 males; Dolega District, Río Majagua, Potrerillos, Banquito de Palmira; 8.68083°N, 82.532528°W; 840 m a.s.l.; 28 Feb.–14 Mar. 2019; T. Ríos, Y. Aguirre, leg.; MUPADI. **Veraguas Province** • 14 males; Cuenca 132; Santa Fe District, Santa Fe National Park, Río Mulaba, 2do Brazo, PSPSCB-NPSF-C-097-2017-007; 8.52577°N, 81.13045°W; 623 m a.s.l.; 19–23 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise trap; in alcohol; COZEM.

Distribution. Costa Rica, Panama.

Remarks. The drawings of *Leucotrichia rhomba* in Harris and Armitage (2019) emphasize the apical phallic sclerite which is somewhat oval in shape. In Thomson and Holzenthal (2015) this sclerite is not emphasized, rather they use the basal sclerites. In Harris and Armitage (2019), these basal sclerites are indicated, but secondarily to the apical sclerite. In examining material from Panama, the apical sclerite proved to be the best character for identifying the species. The other genitalic features are similarly drawn in these two papers. The minor difference in figures could be attributed to artistic interpretation of taxonomic features.

***Leucotrichia ruiteri* sp. nov.**

<http://zoobank.org/F7961E34-1751-4095-A5D1-27D5E29B698D>

Figs 2A, 14

Type locality. PANAMA: **Chiriqui Province:** Cuenca 108; Boquete District; Quebrada Jaramillo, Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.

Type material. *Holotype:* male, PANAMA: **Chiriqui Province:** Cuenca 108; Boquete District; Quebrada Jaramillo, Finca Monterey; 8.7632°N, 82.41383°W; 1,214 m a.s.l.;

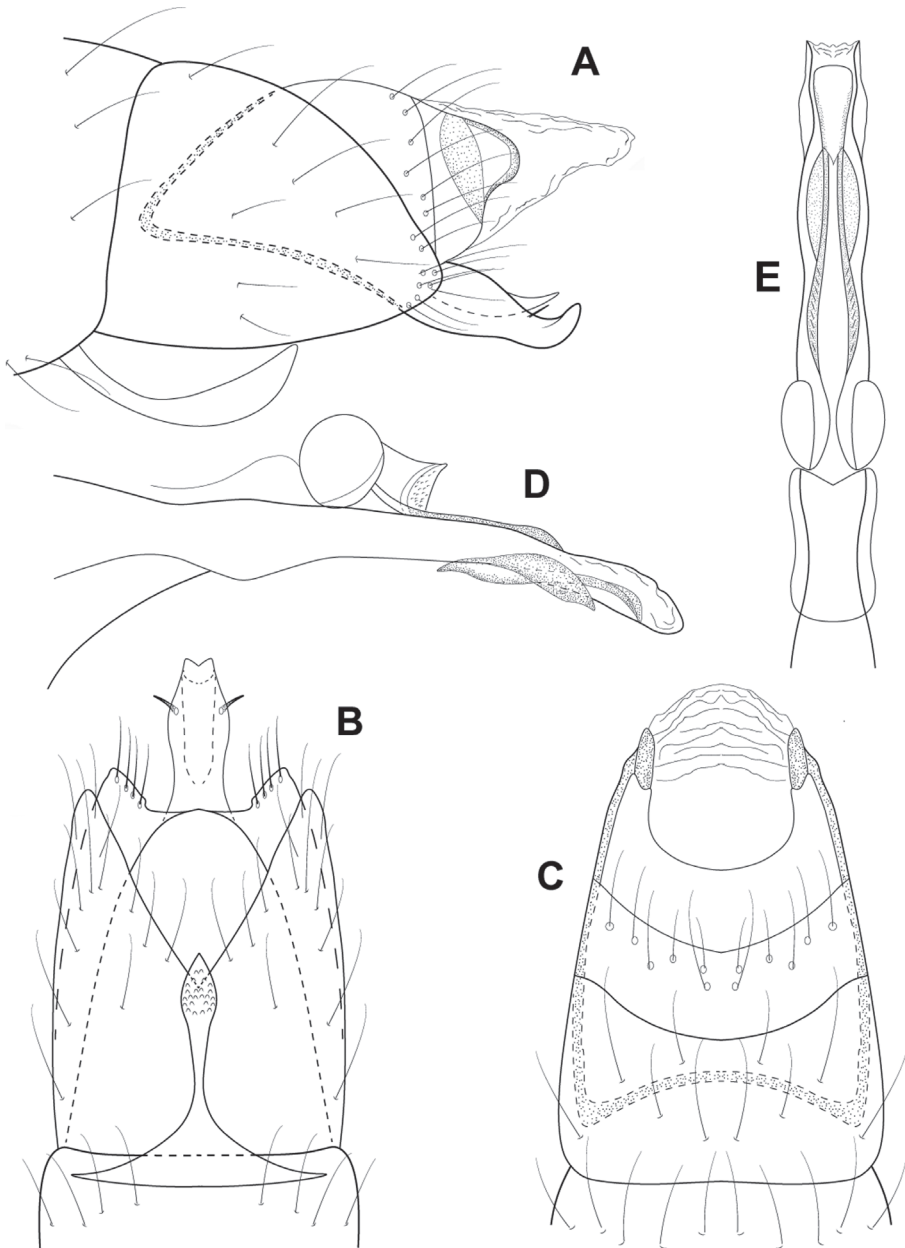


Figure 13. *Leucotrichia rhomba* Thomson & Holzenthal, 2015. Male genitalia: **A** segments VII–X, lateral **B** segments VII–IX, ventral **C** segments VII–X, dorsal **D** phallus, lateral **E** phallus, dorsal. Modified from Harris and Armitage (2019).

8–12 Jun. 2018, K. Collier, leg.; Malaise trap; in alcohol; MIUP-004-T-2021. **Para-**
type: same data as for holotype; 1 male; UMSP.

Other material examined. PANAMA: Chiriqui Province • 1 male; Cuenca 102, Renacimiento District; La Amistad International Park, Río Candela, Finca Felix,

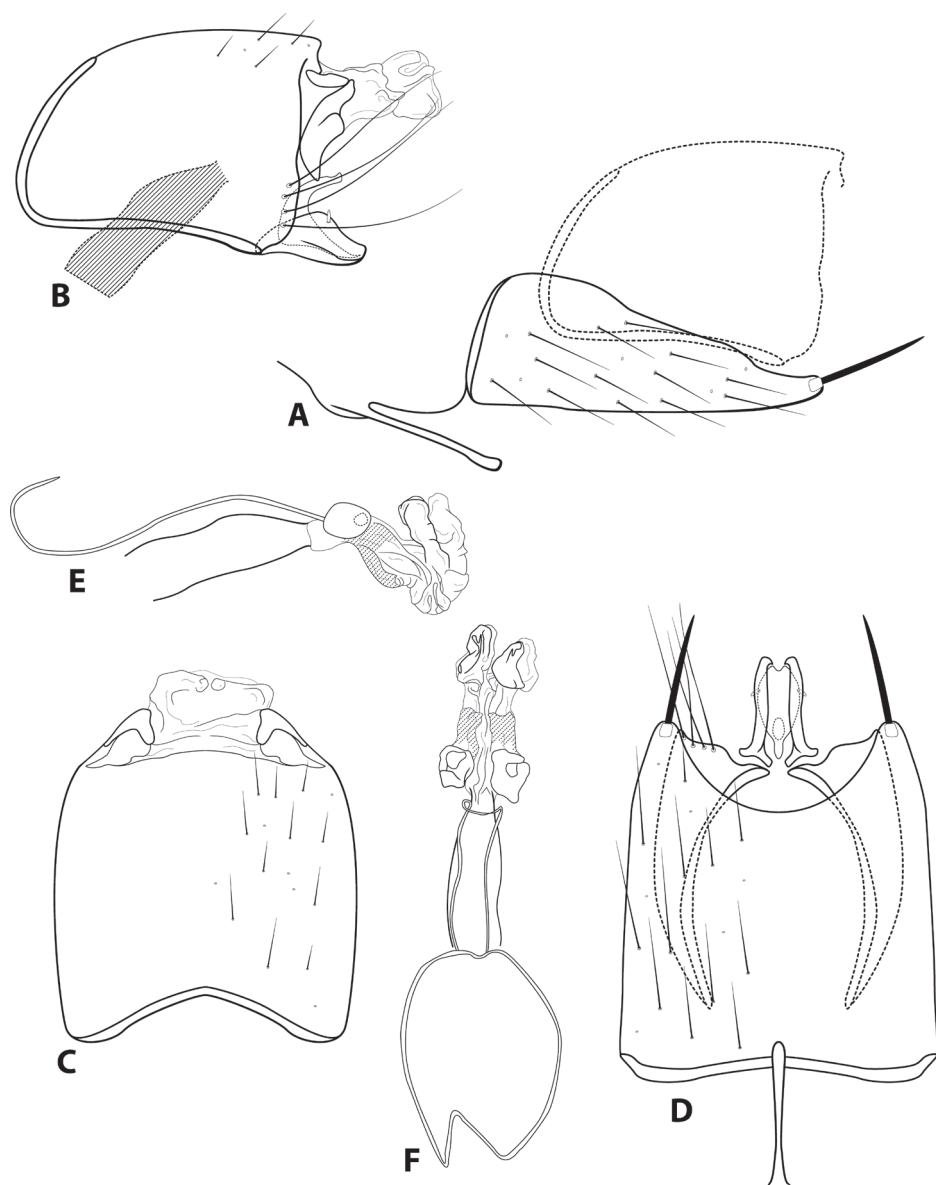


Figure 14. *Leucotrichia ruiteri* sp. nov. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal.

PSPSCB-PILA-C102-2017-021; 8.90614°N, 82.72882°W; 1,799 m a.s.l., 1–5 Sep. 2017; E. Álvarez, T. Ríos, E. Pérez, leg.; Malaise trap; in alcohol; COZEM. **Veraguas Province** • 1 male; Cuenca 132, Santa Fe National Park, Río Mulaba, 2do Brazo, PSPSCB-NPSF-C-097-2017-007; 8.52577°N, 81.13045°W; 623 m a.s.l.; 19–23 Apr. 2017; A. Cornejo, T. Ríos, E. Álvarez, C. Nieto, leg.; Malaise trap; in alcohol; MUPADI.

Diagnosis. *Leucotrichia ruiteri* sp. nov. is most similar to *L. hispida*, as both species bear prominent setae on the posteroventral production of sternum VIII, a bilobed phallus apex, and a similar shaped inferior appendage. *Leucotrichia ruiteri* can be separated by the single, elongate seta on sternum VIII compared to the cluster of setae present on *L. hispida*. Additionally, the forewings of *L. ruiteri* are modified with a large setae-filled pocket, while those of *L. hispida* are unmodified.

Description. Male. Length of forewing 2.0–2.1 mm ($n = 4$). Forewing with large pocket filled with scales (Fig. 2A); hindwing unmodified. Head unmodified, with three ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown.

Genitalia. Abdominal sternum VII slender, elongate (Fig. 14A, D). Sternum VIII with posteroventral production bearing prominent apical seta (Fig. 14A); in ventral view posterior margin concave (Fig. 14D). Segment IX anterolateral margin convex, posterolateral margin straight with slight irregularity (Fig. 14B); dorsally, anterior margin concave, posterior margin broadly convex (Fig. 14C). Tergum X with dorsal sclerite with irregular dorsal margin; ventral sclerite semi-elliptic with knoblike projection mesally on posterior margin; membranous apex subquadrate (Fig. 14B, C). Subgenital plate with dorsal arm simple, with slight preapical emargination on dorsal margin, apex truncate (Fig. 14B); ventral arm narrowing apically, ventral margin slightly sinuate, in ventral view subovate with narrow basal projection and small rounded apical emargination (Fig. 14B, D). Inferior appendage broadest mesally, with small dorsal subapical peg-like seta, apex rounded (Fig. 14B); ventrally slender, with digitate basal projections, apex slightly hooked on inner margin (Fig. 14D). Phallus tubular basally, constricted at midlength with typical median complex bearing basal loop and pair of spherical “windows”; apex membranous with internal sclerotized structures and two apical lobes extending dorsad (Fig. 14E, F).

Distribution. Panama.

Etymology. This species is named in honor and memory of Dave Ruiter, a passionate and enthusiastic caddisfly researcher and good friend, who recently passed away.

Leucotrichia viridis Flint, 1967

Fig. 15

Diagnosis. Due to the similar overall appearance of the phallus, *L. viridis* is most similar to *L. botosaneanui*, *L. hispida*, and *L. chiriquiensis*, as discussed under *L. botosaneanui*. *Leucotrichia viridis* has two dorsal spines on the inferior appendage, while the other species each bear only a single spine.

Material examined. PANAMA: Bocas del Toro Province • 21 males; Cuenca 093, Chiriqui Grande District, Quebrada Rambala, Rambala Jungle Lodge; 8.91627°N, 82.15469°W; 120 m a.s.l.; 9 Aug. 2014; E. Carlson, leg.; Malaise trap; in alcohol; MUPADI • ibid., 3 males; 28 Mar. 2015; UV light trap • ibid., 3 males; 31 Mar.–11 Apr. 2015; Malaise trap. **Chiriqui Province** • 1 male; Cuenca 108; Dolega District; Río Majagua; Potrerillos, Banquito de Palmira; 8.68083°N, 82.53253°W; 840 m a.s.l.; 28 Feb.–14 Mar. 2019; T. Ríos, Y. Aguirre, leg.; Malaise trap; in alcohol; MUPADI.

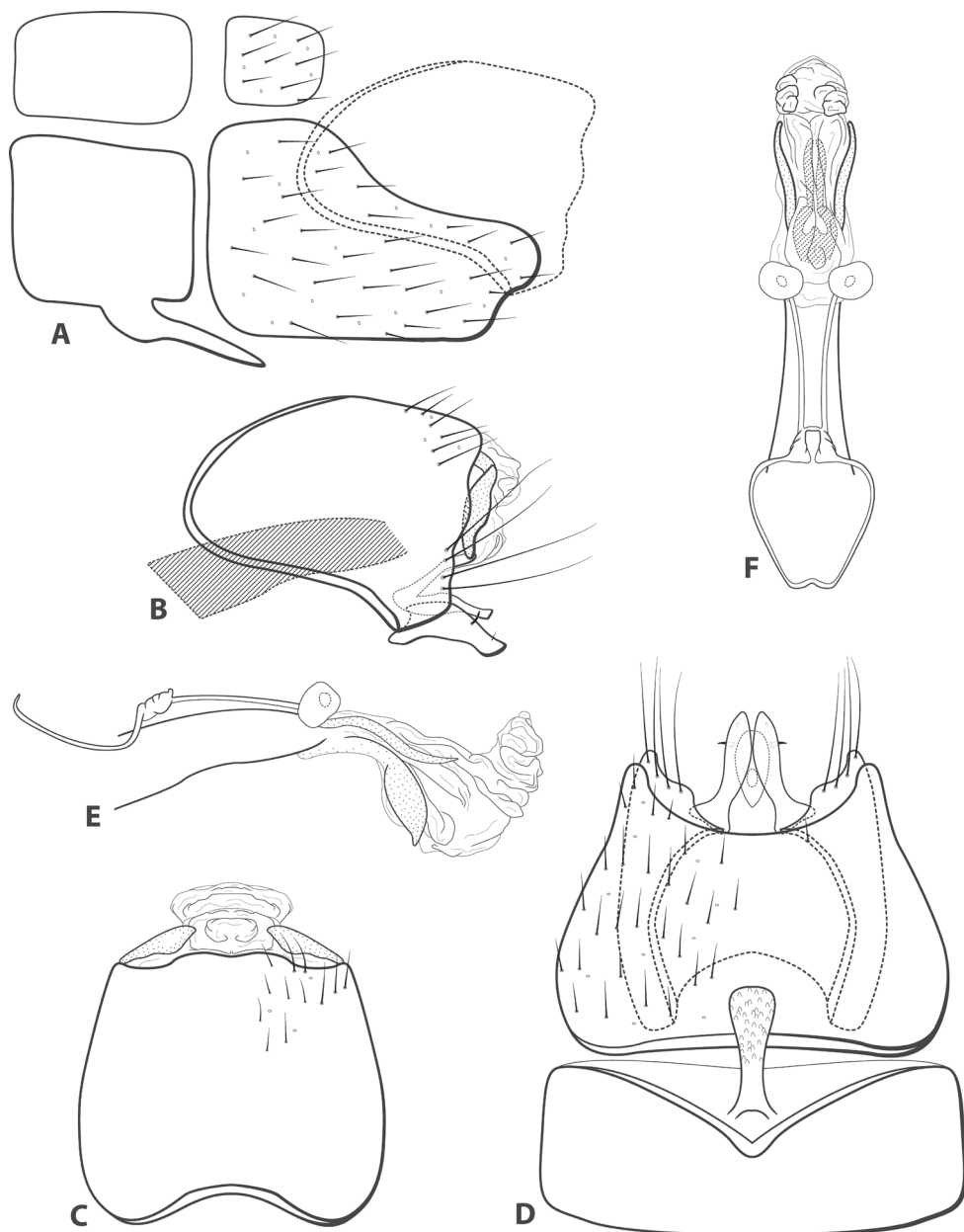


Figure 15. *Leucotrichia viridis* Flint, 1967. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

–**Veraguas Province** • 3 males; Cuenca 132; Santa Fe District, Santa Fe National Park, Río Mulaba, afl. 1er Brazo; PSPSCB-NPSF-C-097-2017-008; 8.51706°N, 81.1214°W; 770 m a.s.l.; E. Álvarez, E. Pérez, T. Ríos, leg.; 19–23 Apr. 2017; in alcohol; COZEM.

Distribution. El Salvador, Guatemala, Mexico, Panama.

Leucotrichia pictipes group*Leucotrichia fairchildi* Flint, 1970

Figs 2C, 16

Diagnosis. *Leucotrichia fairchildi* is currently the only member of the *L. pictipes* Group recorded in Panama. *Leucotrichia pictipes* known distribution includes Mexico, while

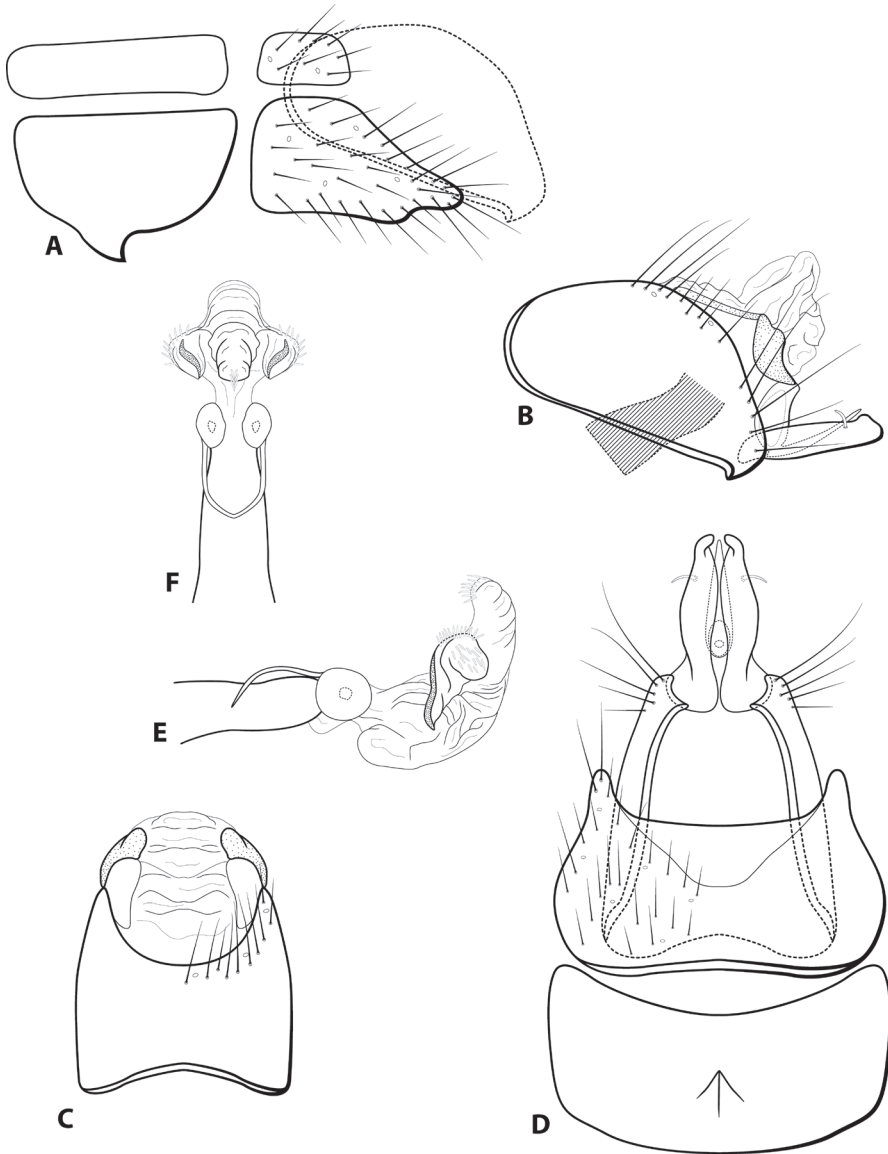


Figure 16. *Leucotrichia fairchildi* Flint, 1970. Male genitalia: **A** segments VII–VIII and segment IX margin, lateral **B** segments IX–X, lateral (base of phallus crosshatched) **C** segments IX–X, dorsal **D** segments VII–IX, ventral **E** phallus, lateral **F** phallus, dorsal. Modified from Thomson and Holzenthal (2015).

L. imitator Flint, 1970 and *L. sarita* Ross, 1944 have been recorded in nearby Costa Rica. All species in this group bear only two ocelli and share similar shapes to the inferior appendage and sternum VII, when viewed laterally. The modified basal antennal segments and setiferous production on the dorsum of the head can be used to easily separate *L. fairchildi* from each of the three other species.

Material examined. PANAMA: **Bocas del Toro Province** • 16 males; Cuenca 093; Chiriqui Grande District; Quebrada Rambala; Rambala Jungle Lodge; 8.91627°N, 82.15469°W; 120 m a.s.l.; 21–31 Dec. 2016; E. Carlson, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 3 males; 6–12 Feb. 2017 • *ibid.*, 1 male; 12–15 Jun. 2017 • 2 males; 28–30 Jun. 2017. **Comarca Ngäbe Buglé** • 3 males; Quebrada Martinez, Bosque Protector Palo Seco, Alto de Valle, detrás de las caseta de MiAmbiente; 8.79484°N, 82.19391°W, 480 m a.s.l.; 16–30 Aug. 2019; Y. Aguirre, T. Ríos, leg.; Malaise trap; in alcohol; MUPADI • *ibid.*, 2 males; 30 Aug.–13 Sep. 2019 • *ibid.*, 2 males; 13–27 Sep. 2019. **Veraguas Province** • 1 male; Cuenca 097; Santa Fe District; Santa Fe National Park; Río Piedra de Moler; PSPSCB-NPSF-C-097-2017-011; 8.55343°N, 81.17675°W; 395 m a.s.l.; 20 Apr. 2017; T. Ríos, E. Álvarez, C. Nieto, leg.; UV light trap; in alcohol; COZEM.

Distribution. Colombia, Costa Rica, Ecuador, El Salvador, Grenada, Panama, Tobago, Trinidad, Venezuela.

Remarks. A pharate female in a pupal case was identified by Botosaneanu and Alkins-Koo (1993) as “*Leucotrichiini*—case 2”. Subsequently, Flint (1996) associated this female with *L. fairchildi*, in addition to collecting adult material from Trinidad and Venezuela.

Discussion

Leucotrichia – A mystery wrapped in an enigma

The colloquial expression “I know it when I see it” was coined in 1964 by United States Supreme Court Justice Potter Stewart to describe his threshold test for obscenity in *Jacobellis v. Ohio*. As stated in the Results section, a definitive diagnosis for adults of the genus *Leucotrichia* is difficult at this time and could only be objectively based on one or perhaps two characters. But, subjectively it is more easily perceived. And, to support this perception, this position is confirmed by molecular analyses (Santos et al. 2016). This perception was successfully applied to each species included in the Results section in the process of producing this assemblage of *Leucotrichia* species for Panama.

In the course of our studies in Panama, we have added to the confusion by finding several species which are “exceptions to the rule” for characters which normally would be included in a diagnosis for the genus. For example, unmodified wings were a consistent, albeit unremarkable, character for this genus, until we described *L. ruiteri* in this paper. This new species has a forewing which bears a pocket filled with scales.

Another, formerly reliable character typical of *Leucotrichia* is the subgenital plate with dorsal and ventral arms. However, a survey of the genus shows that only 21

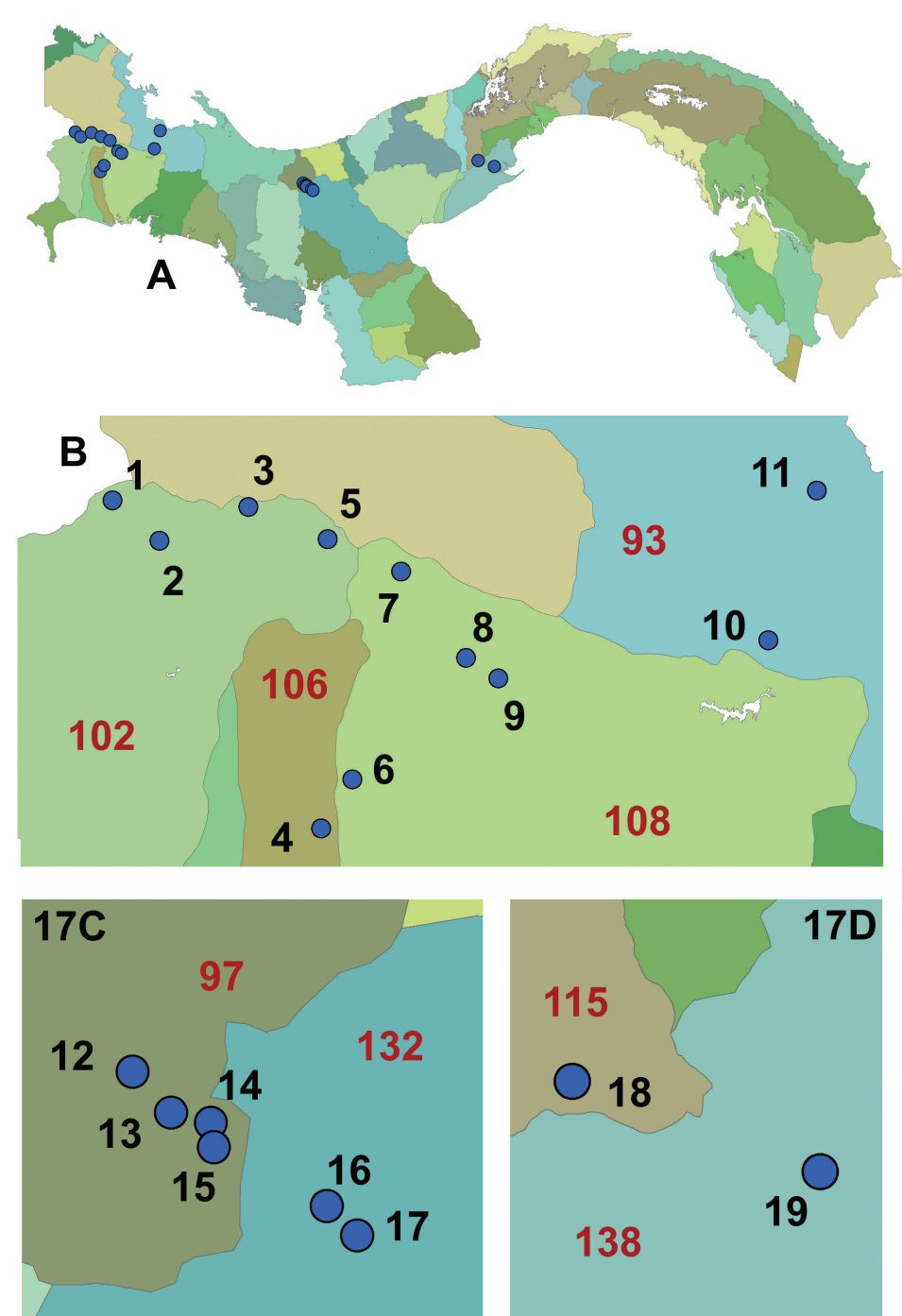


Figure 17. Locations of collection sites for *Leucotrichia* in Panama, sorted and displayed by longitude, then latitude **A** map of Panama showing collection locations **B** enlarged map of western Panama showing locations 1–11 **C** map of the Santa Fe National Park locations 12–17 **D** map of the Altos de Campana National Park locations 18 and 19. Please refer to Tables 1 and 2 for additional information.

species (e.g., the Panamanian species *L. botosaneanui*) have both arms on the subgenital plate. A total of 21 other species (e.g., the Panamanian species *L. melleopicta*) lacks the dorsal arm. And, four species (*L. adela*, *L. inflaticornis*, *L. laposka* Oláh & Johanson, 2011, *L. tubifex* Flint, 1964) are undetermined at this time.

Other characters which could have been used in a diagnosis vary by number or presence. For example, two ocelli are characteristic of the *L. pictipes* group and three ocelli are found in all members of the *L. melleopicta* Group. Inferior appendage segments are fused in 15 species (e.g., the Panamanian species, *L. rhomba*), with separate segments in 29 species (e.g., the Panamanian species *L. chiriquiensis*), and undetermined in two species (*L. adela*, *L. alisensis* Rueda Martín, 2011). There is a dorsal spine on the inferior appendage in 35 species (e.g., *L. melleopicta*), it is lacking in ten species (e.g., *L. inops* Flint, 1991), and is undetermined in one species (*L. adela*). Forty-one species have a ventral process on abdominal segment VII (prominent in 33 species, e.g., *L. melleopicta*; reduced in eight species, e.g., *L. botosaneanui*), and six species have no ventral process.

Finally, there are other characters, like the unmodified wings mentioned above, which seem consistent within *Leucotrichia*, but are shared with other genera. An example of this is the median complex on the phallus bearing sclerotized armature, which is also found in *Zumatrichia* and other members of the Leucotrichiinae.

Of course, the variability that we find within this genus is also common in other genera of insects. However, usually there is a core of morphological characters which consistently define those genera. Even so, in Santos et al. (2016), there was only a single morphological character in the larvae which united the genus. At this juncture, the best we can say is that *Leucotrichia* is a genus consisting of a complex of species, united by perception and supported by molecular analyses, not all of whom share all morphological characters consistently. Future molecular and morphological analyses could alter our definition of this genus, further clarifying its position and uniqueness, or lack thereof, within the Leucotrichiinae. However, until then we are confident that “we know it when we see it”.

How many *Leucotrichia*?

When we first started examining the extent of the hydroptilid fauna of Panama in 2015, we were naively comfortable with the three taxa representing the genus *Leucotrichia*. Two of them (*L. chiriquiensis* and *L. fairchildi*) had been described from this country, and the thought that many more were undetected seemed remote. This presumption was supported by recent papers based on two doctoral studies involving this genus (Thomson and Holzenthal 2015; Santos et al. 2016), neither of which identified new taxa for Panama. Our calm was somewhat disturbed during subsequent years as we began to find new first records for *Leucotrichia* as the result of prolonged sampling at single locations, involving Malaise trapping. Prior to 2012, almost all caddisflies collected and identified from Panama resulted from light trapping or sweeping. We began to see other possibilities in 2020 when we detected our first new species from Panama,

L. cultrata (Thomson and Armitage 2021). However, we were totally unprepared, as we began to address unidentified leucotrichiine specimens in preparation for generating this manuscript, to find we had four additional new species to science and two additional first records for Panama. Where would it end? We now have replaced complacency with anticipation as we collect, process, and identify each new sample. This anticipation is further supported by the fact that Panama's assemblage of *Leucotrichia* species has a low similarity to those found in neighboring countries (see below). More new species to science are possible, while the chance for more first records for Panama seems probable.

The 14 species of this genus in Panama is currently the most for any Latin American country. Impressive as that total is, we must dampen our enthusiasm in at least two regards. Latin America as a whole is considerably under-collected for adult caddisflies. Whereas a number of countries have a published species list (e.g., Bueno-Soria and Flint (1978) for Mexico, Chamorro-Lacayo et al. (2007) for Nicaragua, Holzenthal (1988) for Costa Rica, Muñoz-Quesada (2000) for Colombia, Ríos-Touma et al. (2017) for Ecuador, and Paprocki and França (2014) and Santos et al. (2020) for Brazil), they all are but intermediate waypoints. All imply room for growth. For example, Ríos-Touma et al. (2017) listed 310 species for Ecuador, but based on a non-parametric estimator of true species richness (Chao2; Shen et al. 2003; Gotelli and Colwell 2011), this represents only ~ 54% of its estimated species richness. In Panama, we are quickly approaching 500 total species, with no end in sight; and this for a country ~ 28% the size of Ecuador and with less topographic diversity. In addition, little of the collecting which has taken place in these other countries involved Malaise traps, which we consider a critical factor. As more collecting in other countries takes place, involving prolonged sampling with multiple methods, we anticipate that the *Leucotrichia* assemblages of those countries will increase significantly, and perhaps exceed what we find in Panama.

Coexistence and frequency of occurrence

It is not uncommon to find multiple congeners of many caddisfly genera in the same stream location. Intuitively, there are sufficient resources available to mitigate any possible competition or cropping by predators to keep population levels relatively low. Thus, the competitive exclusion principle (aka Gause's Law; Gause 1932), in most cases, does not apply, particularly for microcaddisflies who cannot be imagined to impact resource levels in all but the most narrow of niches. However, as noted in Table 3, there are on average, roughly three species for each of the 19 streams in which *Leucotrichia* have been found in Panama. The actual tallies can be found in Table 1, and the range is considerable. Two of the streams, Quebrada Jaramillo (1,214 m a.s.l.) and Quebrada Rambala (120 m a.s.l.), both in dendritic watersheds, each have seven species of *Leucotrichia* which have been collected at the same locations. The Río Majagua (840 m a.s.l.), which is a linear watershed coming off of Volcan Baru, has produced six species to date, with identifications on-going. Most of the other streams listed in Table 1 have four or fewer species. Considering that the three streams mentioned above were sampled with both UV light and Malaise traps monthly for at least a year, one might

suspect that the other 16 streams have additional species to reveal if only they were sampled more thoroughly. Regardless, these few examples demonstrate a species packing that exceeds expectations. Whether the small size of these species facilitates the packed nature of their assemblages remains to be determined. This is another pointed example of the need for prolonged sampling with multiple methods to better define caddisfly assemblages at any location.

Altitudinal distribution

There are a number of problems when evaluating the distribution of any group of aquatic insects in relation to altitude. Inadequate and infrequent sampling at representative altitudes, rarely captured or undetected species, low or high altitude outliers caused by meteorological events, differences in stream velocity and riparian corridor composition, and meteorological conditions during sampling are but a few (Janzen 1967; Rahbek 1995; Miserendino and Pizzolón 2001). With those caveats exposed, we present the distribution of *Leucotrichia* species with altitude in Fig. 18. It is apparent that most of the species can be found from low (~ 100 m a.s.l.) to middle

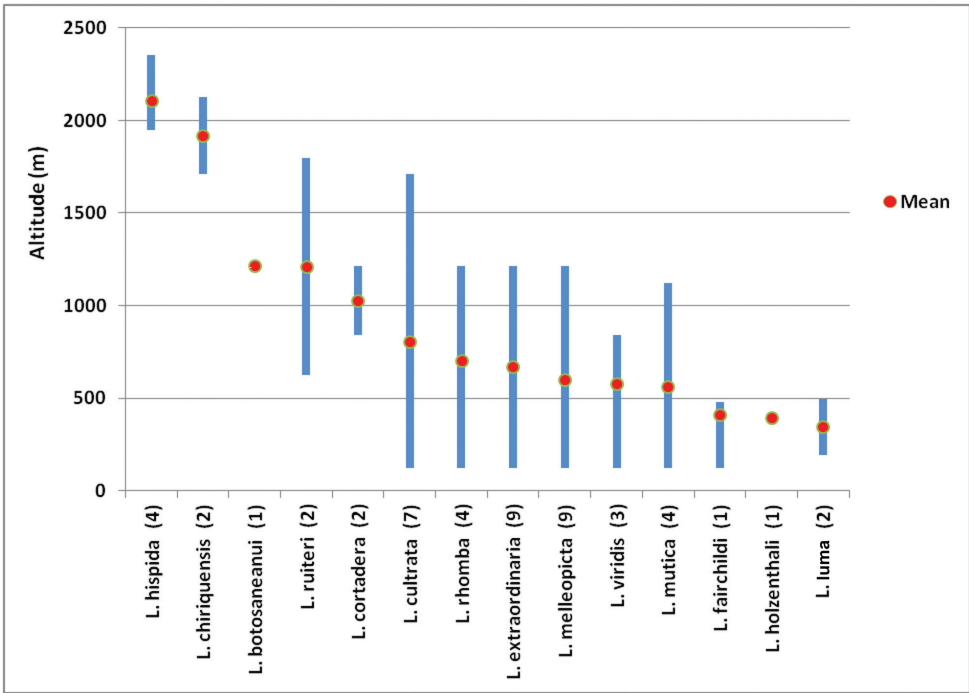


Figure 18. Distribution of *Leucotrichia* species with altitude in Panama, sorted from left to right by mean values. The number of unique streams involved in plotting each species is found in parentheses following each species name. Mean values for each species distribution range are indicated by a red circle. The species name labels orthogonal to the X-axis are not italicized to facilitate readability.

(~ 1,500 m a.s.l.) altitudes. The higher altitudes appear to be populated by very few species consistently, while another few species have only been collected at low altitudes. Approximately 1/3 of the species in Panama are infrequently collected (Table 3), including those that favor low altitudes, so until additional specimens of these species are collected, we reserve judgment about their true range of altitudes occupied. However, we think that sufficient collections have been made overall to make us more confident about the higher altitude proclivities of *L. hispida* and *L. chiriquiensis*. Additional data records from monthly Malaise trap samples over several years bolster our belief in these two species being confined to higher altitudes.

Geographic distributions and affinities

Endemics aside, the current, typical distribution pattern among caddisflies in the northern Neotropics follows a NW to SE axis from Mexico down to Panama, with disjuncts to the north (nearctic North America) and to the south (northern South America). Most of the species of *Leucotrichia* in Panama follow this track. However, there are two species of *Leucotrichia* and roughly two dozen Panamanian caddisfly species which share the Trinidad to Panama connection mentioned in the Results section. To our knowledge, few other northern South American countries between Trinidad and Panama also host these species. We have speculated in the past that the higher velocity trade winds during the dry season (December through April) moving from northern South America west, toward and across Panama, might be involved in this disjunct distribution (Armitage et al. 2020). However, other than recording yet more species which fit this profile, no other additional proof has been obtained.

Leucotrichia species have been found in 22 continental and island countries in Latin America, including the Caribbean Region (Holzenthal and Calor 2017). Surprisingly, none have been found in French Guiana, Suriname, Paraguay, Uruguay, Bolivia, Cuba, Belize, Honduras, and many of the Caribbean Islands. We suspect, in large part, this absence is the result of undercollecting of adults. Also, the majority of our species were collected in Malaise traps, whose use is important for detecting the greatest number of species for this genus at a collecting site, but not commonly employed elsewhere. The lack of affinity among countries for this and other genera appears negatively correlated with the percent of endemics in each country's fauna. In samples from Panama, we have observed from 20–35% endemics. In Brazil (Santos et al. 2020), 538 of the 796 recorded species of caddisflies are endemic (68%). We suggest that as more collecting is done, the affinity among countries will increase and the percent of endemics in each country will go down. We base this statement, in part, on our elimination of “endemic” status from 84 Costa Rican species of caddisflies over the last six years through their discovery in Panama.

An interesting historical aspect of this puzzling genus involves its ancestral home or point of origin and the genesis of its current assemblage of species. If we accept the work of Santos et al. (2016), based on molecular analyses, the Leucotrichiinae began to diversify some 124 ma, after the separation of South America from Africa. Crown diversification of the Leucotrichiini occurred ~ 80 ma. As South America assumed its

current orientation and position, they proposed that the Leucotrichiini or its generic derivatives migrated north, using the proto-Caribbean archipelago as an initial invasion corridor. This is consistent with the theory that Brazil and the Amazon basin are the center of origin or ancestral home for many organismal groups (Antonelli et al. 2018). As mentioned above, the genus *Leucotrichia* in Brazil is at the moment characterized by low diversity and no affinity to other countries in Latin America, and there is the possibility that the genus evolved elsewhere. However, given that all other Leucotrichiini genera are present in South America, with some restricted to this region, it is more plausible that the genus evolved in South America and then dispersed northward (A. Santos, pers. comm.). The only other hard information we have is based on the work of Wells and Wichard (1989) wherein they described the fossil species *Leucotrichia adela* from Dominican amber (20–23 ma), diagnosing it as closest to the extant Panamanian species, *L. chiriquiensis*. Based on all of this, there is a reasonable likelihood that the original migrants from South America initially diversified and underwent rapid radiation in Caribbean and Central America regions, not South America, as the next step in producing the array of species we have today. Then alternating changes in climate during the Pleistocene, and before, with reciprocating northward and southward migrations of floras and faunas (Rocha and Kaefer 2019), could have forced additional speciation, as well as colonization of northern South America by some species which evolved further north. All of this is conjecture, of course, and our understanding of the matter will only become clearer with increased collections and with more geographically inclusive molecular work on the leucotrichiine genera and species.

The composition and structure of the cluster diagram in Fig. 19 will surely change as more sampling and identifications of adult *Leucotrichia* takes place in all Latin American countries. We anticipate a marked increase of similarity values across the board, should that occur. This low similarity between Panama and other Latin American

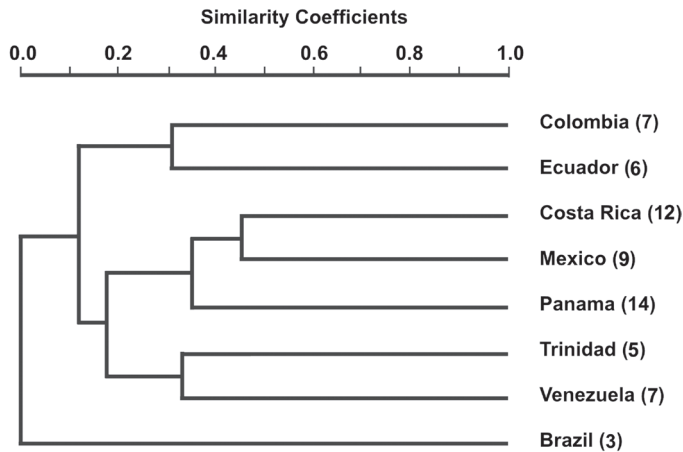


Figure 19. Cluster diagram employing Bray-Curtis similarity values showing the relationships between Latin American countries home to at least four species of *Leucotrichia*, plus Brazil. The number of species in each country is indicated within parentheses at the end of each name.

countries (Fig. 19), also increases the probability that other species, but certainly not all, from outside Panama will eventually be found here. This is based on more than presumption. The majority of the new country records ($n = 156$) we have found during the last six years are species which heretofore were only found in Costa Rica. Thus, other *Leucotrichia* species unique to that country have a higher probability of being found in Panama. This same logic holds, to a lesser degree, with other countries with which Panama currently shares *Leucotrichia* species.

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A preliminary molecular phylogeny of the family Hydroptilidae (Trichoptera): an exploration of combined targeted enrichment data and legacy sequence data

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Abstract

Hydroptilidae is an extremely diverse family within Trichoptera, containing over 2,600 known species, that displays a wide array of ecological, morphological, and habitat diversity. However, exploration into the evolutionary history of microcaddisflies based on current phylogenetic methods is mostly lacking. The purpose of this study is to provide a proof-of-concept that the use of molecular data, particularly targeted enrichment data, and statistically supported methods of analysis can result in the construction of a stable phylogenetic framework for the microcaddisflies. Here, a preliminary exploration of the hydroptilid phylogeny is presented using a combination of targeted enrichment data for ca. 300 nuclear protein-coding genes and legacy (Sanger-based) sequence data for the mitochondrial COI gene and partial sequence from the 28S rRNA gene.

Keywords

Caddisfly, diversity, molecular dataset, systematics

Introduction

Caddisflies, or Trichoptera, are a diverse order of insects with more than 16,000 described species and 100s of new species awaiting placement and description (Morse 1999; Holzenthal 2009; Holzenthal et al. 2015). Moth-like as adults, Trichoptera are closely related to Lepidoptera (butterflies and moths). Larvae are aquatic and produce silk, which is used to construct a wide variety of portable cases and filtering nets (Wiggins 1996, 2004).

As the common name “microcaddisfly” suggests, Hydroptilidae represent the smallest family in the order in terms of body size, with adults ranging from between 1.5 mm to usually no more than 5 mm in length (Holzenthal et al. 2007b). Microcaddisflies are extremely diverse; larvae occur in a wide array of aquatic habitats, display numerous feeding patterns, and last instars construct a variety of larval cases known collectively for the family as “purse-cases” and exhibit an interesting hypermetamorphosis observed within Trichoptera only in Hydroptilidae and its sister group, Ptilocolepidae (Nielsen 1948; Wells 2010).

In terms of species diversity, Hydroptilidae is the largest family in the order Trichoptera, including more than 2,600 species in 76 genera (including three fossil genera) and six subfamilies, found in all faunal regions of the world (Marshall 1979; Morse 1999; Holzenthal et al. 2011) (Table 1). Of the six subfamilies, two are largely endemic to the Neotropical faunal region (Leucotrichiinae and Neotrichiinae), though some of the included species are distributed well into North America. Ochrotichiinae is distributed primarily in the Neotropics, with two genera occurring in Australasia. Hydroptilinae occurs in the Old World, but also includes two large cosmopolitan genera (*Hydroptila* and *Oxyethira*) and several genera endemic to the Australasian or Afrotropical faunal regions. The subfamily Orthotrichiinae is small, but includes the cosmopolitan genus *Orthotrichia*, while the subfamily Stactobiinae is a varied collection of genera that are either endemic to a particular region or occur in a wider distribution throughout multiple regions. The closely related Ptilocolepidae are a small family, formerly considered to be a subfamily within Hydroptilidae, which currently contains the genera *Ptilocolepus* and *Palaeagapetus* distributed throughout the Holarctic faunal region. Since being elevated to family status (Malicky 2001), the placement of Ptilocolepidae and its relationship with Hydroptilidae has been contentious (Holzenthal et al. 2007a; Malicky 2008; Thomas et al. 2020).

Marshall (1979) provided the first comprehensive review of Hydroptilidae at the generic level, including the 42 genera known at the time. The morphology-based phylogeny she proposed was not based on any statistical analyses and therefore offered no support values for any of the proposed relationships (Fig. 1). The only other attempt to provide a family-wide systematic framework for Hydroptilidae was that of Oláh and Johanson (2011), a work in which they described many new species and updated the genera to be included in each subfamily. Several tables were provided, containing either features or character states of species groups, subgenera, or generic clusters; there was no discussion presented regarding the information outlined in the tables. As interpreted from the tables, several genera were transferred between subfamilies or moved from incertae sedis status, but no phylogeny or hypotheses of relationships were included.

Table 1. Currently recognized genera of Hydroptilidae and Ptilocolepidae and family-group classification.

Family	Subfamily	Tribe	Genera	
Hydroptilidae	Hydroptilinae	–	<i>Acanthotrichia</i>	<i>Microptila</i>
			<i>Acritoptila</i>	<i>Missitrichia</i>
			<i>Aenigmatrichia</i>	<i>Mulgravia</i>
			<i>Agraylea</i>	<i>Oxyethina</i>
			<i>Allotrichia</i>	<i>Paroxyethina</i>
			<i>Austratrichia</i>	<i>Paucicalcaria</i>
			<i>Cyclopsiella</i>	<i>Sutheptila</i>
			<i>Dhatrichia</i>	<i>Tangatrichia</i>
			<i>Hellyethina</i>	<i>Tricholeiochiton</i>
			<i>Hydroptila</i>	<i>Ugandatrichia</i>
			<i>Jabitrichia</i>	<i>Vietrichia</i>
			<i>Kholaptila</i>	<i>Wlitrichia</i>
			<i>Maeyaptila</i>	<i>Xuthotrichia</i>
	Leucotrichiinae	Alisotrichiini	<i>Alisotrichia</i>	<i>Cerasmatrichia</i>
			<i>Byrsopteryx</i>	<i>Mejicanotrichia</i>
			<i>Celaenotrichia</i>	<i>Scelobotrichia</i>
		Leucotrichiini	<i>Acostatrichia</i>	<i>Costatrichia</i>
			<i>Anchitrichia</i>	<i>Leucotrichia</i>
			<i>Ascotrichia</i>	<i>Peltopsyche</i>
			<i>Betrichia</i>	<i>Tupiniquintrichia</i>
			<i>Cenatotrichia</i>	<i>Zumatrichia</i>
	Neotrichiinae	–	<i>Kumanskiella</i>	<i>Neotrichia</i>
			<i>Mayatrichia</i>	<i>Taraxitrichia</i>
	Ochrotrichiinae	–	<i>Angrisanoia</i>	<i>Nothotrichia</i>
			<i>Caledonotrichia</i>	<i>Ochrotrichia</i>
			<i>Dibusa</i>	<i>Ragitrichia</i>
			<i>Maydenoptila</i>	<i>Rhyacopsyche</i>
			<i>Metrichia</i>	
	Orthotrichiinae	–	<i>Ithytrichia</i>	<i>Sarangannotrichia</i>
			<i>Orthotrichia</i>	
	Stactobiinae	–	<i>Bredinia</i>	<i>Pseudoxyethina</i>
			<i>Catoxyethira</i>	<i>Orinocotrichia</i>
			<i>Chrysotrichia</i>	<i>Plethus</i>
			<i>Flintiella</i>	<i>Stactobia</i>
			<i>Maetalaiptila</i>	<i>Stactobiella</i>
			<i>Niuginitrichia</i>	<i>Tizatetrichia</i>
Hydroptilidae, incertae sedis	–	–	<i>Burminoptila</i> †	<i>Macrostactobia</i>
			<i>Dicaminus</i>	<i>Novajerseya</i> †
			<i>Electrotrichia</i> †	<i>Orphminotrichia</i>
Ptilocolepidae	–	–	<i>Palaeagapetus</i>	<i>Ptilocolepus</i>

Several subfamilies have a history of being difficult to unite by any morphological features. For example, various Trichoptera researchers have made published comments regarding the difficulty in uniting the subfamily Stactobiinae or finding any derived characters exclusive to the group (Wells 1990; Bowles et al. 1999; Malicky and Chantaramongkol 2007). Leucotrichiinae is the only subfamily that has undergone a detailed phylogenetic analysis; a relatively recent assessment confirmed the monophyly of the family and generic assignment to two newly established tribes (Leucotrichiini and Alisotrichiini) for the first time (Santos et al. 2016).

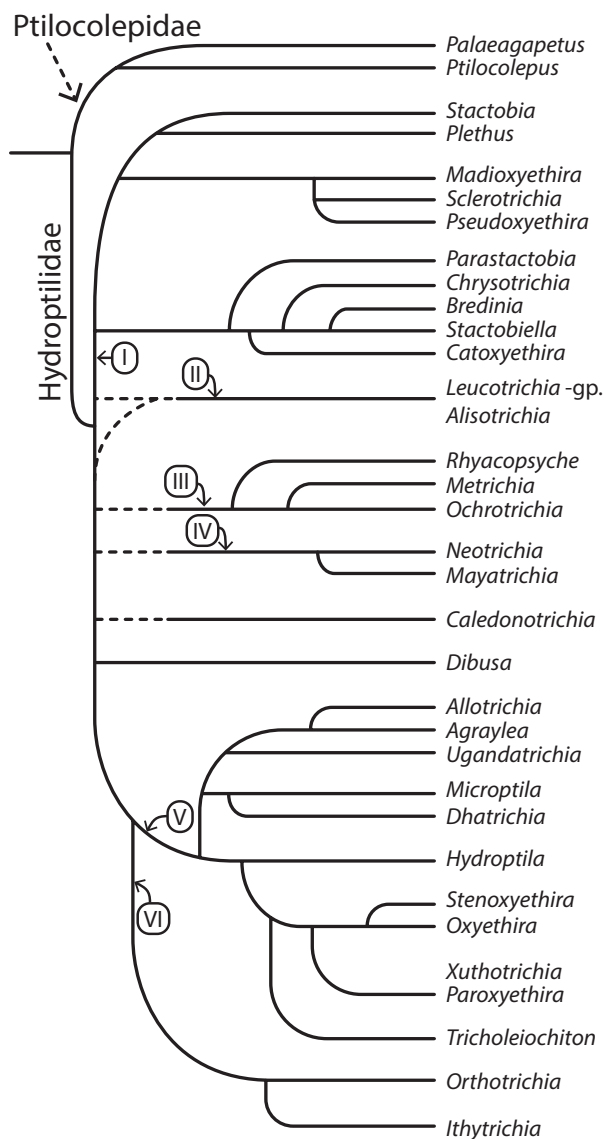


Figure 1. Phylogeny of Hydroptilidae, re-drawn from Marshall (1979). Based on morphological data; generic relationships (I Stactobiini II Leucotrichiini III Ochrotrichiini IV Neotrichiini V Hydroptilini VI Orthotrichiini).

A stable framework based on statistically-supported phylogenetic methods is needed to consistently define taxa and provide context for how they relate to each other and are arranged within the family overall. Wiggins (2004) suggested that a thorough analysis of phylogenetic relationships is important for taxonomic and systematic progression; Hydroptilidae has consistently been supported as monophyletic in studies of family relationships across Trichoptera, but analysis of the relationships within this hyperdiverse family

has long been neglected. The microcaddisflies have shown a long history of instability and tenuous placement within Trichoptera but tended to occur with several families in various arrangements near the base of Trichoptera (Ross 1967; Weaver 1984; Weaver and Morse 1986; Wiggins and Wichard 1989; Frania and Wiggins 1997; Ivanov 1997; Kjer et al. 2001; Malm et al. 2013). In the most recent study using molecular data to explore the relationships among the caddisfly families, Hydroptilidae were grouped with the suborder Integripalpia in an arrangement that was supported by different methods of analysis and independent datasets (Thomas et al. 2020). A stable phylogeny for Hydroptilidae would also be useful for larger questions applied to the order Trichoptera. Targeted enrichment has emerged as a useful and popular tool for sequencing many genes from museum specimens. It allows for sequencing across many hundreds of genes, even for specimens with degraded DNA (Lemmon et al. 2012). Recently, Deng and colleagues applied this approach to the trichopteran genus *Himalopsyche* (Deng et al. 2021). This preliminary study acts as a proof-of-concept that targeted enrichment sequence data using the previously published Trichoptera probe set can be successfully obtained from hydroptilid specimens and, when used in tree construction, can successfully recover expected clades, and produce a phylogeny with high support values. Our specific objectives are to provide a preliminary analysis of the monophyly of Hydroptilidae, Ptilocolepidae, and the hydroptilid subfamilies in their current classification system, and to explore the relationships within and between these taxa.

Materials and methods

Selection of taxa

The taxa included in this study were chosen to represent the overall taxonomic diversity of the family Hydroptilidae by including examples of all subfamilies and as many genera as possible. A list of the specimens from which DNA was sequenced for this study is presented in Table 2.

Targeted enrichment taxon sampling

Ingroup

We sequenced eleven ingroup species of microcaddisflies using targeted enrichment sequencing (Lemmon et al. 2012), including ten species from the family Hydroptilidae and one species from the family Ptilocolepidae. These taxa represent five of six subfamilies, with the exception of Ochrotrichiinae.

Outgroup

We selected an additional five species from four different families as outgroups, including representatives from Rhyacophilidae, Glossosomatidae, Phryganeidae, and Leptoceridae.

Table 2. Determination, depository, and sequencing method of specimens included in phylogenetic analyses. “Composite” refers to instances in which we combined sequence data for two closely related species in the same genus for the sake of matrix completeness.

		Depository	Targeted Enrichment	Sanger	Composite
INGROUP					
Hydroptilidae					
Hydroptilinae					
<i>Agraylea</i>	<i>cognatella</i>	ZMUB		X	
	<i>multipunctata</i>	RUIC	X	X	
	<i>sexmaculata</i>	RUIC		X	
	<i>saltesea</i>	RUIC		X	
<i>Allotrichia</i>	<i>cf. saltesea</i>	BOLD		X	
	<i>vilnensis</i>	BOLD	X	X	
<i>Hellyethira</i>	<i>simplex</i>	UMSP		X	
	<i>Hydroptila</i>				
<i>Hydroptila</i>	<i>ajax</i>	BOLD		X	
	<i>albicornis</i>	BOLD		X	
	<i>ampoda</i>	BOLD		X	
	<i>argosa</i>	BOLD		X	
	<i>consimilis</i>	BOLD		X	
	<i>coweetensis</i>	BOLD		X	
	<i>delineata</i>	BOLD		X	
	<i>forcipata</i>	ZMUB		X	
	<i>gunda</i>	CUAC		X	
	<i>hamata</i>	CUAC		X	
	<i>jackmanni</i>	BOLD		X	
	<i>losida</i>	UMSP		X	
	<i>oguranis</i>	UMSP		X	
	<i>rono</i>	BOLD		X	
	<i>scamandra</i>	UMSP		X	X
	<i>tineoides</i>	ZMUB	X	X	
	<i>vectis</i>	RUIC		X	X
	<i>xera</i>	BOLD		X	
<i>Oxyethira</i>	<i>absona</i>	RUIC		X	
	<i>bidentata</i>	RUIC		X	
	<i>frici</i>	ZMUB		X	
	<i>grisea</i>	CUAC		X	
	<i>janella</i>	CUAC		X	
	<i>rivicola</i>	RUIC		X	
	<i>rossi</i>	RUIC		X	
	<i>Paroxyethira</i>				
<i>Paroxyethira</i>	<i>hendersoni</i>	NMNH		X	
	<i>tillyardi</i>	NMNH		X	
<i>Ugandatrichia</i>	<i>maliwan</i>	RUIC		X	
	sp.	RUIC		X	
Leucotrichiinae					
<i>Abtrichia</i>	<i>antennata</i>	UMSP		X	
	<i>squamosa</i>	UMSP		X	
	<i>veva</i>	NMNH		X	
<i>Alisotrichia</i>	<i>fundorai</i>	NMNH		X	
	<i>hirudopsis aitija</i>	NMNH		X	
<i>Anchitrichia</i>	<i>duplifurcata</i>	UMSP		X	
	<i>spangleri</i>	RUIC		X	
<i>Ascotrichia</i>	<i>surinamensis</i>	NMNH		X	X
	sp.	RUIC		X	X
<i>Byrsoteryx</i>	<i>abrelata</i>	UMSP		X	
	<i>chaconi</i>	UMSP		X	
	<i>esparta</i>	UMSP		X	
	<i>gomezi</i>	UMSP	X	X	
	<i>solisi</i>	UMSP		X	
	<i>tapanti</i>	UMSP		X	
	<i>tica</i>	UMSP		X	
<i>Celaenotrichia</i>	<i>edwardsi</i>	BOLD		X	

		Depository	Targeted Enrichment	Sanger	Composite
<i>Cerasmatrichia</i>	<i>spinosa</i>	BOLD	X	X	
	<i>trinitatis</i>	NMNH		X	
<i>Ceratotrichia</i>	<i>flavicomma</i>	NMNH		X	
<i>Leucotrichia</i>	<i>fairchildi</i>	RUIC		X	X
	<i>pictipes</i>	RUIC		X	X
	<i>sarita</i>	NMNH	X	X	
<i>Zumatrichia</i>	<i>anomalopecta</i>	NMNH		X	
	<i>diamphidia</i>	RUIC		X	X
	<i>rhampoides</i>	UMSP		X	X
Neotrichiinae					
<i>Mayatrichia</i>	<i>ayama</i>	NMNH		X	
	<i>ruvalda</i>	UMSP		X	
<i>Neotrichia</i>	<i>feolai</i>	BOLD	X	X	
	<i>minutisimella</i>	UMSP		X	
	<i>vibrans</i>	UMSP		X	
Ochrotrichiinae					
<i>Dibusa</i>	<i>angata</i>	NMNH		X	
<i>Metrichia</i>	<i>fontismoreaui</i>	NMNH		X	
	<i>neotropialis</i>	UMSP		X	
	<i>nigritta</i>	UMSP		X	
	<i>patagonica</i>	UMSP		X	
	<i>platigona</i>	NMNH		X	
	<i>spica</i>	UMSP		X	
	<i>yalla</i>	NMNH		X	
<i>Nothotrichia</i>	<i>cautinensis</i>	BOLD		X	
<i>Ochrotrichia</i>	<i>alsea</i>	UMSP		X	
	<i>dactylophora</i>	BOLD		X	
	<i>eliaga</i>	RUIC		X	
	<i>logana</i>	RUIC		X	
	<i>limonensis</i>	UMSP		X	
	<i>oregona</i>	UMSP		X	
	<i>panamensis</i>	RUIC		X	
	<i>tarsalis</i>	UMSP		X	
	<i>tenanga</i>	UMSP		X	
<i>Rhyacopsyche</i>	<i>andina</i>	UMSP		X	
	<i>dikrosa</i>	UMSP		X	
	<i>hagenii</i>	UMSP		X	
	<i>mexicana</i>	UMSP		X	
Orthotrichiinae					
<i>Ithytrichia</i>	<i>lamellaris</i>	USDC		X	
<i>Orthotrichia</i>	<i>curvata</i>	BOLD	X	X	
	<i>tragetti</i>	BOLD	X	X	
Stactobiinae					
<i>Stactobia</i>	<i>makartshenkoi</i>	NMNH		X	
	<i>nybomi</i>	NMNH		X	
<i>Stactobiella</i>	<i>delira</i>	UMSP	X	X	
	<i>martynovi</i>	RUIC		X	
	<i>palmata</i>	BOLD		X	
	<i>tshistjakovi</i>	UMSP		X	
Incertae sedis					
<i>Orphninothrichia</i>	<i>squamosa</i>	UMSP		X	
Ptilocolepidae					
<i>Palaeagapetus</i>	<i>celsus</i>	RUIC		X	
	<i>nearcticus</i>	BOLD		X	
	<i>ovatus</i>	NMNH		X	
<i>Prilocolepus</i>	<i>extensus</i>	USDC	X	X	
	<i>granulatus</i>	RUIC		X	
OUTGROUP					
Glossosomatidae					
<i>Agapetus</i>	<i>pinatus</i>	RUIC		X	
<i>Agapetus</i>	<i>tomus</i>	BOLD	X	X	

		Depository	Targeted Enrichment	Sanger	Composite
<i>Anagapetus</i>	<i>bernea</i>	BOLD		X	
	<i>debilis</i>	RUIC		X	
<i>Cariboptila</i>	<i>aurulenta</i>	BOLD		X	
<i>Culoptila</i>	<i>hamata</i>	RUIC		X	
<i>Glossosoma</i>	<i>nigrior</i>	RUIC		X	
<i>Padunia</i>	<i>jeanae</i>	RUIC		X	
<i>Protoptila</i>	<i>laterospina</i>	BOLD		X	
	<i>tenebrosa</i>	RUIC		X	
Hydrobiosidae					
<i>Apatanodes</i>	<i>sociatus</i>	BOLD		X	
<i>Apsilochorema</i>	<i>gisbum</i>	RUIC		X	
<i>Atopsyche</i>	<i>callosa</i>	RUIC		X	
	sp.	RUIC		X	
<i>Taschorema</i>	<i>evansi</i>	RUIC		X	
<i>Ulmerochorema</i>	<i>onychion</i>	RUIC		X	
	<i>rubiconum</i>	BOLD		X	
Rhyacophilidae					
<i>Himalopsyche</i>	<i>malenada</i>	BOLD		X	
<i>Rhyacophila</i>	<i>brunnea</i>	RUIC	X	X	
	<i>coloradensis</i>	RUIC	X	X	
	<i>fuscula</i>	RUIC		X	
Phryganeidae					
<i>Ypbria</i>	<i>californica</i>	BOLD	X	X	
Leptoceridae					
<i>Leptocerus</i>	<i>americanus</i>	BOLD	X	X	
Sericostomatidae					
<i>Myotrichia</i>	<i>murina</i>	BOLD		X	
Limnephilidae					
<i>Limnephilus</i>	<i>externus</i>	BOLD		X	

Sanger sequencing taxon sampling

Ingroup

The ingroup, Hydroptilidae and Ptilocolepidae, included 104 species units representing a total of 32 genera. Representatives from both ptilcolepid genera and all six traditionally recognized hydroptilid subfamilies were included as ingroup taxa. As many genera from each subfamily were obtained as possible and all taxa from which DNA was successfully sequenced and amplified were included in the dataset. Large subfamilies and genera, such as Hydroptilinae, *Hydroptila*, and *Oxyethira*, were sampled more rigorously to account for high species richness. There were some taxa included in the targeted enrichment taxon sampling for which no Sanger sequencing data existed. For the fastRFS analysis, we assigned those taxa to the closest available taxon with available Sanger sequencing data based on their classification (Table 2).

Outgroup

The outgroup consisted of 25 species including members from the families Glossosomatidae, Hydrobiosidae, Rhyacophilidae, Phryganeidae, Leptoceridae, Sericostomatidae, and Limnephilidae.

Depositories

Specimens sequenced for this study were obtained from the National Museum of Natural History, Washington, DC, USA (**NMNH**); University of Minnesota Insect Collection, St. Paul, MN, USA (**UMSP**), Clemson University Arthropod Collection, Clemson, SC, USA (**CUAC**); Zoological Museum, University of Bergen, Bergen, Norway (**ZMUB**); Rutgers University Entomology Museum, New Brunswick, NJ, USA (**RUIC**); and Departamento de Zoología y Antropología Física, Universidad de Santiago de Compostela, Santiago de Compostela, Spain (**USDC**). Additionally, Dave Ruiter, Grants Pass, Oregon, USA; Alice Wells, Australian Biological Resources Study, Canberra, ACT, Australia; and Tomiko Ito, Hokkaido Aquatic Biology, Hokkaido, Japan generously donated several specimens from their private collections to UMSP. Voucher materials from specimens that were successfully sequenced are deposited at the NMNH, UMSP, CUAC, ZMUB, and USDC. All specimens from which DNA was sequenced for this study were affixed with a barcode label (4 mil polyester, 8 × 14 mm, code 49) bearing a unique alphanumeric sequence beginning with the prefix UMSP. The prefix does not imply ownership by UMSP, but only indicates that the specimen was databased at that collection and to provide unique identification code (UID) for entry into a database. Specimen-level taxonomic, locality, and other information are stored in the University of Minnesota Insect Collection database using the software Specify 6.7.02 (Specify Collections Consortium 2022).

DNA Sequences

To create a scaffold of phylogenetic relationships among subfamilies, we used targeted enrichment to capture 302 genes across a subset of the taxa sampled (Table 2).

DNA extraction

DNA was extracted from pinned or 95% ethanol-preserved museum specimens. In cases of ethanol-preserved specimens, attempts were made to use the most recently collected specimens available. Due to the physically minute size of individual specimens, the head, thorax, and legs were all taken for extraction. In all cases, male genitalia were retained as specimen voucher material, and the specimen data were entered into the UMSP Specify database. Genitalia were prepared for preservation following the lactic acid method, procedures for which are explained in detail by Blahnik et al. (2007). DNA was extracted in either the laboratory of Dr. Karl Kjer, Rutgers University, or of Dr. Susan Weller, University of Minnesota. DNA extraction was completed using the DNEasy Blood and Tissue Kit (Qiagen, Inc.) with 20 µl of Proteinase K (Qiagen, Inc.).

Targeted enrichment

We used the Trichoptera probe set published in Deng et al. (2021) for the targeted enrichment analyses. Following DNA extraction, quantification, targeted enrichment,

library preparation, and DNA sequencing were conducted off-site by Rapid Genomics. For sequencing, paired-end 2 × 150 bp reads were sequenced on an Illumina NovaSeq instrument.

PCR and Sanger sequencing

Targeted gene sequences for COI and partial 28S were amplified using polymerase chain reaction (PCR) with Accuzyme Mix (Bioline) and the primers listed in Table 3. An additional 0.25 µl of magnesium per specimen was utilized when amplifying the mitochondrial DNA (COI). The PCR mix underwent the time and temperature cycles listed, with different annealing temperatures for each targeted gene sequence as stated in Table 4. PCR products were cleaned and purified with either the QIAquick PCR Purification Kit (Qiagen, Inc.) or ExoSAP-IT (Affymetrix, Inc.). DNA concentrations were estimated by UV visualization of SYBR Safe (Invitrogen, Life Technologies) stained 1% agarose gel with Tris-borate-EDTA (TBE) electrophoresis buffer using standard techniques. Sequences were visualized and recorded using the Applied Biosystems (ABI) 3730xl Sequencer at the University of Minnesota Genomics Center. Each DNA fragment was sequenced from both directions. We also downloaded public COI sequences from the Barcode of Life Data Systems (BOLD) (Ratnasingham and Hebert 2007) for those taxa represented in our targeted enrichment data set.

Table 3. Primers used in polymerase chain reactions for this study.

Primer	Sequence (5' to 3')	Reference
COI F	TAATTGGAGGATTTGGWAAATG	Kjer et al. 2001
COI R	CCYGGTAAAAATTAAATATAAACTTC	Kjer et al. 2001
D1 up	GGAGGAAAAGAACTAACAAGGATT	Kjer et al. 2001
D1dn	CAACTTTCCCTTACGGTACT	Kjer et al. 2001
D2up4	GAGTTCAAGAGTACGTGAAACCG	Zhou et. al. 2007
D2dnB	CCTTGGTCCGTGTTTCAAGAC	Zhou et. al. 2007
D3up	ACCCGTCCTGAAACACGGAC	Kjer et al. 2001
D3DnTr2	CTATCCTGAGGGAACCTCGGA	Kjer et al. 2001

Table 4. PCR settings (cycles, temperature, time) for each targeted gene sequence.

Repetitions	Temperature (°C)	Time
1 ×	94	3 minutes
40 ×	94	30 seconds
40 ×	52 – COI	30 seconds
40 ×	56 – D1	30 seconds
40 ×	57 – D2	30 seconds
40 ×	61 – D3	30 seconds
40 ×	72	30 seconds
40 ×	72	7 minutes
1 ×	4	hold

Targeted enrichment analysis

Paired-end raw reads were delivered in FASTQ files by Rapid Genomics for the targeted enrichment taxa. We trimmed adapters from the raw reads using TrimGalore! (Babraham Bioinformatics 2019). We then followed the targeted enrichment analysis pipeline published by Breinholt et al. (2018). In brief, we assembled the trimmed reads into targeted gene sequences using iterative baited assembly. Then, for each gene targeted, we searched against the *Stenopsyche tienmushanensis* reference genome assembly (Luo et al. 2018) with BLAST to assess orthology. If a selected gene generated multiple hits in the genome assembly, then that gene was removed from further analysis. We then assessed contamination in the data set by an all-by-all comparison with USEARCH v. 11 (Edgar 2010). If a hit was more than 98% identical over more than 80% of the gene sequence, both gene sequences were removed from further analysis. We combined orthologous sequences into unaligned FASTA files, which were aligned with MAFFT v. 7 (Katoh and Standley 2013) using the “AUTO” alignment setting.

Alignment of Sanger sequencing data

Forward and reverse sequence fragments were edited and aligned in the program Geneious (Geneious Pro, v. 5.6.3, created by Biomatters). Consensus sequences for mitochondrial DNA (COI) were aligned using translation alignment in Geneious, while consensus sequences for ribosomal RNA (D1-3) were aligned using the MUSCLE alignment. Gaps and ambiguous sequences were coded as missing (-). Nucleotides were treated as unordered characters with four alternative states.

Phylogenetic analysis

We generated three phylogenetic estimates from our data: (1) a maximum-likelihood tree based on a concatenated supermatrix of the targeted enrichment data (Fig. 2A), (2) a multispecies coalescent tree generated from maximum-likelihood trees of individual targeted enrichment loci (Fig. 2B), and (3) a fastRFS supertree based on the maximum-likelihood trees of individual targeted enrichment loci and the alignments from Sanger data of COI and 28S (Fig. 3). Single gene alignments and tree files were deposited in the Dryad Data Repository at <https://doi.org/10.5061/dryad.15dv41p0n> (Thomson et al. 2022).

Unfortunately, 100% of the gene fragments chosen for this study were not successfully sequenced for every species in the dataset. In a few situations, genera were represented by only a few species between which the recovered gene sequences did not overlap (ex: COI and D2 for Species 1, D1 and D3 for Species 2). In these instances, voucher material from the individual specimens was examined and identification was re-confirmed before combining the non-overlapping sequences as a single taxon, as indicated in Table 2.

To generate the maximum likelihood phylogenetic estimate for the supermatrix, we first concatenated the individual gene alignments into a concatenated supermatrix using FASconCAT (Kück and Meusemann 2010). We then used the FASconCAT info file to cre-

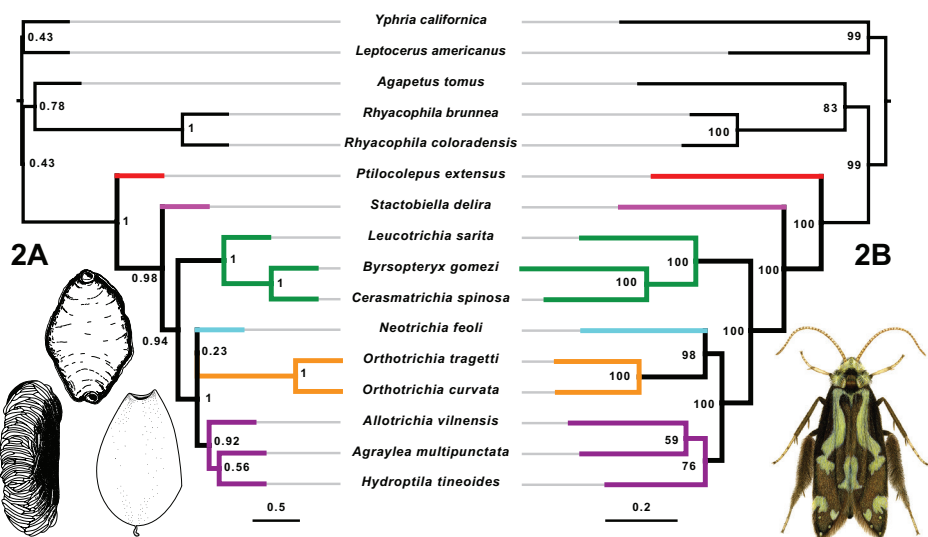


Figure 2. Targeted enrichment data only trees **A** astral multi-species coalescent tree. Support values are local posterior probabilities. Scale bar: coalescent units. Larval cases: *Leucotrichia* (top), *Dibusa* (left), *Ithytrichia* (right) **B** maximum-likelihood tree of concatenated supermatrix. Support values are ultra-fast bootstraps estimated in IQ-TREE. Scale bar: substitution rate. Adult: *Ascotrichia* sp.

are an IQTREE partition definition file. We selected an optimal partitioning scheme using the relaxed clustering algorithm in IQ-TREE v.2.0.6 (Minh et al. 2020) with the options “-mset GTR -m TESTMERGEONLY”. We then selected the best fit substitution model for each subset in the partitioning scheme using ModelFinder as implemented into IQ-TREE v.2.0.6 with the option “-m MFP” (Minh et al. 2020). Using this model, we ran 25 separate maximum likelihood tree searches with 1000 ultrafast bootstrap replicates (option -bb 1000) and chose the tree with the best maximum-likelihood score (Hoang et al. 2017).

To generate a multi-species coalescent species tree, we first generated individual gene trees for each targeted enrichment locus with IQ-TREE v.2.0.6 (Minh et al. 2020). For each tree, we first selected the best substitution model with ModelFinder and then estimated 25 maximum likelihood trees with 1000 ultrafast bootstrap replicates and selected the tree with the maximum likelihood. We then used these trees as input for ASTRAL-III (Zhang et al. 2018).

Finally, we incorporated Sanger sequencing data for 28S and COI into a supertree analysis as described in Letsch et al. (2021). In their paper, they found that the supertree approach fastRFS (Vachaspati and Warnow 2017) generated the most reliable trees when combining Sanger sequencing data for many taxa with a “backbone” phylogenomic dataset that represented a smaller subset of those same taxa. Briefly, we concatenated the four PCR regions (D1, D2, D3 of 28S and COI) into a supermatrix and generated a tree using the same methods outlined above for the targeted enrichment loci. We then used fastRFS (Vachaspati and Warnow 2017) to estimate a “supertree” that considers both the targeted enrichment-based backbone tree and the increased taxon sampling made possible via the Sanger sequencing data.

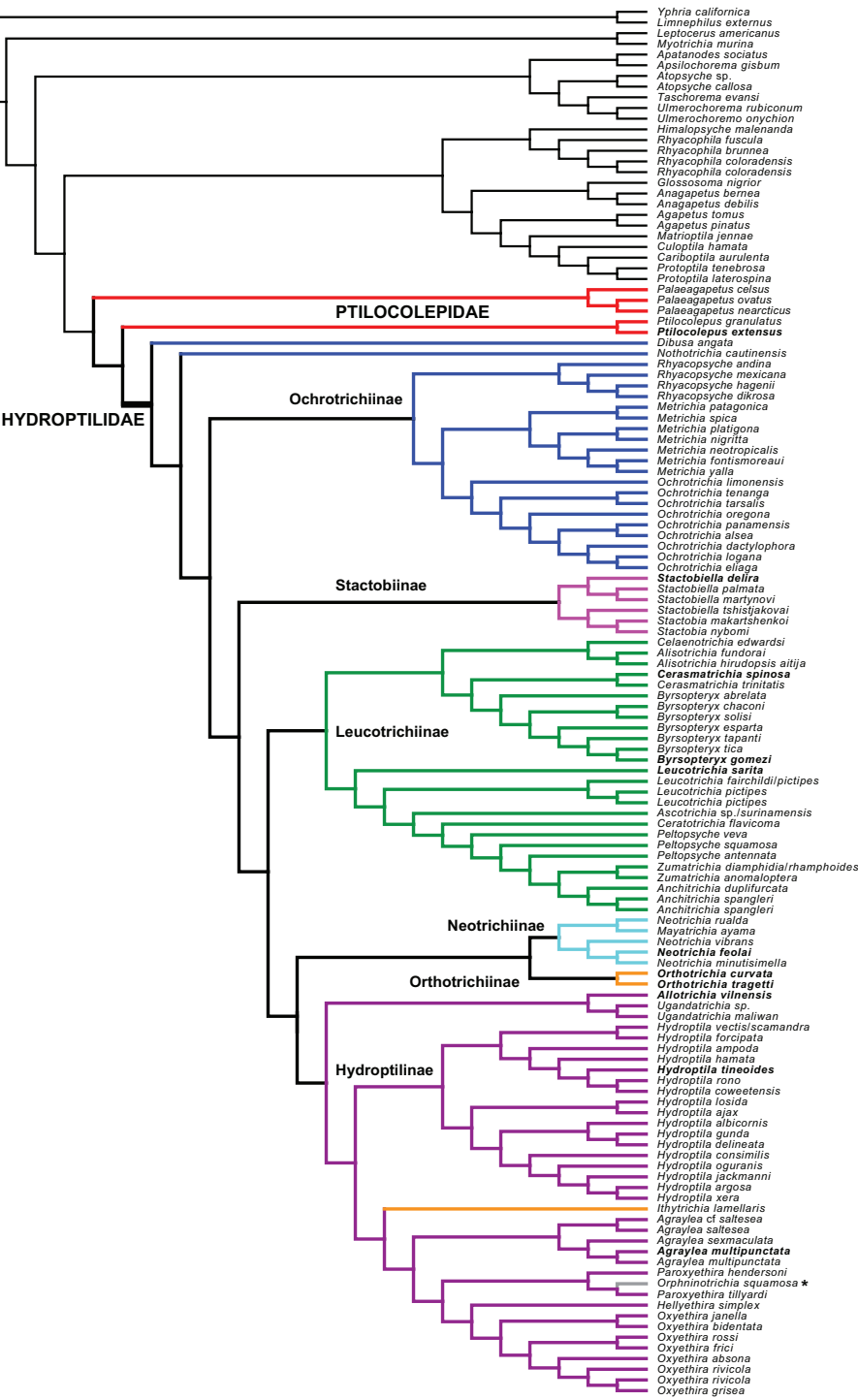


Figure 3. FastRFS majority-rule supertree derived from gene trees generated from both targeted enrichment data and Sanger sequencing data. Bold italic font indicates taxa that include targeted enrichment data. **Orphninothira*, incertae sedis in current classification.

Results

Summary of analyses

Ptilocolepidae

Only a single *Ptilocolepus* species was included in the targeted enrichment dataset, so no conclusions regarding the monophyly of Ptilocolepidae can be made based on the two targeted enrichment trees (Fig. 2A, B). In both targeted enrichment trees, however, *Ptilocolepus* was recovered as sister to Hydroptilidae (PP: 1, BS: 100).

Palaeagapetus and *Ptilocolepus* were each recovered as monophyletic in the fastRFS supertree (Fig. 3), although Ptilocolepidae was recovered as paraphyletic in relation to Hydroptilidae.

Hydroptilidae

A monophyletic Hydroptilidae was recovered in the target enrichment trees (PP: 0.98, BS: 100) and in the fastRFS supertree.

Hydroptilinae

In both targeted enrichment trees, Hydroptilinae formed a monophyly represented by one species each from the genera *Agraylea*, *Allotrichia*, and *Hydroptila* (PP: 0.92, BS: 76).

Hydroptilinae was not recovered as monophyletic due to the inclusion of species of *Ithytrichia* and *Orphminotrichia*. The genera *Hydroptila*, *Agraylea*, and *Oxyethira* were each recovered as monophyletic within Hydroptilinae, each represented by at least five species.

Leucotrichiinae

A monophyletic Leucotrichiinae was recovered in both targeted enrichment trees (PP: 1, BS: 100). The tribe Leucotrichiini was represented by only a single *Leucotrichia* species, so no conclusions regarding the monophyly of the tribe can be made. A monophyletic Alisotrichiini was also supported, based on a single species from each of the genera *Byrsoteryx* and *Cerasmatrichia* (PP: 1, BS: 100).

The fastRFS supertree also presented a monophyletic Leucotrichiinae and included a monophyletic Leucotrichiini sister to a monophyletic Alisotrichiini, with each tribe represented by at least four genera.

Neotrichiinae

Neotrichiinae was represented in the targeted enrichment dataset by only a single *Neotrichia* species, and thus no conclusions can be made on its monophyly. The single

Neotrichia species appeared as sister to *Orthotrichia* in both trees, although with mixed support (PP: 0.23, BS: 98).

In the fastRFS supertree, Neotrichiinae was recovered as both monophyletic and sister to *Orthotrichia*. Neotrichiinae + *Orthotrichia* formed a clade sister to Hydroptilinae (if *Ithytrichia* and *Orphninostrichia* are included within Hydroptilinae).

Ochrotrichiinae

No targeted enrichment data representing members of the Ochrotrichiinae subfamily were available.

Based upon the genera currently included in Ochrotrichiinae, the monophyly of the subfamily was not recovered in the fastRFS supertree. (*Metrichia* + *Ochrotrichia*) + *Rhyacopsyche* formed a distinct clade, but *Nothotrichia* and *Dibusa* failed to group with the rest of the ochrotrichiinae genera. Both latter two genera were recovered near the base of Hydroptilidae, with *Dibusa* sister to the rest of the hydroptilids.

Orthotrichiinae

Orthotrichiinae was represented by only a single genus, *Orthotrichia*, in the targeted enrichment dataset, and thus no conclusions regarding the monophyly of the subfamily can be made based on these trees. In both targeted enrichment trees, *Orthotrichia* formed a cluster with *Neotrichia* and Hydroptilinae (PP: 1, BS: 100).

The monophyly of Orthotrichiinae was not recovered in the fastRFS supertree. *Orthotrichia* was recovered as sister to Neotrichiinae, while *Ithytrichia* was represented by a single species and grouped within Hydroptilinae.

Stactobiinae

No conclusions regarding the monophyly of Stactobiinae can be made based on the total enrichment dataset, as only a single *Stactobiella* species was included. This *Stactobiella* was recovered as sister to the rest of Hydroptilidae (PP: 0.98, BS: 100).

A monophyletic Stactobiinae, represented by the genera *Stactobia* and *Stactobiella*, was recovered in the fastRFS supertree.

Incertae sedis

Of the genera currently considered incertae sedis within Hydroptilidae, only Sanger sequence data for a single species of *Orphninostrichia* was available.

In the fastRFS supertree, this *Orphninostrichia* species was grouped within the genus *Paroxyethira* within Hydroptilinae.

Discussion

Ptilocolepidae

The monophyly of Ptilocolepidae was not recovered in this study, but the 2 ptilocolepid genera did form a monophyletic unit with Hydroptilidae in the fastRFS supertree based on both targeted enrichment and Sanger sequencing data (Fig. 3), thus supporting a previously hypothesized Hydroptiloidea (Thomas et al. 2020). A monophyletic Ptilocolepidae was also not recovered in a previous study exploring the relationships among the families of Trichoptera (Holzenthal et al. 2007a). No members of Ptilocolepidae were represented in the recent Malm et al. (2013) study using molecular data to explore the relationships of the suborders within Trichoptera. Ptilocolepidae has thus far not been recovered as a monophyletic unit in any recent phylogenetic studies employing statistical analyses.

Hydroptilidae

The monophyly of Hydroptilidae was recovered in this study (Figs 2, 3).

Hydroptilinae

A monophyletic Hydroptilinae was recovered in this study in the targeted enrichment trees (Fig. 2A, B). Hydroptilinae was also recovered in the fastRFS supertree (Fig. 3), if the understanding of the subfamily is more loosely interpreted to potentially include the genera *Ithytrichia* and *Orphninostrichia*. It is possible that this represents the appropriate placement of these genera, as the current understanding of the placement of *Orphninostrichia* is uncertain, and Marshall did hypothesize that in the future *Ithytrichia* and *Orthotrichia* might no longer be considered a monophyletic Orthotrichiinae (Marshall 1979). Further sampling of both genera would help to make a more confident conclusion about their placement.

Hydroptilinae is a very diverse and widely distributed group, sequencing still more taxa would allow us to further resolve its topology. In her review, Marshall (1979) noted the group's success in diversity and distribution and the very heterogeneous appearance of the subfamily when viewed as a whole. She also commented that the group could consist of three subgroups distinguishable by affinities in the male and female genitalia and the general appearance and habits of the larvae: the *Agraylea* group, the *Hydroptila* group, and the *Oxyethira* group. The potential for these three subgroups can be seen in the supertree, but additional sampling to include representation of more Hydroptilinae genera is needed.

Leucotrichiinae

The subfamily Leucotrichiinae was recovered in both the targeted enrichment trees and the fastRFS supertree. Additionally, the tribes Alisotrichiini and Leucotrichiini were also recovered as monophyletic sisters in the supertree, in agreement with Santos et al.

(2016). This reinforces Marshall's (1979) comment that, although the morphological boundaries of some of the leucotrichiine genera themselves are not always distinct and clear-cut, the subfamily itself does appear to form a unique clade within Hydroptilidae.

Neotrichiinae

The subfamily Neotrichiinae was recovered as monophyletic in the fastRFS supertree, but additional sampling to include more genera would help to strengthen this conclusion. In both the targeted enrichment trees and the supertree, Neotrichiinae, however represented, appeared as sister to *Orthotrichia*. Marshall (1979) included *Orthotrichia* as a member of Orthotrichiinae, but also mused that the genera included in that subfamily might be considered to be separate groups in the future. Additional sampling may help to resolve whether *Orthotrichia* truly is sister to Neotrichiinae, or should perhaps be considered as a member of the neotrichiine subfamily.

Ochrotrichiinae

Unfortunately, no targeted enrichment data were obtained for any member of Ochrotrichiinae. Within the fastRFS supertree, however, the genera *Metrichia*, *Ochrotrichia*, and *Rhyacopsyche* were recovered as a clade. When Ochrotrichiinae was first established by Marshall (1979), she stated that the features on which she based the group may one day prove to be secondarily derived from the general form of the Hydroptilinae and that Ochrotrichiinae may indeed prove to be a subgroup of Hydroptilinae. At least in this study, based on the three genera included in Marshall's original Ochrotrichiinae, the evidence does not support this conjecture.

Nothotrichia and *Dibusa* did not form a monophyletic Ochrotrichiinae with the other three included genera. The genus *Nothotrichia* was originally left unplaced within Hydroptilidae by Marshall (1979); Harris and Armitage (1997) later added *Nothotrichia* to Ochrotrichiinae but stated that they were still attempting to determine synapomorphies for the group. Marshall also left *Dibusa* unplaced within Hydroptilidae, but noted similarities between *Dibusa*, *Nothotrichia*, and the hydroptiline genus *Agraylea* (1979); *Dibusa* was later added to Ochrotrichiinae by Oláh and Johanson (2011), but no explanation for the inclusion was provided. Additional exploration is needed to determine if *Dibusa* and *Nothotrichia* should remain included in Ochrotrichiinae, or if they should be formally placed elsewhere.

Orthotrichiinae

The subfamily Orthotrichiinae was not recovered as a monophyletic unit. Nielsen (1948) considered the two genera for which Orthotrichiinae was originally established (*Ithytrichia* and *Orthotrichia*) to be derived from a common ancestor because of a large number of shared larval features. However, in Marshall's (1979) opinion, while the larvae do share a number of morphological and behavioral similarities, both the larvae

and adults are distinct for each genus and Orthotrichiinae might not be considered a cohesive unit. Additional sampling from both genera, and the potential inclusion of the third genus *Saranganotrichia*, may be necessary to understand the phylogenetic placement of Orthotrichiinae.

Stactobiinae

The subfamily Stactobiinae was recovered as monophyletic in the fastRFS supertree. Given previous researchers' difficulty in finding morphological features that could be used to unite this group (Wells 1990; Bowles et al. 1999; Malicky and Chantaramongkol 2007), further work and detailed observations are needed to more clearly define this subfamily.

In the targeted enrichment trees, Stactobiinae was recovered as sister to the rest of Hydroptilidae, which was not in agreement with the arrangement of the fastRFS supertree. This discrepancy is likely due to the difference in taxon coverage between the targeted enrichment sequences and the Sanger sequences; additional targeted enrichment data sampled from across all six subfamilies may resolve this disagreement.

Incertae sedis

The genus *Orphninostrichia*, though only represented in this study by a single species, was recovered within a clade of hydroptiline genera (Fig. 3). This placement is independently corroborated by Marshall's (1979) consideration that the genus shared similarities with other members of Hydroptilinae. There are two additional extant genera currently considered incertae sedis within Hydroptilidae, *Dicaminus* and *Macrostactobia*, but no sequence data was available for these. The three extinct incertae sedis genera, *Burminoptila*, *Electrotrichia*, and *Novajerseya*, cannot be placed using molecular data.

Conclusions

The objectives of this paper were to provide a preliminary analysis 1) testing the monophyly of both Hydroptilidae and Ptilocolepidae, 2) evaluating the monophyly of the traditionally recognized subfamilies within Hydroptilidae, and 3) inferring relationships within and between Hydroptilidae, its included subfamilies, and Ptilocolepidae. This was the first study to explore a phylogenetic assessment of the family Hydroptilidae using modern statistical methods and molecular data. We show that an existing targeted enrichment probe set worked well on Hydroptilidae and provided strong support for the deeper relationships in the family. Further planned advancements of this study focusing on targeted enrichment data will confer taxonomic stability to the family, refine the current classification system, and provide a new phylogenetic framework in which to place new species and genera. Additionally, given the

level of diversity and global distribution of Hydroptilidae, the extensive inclusion of more taxa may also produce a more strongly supported topology. A phylogenetic assessment of the relationships within the microcaddisflies will define the natural limits of the genera and subfamilies and their evolutionary relationships within the family, which in turn will support a stable classification of the hydroptilids. This provides an evolutionary framework in which to place undescribed microcaddisfly species, of which there are 100s, many of which occur in threatened ecosystems. It will also provide an evolutionary framework to investigate the unique life history features of the family, its diversity of larval case morphology, feeding strategies, male genitalia morphology, male secondary sexual characteristics, and patterns of regional endemism and other distributions.

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