



A new genus of Chamaemyiidae (Diptera: Lauxanioidea) predaceous on Adelgidae (Hemiptera), with a key to chamaemyiid species associated with Pinaceae-feeding Sternorrhyncha

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Abstract

A new genus of Chamaemyiidae (Diptera: Lauxanioidea) is described, namely *Leucotaraxis* **gen. nov.** (type species *Leucopsis atrifacies* Aldrich; other included species *Leucotaraxis argenticollis* (Zetterstedt), **comb. nov.**, *Leucotaraxis piniperda* (Malloch), **comb. nov.**, and *Leucotaraxis sepiola* **sp. nov.**). These species are predators of Adelgidae (Hemiptera) infesting Pinaceae. *Leucotaraxis argenticollis* is Holarctic, while the other three species are Nearctic. The phylogeny of *Leucotaraxis* with other representatives of Chamaemyiidae was elucidated using mitochondrial and nuclear DNA sequences and the genus was found to be monophyletic. Egg and puparial stages are discussed or described and illustrated for all species except *Leucotaraxis sepiola*. A key is provided to all species of Chamaemyiidae known to attack Pinaceae-infesting Sternorrhyncha, an annotated list of these taxa is provided, and a habitus photograph is provided for each genus with such species. In addition, a lectotype is designated for *Leucopsis olivacea* Meijere, and it is synonymized under *Neoleucopsis obscura* (Haliday), **syn. nov.**

Key words: new genus, new species, key, lectotype, new combinations, new synonym, immature stages, silver fly

Introduction

Chamaemyiidae (Diptera), or silver flies, represents a group of larval predators attacking sternorrhynchus Hemiptera, such as aphids, adelgids, scale insects, and mealybugs. Although the species of some chamaemyiid genera are quite general in their feeding habits, many genera are restricted to a particular sternorrhynchan prey lineage. There are currently 32 described genera and subgenera of Chamaemyiidae worldwide, with more than 340 valid species. The vast majority of species-level work has been undertaken in the Palearctic Region (e.g., Tanasijtshuk 1986). For the New World fauna, few comprehensive treatments have been published. Tanasijtshuk (2002) summarized the Nearctic species of *Leucopsis* Meigen, published before 1965, and then Tanasijtshuk (2003, 2005, 2006) proceeded to describe 21 new species of *Leucopsis* from this part of the world, leaving many more still in need of description, and with no keys to species. The Chamaemyiidae chapter (Gaimari 2010) in the second volume of the *Manual of Central American Diptera* includes a key to all New World genera. This paper serves to make available one of the recognized new genera (*Leucotaraxis* **gen. nov.**, indicated there as “Undescribed Genus C”) in that work, with several new combinations and one new species. One of the other undescribed genera from South America in that work (undescribed genus A) was described as *Chamaeleucopsis* Gaimari (Gaimari 2012), and two others (undescribed genera B and D) were recently described as *Vitaleucopsis* Gaimari and *Chamaethrix* Gaimari, respectively (Gaimari 2020).

The biology of species of Chamaemyiidae was reviewed by Gaimari (2010, 2021). A review of the use of chamaemyiids for biological control of adelgids was provided by Ross *et al.* (2011) and Gaimari (2021). Examples of adelgids that serve as prey for chamaemyiids in their native ranges include the balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Eichhorn 1968) and the pine adelgid, *Pineus pini* (Goeze) (Wilson 1938) in Europe, the fir

adelgids *A. knucheli* Schneider-Orelli & Schneider and *A. joshii* Schneider-Orelli & Schneider in the Himalayas (Rao & Ghani 1972), and the pine bark adelgid, *Pineus strobi* (Hartig), in eastern North America (Sluss & Foote 1973; Wantuch *et al.* 2019). Chamaemyiids have been evaluated for introduction as biological control agents for several exotic adelgid species. In fact, the only instances of successful biological control of adelgids utilized chamaemyiids from Europe: *Pineus boernerii* Annand was regulated below economically injurious levels in pine plantations in Chile with *Neoleucopis obscura* (Haliday) (Mills 1990); and *P. pini* was controlled in Hawaii with *N. obscura* (Culliney *et al.* 1988) and in New Zealand with *N. tapiae* (Blanchard) (Zondag & Nuttall 1989). Two species of *Leucotaraxis* discussed here, *L. argenticollis* (Zetterstedt) and *L. piniperda* (Malloch), are being evaluated as biological control agents of the hemlock woolly adelgid, *Adelges tsugae* Annand (Kohler *et al.* 2008; Grubin *et al.* 2011; Ross *et al.* 2011; Motley *et al.* 2017; Neidermeier *et al.* 2020; Dietschler *et al.* 2021). Additional details on the biology of chamaemyiids attacking Pinaceae-feeding Sternorrhyncha are provided herein, along with the description of *Leucotaraxis* **gen. nov.** containing four species, one of which is new. The four species are described or rediagnosed herein (noting that full descriptions of three of the species are in McAlpine & Tanasijtshuk (1972) and Tanasijtshuk (2002)), and the phylogeny of *Leucotaraxis*, in context with other representatives of Chamaemyiidae, was elucidated using mitochondrial and nuclear DNA sequences. A key is provided to all known chamaemyiid species attacking Pinaceae-feeding Sternorrhyncha, as well as an annotated list of these species.

Materials and methods

Many specimens for this study were collected or reared by the authors and various colleagues (Table 1 contains the names of collectors for those specimens used in the molecular aspects of this work, for the *Leucotaraxis* species and the other included taxa). Additional material was provided from several insect collections, some of which maintain types for species included in this work, including: California Academy of Sciences, San Francisco, California, USA (CAS); California State Collection of Arthropods, Sacramento, California, USA (CSCA) and its associated Frozen Tissue Collection (CSCA-FTC); Canadian National Collection of Insects, Arachnids & Nematodes, Agriculture & Agri-Food Canada, Ottawa, Ontario, Canada (CNC); Cornell University Insect Collection, Ithaca, New York, USA (CUIC); Illinois Natural History Survey, Urbana, Illinois, USA (INHS); Lund University Museum of Zoology, Lund, Sweden (MZLU); Pacific Forestry Centre Arthropod Reference Collection, Canadian Forest Service, Victoria, British Columbia, Canada (PFCA); Collection Entomologique Ouellet-Robert, Université de Montréal, Montréal, Québec, Canada (QMOR); University of Arizona Insect Collection, Tucson, Arizona, USA (UAIC); National Museum of Natural History, Washington, DC, USA (USNM); and Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM). Additional collections housing types cited herein include: Dipartimento di Coltivazione e Difesa delle Specie Legnose, Sezione Entomologia Agraria, Università di Pisa, Italy (DCDS); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Bangalore Biological Control Research Institute – Entomology, Bangalore, India (ICPR); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN); Museo di Zoologia, Università di Bologna, Italy (MZUB); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); National Museum of Ireland, Dublin, Ireland (NMID); Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia (ZISP); and Zoologisch Museum – Entomology, Instituut voor Taxonomische Zoologie, Universiteit van Amsterdam, Amsterdam, Netherlands (ZMAN).

For all specimens where abdomens were dissected and macerated using lactic acid, the partial abdomen and genitalia are stored in glycerin in a glass vial mounted on the same pin. Adult specimens in the *Specimens examined* sections indicated as “[molecular voucher]” are only the abdomen, head, wings and some legs (and puparium in some cases) in a glycerin vial mounted on a pin and deposited in the CSCA; the thorax of each was used in the molecular portions of this and other ongoing work. These specimens, along with other specimens being preserved for molecular work, are indicated with a unique “specimen #”, which correspond to an entry in the CSCA-FTC database. Some complete specimens in the CSCA-FTC are indicated with a unique “specimen #”, or for series in the same vial with a “voucher #”, which correspond to samples in the freezer and database, whether or not used in these analyses. Note, some pinned specimens in CSCA also have a “specimen #”, indicating their data being recorded in the CSCA-FTC database. Larval and puparial specimens indicated as “[molecular voucher]” are slide mounted in Canada balsam after non-destructive DNA extraction. Molecular vouchers with specimen numbers beginning with “ENT” are held in YPM.

TABLE 1. Collection and voucher information for specimens included in the molecular phylogeny. Vouchers are deposited at the California State Collection of Arthropods (CSCA) or Yale Peabody Museum (YPM).

Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Coelopa vanduzeei</i> Cresson [Coelopidae]	CSCA#14Q855	USA; California; Mission Beach on Mission Bay; 15 April 2003; coll. Stephen D. Gaimari, Alexander V. Gaimari	MZ298227	MZ296030	MZ295995
<i>Minettia flaveola</i> (Coquillett) [Lauxaniidae]	CSCA#10F152	USA; California; Sonoma; Annadel State Park; 17 May–7 June 2007; coll. Peter Kerr, Stephan Blank	MZ298247	N/A	MZ296023
<i>Anchileucopsis geniculata</i> (Zetterstedt)	CSCA#09E481	UNITED KINGDOM; England; Suffolk County; RAF Barnham Camp; 13 May 1995; coll. Ian F.G. McLean	MF468329	MF468329	MF468985
<i>Chamaemyia polystigma</i> (Meigen)	CSCA#11G567	USA; New Mexico; Sandoval County; Santa Fe National Forest; 24 July 1995; coll. Stephen D. Gaimari	MZ298226	MZ296029	MZ295994
<i>Leucopsis decipiens</i> Tanasijtshuk	CSCA#10F139	USA; California; Del Norte County; Siskiyou National Forest; 3 June 2009; coll. Peter Kerr, Owen Lonsdale	MZ298228	MZ296031	MZ295996
<i>Leucopsis hennigrata</i> McAlpine	CSCA#10F190	TURKEY; Bolu Province; Sultankoy; 15 May 2007; coll. Hans Peter Ravn	MZ298229	MZ296032	MZ295997
<i>Leucopsis ninae</i> Tanasijtshuk	CSCA#11G534	RUSSIA; Tashkent; lab reared at USDA-APHIS-PPQ National Biological Control Laboratory, Niles, Michigan; 1995	MZ298230	MZ296033	MZ295998
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E492	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468346	MF468954	MZ296003
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#10F132	USA; Washington; Thurston County; Olympia; 8 August 2009; coll. Sarah M. Grubin	MF468351	MF468959	MZ296004
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#10F659	USA; Washington; Pierce County; Tacoma; Point Defiance Park; 20 May 2010; coll. Sarah M. Grubin	MZ298231	MZ296034	MZ296005
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#10F671	USA; Washington; Pierce County; Tacoma; Point Defiance Park; 4 June 2010; coll. Sarah M. Grubin	MZ298232	MZ296035	MZ296006
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856455	USA; Connecticut; Litchfield County; Bridgewater; 6 July 2002; coll. Nathan P. Havill	MF468330	MF468937	MZ296009

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TABLE 1. (Continued)

Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856456	USA; Minnesota; Stearns County; Birch Lakes State Forest; 23 June 2008; coll. Robert Tiplady	MF468331	MF468943	MF468987
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856414	USA; Minnesota; Stearns County; Birch Lakes State Forest; 23 June 2008; coll. Robert Tiplady	MF468332	MF468944	MZ296007
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856417	USA; Minnesota; Stearns County; Birch Lakes State Forest; 23 June 2008; coll. Robert Tiplady	MF468335	MF468945	MZ296008
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E490	USA; Pennsylvania; Centre County; Boalsburg; 11 April 2009; coll. Nathan P. Havill, Maya Nehme	MF468337	MF468946	MZ296002
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E488	USA; Minnesota; Crow Wing County; Cross Lake; 28 May 2009; coll. Nathan P. Havill, Jana Albers	MF468340	MF468949	MZ296000
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E489	USA; Minnesota; Crow Wing County; Cross Lake; 28 May 2009; coll. Nathan P. Havill, Jana Albers	MF468341	MF468950	MZ296001
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E484	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468342	MF468951	MZ295999
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E485	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468343	MF468952	MF468994
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E486	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468344	MF468953	MF468995
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E493	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468347	MF468955	MF468997
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E494	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468348	MF468956	MF468998

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TABLE 1. (Continued)

Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E495	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468349	MF468957	MF468999
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	CSCA#09E496	USA; Minnesota; Stearns County; Birch Lakes State Forest; 30 May 2009; coll. Nathan P. Havill, Robert Tiplady	MF468350	MF468958	MF469000
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856464	USA; Washington; Clark County; Vancouver; 23 October 2012; coll. Glenn Kohler	MF468361	MF468963	MZ296010
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856471	USA; Washington; Clark County; Vancouver; 23 October 2012; coll. Glenn Kohler	MF468370	MF468964	MF469003
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856419	USA; Washington; Thurston County; Tumwater Falls Park; 21 June 2013; coll. Darrell Ross	MF468400	MF468965	MF469004
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856425	USA; Washington; Thurston County; Tumwater Falls Park; 21 June 2013; coll. Darrell Ross	MF468406	MF468966	MF469005
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856427	USA; Washington; Thurston County; Tumwater Falls Park; 21 June 2013; coll. Darrell Ross	MF468408	MF468967	MF469006
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856591	USA; Washington; Thurston County; Tumwater Falls Park; 21 June 2013; coll. Darrell Ross	MF468412	MF468968	MF469007
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT856601	USA; Washington; Thurston County; Tumwater Falls Park; 21 June 2013; coll. Darrell Ross	MF468423	MF468969	MF469008
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT791609	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468465	MF468972	MF469009
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT791540	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468472	MF468975	MF469010
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT791572	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468498	MF468976	MF469011

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Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT791575	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468502	MF468977	MF469012
<i>Leucotaraxis argenticollis</i> (Zetterstedt)	YPM#ENT857047	USA; Colorado; Larimer County; Zimmerman Lake trail; 27 July 2016; coll. Nathan P. Havill	MF468935	MF468981	MZ296011
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#09E474	USA; New Mexico; Lincoln County; Lincoln National Forest; 24 June 1995; coll. Stephen D. Gaimari	MZ298233	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#09E478	USA; New Mexico; Lincoln County; Lincoln National Forest; 24 June 1995; coll. Stephen D. Gaimari	MF468625	MF468983	MF469014
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#09E479	USA; New Mexico; Lincoln County; Lincoln National Forest; 24 June 1995; coll. Stephen D. Gaimari	MZ298234	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#09E480	USA; New Mexico; Lincoln County; Lincoln National Forest; 25 June 1995; coll. Stephen D. Gaimari	MZ298235	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F335	USA; New Mexico; Lincoln County; Lincoln National Forest; 25 June 1995; coll. Stephen Gaimari	MZ298236	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F336	USA; New Mexico; Lincoln County; Lincoln National Forest; 25 June 1995; coll. Stephen Gaimari	MZ298237	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F340	USA; New Mexico; Lincoln County; Lincoln National Forest; 25 June 1995; coll. Stephen Gaimari	MZ298238	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F341	USA; New Mexico; Lincoln County; Lincoln National Forest; 25 June 1995; coll. Stephen Gaimari	MZ298239	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F348	USA; New Mexico; Lincoln County; Lincoln National Forest; 26 June 1995; coll. Stephen Gaimari	MZ298240	MZ296036	MZ296012
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F349	USA; New Mexico; Lincoln County; Lincoln National Forest; 26 June 1995; coll. Stephen Gaimari	MZ298241	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F351	USA; New Mexico; Lincoln County; Lincoln National Forest; 26 June 1995; coll. Stephen Gaimari	MZ298242	N/A	N/A
<i>Leucotaraxis atrifacies</i> (Aldrich)	CSCA#10F353	USA; New Mexico; Lincoln County; Lincoln National Forest; 26 June 1995; coll. Stephen Gaimari	MZ298243	N/A	N/A

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TABLE 1. (Continued)

Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Leucotaraxis atrifacies</i> (Aldrich)	YPM#ENT960794	USA; Washington; Ferry County; Colville Reservation; 22 July 2019; coll. Darci Dickinson	MZ298244	N/A	N/A
<i>Leucotaraxis piniperda</i> (Malloch)	CSCA#09E471	USA; Connecticut; New Haven County; Hamden; 16 June 2009; coll. Michael E. Montgomery	MF468660	MF468948	MZ296013
<i>Leucotaraxis piniperda</i> (Malloch)	CSCA#09E475	USA; Minnesota; Beltrami County; Bemidji; 29 May 2009; coll. Nathan P. Havill	MF468659	MF468947	MZ296014
<i>Leucotaraxis piniperda</i> (Malloch)	CSCA#10F134	USA; Washington; Pierce County; Tacoma; 25 April 2009; coll. Sarah M. Grubin	MF468665	MF468960	MZ296015
<i>Leucotaraxis piniperda</i> (Malloch)	CSCA#10F656	USA; Washington; Pierce County; Tacoma; 5 May 2010; coll. Sarah M. Grubin	MZ298245	MZ296037	MZ296016
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856378	USA; Maryland; Baltimore County; Cylburn Arboretum; 28 May 2008; coll. Melody Keena	MF468628	MF468938	MZ296017
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856380	USA; Maryland; Baltimore County; Cylburn Arboretum; 28 May 2008; coll. Melody Keena	MF468630	MF468939	MZ296016
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856388	USA; West Virginia; Jefferson County; Shepherdstown; 28 May 2006; coll. Melody Keena	MF468636	MF468940	MZ296018
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856401	USA; Washington; Pierce County; Tacoma; 12 May 2008; coll. Michael E. Montgomery, Richard McDonald	MF468646	MF468941	MF469018
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856408	USA; Washington; Pierce County; Tacoma; 12 May 2008; coll. Michael E. Montgomery, Richard McDonald	MF468653	MF468942	MZ296019
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856705	USA; Virginia; Montgomery County; Blacksburg; 18 May 2010; coll. Melissa Fischer	MF468672	MF468961	MZ296020
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856706	USA; Virginia; Montgomery County; Blacksburg; 18 May 2010; coll. Melissa Fischer	MF468673	MF468962	MZ296021
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT791591	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468742	MF468970	MF469025

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TABLE 1. (Continued)

Species	Voucher Accession	Collection information	GenBank Accession No.		
			COI	TPI	CAD
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT791607	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468753	MF468971	MF469026
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT791616	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; coll. Darrell Ross, Arielle Arsenault	MF468761	MF468973	MF469027
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT791620	USA; Washington; Pierce, King, and Thurston Counties; 11 April–25 May 2015; Coll, Darrell Ross, Arielle Arsenault	MF468765	MF468974	MF469028
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856920	USA; Washington; Pierce County; Tacoma; 1 January 2016; coll. Rachel Brooks	MF468918	MF468978	MF469029
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856921	USA; Washington; Pierce County; Tacoma; 1 January 2016; coll. Rachel Brooks	MF468919	MF468979	MF469030
<i>Leucotaraxis piniperda</i> (Malloch)	YPM#ENT856928	USA; New York; Tompkins County; Ithaca; 3 June 2016; coll. Nathan Havill, Mark Whitmore, Amalia Havill	MF468926	MF468980	MF469031
<i>Leucotaraxis sepiola</i> sp. nov.	CSCA#10F352	USA; New Mexico; Lincoln County; Lincoln National Forest; 26 June 1995; coll. Stephen D. Gaimari	MZ298246	MZ296038	MZ296022
<i>Lipoleucopsis praecox</i> Meijere	CSCA#09E465	UNITED KINGDOM; England; Norfolk County; Thetford Forest; 8 April 1996; coll. Ian F.G. McLean	MF468936	MF468984	MF469032
<i>Neoleucopsis atratula</i> (Ratzeburg)	YPM#ENT996100	USA; California; Mendocino County; 8 December 2011; coll. Karen Hutten	MZ298248	MZ296039	MZ296024
<i>Neoleucopsis pinicola</i> (Malloch)	CSCA#09E460	USA; Connecticut; New Haven County; Bethany; 29 April 2008; coll. Michael E. Montgomery	MZ298249	MZ296040	MZ296025
<i>Neoleucopsis tapiae</i> (Blanchard)	CSCA#10F150	USA; Hawaii; Hilo; Waimea; 25 January 2010; coll. Zvi Mendel	MZ298250	MZ296041	MZ296026
<i>Pseudodima occidentalis</i> Barber	CSCA#11G543	USA; California; Sacramento County; Cosumnes River Preserve; 22 June 2004; coll. Stephen D. Gaimari	MZ298251	MZ296042	MZ296027
<i>Vitaleucopsis nidolkah</i> Gaimari	CSCA#09E462	USA; New Mexico; Lincoln County; Lincoln National Forest; 24 June 1995; coll. Stephen D. Gaimari	MZ298252	MZ296043	MZ296028

Terminology. Basic terminology follows Cumming & Wood (2009) and Gaimari (2010). Body length was measured in lateral view by adding the length of the head (without antennae) through the thorax with the abdominal length, to account for differential curling of the abdomens. For head ratios: the head length and height were measured from a lateral view, respectively, from the lunule through the posterior occiput, and from the dorsal edge of the head through the ventral edge of the gena; the frons width and length were measured from an anterodorsal view, with the frons width through the anterior ocellus, and the frons length from the anterior ocellus through the anterior edge of the frons. On the thorax, the scutal width is measured at the level of the supra-alar setae, and the scutellar width is measured through the area of contact with the scutum. Wing width was measured at the widest level just proximal to the apex of CuA₁. All other measurements were made through their maximum values.

All chamaemyiid taxa in the *Annotated list of species of Chamaemyiidae feeding on Pinaceae-infesting Sternorrhyncha* section appear with full authority and date information, current and original genus combinations, type information, and notes on distribution and biology. As such, the date is not given for those genus and species names in the text.

Molecular phylogeny. The phylogeny of *Leucotaraxis* with other representatives of Chamaemyiidae and two non-chamaemyiid outgroup taxa was elucidated using sequence data from one mitochondrial and two nuclear genes. For adult flies, DNA was extracted from the ground-up thorax. For larval flies, DNA was extracted non-destructively by cutting a small slit in the specimen with a scalpel and retaining the cuticle after proteinase K digestion. In both cases, extraction was performed using DNA IQ Extraction Kit (Promega). The 5' end of the mitochondrial cytochrome c oxidase subunit I gene (COI) was amplified using the primers LepF1 and LepR1 (Hebert *et al.* 2004). A portion of the nuclear triose phosphate isomerase (TPI) gene was amplified using primer 111Fb (Bertone *et al.* 2008), and Cham275R (GCCCAGACGGGCTYGTAGGC) modified from 275R (Bertone *et al.* 2008). A portion of the nuclear carbamoylphosphate synthetase domain of the CAD (rudimentary) gene was amplified in two overlapping fragments using the primers 787F and Cham1098R, and 1057F and 1278R. Primers were designed by Moulton & Wiegmann (2004) with the exception of Cham1098R (TTAGGTAGCTGCCCTCCCAT), which was modified from their primer 1098R. Sequencing reactions were performed using the BigDye Terminator kit (Applied Biosystems, Foster City, California) and analyzed on an Applied Biosystems 3730 automated sequencer at the DNA Analysis Facility on Science Hill at Yale University, New Haven, Connecticut. Sequences from each gene were aligned using MUSCLE 3.6 (Edgar 2004). Maximum likelihood analysis was performed using the concatenated sequence data using IQ-TREE v.2.1.3 (Nguyen *et al.* 2015). Node support was generated with 1,000 UFBoot replicates. *Coelopa vanduzeei* Cresson (Coelopidae) and *Minettia flaveola* (Coquillett) (Lauxaniidae) were included as outgroup taxa, the latter being a fellow member of the Lauxanioidea, and the former a member of the related superfamily Sciomyzoidea. Many of the *Leucotaraxis* sequences were reported previously in Havill *et al.* (2018). All new sequences generated for this study were deposited in GenBank, and collection and voucher data for included specimens are shown in Table 1.

***Leucotaraxis* gen. nov.**

urn:lsid:zoobank.org:act:C920C4F9-D987-4926-B4FB-C5BB4DC5E7B4

“Undescribed Genus C” – Gaimari, 2010: 1005.

Type species. *Leucopis atrifacies* Aldrich, by present designation.

Etymology. The prefix *Leuco-*, in reference to the genus *Leucopis*, appended with the feminine Greek noun *taraxis*, meaning “confusion, disturbance.” The name refers to the historical confusion surrounding the proper genus placement of the included species.

Diagnosis. The body is compact and small (2.1 mm or less), but more delicate than typical leucopines. Postocellar and ocellar setae are absent. The frons is flat and meets the lunule at nearly a 90° angle. The fronto-orbital and median areas of the frons have long, erect white setulae, but lack setae. The lunule has a straight to slightly curved upper margin, appearing squared, and in some species is dark brown to black along with the face, parafacial and medial part of the gena. The face has deep antennal grooves and is either all black or all silvery pruinose. The mouthparts are very small and held within the oral cavity above the small cylindrical palpi. The antennae are black. The scutum is entirely silvery-grey pruinose, lacking dorsocentral vittae, and with 2 pairs of dorsocentral setae in

the posterior part of the scutum. Prescutellar setae are absent. Prescutellum present. Scutellum concolorous with scutum. The abdominal tergites are dark silvery-grey pruinose, except the dorsal parts of syntergite 1+2 and tergite 3 are bronzy pruinose. In the male genitalia, the phallus is always elongated, and can be either gently or strongly curved, and some species lack a pregonite. In the female, sternite 6 is wider than preceding sternites, tergite 7 is strap-like when present, sternite 7 is arcuate when present, all setulae of the pseudo-ovipositor are tiny, and spermathecae are 2+2.

Immatures. The eggs and puparia are known for three of the species included in this genus, with the following generalities in common. *Egg* (Fig. 1A). With series of 11–13 longitudinal ridges frequently anastomosing into a diagonally reticulated pattern, most densely at posterior pole. *Puparium* (Fig. 1B). The puparium is barrel-shaped, slightly flattened, with a convex dorsal surface which is smooth except for tiny spicules. The dehiscent anterior segments (dorsal and ventral) each slope in lateral view into a thin anterior-most part. Anterior spiracle with slit-like spiracular opening at tip of each of 3–5 finger-like lobes. The posterior spiracles are on separated, raised tubercles with sharp strong spinules in the distal half (Figs 1C–D); distally, spiracle trilobed, with slit-like spiracular opening at tip of each finger-like lobe.

Biology. Species of this genus are known as larval predators of Adelgidae on Pinaceae, with three species also associated with aphids in the genus *Cinara* Curtis. Although never reared from *Cinara* as prey, adults have been collected from *Cinara*-infested pines.

Remarks. Contrary to Tanasijtshuk (1986) placing *Leucopis adelgivora* Tanasijtshuk in his “*argenticollis*-group” with an implied close relationship, that species is a typical *Leucopis* (*Leucopis*) that happens to feed on adelgids and does not belong to this new genus. In describing *Leucopis astonea* McAlpine, McAlpine (1977) posited its relationship with the group of species now included in this genus. However, despite several characteristics held in common, it is included in the discrete genus *Vitaleucopis*, which differs in several substantial respects from *Leucotaraxis*, including egg and puparial morphology, as well as adult external and genitalic morphology. However, it does seem possible that both genera belong to a complex of related genera with similar feeding habits, also including *Anchioleucopis* Tanasijtshuk, *Lipoleucopis* Meijere and *Neoleucopis* Malloch. The key to species of *Leucotaraxis* is included as couplets 38–43 in the key to chamaemyiid species associated with Pinaceae-infesting Sternorrhyncha, below.

***Leucotaraxis argenticollis* (Zetterstedt), comb. nov.**

(Figs 1B–C, 2A–B, 3A, 3D–E)

Leucopis argenticollis Zetterstedt 1848: 2714. Sweden. Gottlandia (LT ♂, MZLU). References – Czerny 1936: 10 (key), 11 (redescription); McAlpine & Tanasijtshuk 1972: 1865 (redescription), 1870 (lectotype designation), fig. 1 (head), fig. 3 (abdomen), figs 5–6 (female terminalia), figs 8–16, 19 (male genitalia), figs 20–27 (immatures); Tanasijtshuk 1986: 201 (redescription), figs 333–337 (male genitalia), figs 338–345 (larval); Papp 1979: 82 (key, description), fig. 54A (abdomen), fig. 54B (male genitalia); Kohler *et al.* 2008: 494 (biology); Grubin *et al.* 2011: 1410 (biology); Havill *et al.* 2018 (biology, population genetics); Neidermeier *et al.* 2020 (biology, biological control); Dietschler *et al.* 2021 (biology, biological control).

Leucopis orbitalis Malloch 1921: 352. United States. Illinois: Dundee (HT ♂, INHS). References – McAlpine 1965: 709 (catalog); McAlpine & Tanasijtshuk 1972: 1865 (synonymy).

Leucopis sp. nr. *orbitalis*. References – Rao 1965: 43; McAlpine & Tanasijtshuk 1972: 1865 (identity).

Diagnosis. The face and lunule (Fig. 2B) are silvery-grey pruinose. The postpronotum (Fig. 2A) has 1 to several long setulae (longer than the setulae on the scutum) medially from the postpronotal seta. In the male (see figs 8–16, 19 in McAlpine & Tanasijtshuk 1972), the epandrial complex is simple, small, and yellowish- to silvery-grey pruinose, with no central epandrial process; the surstylar lobe is short and slender, the phallus (Fig. 3A) is broad in lateral view with a wedge-shaped anterobasal process at a 90° angle from the thin elongate pointed process. In the female (Figs 3D–E), tergites (Fig. 3E) with tergite 6 enlarged and slightly less than 2 X wider than long, tergite 7 present and strap-like, tergite 8 longer than wide, slightly tapering distally; sternites (Fig. 3D) with sternite 6 enlarged and about 2 X wider than long, sternite 7 present and arcuate.

Immatures. *Egg.* Measurements as in *Leucotaraxis atrifacies* (Fig. 1A). *Larvae.* Described and figured in McAlpine & Tanasijtshuk (1972). *Puparium* (Fig. 1B). Length 2.3–2.8 mm, width 0.9–1.0 mm. Dehiscent anterior segments (dorsal and ventral) 0.05–0.06 mm long. Raised posterior spiracular tubercles (Fig. 1C) 0.12–0.16 mm long, darkly sclerotized.

Biology. Predators as larvae on species of *Adelges* Vallot and *Pineus* Shimer (Hemiptera: Adelgidae) on Pinaceae (*Abies*, *Picea*, *Pinus*, *Tsuga*). Specific records (including our own rearings) include: *Adelges piceae* on *Abies balsamea*; *Adelges tsugae* on western hemlock, *Tsuga heterophylla* (Kohler *et al.* 2008); *Pineus abietinus* Underwood & Balch on *Abies lasiocarpa*; *Pineus boernerii* on *Pinus henryi*; *Pineus coloradensis* (Gillette) on *Pinus banksiana*, *Pinus contorta*, *Pinus flexilis*, *Pinus monticola*, and *Picea engelmannii*; *Pineus pineoides* (Cholodkovsky) on *Picea* sp.; *Pineus pini* on *Pinus sylvestris*; *Pineus similis* (Gillette) on *Picea glauca* and *Picea abies*; *Pineus strobii* on *Pinus strobus* (Wantuch *et al.* 2019); *Pineus* spp. on *Picea glauca*, *Pinus contorta*, *Pinus insularis*, *Pinus pentaphylla*, *Pinus resinosa*, *Pinus strobus* and *Pinus sylvestris* (McAlpine & Tanasijtshuk 1972).

Several specimens were swept from infestations of *Cinara ponderosae* (Williams) in young stands of *Pinus ponderosa* (e.g., height less than 5 m throughout the large stand), but despite rearing >150 chamaemyiid larvae from this host, none were this species but were instead *Vitaleucopis nidolkah* Gaimari and an undescribed species of *Leucopis* (*Leucopis*). It remains a possibility that *Leucotaraxis argenticollis* is also a predator in that system, whether on the *Cinara* aphids or on adelgids unseen by the first author while collecting.

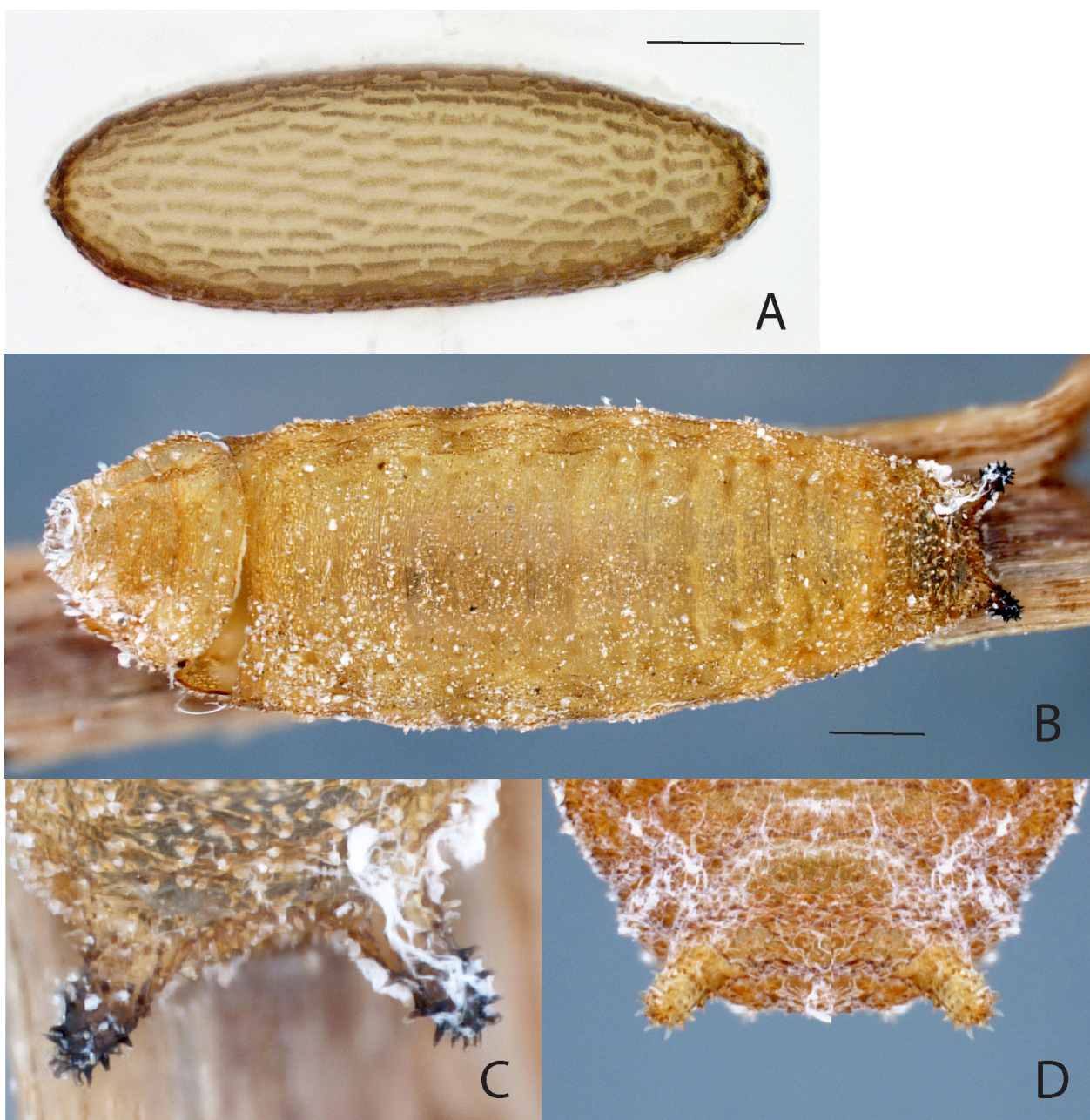


FIGURE 1. Immature stages of *Leucotaraxis* species. A. *L. atrifacies*, egg, dorsal view, posterior pole right (measure bar = 0.1 mm). B–C. *L. argenticollis*, puparium, dorsal view: B. habitus (measure bar = 0.2 mm); C. posterior spiracles. D. *L. piniperda*, puparial posterior spiracles, dorsal view.

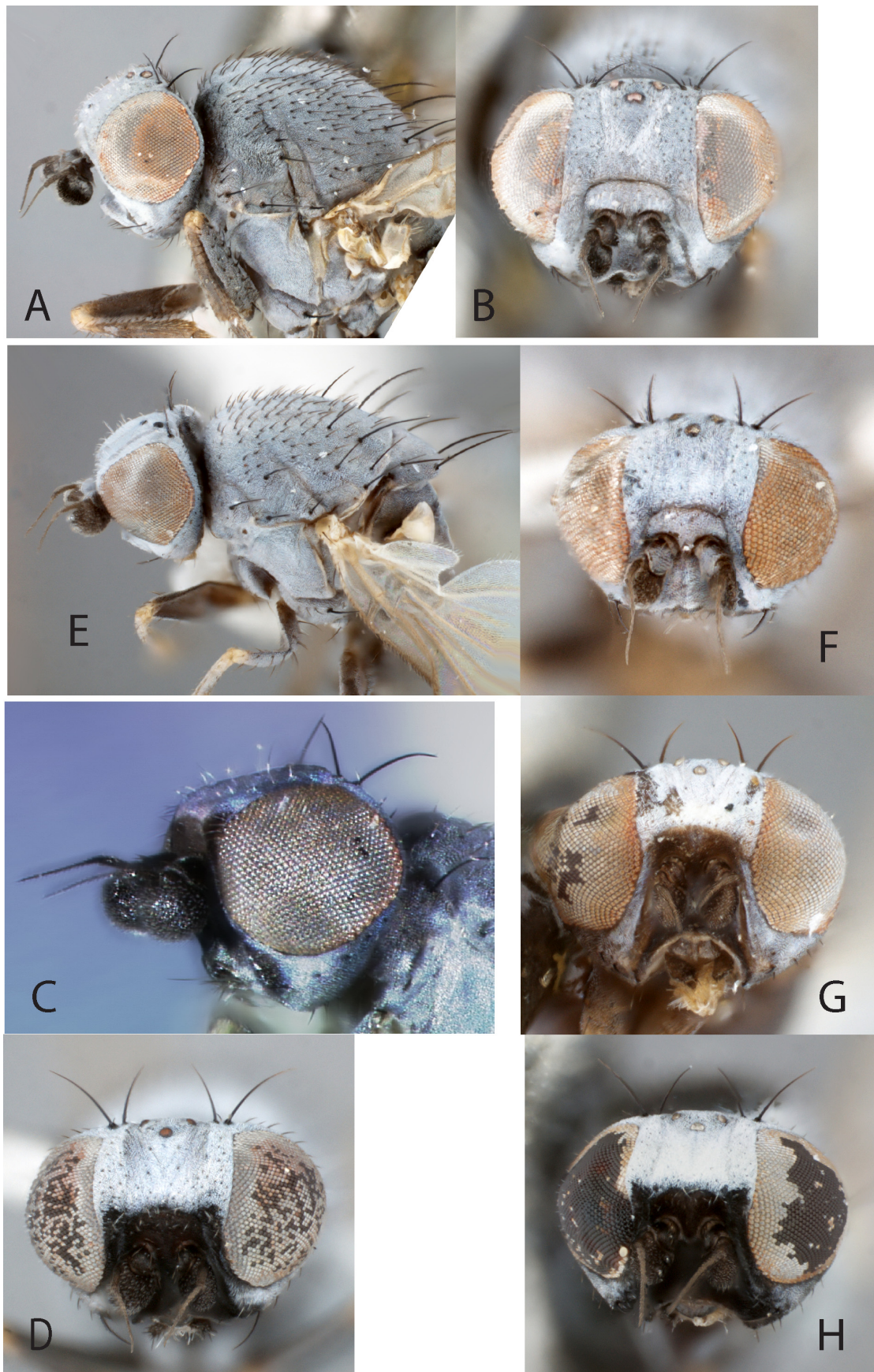


FIGURE 2. *Leucotaraxis* species. A–B. *L. argenticollis*: A. head and thorax, lateral view; B. head, anterior view. C–D. *L. atrifacies*: C. head and anterior thorax, lateral view; D. head, anterior view. E–H. *L. piniperda*: E. head and thorax, lateral view; F–H. heads, anterior view: F. eastern form; G. mixed form; H. western form.

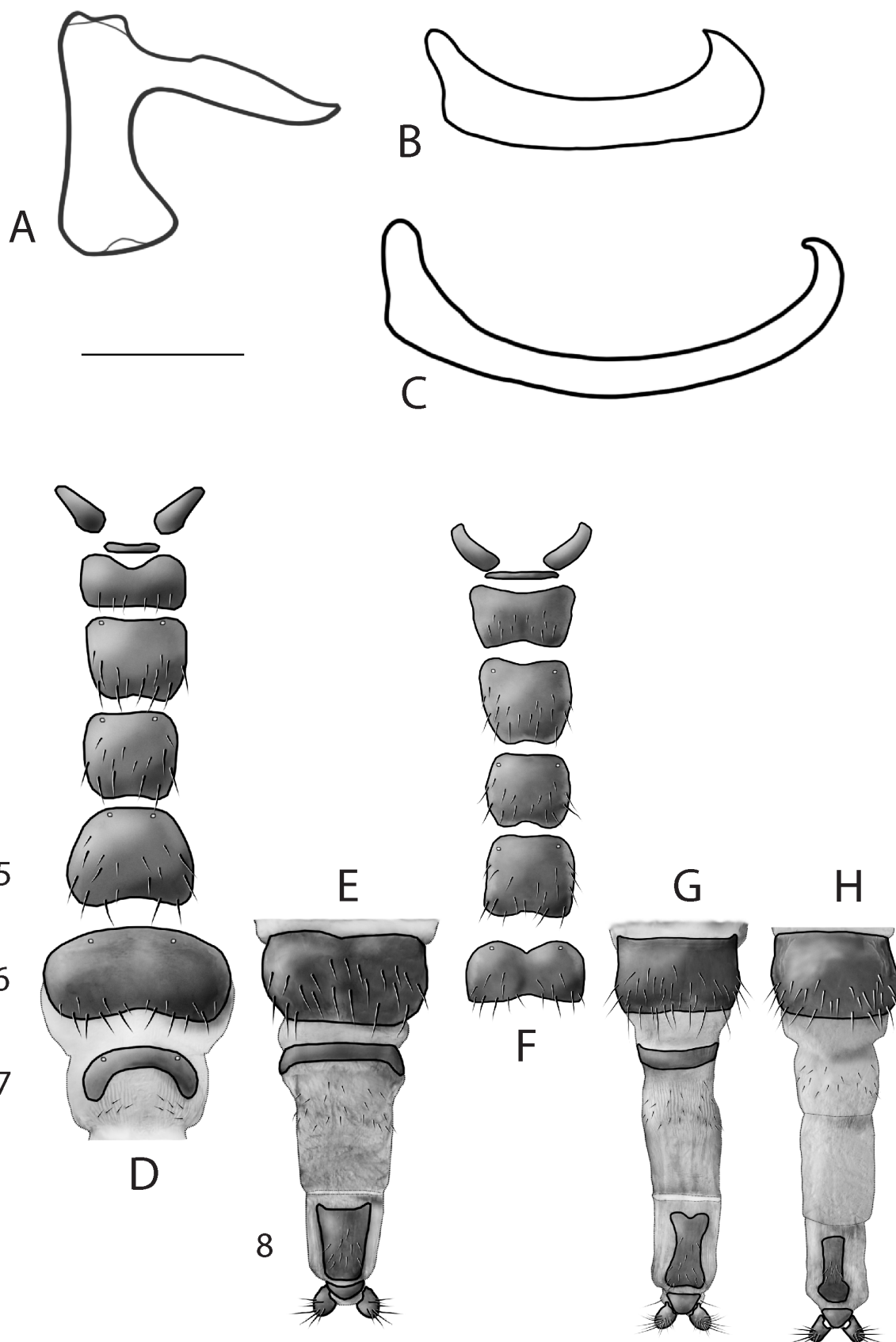


FIGURE 3. Terminalia of *Leucotaraxis* species. A–C. Male, phallus, oriented with distal part right (measure bar = 0.1 mm): A. *L. argenticollis*; B. *L. atrifacies*; C. *L. piniperda*. D–H. Female, terminalia. D–E. *L. argenticollis*: D. ventral view; E. dorsal view. F–G. *L. atrifacies*: F. ventral view; G. dorsal view. H. *L. piniperda*, dorsal view. Numbers to the left indicate segments (D, F are sternites; E, G, H are tergites).

Remarks. At two different localities (one in New Mexico and one in Arizona), this species was collected together with *Chamaethrix necopina* Gaimari, *Leucotaraxis atrifacies* and *Vitaleucopsis nidolkah*, and at the New Mexico locality also with *Leucotaraxis sepiola*. The puparial stage is distinguishable from that of *Leucotaraxis atrifacies* and *L. piniperda* by the slightly longer posterior spiracular tubercle, which is more darkly sclerotized distally in this species, and the slightly larger size. The three specimens from Coconino County, Arizona, were mistakenly listed by Tanasijtshuk (2002) as *Leucopsis piniperda*.

Distribution. **Nearctic:** Canada (Alberta, British Columbia, Manitoba, Newfoundland, New Brunswick, Northwest Territories, Ontario, Quebec). USA (Alaska, Arizona, California, Colorado, Connecticut, Georgia, Idaho, Illinois, Massachusetts, Minnesota, Montana, New Hampshire, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Utah, Virginia, Washington, Wyoming). **Oriental.** India (Rao 1965). **Palaearctic:** England (McLean 1982), Japan, Russia (McAlpine & Tanasijtshuk 1972), Sweden.

Specimens examined. Nearly all specimens from McAlpine & Tanasijtshuk (1972) were examined, with additional specimens as follows. CANADA: **ALBERTA.** Seele, H₂O Rd, 12.i.1971, coll. L.S. Skaley, ex. duff around *P[inus]. contorta*, 3916, 74-726 15 (1 ♀, CNC). **BRITISH COLUMBIA.** Atlin, 2200 ft., 2.vi.1955, coll. H. Huckel (1 ♀, CNC). Burns Lake, 8.vii.1993, coll. L.M. Humble, ex. *Pinus contorta* foliage, emerged 20.vii.1993, FIDS No. 93-0504-02 (1 ♀, PFCA). Kitimat, 2.vi.1960, coll. R. Pilfrey (1 ♂, CNC), coll. J.G. Chillcott, ex. hemlock forest (1 ♀, CNC). Princeton, 19.v.1986, ex. pine leader (1 ♀, CNC). Saanichton, 26.iii.1993, coll. L.M. Humble, ex. beating of hemlock foliage infested with *Adelges tsugae*, FIDS No. 93-0005-01 (1 ♂, 1 ♀, CSCA; 1 ♂, 2 ♀, PFCA), 30.iv.1993, FIDS No. 93-0037-02 (2 ♂, 2 ♀, PFCA), 11.vi.1993, FIDS No. 93-0204-01 (1 ♀, PFCA), 28.v.1993, ex. puparia in *Adelges tsugae* wool on *Tsuga heterophylla*, emerged 31.v.1993, FIDS No. 03-0102-01 (1 ♂, 1 ♀, CSCA; 1 ♂, 1 ♀, PFCA). Summit Lake, Mile 392 Alaska Highway, 4200 ft., 21.vii.1959, R.E. Leech (1 ♂, 2 ♀, CNC), 5000 ft., 6.vii.1959, coll. R.E. Leech (1 ♂, CNC). **ONTARIO.** Ottawa, 4.vii.1963, coll. J.R. Vockeroth, ex. *Pineus similis* on *Picea glauca*, emerged 15.vii.1963 (1 ♀ with puparium, CNC). Ottawa, 17.vii.1963, coll. J.R. Vockeroth (3 ♂, 4 ♀, CNC), 22.vii.1963 (3 ♂, CNC), 23.vii.1963 (1 ♂, 1 ♀, CNC). Hazeldean, 23.vi.1963, coll. A.W. Steffan, ex. reared on *Pineus similis* on *Picea abies*, emerged 7.vii.1963 (1 ♀, CNC). **QUEBEC.** Duchesnay, 21.vii.1942, coll. Jos. I. Beaulne (1 ♂, QMOR). Gatineau County, Masham Township, 21.v.1974, coll. D.M. Wood (1 ♀, CNC). USA: **ALASKA. Matanuska-Susitna Borough,** Big Lake, 10.vii.2020, coll. Jason Moan, ex. *Pineus coloradensis* on *Pinus contorta* (1 larva [molecular voucher], YPM; ENT996080). **ARIZONA. Apache Co.,** Apache National Forest, 0.3 mi. S mi. 249 on US Route 191, 5 mi. S Alpine, along Coleman Creek, 33°47'24"N 109°10'01"W, 2500 m, 30.vi.1995, coll. S.D. Gaimari, ex. sweep *Pinus ponderosa* (2 ♀, CSCA), 1.vii.1996 (1 ♀, CSCA); clearing 6.4 mi. N southern junction Forest Roads 24 & 25 on Road 24, 33°39'22"N 109°21'38"W, 2725 m, 2.vii.1995, coll. S.D. Gaimari, ex. sweep vegetation, including *Pinus ponderosa* (2 ♀, CSCA). **Coconino Co.,** Fort Valley Experiment Station, 13.iii.1929, Lot VII (1 ♀, USNM), 15.iii.1929, Lot VI (1 ♂, USNM), 18.iii.1929, Lot II (1 ♀, USNM). **CALIFORNIA. Riverside Co.,** Riverside, UCR campus, 10.vi.1963, coll. R.C. Dickson (1 ♀, CNC). **COLORADO. Larimer Co.,** Zimmerman Lake trail, 40.5397, -105.8792, 27.vii.2016, coll. Nathan Havill, ex. *Pineus coloradensis* on *Picea engelmannii* (1 larva [molecular voucher], YPM; ENT857047). **CONNECTICUT. Hartford Co.,** Hartford, Cedar Hill Cemetery, 41.7266, -72.6932, 5.vi.2016, coll. M.E. Montgomery, ex. *Pineus strobi* on *Pinus strobus* (6 larvae [molecular voucher], YPM; ENT961206-11). **Litchfield Co.,** Bridgewater, Skyline Ridge Rd., 41.4704, -73.3190, 6.vii.2002, coll. N. Havill, ex. *Pineus strobi* on *Pinus strobus* (1 puparium [molecular voucher], YPM; ENT856455). **GEORGIA. Union Co.,** Byron H. Reese Trailhead, 34.7422, -83.9227, 20.v.2018, coll. Jim Sullivan, ex. *Pineus strobi* on *Pinus strobus* (7 larvae [molecular voucher], YPM; ENT996058-64). **White Co.,** Helen, Chattahoochee National Forest, 34.7930, -83.7558, 13.ix.2019, coll. Jim Sullivan, ex. *Pineus strobi* on *Pinus strobus* (7 larvae [molecular voucher], YPM; ENT979185-88, ENT979191, ENT979199, ENT979204). **IDAHO. Boise Co.,** Boise National Forest, 43.8963, -115.7125, 13.ix.2016, coll. Kelsey Bedford, ex. *Adelges piceae* on *Abies lasiocarpa* (1 larva [molecular voucher], YPM; ENT961177). **Kootenai Co.,** Coeur d'Alene, 47.697, -116.772, 23.v.2013, coll. Gina Davis, ex. *Adelges tsugae* on *Tsuga heterophylla* (5 larvae [molecular voucher], YPM; ENT856473-77). **MASSACHUSETTS. Franklin Co.,** Sunderland, Mt. Toby State Forest, 42.4892, -72.5314, 13.v.2018, coll. Ryan Crandall, ex. *Pineus strobi* on *Pinus strobus* (4 larvae [molecular voucher], YPM; ENT996067-70). **Worcester Co.,** Worcester, 42.2790, -71.7733, 12.v.2018, coll. Felicia Andre, ex. *Pineus strobi* on *Pinus strobus* (1 puparium, 3 larvae [molecular voucher], YPM; ENT996065-67). **MINNESOTA. Crow Wing Co.,** Kettleston's, 46.65631°N 94.06856°W, 28.v.2009, coll. N. Havill & J. Albers, ex. reared from *Pineus strobi* on *Pinus strobus*, N. Havill sample 09-135, Specimen #09E489 (1 ♂ [molecular voucher], CSCA), Specimen #09E488 (1 ♂ [molecular

voucher], CSCA), Specimen #09E504 (1 ♂ [molecular voucher], CSCA), Specimen #09E525 (1 ♀, CSCA-FTC). **Itasca Co.**, Grand Rapids, UMN North Central Research and Outreach Center, 47.2517, -93.5103, 28.v.2009, coll. Nathan Havill, Jana Albers, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT856650). **Stearns Co.**, Birch Lakes State Forest, 45°45'51"N 94°46'03"W, 23.vi.2009, coll. R. Tiplady, ex. reared from *Pineus strobi* on *Pinus strobus* (1 puparium, 2 adults [molecular voucher], YPM; ENT856456 (puparium), ENT856414, ENT856417), 30.v.2009, coll. N. Havill & R. Tiplady, ex. reared from *Pineus strobi* on *Pinus strobus*, N. Havill sample 09-136, Specimen #09E484 (1 ♂ [molecular voucher], CSCA), Specimen #09E485 (1 ♂ [molecular voucher], CSCA), Specimen #09E486 (1 ♂ [molecular voucher], CSCA), Specimen #09E487 (1 ♂ [molecular voucher], CSCA), Specimen #09E492 (1 ♂ [molecular voucher], CSCA), Specimen #09E493 (1 ♂ [molecular voucher], CSCA), Specimen #09E494 (1 ♂ [molecular voucher], CSCA), Specimen #09E495 (1 ♂ [molecular voucher], CSCA), Specimen #09E496 (1 ♂ [molecular voucher], CSCA), Specimen #09E497 (1 ♂ [molecular voucher], CSCA), Specimen #09E501 (1 ♂ [molecular voucher], CSCA), Specimen #09E502 (1 ♂ [molecular voucher], CSCA), Voucher #09E509 (13 ♀, CSCA-FTC). **MONTANA. Park Co.**, Yellowstone National Park, Cascade Lake Trail, 44.7518, -110.4863, 19.ix.2016, coll. Gina Davis, Lee Pederson, ex. *Pineus coloradensis* on *Pinus contorta* (1 larva [molecular voucher], YPM; ENT96215). **Teton Co.**, Choteau 47.8976, -112.5721, 24.viii.2017, coll. Gina Davis, ex. *Pineus coloradensis* on *Pinus flexilis* (2 larvae [molecular voucher], YPM; ENT996081–82). **NEW HAMPSHIRE. Hillsborough Co.**, Hillsboro, Fox State Forest, 43.1316, -71.9286, 29.viii.2016, coll. Jennifer Weimer, ex. *Pineus strobi* on *Pinus strobus* (3 larvae [molecular voucher], YPM; ENT961212–14). **Rockingham Co.**, Pawtuckaway State Park, 43.0869, -71.1574, 30.iv.2019, coll. Jennifer Weimer, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT961221). **NEW MEXICO. Lincoln Co.**, Lincoln National Forest, 2.4 km W Angus, Mills Canyon, along Rio Bonito, 33°27'05"N 105°41'46"W, 2130 m, 18–19.vi.1995, coll. S.D. Gaimari, ex. sweep colonies of *Cinara ponderosae* on *Pinus ponderosa* (1 ♂, CSCA), 26.vi.1995 (3 ♀, CSCA-FTC). **McKinley Co.**, Cibola National Forest, Zuni Mountains, 4.4 mi. SE Fort Wingate, 35°25'49"N 108°29'17"W, 7300 ft., 25.vi.1996, coll. S.D. Gaimari, ex sweep *Pinus edulis* (1 ♂, 1 ♀, CSCA). **NEW YORK. Monroe Co.**, Rochester, Highland Park, 43.1278, -77.6122, 8.vii.2017, coll. Cynthia Smith, ex. *Pineus strobi* on *Pinus strobus* (1 puparium [molecular voucher], CUIC). **OHIO. Portage Co.**, Kent, 13.vii.1969, coll. T.P. Sluss (1 ♂, UAIC). **OREGON. Deschutes Co.**, Deschutes River, 1 mi. SW Pringle Falls, 4250 ft., 31.vii.1970, coll. Paul H. Arnaud, Jr., ex. flight trap (1 ♀, CAS). **Lake Co.**, Fort Rock, Deschutes National Forest, 43.5651, -121.1768, 25.iv.2104, coll. Glenn Kohler, ex. *Pineus coloradensis* on *Pinus contorta* (1 puparium [molecular voucher], YPM; ENT996083). **PENNSYLVANIA. Centre Co.**, Boalsburg, Shingletown Rd. & West Main St., 40°46'27"N 77°48'44"W, 11.iv.2009, coll. N. Havill & M. Nehme, ex. swept *Pineus strobi* on *Pinus strobus*, N. Havill sample 09-42, Specimen #09E490 (1 ♂ [molecular voucher], CSCA), Specimen #09E491 (1 ♂ [molecular voucher], CSCA). **UTAH. Weber County, Eden**, 41.3715, -111.9228, iv.2020, coll. Justin Williams, ex. *Adelges piceae* on *Abies lasiocarpa* (1 larva [molecular voucher], YPM; ENT996084). **VIRGINIA. Giles Co.**, Jefferson National Forest, Dismal Falls, 37.19263, -80.8923, 13.iv.2016, coll. Holly Wantuch, ex. *Pineus strobi* on *Pinus strobus* (6 larvae [molecular voucher], YPM; ENT906890, ENT906894–95, ENT906897, ENT906899–900). **Pulaski Co.**, Pulaski, Gatewood Park and Reservoir, 37.0622, -80.8363, 2.vii.2014, coll. Holly Wantuch, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT906874). **Wythe Co.**, Speedwell, Mt. Rogers National Recreation Area, 36.7722, -81.1752, 23.vi.2014, coll. Holly Wantuch, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT906876). **WASHINGTON. Clallam Co.**, Blyn, 48°04.120'N 122°57.400'W, 2.iv.2005, coll. Glenn Kohler (1 ♀ (SDG dissection 1384), CSCA), 9.vi.2005 (1 ♂ (SDG dissection 1274), CSCA). Seguin, 48°06.480'N 123°12.580'W, 25.vii.2005, coll. Glenn Kohler (1 ♀, CSCA). **Clark Co.**, Vancouver, 45.7037, -122.6695, 23.x.2012, coll. Glenn Kohler, ex. *Adelges tsugae* on *Tsuga heterophylla* (2 larvae [molecular voucher], YPM; ENT856464, ENT856471). **Island Co.**, Coupeville, 48°12.050'N 122°37.550'W, 26.vii.2005, coll. Glenn Kohler (2 ♂, CSCA). **King Co.**, Vashon, 47°27.200'N 122°26.950'W, 9.vi.2005, coll. Glenn Kohler (1 ♀, CSCA). **Pierce Co.**, Ruston, 47°18'02.86"N 122°31'01.31"W, 7.vii.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample SU147, Specimen #10F867 (1 ♂ with puparium [molecular voucher], CSCA), 22.vii.2010, Specimen #10F876 (1 ♂ with puparium, CSCA-FTC). Tacoma, 47°16'41.02"N 122°31'01.69"W, 21.vi.2010, coll. S.M. Grubin, ex. *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample L28 (1 ♀ with puparium, CSCA), 7.vii.2010, S. Grubin sample L40 (1 ♂ with puparium, CSCA), 22.vii.2010, S. Grubin sample L42, Specimen #10F877 (1 ♀ with puparium, CSCA-FTC), no date, S. Grubin sample L54 (1 ♀ with puparium, CSCA). Tacoma, Point Defiance, 47°18.246'N, 122°30.979'W, 4.v.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on

Tsuga heterophylla, S. Grubin sample SP047, Specimen #10F694 (1 ♀ with puparium, CSCA-FTC), S. Grubin sample SP059, Specimen #10F693 (1 ♀ with puparium, CSCA-FTC), 20.v.2010, Specimen #10F674 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F675 (1 ♂ with puparium, CSCA-FTC), S. Grubin sample L20, Specimen #10F679 (1 ♀ with puparium, CSCA-FTC), S. Grubin sample L22, Specimen #10F681 (1 ♀ with puparium, CSCA-FTC), S. Grubin sample L24, Specimen #10F680 (1 ♀ with puparium, CSCA-FTC), S. Grubin sample SP075, Specimen #10F683 (1 ♂ with puparium [molecular voucher], CSCA), S. Grubin sample SP077, Specimen #10F682 (1 ♂ with puparium [molecular voucher], CSCA), 4.vi.2010, Specimen #10F671 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F672 (1 ♂ with puparium, CSCA-FTC), Specimen #10F673 (1 ♂ with puparium, CSCA), S. Grubin sample SP079, Specimen #10F700 (1 ♂ with puparium [molecular voucher], CSCA). Tacoma, Point Defiance, 47°16'41.02"N, 122°31'1.69"W, 20.v.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, Specimen #10F659 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F660 (1 ♀ with puparium [molecular voucher], CSCA), Specimen #10F661 (1 ♀ with puparium, CSCA), 7.vii.2010, S. Grubin sample L38, Specimen #10F881 (1 ♂ with puparium, CSCA-FTC). Tacoma, 47°16'49.80"N, 122°30'58.96"W, 24.iv.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample SP009, Specimen #10F688 (1 ♀, CSCA-FTC), S. Grubin sample SP029, Specimen #10F687 (1 ♀ with puparium, CSCA-FTC), 4.v.2010, S. Grubin sample SP064, Specimen #10F702 (1 ♂ with puparium [molecular voucher], CSCA), 9.iv.2010, S. Grubin sample SP011, Specimen #10F686 (1 ♀ with puparium, CSCA), S. Grubin sample SP013, Specimen #10F685 (1 ♀, CSCA-FTC), S. Grubin sample SP017, Specimen #10F684 (1 ♀, CSCA-FTC), 22.vii.2010, S. Grubin sample L56 (1 ♀ with puparium, CSCA), Specimen #10F875 (1 ♂ with puparium, CSCA-FTC). **Thurston Co.**, Olympia, 47°01'03.42"N, 122°54'10.50"W, 24.iv.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample SP025, Specimen #10F699 (1 ♀ with puparium [molecular voucher], CSCA), S. Grubin sample SP039, Specimen #10F695 (1 ♂ with puparium, CSCA), Specimen #10698 (1 ♂ with puparium [molecular voucher], CSCA), S. Grubin sample SP041, Specimen #10F697 (1 ♂ with puparium [molecular voucher], CSCA), S. Grubin sample SP042, Specimen #10F696 (1 ♂ with puparium, CSCA), 5.v.2010, Specimen #10F676 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F677 (1 ♀ with puparium [molecular voucher], CSCA), S. Grubin sample SP060, Specimen #10F691 (1 ♂ with puparium, CSCA-FTC), S. Grubin sample SP062, Specimen #10F690 (1 ♀ with puparium, CSCA-FTC), S. Grubin sample SP063, Specimen #10F689 (1 ♂ with puparium, CSCA-FTC), S. Grubin sample SP065, Specimen #10F692 (1 ♀ with puparium, CSCA), 20.v.2010, Specimen #10F662 (1 ♂ with puparium, CSCA), 21.vi.2010, S. Grubin sample SU088, Specimen #10F869 (1 ♂ with puparium [molecular voucher], CSCA), 22.vii.2010 (1 ♂, CSCA). Olympia, 47°02.454'N 122°54.054'W, 8.vii.2009, coll. S.M. Grubin, ex. reared from *Adelges tsugae*, N. Havill sample 10-01, Specimen #10F131 (1 ♂ [molecular voucher], CSCA), N. Havill sample 10-04, Specimen #10F132 (1 ♂ [molecular voucher], CSCA), 24.vi.2009, N. Havill sample 10-03, Specimen #10F130 (1 ♂ [molecular voucher], CSCA), no date, S. Grubin sample L30, Specimen #10F873 (1 ♂ with puparium, CSCA-FTC). Tumwater, Tumwater Falls Park, 47.0379, -122.896521, vi.2013, coll. D. Ross, (2 larvae, 3 adults [molecular voucher], YPM; ENT856591, ENT856601 (larvae), YPM; ENT856419, ENT856425, ENT856427). **Pierce, King, and Thurston Cos.**, 11.iv–25.v.2015, from lab colony, coll. D. Ross, A. Arsenault, (4 adults [molecular voucher], YPM; ENT791609, ENT791540, ENT791572, ENT791575). **WYOMING. Teton Co.**, Caribou-Targhee National Forest, 43.7047, -110.9847, 18.x.2017, coll. Laura Lowrey, ex. *Pineus abietinus* on *Abies lasiocarpa* (5 puparia [molecular voucher], YPM; ENT996085–89).

***Leucotaraxis atrifacies* (Aldrich), comb. nov.**

(Figs 1A, 2C–D, 3B, 3F–G)

Leucopis atrifacies Aldrich 1925: 152. United States. California: San Francisco (HT ♀, USNM). References – McAlpine 1965: 709 (catalog); Cole & Schlinger 1969: 376 (note); Tanasijtshuk 2002: 194 (redescription), figs 1–2 (head), figs 3–5 (♂ genitalia); Havill *et al.* 2018: 26 (relationships).

Diagnosis. The face and lunule (Figs 2C–D) are dark brown to black pruinose. The postpronotum (as in Fig. 2E) has 1 strong postpronotal seta, and no additional setulae longer than those on the scutum. In the male (see figs 3–5 in Tanasijtshuk 2002), the epandrial complex is simple, small, and yellowish- to silvery-grey pruinose, with no central epandrial process; the surstylar lobe is short and stout; the phallus (Fig. 3B) is long and thick in lateral view, less than 8 X longer than its height at the middle, and is straight-sided until an abrupt distal curve to a pointed tip. In the

female (Fig. 3G), tergite 6 enlarged and about 1.6 X wider than long, tergite 7 present and strap-like, tergite 8 longer than wide, bone-shaped, narrowest through middle; sternites (Fig. 3F) with sternite 6 more than 2 X wider than long and slightly concave medially on both anterior and posterior margins, sternite 7 absent.

Immatures. Egg (Fig. 1A). Length 0.42–0.47 mm, width 0.14–0.17 mm. *Puparium*. Length 1.9–2.2 mm, width 0.7–0.9 mm. Dehiscent anterior segments (dorsal and ventral) 0.04–0.06 mm long. Raised posterior spiracular tubercles 0.07–0.11 mm long, with sclerotization concolorous with remainder of puparium (as in Fig. 1D).

Biology. Predators as larvae on species of *Adelges* and *Pineus* on Pinaceae (*Pinus*, *Tsuga*). Specific records include their attacking *Adelges piceae* and a *Pineus* sp., and adelgids (presumably *Pineus* sp.) infesting *Pinus radiata* and *Pinus edulis*. A larva was collected from *Pineus coloradensis* on *Pinus ponderosa*. Many specimens were swept from infestations of *Cinara ponderosae* in young stands of *Pinus ponderosa* (e.g., height less than 5 m throughout the large stand), but despite rearing >150 chamaemyiid larvae from this host, none were this species but were instead *Vitaleucopis nidolkah* and an undescribed species of *Leucopis* (*Leucopis*). It remains a possibility that *Leucotaraxis atrifacies* is also a predator in that system, whether on the *Cinara* aphids or on adelgids unseen by the first author while collecting.

Remarks. This species was originally described from specimens reared by Eric Walther “in connection with *Thecodiplosis pini-radiatae*” (= *Thecodiplosis piniradiatae* (Snow & Mills), Cecidomyiidae), the Monterey pine midge. This midge forms galls at the bases of needles of several species of *Pinus* including *Pinus coulteri*, *P. radiata* and *P. sabiniana*, and although they likely do not share a true association, it makes sense for them to be together on a tree infested with both the midge and adelgids.

At two different localities (one in New Mexico and one in Arizona), this species was collected together with *Chamaethrix necopina*, *Leucotaraxis argenticollis* and *Vitaleucopis nidolkah*, and at the New Mexico locality also with *Leucotaraxis sepiola*. This species was also collected at a different New Mexico locality with *Leucotaraxis sepiola*, and at the southern California locality along with the undescribed species of *Vitaleucopis* cited in Gaimari (2020). The puparial stage is indistinguishable from that of *Leucotaraxis piniperda*, both of which are only distinguishable from *Leucotaraxis argenticollis* by the shorter posterior spiracular tubercle which is not more darkly sclerotized distally, and the slightly smaller size.

Given the few specimens known from Mexico are from the south of the country and quite distant from other known specimens, it is expected that this species inhabits the areas dominated by *Pinus* in Mexico, at least as far south as the Popocatepetl volcano. More rearing and collecting in Mexico will be necessary to understand the extent of its distribution south of the USA.

Distribution. Mexico (Durango, Mexico State). USA (Arizona, California, Colorado, New Mexico, Washington).

Specimens examined. All specimens from Tanasijtshuk (2002) were examined, with additional specimens as follows. MEXICO: MEXICO. San Pedro Nexapa, nr. Amecameca, foot of Popocatepetl (volcano), 19°04'23.89"N 98°42'04.04"W, 2955 m, 7.vii.2011, coll. N.P. Havill, W. Gloria, A. Gloria-Soria, ex. on *Pinus* sp. (5-needle) infested with *Pineus* sp. (2 ♂ with puparia, CSCA). USA: ARIZONA. Apache Co., Apache National Forest, 0.3 mi. S mi. 249 on US Route 191, 5 mi. S Alpine, along Coleman Creek, 33°47'24"N 109°10'01"W, 2500 m, 30.vi.1995, coll. S.D. Gaimari, ex. sweep *Pinus ponderosa* (1 ♀, CSCA), 1.vii.1995 (1 ♀, CSCA); nr. Alpine, 33°51'52"N 109°10'18"W, 2440 m, 28.vi.1995, coll. S.D. Gaimari, ex. sweep young *Pinus ponderosa* (1 ♀, CSCA). CALIFORNIA. Los Angeles Co., La Crescenta, Eagle Canyon, S base Mount Lukens, 29.vi.1994, coll. S.D. Gaimari, ex. Sharkey Malaise trap near stream (1 ♂, CSCA). COLORADO. Alamosa Co., 21 mi. ENE Mosca, 37°45'02"N 105°30'14"W, 8100 ft., 19–22.vi.1996, coll. S.D. Gaimari, ex. Malaise trap (1 ♀, CSCA). NEW MEXICO. Lincoln Co., Lincoln National Forest, 2.4 km W Angus, Mills Canyon, along Rio Bonito, 33°27'05"N 105°41'46"W, 2130 m, 18–19.vi.1995, coll. S.D. Gaimari, ex. sweep colonies of *Cinara ponderosae* on *Pinus ponderosa* (1 ♂, 3 ♀, CSCA), 23.vi.1995 (1 ♂, 3 ♀, CSCA), 24.vi.1995, Specimen #09E474 (1 ♂ [molecular voucher], CSCA), Specimen #09E478 (1 ♂ [molecular voucher], CSCA), Specimen #09E479 (1 ♂ [molecular voucher], CSCA), Voucher #09E519 (2 ♂, 8 ♀, CSCA-FTC), 25.vi.1995, Specimen #09E480 (1 ♂ [molecular voucher], CSCA), Voucher #09E513 (1 ♀ (SDG dissection #1379), CSCA-FTC), Specimen #10F334 (1 ♀, CSCA), Specimen #10F335 (1 ♀ (SDG dissection #1380), CSCA-FTC), Specimen #10F336 (1 ♀ (SDG dissection #1381), CSCA-FTC), Specimen #10F337 (1 ♀, CSCA-FTC), Specimen #10F338 (1 ♀, CSCA-FTC), Specimen #10F339 (1 ♀, CSCA-FTC), Specimen #10F340 (1 ♀ (SDG dissection #1382), CSCA-FTC), Specimen #10F341 (1 ♀ (SDG dissection #1383), CSCA-FTC), Specimen #10F342 (1 ♀, CSCA-FTC), Specimen #10F343 (1 ♀, CSCA-FTC),

Specimen #10F344 (1 ♂, CSCA-FTC), Specimen #10F345 (1 ♂, CSCA-FTC), 26.vi.1995, Specimen #09E523 (1 ♀ (SDG dissection #1372), CSCA-FTC), Specimen #10F346 (1 ♀, CSCA-FTC), Specimen #10F347 (1 ♀ (SDG dissection #1374), CSCA-FTC), Specimen #10F348 (1 ♀ (SDG dissection #1375), CSCA-FTC), Specimen #10F349 (1 ♀ (SDG dissection #1376), CSCA-FTC), Specimen #10F350 (1 ♀ (SDG dissection #1377), CSCA-FTC), Specimen #10F351 (1 ♀ (SDG dissection #1378), CSCA-FTC), Specimen #10F353 (1 ♀ (SDG dissection #1372), CSCA-FTC), Specimen #10F726 (1 ♂, CSCA), Voucher #09E515 (5 ♀, CSCA-FTC); White Mountains, along Fork Creek, 3.1 mi. W Alto, 33°23'31.2"N 105°43'57.0"W, 2365 m, 15.vi.2007, coll. S.D. Gaimari, ex. sweep *Pinus ponderosa* with *Cinara ponderosae* infestation (1 ♂, 1 ♀, CSCA). **McKinley Co.**, Cibola National Forest, Zuni Mountains, 4 mi. SSW Fort Wingate, 35°25'20"N 108°34'38"W, 7900 ft., 24.vi.1996, coll. S.D. Gaimari, ex. sweep *Pinus ponderosa* (8 ♂, 9 ♀, CSCA), 4.4 mi. SE Fort Wingate, 35°25'49"N 108°29'17"W, 7300 ft., 25.vi.1996, ex. sweep *Pinus edulis* (4 ♀, CSCA). **WASHINGTON. Ferry Co.**, Colville Reservation, Inchelium, 48.3109°N 118.2017°W, 22.vii.2019, coll. D. Dickenson, ex. *Pineus coloradensis* on *Pinus ponderosa*, sample 19-176-05 (1 ♂, on slide, YPM; ENT960794).

***Leucotaraxis piniperda* (Malloch), comb. nov.**

(Figs 1D, 2E–H, 3C, 3H)

Leucopis piniperda Malloch 1921: 351. United States. Illinois: Urbana (HT ♀, INHS). References – McAlpine 1965: 709 (catalog); Cole & Schlinger 1969: 376 (note); Tanasijtshuk 2002: 203 (redescription), figs 29–30 (head), figs 31–34 (♂ genitalia). Kohler *et al.* 2008: 494 (biology, as *Leucopis atrifacies*); Grubin *et al.* 2011: 1410 (biology); Havill *et al.* 2018 (biology, population genetics); Neidermeier *et al.* 2020 (biology, biological control); Dietschler *et al.* 2021 (biology, biological control).

Diagnosis. The lunule, face and parafacial are either entirely silvery-grey pruinose (Fig. 2F, eastern form), entirely brown to black pruinose (Fig. 2H, western form), or the lunule and face are brown to black pruinose with the parafacial silvery-grey pruinose (Fig. 2G, mixed form). The postpronotum (Fig. 2E) has 1 strong postpronotal seta, and no additional setulae longer than those on the scutum. In the male (see figs 31–34 in Tanasijtshuk 2002), the epandrial complex is simple, small, and yellowish- to silvery-grey pruinose, with no central epandrial process; the surstylar lobe is short and stout; the phallus (Fig. 3C) is very long and thin in lateral view, more than 10 X longer than its height at the middle, and is gently curved throughout to a pointed tip. In the female (Fig. 3H), tergite 6 enlarged and about 1.5 X wider than long, tergite 7 absent (position represented only by tiny setulae), tergite 8 longer than wide, parallel-sided, with distal end enlarged; sternites as in *Leucotaraxis atrifacies* (Fig. 3F).

Immatures. Egg and puparium as in *Leucotaraxis atrifacies*.

Biology. Predators as larvae on species of *Adelges* and *Pineus* on Pinaceae (*Abies*, *Picea*, *Pinus*). Specific records (including our own rearings) include: *Adelges piceae* on *Abies grandis*; *Adelges tsugae* on *Tsuga heterophylla* (Kohler *et al.* 2008); *Pineus boernerii* on *Pinus densiflora*; *Pineus coloradensis* on *Pinus* sp. (a 5-needle pine, possibly *Pinus lambertiana*) and *Picea engelmannii*; *Pineus pini* on *Pinus sylvestris*; *Pineus similis* on *Picea glauca*; *Pineus strobi* on *Pinus strobus* (Tanasijtshuk 2002; Wantuch *et al.* 2019); *Pineus* sp. on *Pinus sylvestris*. They have also been collected as adults from *Pinus contorta* and *Pinus resinosa*.

Remarks. Unfortunately, the few specimens from Oregon and Washington in the study by Kohler *et al.* (2008) were misidentified as *Leucopis atrifacies*. After examination of the specimens from this work and from Tanasijtshuk (2002), the color of pruinosity on the lunule, face and parafacial are variable, with a distinct distributional pattern. The specimens from eastern North America (Canada – New Brunswick, Quebec; USA – Connecticut, Illinois, Maryland, Minnesota, North Carolina, Ohio, Rhode Island, Virginia) all have uniformly silvery-grey pruinosity (Fig. 2F), while those in western North America (Canada – Alberta, British Columbia; USA – California, Colorado, Idaho, New Mexico, Oregon, Washington, Wyoming) all have uniformly brown to black pruinosity (Fig. 2H). The east-west divergence is also displayed in molecular data (see Havill *et al.* 2018). Only the specimens from Ontario, Canada, have a mixed state (Fig. 2G), with the lunule and face being brown to black pruinose with the parafacial silvery-grey pruinose. Both the male and female genitalia, as well as other external characteristics, make the identity of this species unambiguous despite this variation. The puparial stage is indistinguishable from that of *Leucotaraxis atrifacies*, both of which are only distinguishable from *Leucotaraxis argenticollis* by the shorter posterior spiracular tubercle that is not heavily sclerotized distally, and the slightly smaller size.

Distribution. Canada (Alberta, British Columbia, New Brunswick, Ontario, Quebec, Saskatchewan). USA (Arizona, California, Colorado, Connecticut, Idaho, Illinois, Maryland, Massachusetts, Michigan, Minnesota, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Utah, Virginia, Washington, West Virginia).

Specimens examined. All specimens from Tanasijtshuk (2002) were examined, with additional specimens as follows. CANADA: **ALBERTA.** Seebe, 20.i.1971, ex. duff around *C. com.* infected *P[inus]. contorta*, #2670 (1 ♀, CNC). **ONTARIO.** Chalk River, 1.viii.1951, coll. J.M. Anderson, ex. *Pissodes strobi* (1 ♀, CNC). Ottawa, 29.vi.1994, coll. J.R. Vockeroth, ex. damp second-growth *Acer-Betula* woods (1 ♀, CNC). Sault Ste. Marie, 18.vii.1951, coll. L. Lyons, ex. red pine [= *Pinus resinosa*], No. R-70-19 (1 ♀, CNC). **SASKATCHEWAN.** Smeaton, 53.6181, -104.7409, 9.vi.2010, coll. N. Havill, ex. *Pineus* on *Picea* sp. (1 larva [molecular voucher], YPM; ENT764124). USA. **CALIFORNIA. El Dorado Co.,** Eldorado National Forest, 38.9148, -120.3904, 31.v.2010, coll. Nathan Havill, Stephen Gaimari, ex. *Pineus coloradensis* on *Pinus* sp. (5-needle) (1 larva [molecular voucher], YPM; ENT790140). **COLORADO. Boulder Co.,** Boulder, Flagstaff Canyon, 5800 ft., 10.vi.1961, coll. C.H. Mann, ex. on side of stream (1 ♂, CNC). **Larimer Co.,** Zimmerman Lake trail, 40.5397, -105.8792, 27.vii.2016, coll. Nathan Havill, ex. *Pineus coloradensis* on *Picea engelmannii* (1 larva [molecular voucher], YPM; ENT857046). **CONNECTICUT. Hartford Co.,** Hartford, Cedar Hill Cemetery, 41.7266, -72.6932, 5.vi.2016, coll. M.E. Montgomery, ex. *Pineus strobi* on *Pinus strobus* (8 larvae [molecular voucher], YPM; ENT961079–86). **New Haven Co.,** Hamden, Exeter Rd. & Deerfield Dr., 41.426°N 72.936°W, 16.vi.2009, coll. M.E. Montgomery, ex. reared from *Pineus* sp. on *Pinus sylvestris*, N. Havill sample 09-134, Specimen #09E471 (1 ♂ [molecular voucher], CSCA). **IDAHO. Idaho Co.,** Warm Springs Point, 13.viii.1969, 51-488b (2 ♀, USNM). **ILLINOIS. Champaign Co.** Urbana, 12.vi.1967, coll. J. Appleby, ex. larvae in wax mass of pine aphid (1 ♀ with puparium, 2 ♀, USNM). **Morgan Co.,** Meredosia, 29.v.1917 (1 ♀, INHS). **MARYLAND. Baltimore Co.,** Baltimore, Cylburn Arboretum, 39.532, -76.653, 28.v.2008, coll. Melody Keena, ex. *Pineus boernerii* on *Pinus densiflora* (7 larvae [molecular voucher], YPM; ENT856378–84). **MASSACHUSETTS. Hampshire Co.,** Amherst, 42.3928, -72.5323, 20.v.2018, coll. Ryan Crandall, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT996097). **Worcester Co.,** Worcester, 42.2790, -71.7733, 12.v.2018, coll. Felicia Andre, ex. *Pineus strobi* on *Pinus strobus* (1 larva [molecular voucher], YPM; ENT996096). **MICHIGAN. Benzie Co.,** Lake Ann, 44.7436, -85.9131, 6.xi.2018, coll. Scott Lint, ex. *Pineus strobi* on *Pinus strobus* (2 puparia [molecular voucher], YPM; ENT996098–99). **MINNESOTA. Beltrami Co.,** Bemidji, visitor center nr. Paul Bunyan statue, 47°28'13"N 94°52'43"W, 23.v.2009, coll. N. Havill, ex. old gall of *Adelges* sp. on *Picea* sp., N. Havill sample 09-123, Specimen #09E475 (1 ♂ [molecular voucher], CSCA). **NEW MEXICO: San Miguel Co.,** Las Vegas Hot Springs, 7.viii, coll. H.S. Barber (1 ♂, USNM). **NEW YORK. Cayuga Co.,** McIlroy Bird Sanctuary, 42.6661, -76.2834, 2.vii.2019, coll. Nicholas Dietschler, Marshall Lefebvre, Katharine O'Connor, ex. *Pineus strobi* on *Pinus strobus* (1 puparium [molecular voucher], CUIC). **Monroe Co.,** Rochester, Highland Park, 43.1278, -77.6122, 8.vii.2017, coll. Cynthia Smith, ex. *Pineus strobi* on *Pinus strobus* (3 larvae, 13 puparia [molecular voucher], CUIC). **Steuben Co.,** Addison, McCarthy Hill State Forest, 42.0975, -77.1938, 26.vii.2018, coll. Nicholas Dietschler, Marshall Bigler-Lefebvre, ex. *Pineus strobi* on *Pinus strobus*, (7 larvae, 2 puparia [molecular voucher], CUIC). **Tompkins Co.,** Ithaca, Cornell campus, 42.4454, -76.4755, 3.vi.2016, coll. Nathan Havill, Mark Whitmore, Amalia Havill, ex. *Pineus strobi* on *Pinus strobus* (12 larvae [molecular voucher], YPM; ENT856925–36). **Ulster Co.,** Woodstock, Overlook Mountain Forest, 42.0760, -74.1259, 31.v.2018, coll. Nicholas Dietschler, Marshall Bigler-Lefebvre, ex. *Pineus strobi* on *Pinus strobus* (5 larvae [molecular voucher], CUIC). **NORTH CAROLINA. Macon Co.,** Highlands, Wightman College, 10.vii.1987, coll. W.W. Wirth, ex. UV light (1 ♀, USNM). **Transylvania Co.,** Sapphire, 20.vii.1990, coll. W.W. Wirth, ex. UV light trap (2 ♀, USNM). **OHIO. Morgan Co.,** Beverly, 39.6431, -81.7060, 26.vi.2019, coll. Page Weckbacher, ex. *Pineus strobi* on *Pinus strobus* (1 larva, 4 puparia [molecular voucher], YPM; ENT961088–92). **Portage Co.,** Kent, 16.vii.1969, coll. T.P. Sluss, biological note 6914 (1 ♂, UAIC). **OREGON. Benton Co.,** Corvallis, 12.v.1951, coll. R.G. Mitchell, ex. reared, predaceous on *Adelges piceae* (1 ♂, CNC). **Multnomah Co.,** Portland, Grant Park, 45°32.450'N 122°37.800'W, 14.iv.2006, coll. G. Kohler, ex. reared from field collected puparium on *Adelges tsugae* (1 ♂ with puparium, CSCA), 12.v.2006, ex. flight caught (2 ♀, CSCA). **PENNSYLVANIA. Greene Co.,** Mt. Morris, 39.7730, -80.1475, 19.vi.2015, coll. Andrew Liebhold, ex. *Pineus strobi* on *Pinus strobus* (2 larvae [molecular voucher], YPM; ENT856919, ENT856697). **RHODE ISLAND. Washington Co.,** University of Rhode Island, Kingston, 12.vi.1982, coll. R. Casagrande (1 ♂, USNM). **UTAH. Davis Co.,** Farmington Canyon, 40.9932, -111.8186, 5.ix.2017, coll. Danielle Malesky, ex. *Adelges piceae* on *Abies lasiocarpa* (1 larva [molecular voucher],

YPM; ENT996095). **VIRGINIA. Fairfax Co.**, Alexandria, 14.vi.1952, coll. W.W. Wirth (1 ♀, USNM), 15.vi.1952 (1 ♂, USNM). **Montgomery Co.**, Blacksburg, Coal Mining Heritage Park, 37.1870, -80.427, 18.v.2010, coll. Melissa Fischer, ex. *Pineus strobi* on *Pinus strobus*. (9 larvae [molecular voucher], YPM; ENT856988–89, ENT856702–08). **WASHINGTON. Clark Co.**, Vancouver, 45.7031, -122.6707, 21.vi.2013, coll. Darrell Ross, ex. *Adelges tsugae* on *Tsuga heterophylla* (1 larva [molecular voucher], YPM; ENT856663). Island County; Camano Island, 48.1474, -122.4411, 4.iv.2017, coll. Mark Whitmore, Isis Caetano, ex. *Adelges tsugae* on *Tsuga heterophylla* (1 larva, 2 puparia [molecular voucher], CUIC). **King Co.**, Vashon, 47°27.200'N 122°26.950'W, 22.iii.2006, coll. G. Kohler, ex. reared from field collected puparium on *Adelges tsugae* (1 ♀ with puparium, CSCA), S. Grubin sample L48, Specimen #10F865 (1 ♂ with puparium [molecular voucher], CSCA), 4.viii.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, Specimen #10F880 (1 ♀ with puparium, CSCA-FTC). **Pierce Co.**, Ruston, 47°18'02.86"N 122°31'01.31"W, 22.vii.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla* (1 ♀ with puparium, CSCA). Tacoma, 47°16'41.02"N 122°31'01.69"W, 7.vii.2010, coll. S.M. Grubin, ex., reared, *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample L44 (1 ♂, CSCA), S. Grubin sample SU132 (1 ♂ with puparium, CSCA), 22.vii.2010 (2 ♂ with puparia, 1 ♀ with puparium, CSCA), S. Grubin sample L50 (1 ♂ with puparium, CSCA), S. Grubin sample SU180 (1 ♂ with puparium, CSCA), S. Grubin sample SU181, Specimen 10F864 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F874 (1 ♀ with puparium, CSCA-FTC), Specimen #10F878 (1 ♂ with puparium, CSCA-FTC). Tacoma, 47°16'49.80"N, 122°30'58.96"W, 24.iv.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla* (2 ♂ with puparia, 2 ♀ with puparia, CSCA), Specimen #10F663 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F664 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F665 (1 ♂ with puparium, CSCA). Tacoma, Masonic Memorial Cemetery, 1.i.2016, coll. Rachel Brooks (2 larvae [molecular voucher], YPM; ENT856920–21). Tacoma, Point Defiance Park, 47.304, -122.516, 12.v.2008, coll. Michael E. Montgomery, Richard McDonald (2 adults [molecular voucher], YPM; ENT856401, ENT856408). Tacoma, Point Defiance, 47°18.300'N 122°30.000'W, 9.vi.2005, coll. G. Kohler (1 ♀, CSCA). Tacoma, Point Defiance, 47°18.246'N 122°30.979'W, 25.iv.2009, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, N. Havill sample 10-05.1, Specimen #10F135 (1 ♀ [molecular voucher], CSCA), N. Havill sample 10-05.2, Specimen #10F133 (1 ♀ [molecular voucher], CSCA), N. Havill sample 10-05.3, Specimen #10F138 (1 ♂ [molecular voucher], CSCA), N. Havill sample 10-05.4, Specimen #10F134 (1 ♀ [molecular voucher], CSCA), N. Havill sample 10-05.5, Specimen #10F137 (1 ♂ [molecular voucher], CSCA), 24.iv.2010, S. Grubin sample SP023, Specimen #10F655 (1 ♂ with puparium, CSCA), 5.v.2010, Specimen #10F656 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F657 (1 ♀ with puparium [molecular voucher], CSCA), Specimen #10F658 (1 ♀ with puparium, CSCA-FTC). **Thurston Co.**, Olympia, 47°01'03.42"N, 122°54'10.50"W, 24.iv.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, Specimen #10F666 (1 ♂ with puparium [molecular voucher], CSCA), Specimen #10F667 (1 ♀ with puparium [molecular voucher], CSCA), Specimen #10F668 (1 ♀ with puparium, CSCA-FTC), Specimen #10F669 (1 ♂ with puparium, CSCA), Specimen #10F670 (1 ♀ with puparium, CSCA), 5.v.2010, Specimen #10F678 (1 ♀ with puparium [molecular voucher], CSCA), 21.vi.2010, S. Grubin sample SU120, Specimen #10F868 (1 ♂ with puparium [molecular voucher], CSCA), 7.vii.2010, S. Grubin sample SU166 (1 ♀ with puparium, CSCA), S. Grubin sample SU162, Specimen #10F879 (1 ♂ with puparium, CSCA-FTC), 22.vii.2010 (1 ♀ with puparium, CSCA). Olympia, 47°00'48.30"N 122°54'18.21"W, 8.vii.2010, coll. S.M. Grubin, ex. reared, *Adelges tsugae* on *Tsuga heterophylla*, S. Grubin sample L34 (1 ♀ with puparium, CSCA). Olympia, 47°02.454'N 122°54.054'W, 29.vii.2009, coll. S.M. Grubin, ex. reared from *Adelges tsugae*, N. Havill sample 10-02, Specimen #10F136 (1 ♀ [molecular voucher], CSCA). **Pierce, King, and Thurston Cos.**, 11.iv–25.v.2015, from lab colony, coll. Darrell Ross, Arielle Arsenaault, (4 adults [molecular voucher], YPM; ENT791591, ENT791607, ENT791616, ENT791620). **WEST VIRGINIA. Jefferson Co.**, Shepherdstown, U.S. Fish & Wildlife National Conservation Training Center, 39.486, -77.805, 28.v.2008, coll. Melody Keena, ex. *Pineus strobi* on *Pinus strobus* (3 ♀ [molecular voucher], YPM; ENT856387–89). **MISC. Oregon/Washington.** Cage reared on *Adelges tsugae*, v–vii.2006, G. Kohler (1 ♂, 3 ♀, CSCA).

Leucotaraxis sepiola sp. nov.

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(Figs 4A–H, 5A–C)

Etymology. From the diminutive of the Latin noun *sepia*, referring to squid ink, in reference to the large, distinctive, shiny black epandrium and cerci in the male of this species; a noun.

Diagnosis. The face and lunule (Figs 4B, D) are dark brown to black pruinose. The postpronotum (Figs 4A, G) has 1 strong postpronotal seta, and no additional setulae longer than those on the scutum. In the male genitalia (Figs 5A–C), the epandrial complex is large, conspicuous and polished black, with the epandrium extending into a central process bearing the cerci at a distinct upward angle; the surstylar lobe is articulated with the epandrium and is long and thin.

Adults, ♂ (♀ unknown). Body length 1.8 mm.

Head (Figs 4B–F). 1.4 X higher than long; 1.3 X wider than high; mostly dark silvery grey with exceptions following. Vertex with outer vertical seta longer than inner one by 1.5 X. Postocellar setae absent. Ocellar triangle tapering to about midpoint of frons, slightly raised from fronto-orbital plate; posterior ocelli farther apart than distance to anterior ocellus by 1.5 X; anterior ocellus slightly smaller than posterior; posterior ocelli placed slightly anterior to vertex, with area between and behind posterior ocelli lacking setulae. Ocellar setae absent. Eye with length and width subequal; height 2.6 X genal height. Frons with reddish grey strip along edge of ocellar triangle (Fig. 4F); 1.3 X wider than long; with lateral edges only slightly diverging anteriorly, 1.1 X wider at level of lunule than at level of anterior ocellus; meeting lunule at 90° angle. Fronto-orbital setae lacking; area setulose (setulae erect, white) distally (Figs 4C, E). Lunule (Figs 4B–D) dark brown pruinose above antennae; anterior edge straight, height 0.5 X frons length; with few small, fine setulae. Antennae entirely dark brown to black; separated by distance less than 0.5 X antennal socket width, lacking carina, with area between antennal bases darkening to black pruinose ventrally (as in face); 1st flagellomere short, rounded, covered with short brown hairs; arista with distal segment 3.0 X longer than basal. Face black pruinose; with deep antennal grooves. Parafacial black pruinose; about half width of facial width. Gena with one strong genal seta in addition to one strong setula and several small setulae behind. Clypeus black with sparse covering of dark grey pruinosity; small, exposed. Palpus dark brown; cylindrical; setulose. Mouthparts very small and held within oral cavity above palpi; prementum dark, small; labellum small, yellow.

Thorax (Figs 4A, D). Scutum uniformly dark silvery-grey pruinose; 1.3 X longer than wide; 4.0 X scutellar length; setulose; dorsocentral vittae absent. Prescutellum present. Scutellum concolorous with scutum; 1.7 X wider than long. Pleuron concolorous with scutum. Chaetotaxy: 0+2 dorsocentral setae, posterior seta 1.5 X longer than anterior one; one postpronotal seta; two notopleural setae, in anterior and posterior corners, anterior one 3.0 X longer than posterior one; one pre- and one postsutural supra-alar seta; two postalar setae; prescutellar acrostichal seta absent; proepisternum, anepisternum and anepimeron lacking setae; one strong katapisternal seta along upper edge, with 3 or 4 small setulae in row anterior to seta; two pairs scutellar setae. *Legs*. Entirely dark brown, except for femora and tibiae dark grey pruinose with orange distal tips of femora and basal parts of tibiae, with basal parts of basotarsomeres lighter brown. *Wing*. Length 1.6 mm; 2.6 X longer than wide. Hyaline, with veins brown. Veins R₂₊₃, R₄₊₅ and M₁ parallel in distal half of wing. Crossvein r-m located slightly basad of halfway point of wing length, and at 3/5 point of cell dm length. Vein CuA₁ extends to wing margin; apical section 2.0 X longer than crossvein dm-cu. Halter yellow, with stalk slightly darker.

Abdomen (Fig. 4H). Tergites uniformly setulose, except setulae very slightly enlarged along posterior margin and laterally. Syntergite 1+2 and tergite 3 bronzy pruinose, except lateral parts dark silvery-grey pruinose; tergites 4–6 dark silvery-grey pruinose. Syntergite 1+2 and tergite 3 lacking patch of microtrichiae on lateral edge. Sternites dark silvery-grey pruinose.

Male genitalia (Figs 5A–C). Epandrium large, convex posteriorly, entirely shiny black, with series of very small setulae along posterior edge; extending distomedially into blunt projection which bears cerci on ventral surface, with small central depression on anterodorsal surface; with long, narrow, medially-oriented surstylar lobe. Cercus large, pad-like; shiny black, oriented downwards from posterior surface of distomedial extension of epandrium; in lateral view, subequal in size and general shape to hypandrium. (Note, phallus complex severely over-macerated after soaking in KOH with heavy and dark epandrial complex, resulting in the structures shrivelling and becoming twisted. As such, the following characteristics were not illustrated, but are described as well as possible after thorough examination, to be verified when this species is again collected: Hypandrium in dorsal view subovate, 1.3 X longer than wide,

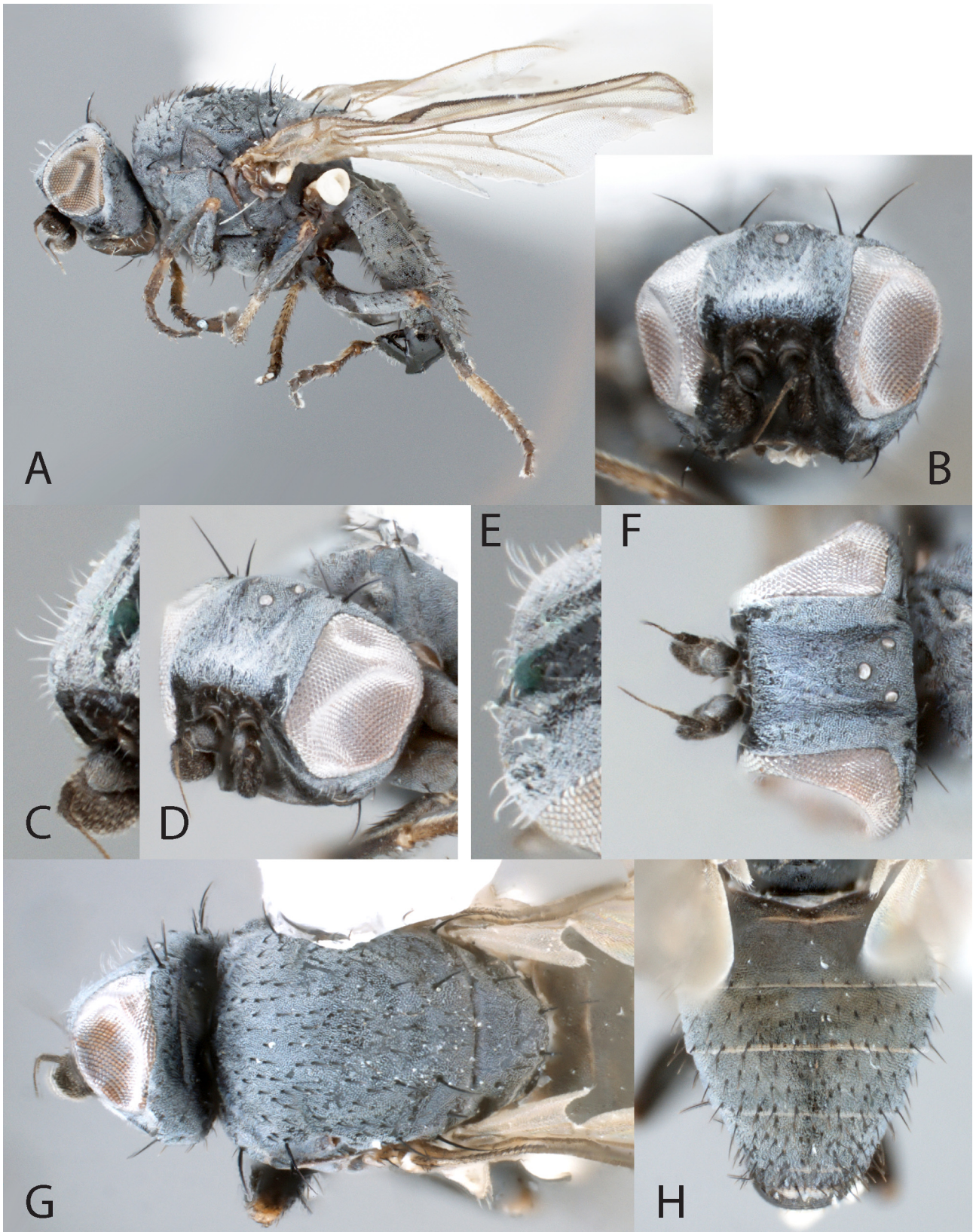


FIGURE 4. *Leucotaraxis sepiola*, male, external features. A. Habitus, lateral view (paratype). B–F. Head: B. anterior view (holotype); C–D. oblique view: C. showing setae along edge of frons (paratype); D. entire (holotype); E–F. dorsal view: E. showing setae along edges of frons (paratype); F. entire (holotype); G–H. dorsal view (holotype): G. head and thorax; H. abdomen.

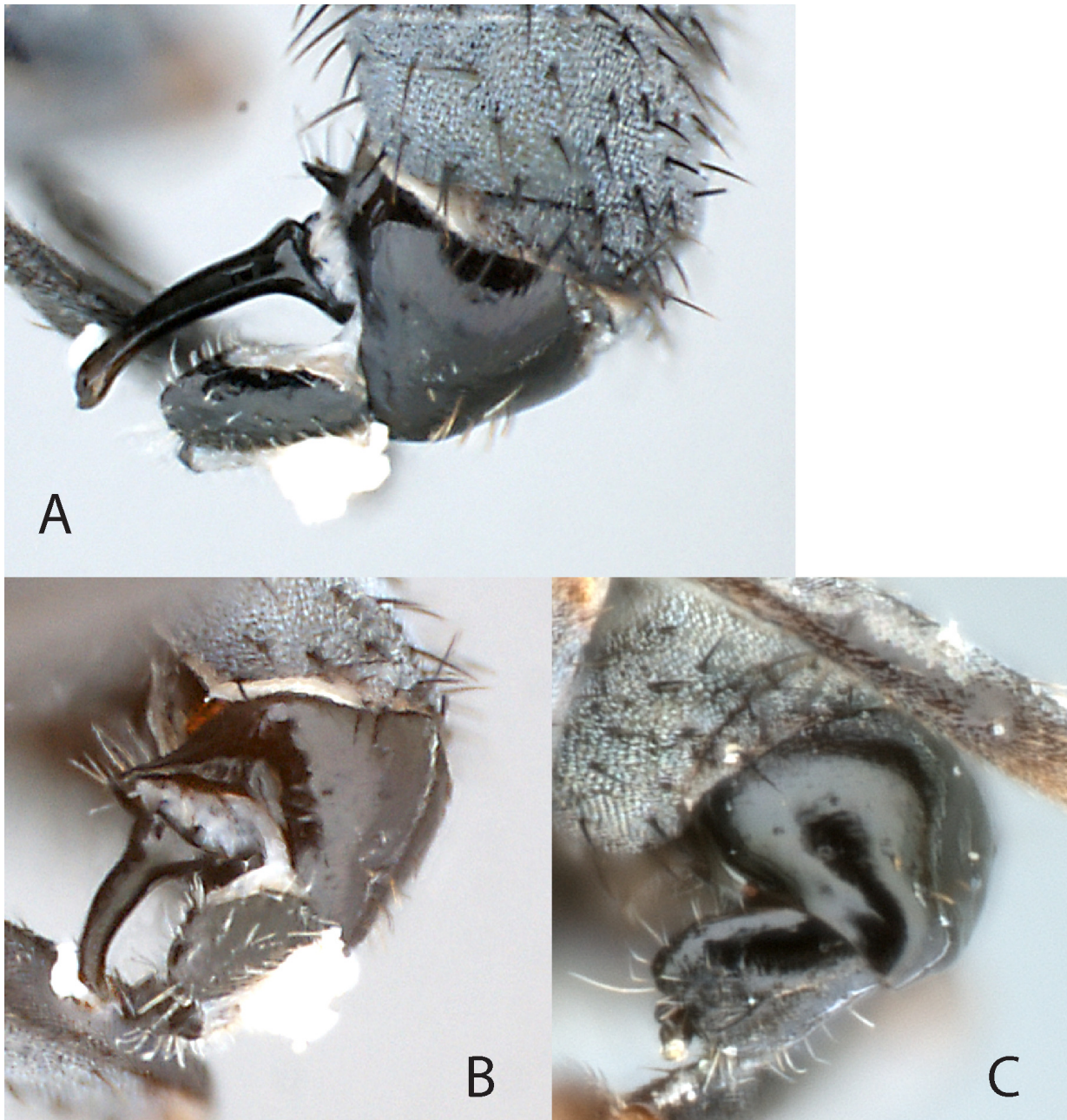


FIGURE 5. *Leucotaraxis sepiola*, male, genitalic features. A–B. Holotype: A. lateral view; B. posterolateral view. C. Paratype, posterolateral view, with surstylus oriented medially under cercus.

with lateral arms very thick to point of articulation with postgonite, becoming abruptly thin posteriorly; in profile, subquadrate, evenly wide. Pregonite absent. Postgonite flattened, curved, with blunt tip; dorsally setulose; lightly sclerotized. Phallapodeme about 2 X longer than high from lateral view, parallel-sided; in ventral view, bone-shaped, about 3 X longer than wide. Phallus from ventral view parallel-sided to blunt tip, 2.2 X longer than wide; from lateral view, length 4.0 X height of basiphallus, basiphallus extending into small subtriangular lobe, distiphallus slightly curved, evenly narrow to blunt tip).

Immatures. Unknown.

Biology. All known specimens were swept from infestations of *Cinara ponderosae* in young stands of *Pinus ponderosa* (e.g., height less than 5 m throughout the large stand), but despite rearing >150 chamaemyiid larvae from this host, none were this species, but were instead *Vitaleucopsis nidolkah* and an undescribed species of *Leucopsis* (*Leucopsis*). It remains a possibility that *Leucotaraxis sepiola* is a predator in that system, whether on the *Cinara* aphids or on adelgids unseen by the first author while collecting.

Remarks. At one locality in New Mexico, this species was collected together with *Chamaethrix necopina*, *Leucotaraxis argenticollis*, *Leucotaraxis atrifacies* and *Vitaleucopis nidolkah*, and at an additional New Mexico locality along with *Leucotaraxis atrifacies*.

Distribution. Known only from New Mexico.

Type material. Holotype ♂ (point mounted, very good condition), deposited in CSCA, with the following labels: “USA. NEW MEXICO. Lincoln Co., 2.4 km W Angus, Lincoln Nat’l For., White Mts. Wilderness, head of Mills Cyn. trail along Rio Bonito, el. 2130 m, 33°27’05”N 105°41’46”W, 26 JUN 1995, S.D. Gaimari, ex. sweep *Cinara ponderosae* on *Pinus ponderosa*” / “HOLOTYPUS ♂ *Leucotaraxis sepiola* Gaimari” (red label). Paratypes: USA: **NEW MEXICO. Lincoln Co.**, 2.4 km W Angus, Lincoln National Forest, White Mountains Wilderness, head of Mills Canyon trail, along Rio Bonito, 33°27’05”N 105°41’46”W, 2130 m, 26.vi.1995, coll. S.D. Gaimari, ex. sweep *Cinara ponderosae* on *Pinus ponderosa* [same data as holotype], Specimen #10F352 (1 ♂ [molecular voucher] (SDG dissection 1371), CSCA). **McKinley Co.**, 4 mi. SSW Fort Wingate, Cibola National Forest, Zuni Mountains, 35°25’20”N, 108°34’38”W, 2408 m, 24.vi.1996, coll. S.D. Gaimari, ex. sweep *Pinus ponderosa* (1 ♂, CSCA).

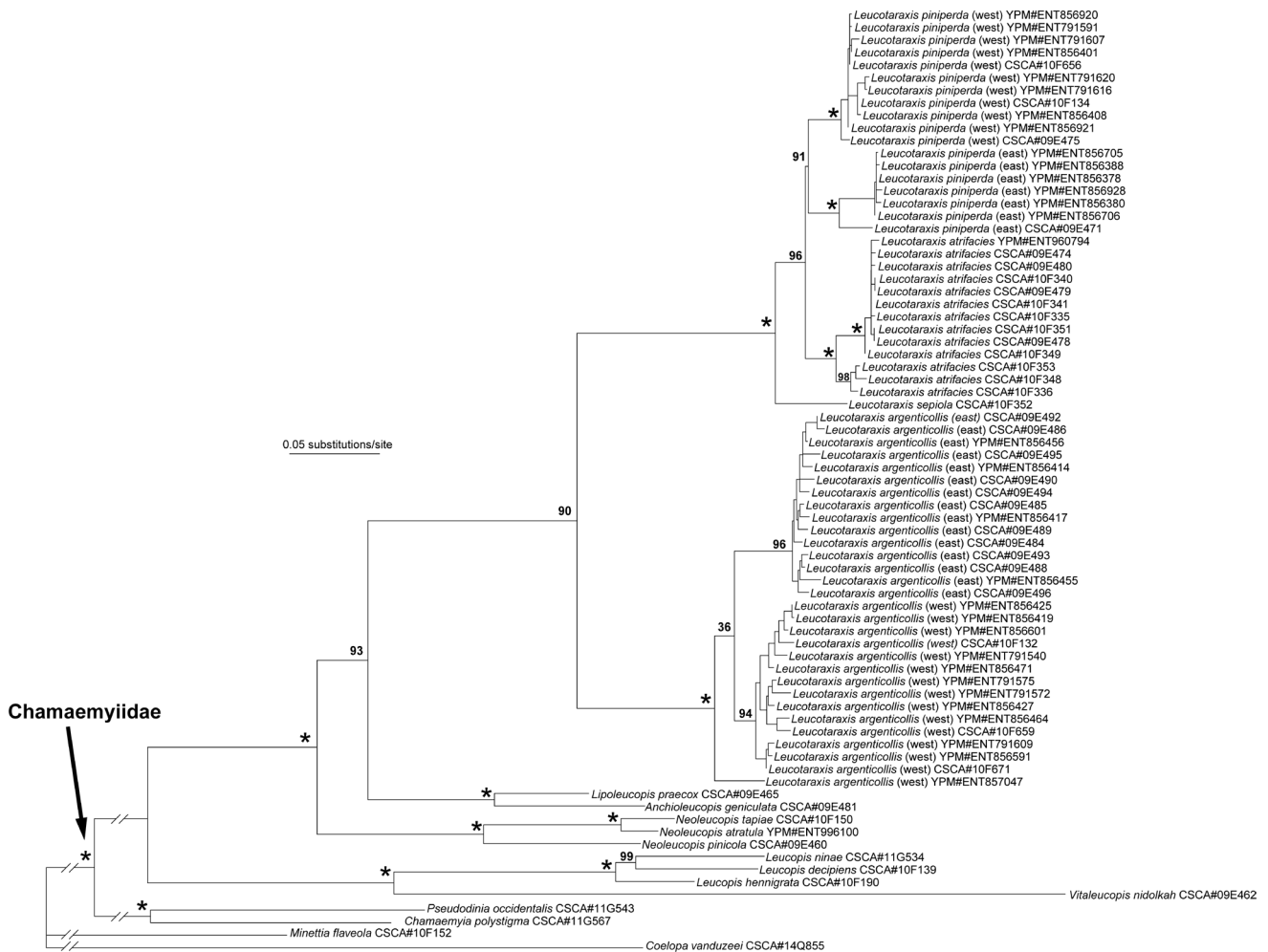


FIGURE 6. Phylogeny of *Leucotaraxis* showing its position in Chamaemyiidae and the relationships among species. Maximum likelihood tree inferred from the concatenated alignment of one mitochondrial and two nuclear genes. The numbers at the major nodes show the UFBoot support values (* for 100%).

Molecular phylogeny

COI sequences were generated for all specimens included in the phylogeny. TPI sequences were generated for all specimens but *Minettia flaveola* plus 11 of 13 *Leucotaraxis atrifacies*, and CAD sequences were generated for all specimens but 11 of 13 *L. atrifacies*. The lack of TPI and CAD data for some *L. atrifacies* specimens should not

impact its placement in the phylogeny because these genes are less variable than COI, and their inclusion for two representatives of the species acts as a ‘backbone’ for higher-level relationships (Talavera et al. 2021). The topology of the maximum likelihood tree (Fig. 6) shows strong support for the monophyly of *Leucotaraxis*. This new genus is not sister to *Leucopis*, to which *Leucotaraxis argenticollis*, *L. atrifacies*, and *L. piniperda* previously belonged. *Leucotaraxis atrifacies* is sister to *L. piniperda*, consistent with these species being morphologically similar. As previously reported in Havill et al. (2018), both *L. argenticollis* and *L. piniperda* have distinct western and eastern clades in North America. In the West, both species can be readily collected feeding on hemlock woolly adelgid, while in the East, they have not been observed feeding on hemlock woolly adelgid. It therefore appears that western and eastern North American populations of these species have different adelgid prey preferences. The new species *Leucotaraxis sepiola* is sister to the *L. atrifacies* + *L. piniperda* clade, while *L. argenticollis* is sister to those three species. It is worth noting that the phylogeny presented here shows a specimen of *L. argenticollis* collected from *Pineus coloradensis* on *Picea engelmannii* in Colorado, USA (molecular voucher, YPM; ENT857047), as sister to the rest of the species, which raises the possibility of additional intraspecific variation associated with geography and/or prey preference. It will also be interesting to see the possible variation with the as yet unsampled Palearctic populations of *L. argenticollis*.

Key to Chamaemyiidae feeding on Pinaceae-infesting Sternorrhyncha

Members of Chamaemyiini are not keyed past the second couplet, since all of those with known biology are predators on Sternorrhyncha in grasses, although occasionally species of some genera will go to Sternorrhyncha on Pinaceae for honeydew as an adult sugar source, e.g., *Chamaemyia fumicosta* Malloch was collected by the first author on several occasions sweeping *Cinara*-infested ponderosa pine. A list of the species included is provided after the key, annotated with their known biology, distribution, and other relevant information. The taxa in brackets [] have not been specifically reared from Pinaceae-attacking Sternorrhyncha, but are considered likely to be predators in this system; further information is provided in the post-key list, and habitus photographs are provided (Figs 7–14) for all of the relevant genera, with those for *Leucotaraxis* species in Figs 2–5. The taxa in parentheses () are not thought to be associated with Pinaceae, but are included in the key to account for incidental visitors occasionally taken in sweep samples. The key presented below is based upon study of most included species, with some aspects based on modifications of published keys of McAlpine (1971), Papp (2010), and Tanasijtshuk (1986), and notes and draft keys of McAlpine and the first author.

1. Head largely yellow, except for grey pruinose ocellar triangle; eye much longer than high; gena higher than eye height. Prescutellum and presutural supra-alar seta absent. Male with articulated bilobate surstylus and flexible phallus with spinelike subapical armature. CREMIFANIINAE. Holarctic *Cre semifania* Czerny...52
- Head color light grey to black, but never yellow; eye dimensions variable, but eye height greater than genal height. Prescutellum present or absent, but presutural supra-alar seta always present. Male usually with fixed non-bilobate surstylus (articulated in *Vitaleucopis*), phallus rigid and without spinelike armature. CHAMAEMYIINAE ...2
- 2 (1). Body elongate, tapering posteriorly. Head with lunule low, bare; 1 or 2 strong fronto-orbital setae present; postocellar setae present; ocellar setae strong, proclinate (absent or minute in some species of *Plunomia* Malloch and *Pseudodinia* Melander). Scutum usually with a presutural dorsocentral seta (Chamaemyiini)
- Body compact, stout posteriorly. Head with lunule high and often with setulae; fronto-orbital setae present or absent, sometimes with 1 or 2 enlarged setulae on upper part of fronto-orbital area; postocellar setae absent; ocellar setae absent or small. Scutum lacking a presutural dorsocentral seta. Leucopini ...3
- 3 (2). Prescutellum present. 9
- Prescutellum absent 4
- 4 (3). Costal wing vein reaching vein M_1 6
- Costal wing vein ending at vein R_{4+5} . Palearctic *Lipoleucopis* Meijere ...5
- 5 (4). Scutum densely setulose; with three pairs of dorsocentral setae; prescutellar acrostichal seta present. Surstylus beak-shaped, arcuate. *Lipoleucopis praecox* Meijere
- Scutum with very sparse setulae; with one pair of dorsocentral setae; prescutellar acrostichal seta absent. Surstylus hammer-shaped, with broad basiphallus tapering to sharpened tip [*Lipoleucopis pulchra* Raspi]
- 6 (4). Small, 2 mm or less in length. Ocellar seta present, reclinate. Upper part of fronto-orbital area with 1 or 2 enlarged, laterocline setulae. Palearctic (in part) *Neoleucopis* Malloch, in part...8
- Larger than 2 mm. Lacking ocellar setae. Lacking enlarged setulae on fronto-orbital area. Holarctic *Anchioleucopis* Tanasijtshuk ...7

7 (6).	Frons pale grey with dark elongate triangle of ocellar plate reaching lunule. Legs black with femora yellow at apex. In male genitalia, apex of surstylar lobe pointed <i>Anchioleucopis geniculata</i> (Zetterstedt)	
-	Frons pale grey with greyish ocellar plate visible only in dorsal view. Legs black except tibiae with yellow bases and apices, and basotarsomere yellow. In male genitalia, apex of surstylar lobe rounded. <i>Anchioleucopis macalpinei</i> Tanasijtshuk	
8 (6).	Ocellar seta small, 1/3 length of inner vertical seta. Fore tarsus yellow. In male, phallus strongly recurved in lateral view, with large ventral lobe with toothed distal edge. In female, sternite 7 divided medially by membranous strip	[<i>Neoleucopis orbiseta</i> (McAlpine)]
-	Ocellar seta large, subequal in length to inner vertical seta. Fore tarsus brown. In male, phallus simple, comma-shaped in lateral view. In female, sternite 7 entire	<i>Neoleucopis freyi</i> (McAlpine)
9 (3).	Body and head shiny black. Frons with 1 strong fronto-orbital seta present. Crossvein bm-cu stub-like, incomplete, not fully separating cells dm and bm. Neotropical (predators of Ortheziidae)	(<i>Melaleucopis</i> Sabrosky)
-	Body and head predominantly pruinose, at most with abdomen shiny black. Fronto-orbital setae absent, or with more than 1. Crossvein bm-cu complete, separating cells dm and bm	10
10 (9).	Anepisternum with 1 to several setae, setulae, or both, along posterior edge. Afrotropical, Neotropical (predators of Coccoidea)	(<i>Leucopis</i> (<i>Leucopella</i>) Malloch)
-	Anepisternum lacking setae or setulae	11
11 (10).	Frons lacking strong fronto-orbital setae, although slightly enlarged setulae may be present in upper part. Ocellar setae absent, or present and reclinate.	13
-	Frons with 2 or more strong fronto-orbital setae. Ocellar setae small, proclinate and diverging	12
12 (11).	Frons with 2 fronto-orbital setae present, with anterior seta equidistant between posterior seta and lunule. Prescutellar acrostichal seta present. Abdominal tergites shiny black. Neotropical (predators of <i>Ceroplastes</i> Gray scales)	(<i>Chamaeleucopis</i> Gaimari)
-	Frons with series of 5 or 6 evenly spaced, strong fronto-orbital setae. Prescutellar acrostichal seta absent. Abdominal tergites silvery-grey pruinose with darkened pruinose spots on tergite 3. Nearctic	[<i>Chamaethrix necopina</i> Gaimari]
13 (11).	Prescutellar acrostichal seta absent	26
-	Prescutellar acrostichal seta present	14
14 (13).	Body and head silvery-grey pruinose; scutum with dorsocentral vittae; abdomen with paired dark spots on tergite 3. Ocellar seta absent. Holarctic (predators of eggs within coccoid ovisacs)	(<i>Leucopomyia</i> Malloch)
-	Body and head dull, dark grey to brown pruinose; scutum lacking dorsocentral vittae; abdomen lacking paired spots on tergite 3. Ocellar seta present. Holarctic, Neotropical	<i>Neoleucopis</i> Malloch, in part ... 15
15 (14).	Ocellar seta weak, shorter than distance from anterior ocellus to vertex, frequently pale and very fine	18
-	Ocellar seta strong, as long or longer than distance from anterior ocellus to vertex, black	16
16 (15).	Antennal pedicel light brown, distinctly paler than first flagellomere. In lateral view of male genitalia, epandrium large, with 10 or more setae on dorsal surface; phallus sickle-shaped	<i>Neoleucopis hadzibeiliae</i> (Tanasijtshuk)
-	Antennal pedicel concolorous with first flagellomere, silvery grey at some angles. In lateral view of male genitalia, epandrium large or narrow, with fewer than 8 setae on dorsal surface; phallus not sickle-shaped	17
17 (16).	Setulae on the frontal plate and along the eye margin weak and pale. Ocellar triangle sparsely and weakly setulose. In lateral view of male genitalia, epandrium large with convex dorsum, with surstylar lobe narrow; phallus widest at middle. In female, sternite 7 entire	<i>Neoleucopis pinicola</i> (Malloch)
-	Setulae on the frontal plate and along the eye margin coarse and black. Ocellar triangle densely and strongly setulose. In lateral view of male genitalia, epandrium narrow, smoothly tapering through surstylar lobes; phallus widest basally. In female, sternite 7 divided medially	<i>Neoleucopis obscura</i> (Haliday)
18 (15).	Lunule and face grey to greyish brown. Ocellar hairs yellowish or blackish	20
-	Lunule and face jet black. Ocellar hairs pale to silky yellow	19
19 (18).	Ocellar hairs distinctly longer and stronger than adjacent hairs. Posterior ocelli farther apart than distance to anterior ocellus. Prescutellar acrostichal seta easily distinguished from surrounding setulae	<i>Neoleucopis milita</i> (McAlpine)
-	Ocellar hairs scarcely distinguishable from adjacent hairs. Distance from anterior ocellus to a posterior ocellus greater than distance between posterior ocelli. Prescutellar acrostichal seta usually indistinguishable from surrounding setulae	<i>Neoleucopis nigralhuna</i> (McAlpine)
20 (18).	Setulae on frons and lunule yellowish	24
-	Setulae on frons and lunule black	21
21 (20).	In male, sternites 4 and 5 each with paired dense patches of thick, medially-oriented setulae; epandrium in lateral view large, extending through thick surstylar lobes; phallus with extremely enlarged basal lobe, constricted relative to long thin distiphallus. In female, medial third of tergite 6 lacking pruinosity and only lightly sclerotized; tergite 7 with distinct jet-black longitudinal striations; tergite 8 deeply cleft anteriorly; sternite 7 medially separated into two halves	<i>Neoleucopis kartliana</i> (Tanasijtshuk)
-	In male, sternites 4 and 5 with normal setulae, neither dense, thick, in patches, nor medially oriented; epandrium with surstylar lobe distinctly tapering; phallus variable, but basal lobe neither massive nor constricted relative to distiphallus; distiphallus not long and thin. In female, tergite 6 pruinose and sclerotized throughout; tergite 7 grey to brown pruinose, lacking longitudinal striations; tergite 8 not cleft anteriorly; sternite 7 entire	22
22 (21).	Ocellar setae subequal to or slightly longer than adjacent setulae. Fronto-orbital area with 1 or more slightly enlarged setulae in upper part. Distiphallus abruptly tapered. Spermathecae small and spherical	<i>Neoleucopis atratula</i> (Ratzeburg)
-	Ocellar setae at least 2 X longer than adjacent setulae. Fronto-orbital area lacking enlarged setulae. Distiphallus variable, gradually or abruptly tapered. Spermathecae variable	23

- 23 (22). Basal two segments of fore tarsus and basal three segments of mid and hind tarsi yellow. Epandrium conical in lateral view. Basiphallus moderately swollen, with distiphallus gradually tapered. Spermathecae small and spherical *Neoleucopis ancilla* (McAlpine), in part
- Basal segment of fore tarsus and basal two segments of mid and hind tarsi yellow. Epandrium parallel-sided. Basiphallus strongly swollen, with distiphallus abruptly tapered. Spermathecae large and ovoid *Neoleucopis tapiae* (Blanchard)
- 24 (20). Ocellar setae black, larger than adjacent setulae. Epandrium in lateral view half as high as long *Neoleucopis ancilla* (McAlpine), in part
- Ocellar setae weak and pale, scarcely distinguishable from adjacent setulae. Epandrium in lateral view up to 1/3 as high as long 25
- 25 (24). Setulae of frons along eye margin long and erect (length subequal to distance between posterior ocelli). Central part of scutum brownish. Epandrium in lateral view with dorsal edge relatively straight *Neoleucopis manii* (Tanasijshtshuk)
- Setulae of frons along eye margin short and depressed forward (length less than half distance between posterior ocelli). Scutum uniformly silvery grey. Epandrium in lateral view with dorsal edge rounded *Neoleucopis aciliosa* (McAlpine)
- 26 (13). Ocellar setae absent in both sexes, and ocellar triangle neither densely pilose nor fuzzy in males, but if moderately fuzzy (*i.e.*, not completely and uniformly covering the area), then posterior ocelli equidistant in comparison with distance from one posterior ocellus to anterior ocellus 31
- Ocellar setae small and reclinate, or ocellar triangle (in males) densely and uniformly pilose and fuzzy with posterior ocelli widely separated 27
- 27 (26). Fronto-orbital area lacking enlarged setulae. Ocellar plate greatly expanded, with posterior ocelli widely spread, much farther apart than distance between anterior and one posterior ocellus. Ocellar seta present in females, but usually absent in males that instead have ocellar plate densely pilose and fuzzy. Nearctic, Neotropical. (*Leucopina* Malloch)
- Fronto-orbital area with 1 or 2 (rarely 0 or 3) enlarged setulae dorsally. Ocellar plate not expanded, pilose nor densely fuzzy, but posterior ocelli sometimes slightly farther apart than distance to anterior ocellus. Ocellar seta present or absent 28
- 28 (27). Head high, height to length ratio nearly 2:1. Eye height to length ratio 2:1. Lunule subequal in height to length to frons, with conspicuous proclinate black setulae. Ocellar seta absent. Anterior ocellus surrounded by ring of short black setulae. Neotropical (predators of eggs within coccoid ovisac) (*Echinoleucopis* Gaimari & Tanasijshtshuk)
- Neither head, eye nor lunule so high. Lunule with small setulae inconspicuous. Ocellar seta present. Anterior ocellus lacking ring of setulae 29
- 29 (28). Lunule with numerous erect black setulae. Scutum and scutellum dark brown pruinose. Legs entirely jet black [*Neoleucopis setigera* (McAlpine)]
- Lunule with small setulae inconspicuous. Scutum grey pruinose, with goldish dorsocentral vittae. Legs with tips of femora, bases of tibiae and at least basal two tarsomeres yellow. Nearctic, Neotropical (feed on Coccoidea); Palearctic *Leucopis* (*Xenoleucopis*) Malloch ...30
- 30 (29). Dorsocentral vitta with diffuse edges, blending into goldish shade over posterior part of scutum and scutellum. Eye 4 X higher than gena. Distal section of vein CuA₁ 2 X longer than length of crossvein dm-cu [*Leucopis* (*Xenoleucopis*) *setifrons* Tanasijshtshuk]
- Dorsocentral vitta sharply outlined, continuing through grey scutum. Scutellum grey. Eye at least 5 X higher than gena. Distal section of vein CuA₁ up to 1.5 X longer than length of crossvein dm-cu *Leucopis* (*Xenoleucopis*) *raoi* Tanasijshtshuk
- 31 (26). Abdomen silvery-grey to grey pruinose, often with spots on tergite 3. Frons not protruding over lunule, lacking stiff laterocline setulae, and lacking enlarged laterally directed setulae in anterolateral corners. Maxillary palpus normal, much smaller than antennal first flagellomere 37
- Abdomen shiny black with only sparse pruinosity. Frons with 1 or 2 rows of stiff black laterocline setulae along eye margin. In male, frons protruding roof-like over lunule, and with enlarged laterally directed setulae in anterolateral corners (sometimes clumped into horn-like pencils). In female, maxillary palpus greatly enlarged (subequal to antennal first flagellomere) and flattened. Nearctic. *Vitaleucopis* Gaimari ...32
- 32 (31). Male (unknown for undescribed species) 35
- Female (unknown for *Vitaleucopis scopula* Gaimari) 33
- 33 (32). Upper face (between antennal sockets) silvery pruinose; antenna light brown, except basal part orange; palpus orange, with distal part light brown; scutum and scutellum bronzy pruinose, distinctly differentiated from silvery-grey pruinose pleuron [undescribed species]
- Upper face (between antennal sockets) shiny black, lacking pruinosity; antenna and palpus black; scutum, scutellum and pleuron concolorous silvery-grey pruinose 34
- 34 (33). At least basotarsomere of each leg yellow [*Vitaleucopis astonea* (McAlpine)]
- Tarsi entirely dark brown (hind basotarsomere sometimes dark orange basally) *Vitaleucopis nidolkah* Gaimari
- 35 (32). Anterolateral part of frons with cluster of 2–4 laterocline setae, whisker-like (not clustered to appear as 1 very thick seta), with length less than length of inner vertical seta *Vitaleucopis nidolkah* Gaimari
- Anterolateral corner of frons with distinct tight cluster of 4 or 5 laterocline setae (appearing like 1 very thick seta), with length 1.5 X that of inner vertical seta 36
- 36 (35). Frons with width and length subequal; distance from vertex to anterior tip of frons 1.7 X width of frons at level of anterior ocellus. [*Vitaleucopis scopula* Gaimari]
- Frons 1.4 X wider than long; distance from vertex to anterior tip of frons 1.3 X width of frons at level of anterior ocellus [*Vitaleucopis astonea* (McAlpine)]
- 37 (31). Scutum with dorsocentral vittae (rarely absent) and pair of anterior median vittae. Frons gently curved and sloping through lunule. Plane of face and parafacial at obtuse angle with frons. Cosmopolitan. *Leucopis* Meigen, in part ...44

-	Scutum unicolorous grey, lacking vittae. Frons flat, sometimes slightly concave medially, ending at 90° angle with upper edge of lunule. Plane of face and parafacial are at an acute angle with the frons. Holarctic	<i>Leucotaraxis</i> gen. nov. ...	38
38 (37)	Lunule and face dark brown to black		40
-	Lunule and face silvery grey		39
39 (38)	Postpronotum with 1 to several long setulae (longer than setulae on scutum) medially from postpronotal seta. In male, phallus from lateral view with broad wedge-shaped anterobasal process at 90° angle from thin elongate pointed process. In female, tergite 7 present and strap-like, and sternite 7 present and arcuate	<i>Leucotaraxis argenticollis</i> (Zetterstedt)	
-	Postpronotum lacking setulae, or with only tiny setulae (much smaller than setulae on scutum) medially from postpronotal seta. In male, phallus from lateral view elongate and thin, curving gently to pointed tip. In female, tergite and sternite 7 absent	<i>Leucotaraxis piniperda</i> (Malloch)	
40 (38)	Male.		42
-	Female (unknown for <i>Leucotaraxis sepiola</i> sp. nov.)		41
41 (40)	Tergite 7 absent	<i>Leucotaraxis piniperda</i> (Malloch)	
-	Tergite 7 present and strap-like	<i>Leucotaraxis atrifacies</i> (Aldrich)	
42 (40)	Epandrial complex large and polished black, with epandrium extending into central process bearing cerci at upward angle. Surstylar lobe long and thin	[<i>Leucotaraxis sepiola</i> sp. nov.]	
-	Epandrial complex simple, small, yellowish- to silvery-grey pruinose, with no central epandrial process. Surstylar lobe short, stout		43
43 (42)	Phallus in lateral view very long and thin, more than 10 X longer than height at middle, gently curved throughout to pointed tip	<i>Leucotaraxis piniperda</i> (Malloch)	
-	Phallus in lateral view long and thick, less than 8 X longer than height at middle, straight-sided until abrupt curve to pointed tip	<i>Leucotaraxis atrifacies</i> (Aldrich)	
44 (37)	Frons with surface covered with long, thin, reclinate silvery setulae. In male, phallus with two prominent, curved, tusk-like rods laterally. Palearctic	(<i>Leucopsis (Metaleucopsis) plumifrons</i> Tanasijtshuk)	
-	Frons lacking thin, reclinate silvery setulae. In male, phallus simple, lacking lateral rods. Cosmopolitan.	<i>Leucopsis (Leucopsis) Meigen</i>	45
45 (44)	Scutum reddish brown to brown, lacking dorsocentral vittae or very faintly visible. Gena less than 1/5 eye height. Tibiae and tarsi yellow. In male, abdominal tergite 3 brownish grey without spots; phallus awl-shaped, smoothly curved	<i>Leucopsis (Leucopsis) adelgivora</i> Tanasijtshuk	
-	Scutum silvery grey to greyish brown, with distinct dorsocentral vittae, which may be faint. Gena more than 1/5 eye height. Tibiae and tarsi predominantly dark brown. In male, tergite 3 either brownish or silvery grey with paired spots; phallus variable, not shaped like a smoothly curved awl		46
46 (45)	Body greyish brown, with dark goldish-brown dorsocentral vittae that diffuse together in posterior part of scutum. Gena high, about 1/2 eye height. Scutellum goldish brown. Abdomen uniformly brown	<i>Leucopsis (Leucopsis) hennigrata</i> McAlpine	
-	Body light grey to silvery grey. Gena 1/4–1/3 eye height. Dorsocentral vittae variable, but never diffusing together in posterior part of scutum. Scutellum silvery grey. Abdomen with tergites 3–5 silvery grey, with paired dark spots on tergite 3 (except for peculiar specimens lacking spots)		47
47 (46)	Ocellar plate with patch of short stiff setae lateral to anterior ocellus. Abdominal tergites covered with long strong setae (mostly half length of tergite). In male, phallus narrow in lateral view	[<i>Leucopsis (Leucopsis) spinifrons</i> Tanasijtshuk]	
-	Ocellar plate lacking short stiff setae lateral of anterior ocellus, instead bare to slightly fuzzy. Abdominal tergites with normal setae (much shorter than half length of tergite). Phallus variable (only males key from here)		48
48 (47)	Surstylar lobe broad, extended from narrow epandrium, parallel-sided all the way to large blunt tip from lateral view	<i>Leucopsis (Leucopsis) aphidiperda</i> Rondani	
-	Surstylar lobe extended from convex epandrium, tapering to narrow or sharpened tip.		49
49 (48)	Surstylar lobe beak-like, with a wide base and tapering to tip. Phallus either with very strong, angular, subbasal ventral expansion, or with ventrobasal part not expanded		51
-	Surstylar lobe narrow from base to tip. Phallus with subbasal ventral expansion small, smoothly rounded		50
50 (49)	Dorsocentral vittae varying from olive brown to pale goldish brown, with dark grey median vittae. Distiphallus from lateral view slightly curved to blunt (sometimes slightly dilated) tip	<i>Leucopsis (Leucopsis) ninae</i> Tanasijtshuk	
-	Dorsocentral vittae grey, concolorous with median vittae. Distiphallus from lateral view straight and narrow to sharpened tip	[<i>Leucopsis (Leucopsis) griseostriata</i> Tanasijtshuk]	
51 (49)	Phallus with strongly produced, angular subbasal ventral expansion.	<i>Leucopsis (Leucopsis) cinarophaga</i> Tanasijtshuk	
-	Phallus narrow throughout in lateral view	<i>Leucopsis (Leucopsis) glyphinivora</i> Tanasijtshuk	
52 (1)	Scutum with 4 or more pairs of postsutural dorsocentral setae, shortening anteriorly. Wing hyaline. Anepisternum with several fine hair-like setulae in anterodorsal corner. Anepimeron bare. Calypter entirely white	[<i>Cre semifania nearctica</i> McAlpine]	
-	Scutum with 1 or 2 pairs of dorsocentral setae. Wing with dark markings at least in subcostal cell and/or costal cell, or wing more extensively patterned. Anepisternum bare in anterodorsal corner. Anepimeron with or without a setula medioventrally. Calypter color variable		53
53 (52)	Antennal arista lanceolate, with 3rd segment flattened, broadened and pointed apically. Costal cell with a central diffuse dark spot; subcostal cell with large black spot apically and a small subbasal spot confluent with dark spot in costal cell. Scutum with 1 pair of dorsocentral setae. Anepimeron lacking medioventral setula. Calypter and fringe entirely whitish yellow.	[<i>Cre semifania lanceolata</i> Papp]	
-	Antennal arista normal, or only basal part thickened. Costal cell hyaline; subcostal cell entirely darkened. Scutum with 2 pairs of dorsocentral setae.		54

- 54 (53). Ocellar triangle small, with grey pruinosity only surrounding ocelli. Lacking interfrontal setae. Wing membrane not patterned outside of subcostal cell. Anepimeron with 1 or more setulae medioventrally. Calypter with margin and fringe dusky *Cre semifania nigrocellulata* Czerny
- Ocellar triangle elongated, with grey pruinosity extending anteriorly nearly to lunule. Anterior tip of ocellar triangle with a pair of strong, proclinate interfrontal setae. Wing membrane darkened at least around distal part of vein R_{2+3} and surrounding crossvein dm-cu. Anepimeron bare. Calypter with margin and fringe pale [*Cre semifania bulgarica* Papp]

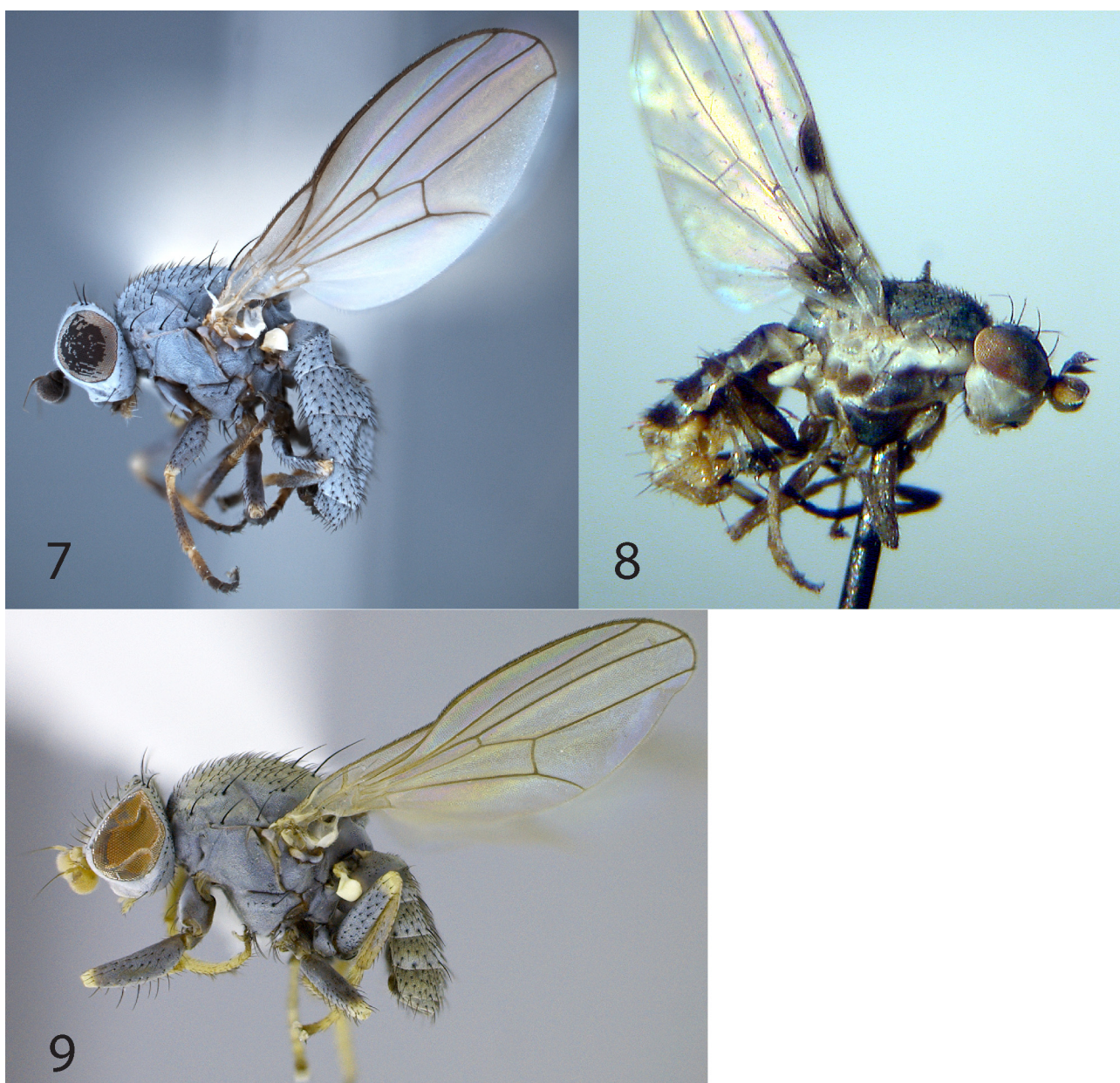
Annotated list of species of Chamaemyiidae feeding on Pinaceae-infesting Sternorrhyncha

Anchioleucopis Tanasijtshuk, 1997: 115 (Fig. 7)

Anchioleucopis geniculata (Zetterstedt, 1855: 4810; *Leucopis*)

Type locality: Sweden (HT ♀, MZLU).

This species occurs in northern Europe, and although it has not been reared, it is very likely a predator of adelgids, and has been collected from canopies of Scots pine, *Pinus sylvestris* (Thunes *et al.* 2004) and swept from the same species infested with *Pineus pini* (McLean 1982).



FIGURES 7–9. Chamaemyiidae genera, lateral habitus. 7. *Anchioleucopis geniculata* (Zetterstedt), female. 8. *Cre semifania lanceolata* Papp, holotype male. 9. *Chamaethrix necopina* Gaimari, holotype male.

Anchioleucopis macalpinei Tanasijtshuk, 2001: 904

Type locality: USA: Ohio (HT ♂, CNC).

This species occurs in eastern North America, and has been reared only from *Pineus strobi*, which most commonly infests eastern white pine, *Pinus strobus*.

Chamaethrix Gaimari, 2020: 62 (Fig. 9)

[*Chamaethrix necopina* Gaimari, 2020: 62]

Type locality: USA: Arizona (HT ♂, CSCA).

This species occurs in the southwestern United States in areas above 2100 m elevation. All known specimens were swept from infestations of *Cinara ponderosae* in young stands of *Pinus ponderosa*, but despite rearing >150 chamaemyiid larvae from this host by the first author, none were this species. It remains a possibility that this species is a predator in that system.

Cremifania Czerny, 1904: 169 (Fig. 8)

[*Cremifania bulgarica* Papp, 2010: 195]

Type locality: Bulgaria (HT ♂, HNHM).

This species is known only from Bulgaria, collected at an elevation of 2250 m in a Pinaceae-dominated habitat. Although never reared, it is likely a predator of adelgids.

[*Cremifania lanceolata* Papp, 1994: 105]

Type locality: Hungary (HT ♂, HNHM).

This species is known only from Hungary, originally collected in an oak forest with Pinaceae present within about 1 km. Although never reared, it is likely a predator of adelgids.

[*Cremifania nearctica* McAlpine, 1963: 252]

Type locality: USA: New Mexico (HT ♂, USNM).

This species is known only from the southwestern United States, and was collected at higher elevations in an area dominated by Pinaceae. Although never reared, it is likely a predator of adelgids.

Cremifania nigrocellulata Czerny, 1904: 170

Type locality: Austria (HT ♀, NHMW).

This species is native to central Europe and was introduced and established in both eastern and western North America (Harris & Dawson 1979, Humble 1994). Much attention was paid to this species in the 1950s due to extensive biological control efforts against balsam woolly adelgid, *Adelges piceae*, attacking several species of fir, *Abies* spp., in North America.

Leucopis (Leucopis) Meigen, 1830: 133 (Fig. 10)

Leucopis (Leucopis) adelgivora Tanasijtshuk, 1986: 204

Type locality: Russia: Sakhalin (HT ♂, ZISP).

Known only from the Russian Far East (Sakhalin), this species is reported as a predator of *Adelges japonicus* (Monzen) on Ayan fir, *Abies ajanensis* (Tanasijtshuk 1986), but *A. japonicus* feeds on *Larix* and *Picea* (Sano *et al.* 2008), so the specific prey is unclear.

Leucopis (Leucopis) aphidiperda Rondani, 1848: 435

Type locality: Italy: Parma (LT ♂, MZUB).

This is a widespread species, found in southern and eastern Europe, the eastern Palearctic and the Near East. It is known mainly as a predator of aphids on angiosperms, but has been reared from a species of *Cinara* on *Abies* (Tanasijtshuk 1986).

Leucopis (Leucopis) cinarophaga Tanasijtshuk, 1962: 225

Type locality: Russia: Leningrad region (HT ♂, ZISP).

This species is found mainly in northern Europe, although it has also been found in southern Europe. As the name implies, it is a predator of *Cinara* species. Specifically, it has been reared from *Cinara brauna* Börner on *Pinus laricio*, *Cinara pini* (L.) and *Cinara pinea* (Mordvilko) on *Pinus sylvestris*, and on *Cinara costata* (Zetterstedt) and *Cinara pruinosa* (Hartig) on *Picea excelsa* (Tanasijtshuk 1986).

Leucopis (Leucopis) glyphinivora Tanasijtshuk, 1958: 92

Type locality: Russia: Leningrad region (HT ♂, ZISP).

This is a very widespread species throughout Europe, the eastern Palearctic, the Near East, North America and in South Africa and the Oriental Region. Some of this distribution may be due to introductions, and this species has been considered as a possible biocontrol agent against pest aphids (Barriault *et al.* 2018). This is a polyphagous species, being known to attack more than 70 species of aphids on more than 100 species of plants (Tanasijtshuk 1986). Among these records is a species of *Cinara* infesting *Pinus sylvestris*.

[*Leucopis (Leucopis) griseostriata* Tanasijtshuk, 2006: 282]

Type locality: USA: New Hampshire (HT ♂, USNM).

This species is known only from the eastern United States. Although it was never reared, it is thought to be a predator of adelgids because it had identical collection labels as a series of specimens belonging to *Neoleucopis pinicola* and *Leucotaraxis argenticollis*.

Leucopis (Leucopis) hennigrata McAlpine, 1978: 350

Type locality: Germany (HT ♂, CNC).

This species is known from central and southern Europe, and was introduced into eastern and western Canada as a biological control agent against balsam woolly adelgid, *Adelges piceae* on several species of fir, *Abies* spp. This species has a rather wide adelgid host range, including: *Adelges piceae* and *Adelges nordmannianae* (Eckstein) infesting several species of fir, as well as *Adelges (Sacchiphantes) viridis* (Ratzeburg) infesting larch, *Larix* spp.

Leucopis (Leucopis) ninae Tanasijtshuk, 1966: 234

Type locality: Kazakhstan (HT ♂, ZISP).

This is a very widespread species, occurring in central and southern Europe, the eastern Palearctic, Near East, and north Africa, and has been introduced into the Nearctic and Afrotropical Regions. It is polyphagous, known to feed on more than 50 species of Sternorrhyncha, particularly aphids, but also has been reared from *Pinus pini* infesting *Pinus sylvestris*, as well as some Coccoidea (Tanasijtshuk 1986).

[*Leucopis (Leucopis) spinifrons* Tanasijtshuk, 2006: 284]

Type locality: Canada: Manitoba (HT ♂, CNC).

This species is known from south-central Canada. It is thought to be a predator of adelgids because it was collected by sweeping white spruce, *Picea glauca*.

***Leucopis (Xenoleucopis)* Malloch, 1933: 384 (Fig. 11)**

Leucopis (Xenoleucopis) raoi Tanasijtshuk, 1986: 182

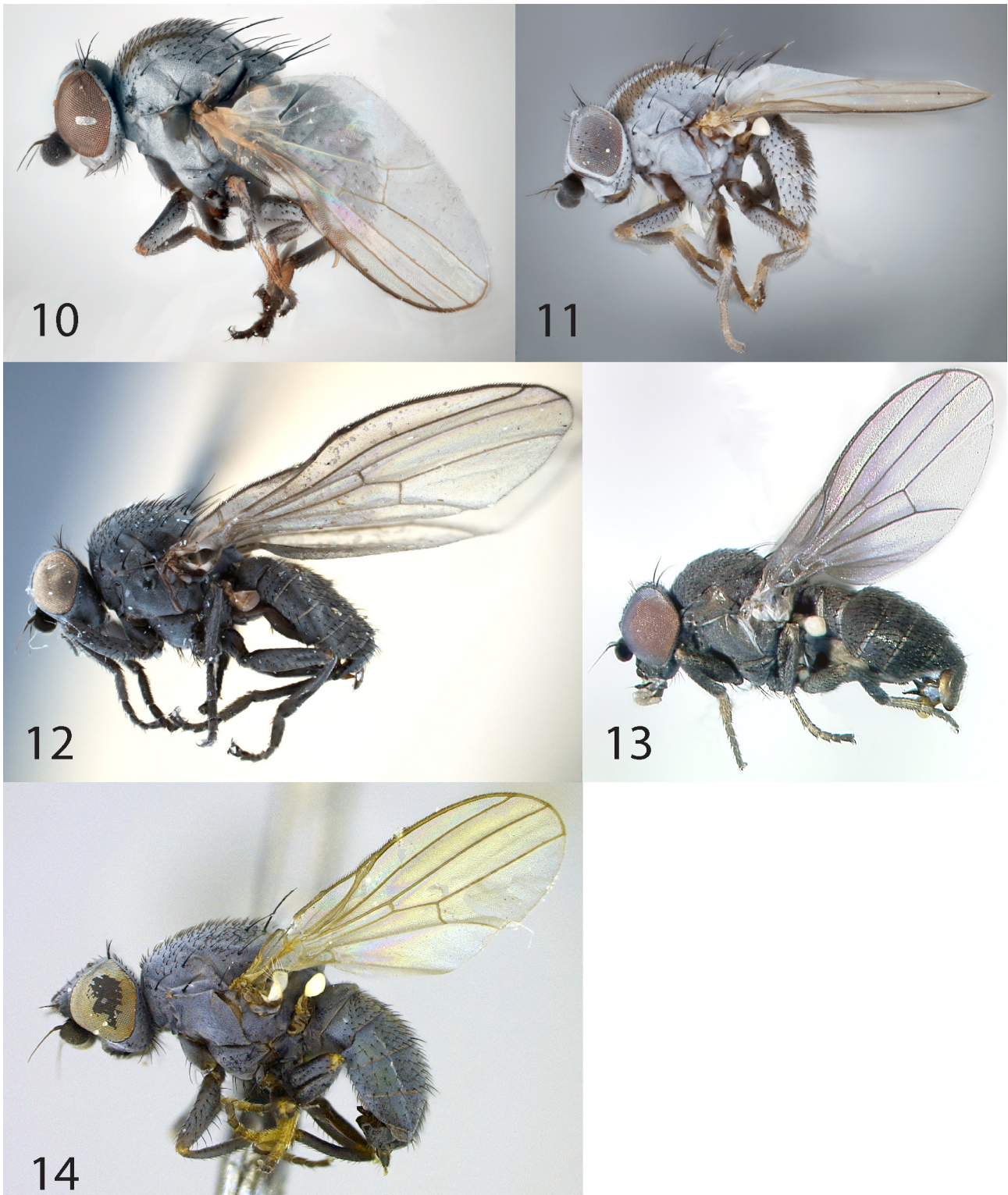
Type locality: India: Himachal Pradesh (HT ♂, ICPR)

This species is known only from India, and has been reported in the Himalayas as an important predator of *Adelges knucheli* on Morinda spruce, *Picea smithiana*, and on silver fir, *Abies pindrow* (Krishnaswamy & Chacko 1988).

[*Leucopis (Xenoleucopis) setifrons* Tanasijtshuk, 1986: 181]

Type locality: Kyrgyzstan (HT ♂, ZISP).

Known only from Kyrgyzstan, this species is assumed to be a predator of adelgids due to having been swept from Tien-Shan fir, *Abies sibirica* var. *semenovii*.



FIGURES 10–14. Chamaemyiidae, genera and subgenera, lateral habitus. 10. *Leucopis (Leucopis)* sp., male. 11. *Leucopis (Xenoleucopis) cilifemur* Malloch, male. 12. *Lipoleucopis praecox* Meijere, male. 13. *Neoleucopis kartliana* (Tanasijtshuk), male. 14. *Vitaleucopis astonea* (McAlpine), holotype male.

***Leucotaraxis* gen. nov.** (Figs 1–5)

Leucotaraxis argenticollis (Zetterstedt, 1848: 2814; *Leucopis*), **comb. nov.**

Type locality: Sweden (LT ♂, MZLU).

This species is widespread in North America, and occurs in northern Europe, the far eastern Palearctic, and India. They are predators of species of *Adelges* and *Pineus* infesting *Abies*, *Picea*, *Pinus*, and *Tsuga* (details provided above). They have also been swept from *Cinara ponderosae* infesting young stands of *Pinus ponderosa*.

Leucotaraxis atrifacies (Aldrich, 1925: 152; *Leucopis*), **comb. nov.**

Type locality: USA: California (HT ♀, USNM).

This species is known only from western North America, attacking species of *Adelges* and *Pineus* infesting *Tsuga* and *Pinus* (details provided above). They have also been swept from *Cinara ponderosae* infesting young stands of *Pinus ponderosa*.

Leucotaraxis piniperda (Malloch, 1921: 351; *Leucopis*), **comb. nov.**

Type locality: USA: Illinois (HT ♀, INHS).

This species is widespread in both eastern and western North America, attacking species of *Adelges* and *Pineus* infesting *Abies*, *Picea*, *Pinus*, and *Tsuga* (details provided above).

[*Leucotaraxis sepiola* **sp. nov.**]

Type locality: USA: New Mexico (HT ♂, CSCA).

This species is known only from the southwestern United States. Although never reared, it has been swept from *Cinara ponderosae* infesting young stands of *Pinus ponderosa*, which may have also been infested with adelgids.

***Lipoleucopis* Meijere, 1928: 76 (Fig. 12)**

Lipoleucopis praecox Meijere, 1928: 76

Type locality: Netherlands (2ST ♂, 2ST ♀, 1ST sex?, ZMAN).

This species is native to northern Europe, and is a predator of *Pineus pini* on *Pinus sylvestris*.

[*Lipoleucopis pulchra* Raspi, 2008: 664]

Type locality: United Arab Emirates (HT ♂, DCDS).

This species is known only from the Arabian Peninsula and Morocco (Ebejer 2016), and has never been reared. The lack of native Pinaceae would suggest a different host than adelgids if *Lipoleucopis pulchra* is native to the UAE or Morocco, but the possibility remains that the species is more widespread, and feeds on adelgids infesting ornamental Pinaceae in its currently known range.

***Neoleucopis* Malloch, 1921: 357 (Fig. 13)**

Neoleucopis aciliosa (McAlpine, 1971: 1871; *Leucopis*)

Type locality: Japan (HT ♂, CNC).

This species is known only from Japan, and has been reared from species of *Pineus* infesting *Pinus pentaphylla* and *Pinus koraiensis*.

Neoleucopis ancilla (McAlpine, 1971: 1869; *Leucopis*)

Type locality: USA: Oregon (HT ♂, USNM).

This species is known from western North America, as predators of species of *Pineus*.

Neoleucopis atratula (Ratzeburg, 1844: 170; *Musca*)

Type locality: Germany (NT ♂, CNC).

This species is widespread in Europe, the Near East, and the eastern Palearctic, and has been introduced into Australia and New Zealand, Argentina, and in several parts of North America. This species was among the predators introduced and established for biological control of *Adelges piceae* attacking true firs, *Abies* spp., in North America (Humble 1994). Rearing indicates that *Adelges piceae* is a primary host for this species. In addition, it is known as a predator of species of *Pineus* (such as *Pineus strobi*) infesting species of *Pinus*, and of other species of *Adelges* infesting species of *Abies*. The species has been collected from canopies of Scots pine, *Pinus sylvestris* (Thunes *et al.* 2004).

Neoleucopis freyi (McAlpine, 1971: 1869; *Leucopis*)

Type locality: Switzerland (HT ♂, CNC).

This species is known only from northern Europe, as predators of *Adelges* (*Sacchiphantes*) *viridis* on Japanese larch, *Larix kaempferi*.

Neoleucopis hadzibeiliae (Tanasijtshuk, 1986: 173; *Leucopis*)

Type locality: Georgia (HT ♂, ZISP).

This species is known from the Caucasus region, as a predator in ovisacs of *Marchalina caucasica* Hadzibeili (Margarodidae) infesting Nordmann fir, *Abies nordmanniana*, and Oriental spruce, *Picea orientalis*.

Neoleucopis kartliana (Tanasijtshuk, 1986: 175; *Leucopis*)

Type locality: Georgia (HT ♂, ZISP).

This species is known from Georgia through Greece, and Italy. Gaimari *et al.* (2007) gave detailed life history information, having reared the species from the scale *Marchalina hellenica* (Gennadius) (Margarodidae) on *Pinus halepensis*. The species was subsequently introduced into Italy to combat this pest (Viggiani & Mustica 2008). The species was also reared from a puparium found on Oriental spruce, *Picea orientalis*.

Neoleucopis manii (Tanasijtshuk, 1968: 6; *Leucopis*)

Type locality: India: Assam (HT ♂, ICPR).

This species is known only from Assam, India, as a predator of species of *Pineus* infesting *Pinus insularis*.

Neoleucopis militia (McAlpine, 1971: 1855; *Leucopis*)

Type locality: Pakistan (HT ♂, CNC).

This species is known only from Pakistan, although it was released against *Adelges piceae* in western North America, where it is not known to have established. It is known as a predator of species of *Adelges* infesting *Abies pindrow*.

Neoleucopis nigriluna (McAlpine, 1971: 1857; *Leucopis*)

Type locality: India: Assam (HT ♂, CNC).

This species is native to India and Pakistan and has been introduced into Hawaii and eastern North America. The species has been reared from species of *Pineus* infesting *Pinus insularis* (McAlpine 1971) and from *Pineus simmondsi* Yaseen & Ghani (Greathead 1995). This species was released and established against *Adelges piceae* in North America, and against a *Pineus* species attacking *Pinus pinaster* in Hawaii.

Neoleucopis obscura (Haliday, 1833: 173; *Leucopis*)

Type locality: Ireland (LT ♂, NMID).

This species is widespread in Europe, and has been introduced into Hawaii, and the eastern and western parts of North America. For Hawaii, although a small percentage of the vouchers from these releases are this species, most turned out to be *N. tapiae*. This species was also among the predators introduced and established for biological control of *Adelges piceae* attacking balsam fir, *Abies balsamea*, in North America. It is known to attack various species of *Adelges* infesting species of *Abies*, and less frequently species of *Pineus* infesting *Pinus*.

Leucopis olivacea Meijere 1928: 75, **syn. nov.** Type locality: Netherlands (LT ♂, ZMAN). The following lectotype is designated here to stabilize the concept of the species, due to the importance of male characteristics to properly identify species in this genus: ♂ specimen, double mounted on minuten into left pleuron, with the

following labels: 1) “Diemen / 3.VIII.18 / deMeijere”, 2) “ZMA040”, 3) “Lectotypus ♂ / *Leucopis* / *olivacea* / de Meijere / des. Gaimari & Havill”. The paralectotype is female, with the same first label as the lectotype, and the following additional labels: 2) “L. *olivacea* / d.M. ”, 3) “ZMA041”, 4) “Paralectotypus ♀ / *Leucopis* / *olivacea* / de Meijere / des. Gaimari & Havill”, 5) “*Neoleucopis* / *obscura* / (Haliday) / det. SD Gaimari, 2011”.

[*Neoleucopis orbiseta* (McAlpine, 1971: 1862; *Leucopis*)]

Type locality: Finland (HT ♂, CNC).

This species is known from northern Europe, and its biology is not known, but likely feeds on adelgids, following the same pattern as all other members of the genus found on Pinaceae.

Neoleucopis pinicola (Malloch, 1921: 357; *Leucopis*)

Type locality: USA: Illinois (HT ♂, INHS).

This species is known from eastern North America and may be present in parts of Europe. It is known to prey on *Pineus strobi* infesting *Pinus strobus*, as well as *Adelges piceae* on balsam fir, *Abies balsamea* (McAlpine 1971, Sluss & Foote 1973). The immature stages and biology were thoroughly described by Sluss & Foote (1973), although the descriptions do not compare the species with congeners.

[*Neoleucopis setigera* (McAlpine, 1971: 1872; *Leucopis*)]

Type locality: Argentina: Tierra del Fuego (HT ♂, CNC).

This species is only known from the type locality in Argentina, and nothing is known of its biology.

Neoleucopis tapiae (Blanchard, 1964: 137; *Leucopis*)

Type locality: Argentina: Nahuel Huapi (22 ST ♂/♀, MACN).

Although described from Argentina, this was likely due to an early introduction with the planting of species of *Pinus* for lumber. This species is widespread in Europe and has been purposely introduced as a predator of species of *Pineus* infesting *Pinus* species in Hawaii, western North America, Malawi, South Africa and New Zealand (Greathead 1995). In Hawaii, this species was introduced under the name *Neoleucopis obscura* (along with the real *N. obscura*), only subsequently having been found to be this species (Greathead 1995). Specific rearing records include *Pineus pini* infesting *Pinus radiata*, *Pineus strobi* infesting *Pinus strobus* and *Pinus sylvestris*, *Pineus cembrae* (Cholodkovsky) infesting *Pinus cembra*, *Pineus laevis* (Maskell) infesting *Pinus sylvestris* and *Pinus radiata*, *Pineus orientalis* (Dreyfus) infesting a species of *Pinus*, *Pineus boernerii* infesting *Pinus patula*, *Pineus havrylenkoi* Blanchard infesting a species of *Pinus*.

Vitaleucopis Gaimari, 2020: 67 (Fig. 14)

[*Vitaleucopis astonea* (McAlpine, 1977: 14; *Leucopis*)]

Type locality: Canada: British Columbia (HT ♂, CNC).

This species is known only from western Canada. Although there is no rearing information, it was collected in a place characterized by Pinaceae, and can be assumed to be a predator of adelgids or *Cinara* aphids.

Vitaleucopis nidolkah Gaimari, 2020: 72

Type locality: USA: New Mexico (HT ♂, CSCA).

This species is known only from the southwestern United States in areas above 2100 m elevation. The first author reared numerous individuals from field-collected larvae attacking *Cinara ponderosae* infesting *Pinus ponderosa*.

[*Vitaleucopis scopulus* Gaimari, 2020: 78]

Type locality: USA: California (HT ♂, CSCA).

This species is known only from western United States. Given the association with “aborted sugar pine cones”, this species is likely a predator on adelgids or *Cinara* aphids attacking sugar pine, *Pinus lambertiana*, since they sometimes infest areas at the bases of new cones and can stunt or abort their development.

[undescribed species (Gaimari 2020: 68)]

Locality: USA: California (♀ specimen, CSCA).

The single specimen is known from the western United States (southern California), but there is no further biological information.

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References

- Aldrich, J.M. (1925) A new *Leucopis* from San Francisco. *Pan-Pacific Entomologist*, 1 (4), 152.
- Barriault, S., Soares, A.O., Gaimari, S.D. & Lucas, E. (2018) *Leucopis glyphinivora* Tanasijtshuk (Diptera: Chamaemyiidae), a new aphidophagous biocontrol agent; development, survival and comparison with *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae). *Bulletin of Entomological Research*, 109 (4), 472–478.
<https://doi.org/10.1017/S0007485318000767>
- Bertone, M.A., Courtney, G.W. & Wiegmann, B.M. (2008) Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology*, 33, 668–687.
<https://doi.org/10.1111/j.1365-3113.2008.00437.x>
- Blanchard, E.E. (1964) Nuevos predadores de la familia Chamaemyiidae con información sobre otras especies argentinas (Dipt.). *Revista de Investigaciones Agropecuarias, Serie 5, Patología Vegetal*, 1, 133–150. [in Spanish]
- Cole, F.R. & Schlinger, E.I. (1969) *The Flies of Western North America*. University of California Press, Berkeley and Los Angeles, California, 693 pp.
- Culliney, T.W., Beardsley Jr., J.W. & Drea, J.J. (1988) Population regulation of the Eurasian pine adelgid (Homoptera: Adelgidae) in Hawaii. *Journal of Economic Entomology*, 81, 142–147.
<https://doi.org/10.1093/jee/81.1.142>
- Cumming, J.M. & Wood, D.M. (2009) Adult Morphology and Terminology. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M. (Eds.), *Manual of Central American Diptera. Vol. 1*. NRC Research Press, Ottawa, pp. 9–50.
- Czerny, L. (1904) *Cremifania nigrocellulata*, eine neue Ochthiphiline. Systematische Stellung und Gattungen-Diagnose der Ochthiphilinen. *Wiener entomologische Zeitung*, 23, 167–170.
<https://doi.org/10.5962/bhl.part.27205>
- Czerny, L. (1936) 51. Chamaemyiidae (Ochthiphilidae). In: Lindner E. (Ed.), *Die Fliegen der Palaearktischen Region. Vol. 103*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 1–25.
- Dietschler, N.J., Bittner, T.D., Trotter III, R.T., Fahey, T.J. & Whitmore, M.C. (2021) Biological control of hemlock woolly adelgid: Implications of adult emergence patterns of two *Leucopis* spp. (Diptera: Chamaemyiidae) and *Laricobius nigrinus* (Coleoptera: Derodontidae) larval drop. *Environmental Entomology*, 50 (4), 803–813.

<https://doi.org/10.1093/ee/nvab037>

- Ebejer, M.J. (2016) The first record of the genus *Melanochthiphila* Frey (Diptera: Chamaemyiidae) from the Palaearctic, and new data on other Chamaemyiidae from Morocco. *Studia dipterologica*, 22 (1), 111–120.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
<https://doi.org/10.1093/nar/gkh340>
- Eichhorn, O. (1968) Problems of the population dynamics of silver fir woolly aphids, genus *Adelges* (= *Dreyfusia*), Adelgidae. *Zeitschrift für Angewandte Entomologie*, 61, 157–214.
<https://doi.org/10.1111/j.1439-0418.1968.tb03886.x>
- Gaimari, S.D. (2010) Chamaemyiidae. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M. (Eds.), *Manual of Central American Diptera. Vol. 2*. NRC Research Press, Ottawa, pp. 997–1007.
- Gaimari, S.D. (2012) A new genus and species of Chamaemyiidae (Diptera: Lauxanioidea) from South America feeding on *Ceroplastes* wax scales (Hemiptera: Coccidae), and status of the genus *Ortalidina* as a chamaemyiid. *Zootaxa*, 3342 (1), 39–50.
<https://doi.org/10.11646/zootaxa.3342.1.2>
- Gaimari, S.D. (2020) Two new genera of Nearctic Chamaemyiidae (Diptera: Lauxanioidea) associated with *Cinara* aphids (Hemiptera) on *Pinus*. *Zootaxa*, 4852 (1), 61–82.
<https://doi.org/10.11646/zootaxa.4852.1.3>
- Gaimari, S.D. (2021 in press) 76. Chamaemyiidae (Silver Flies). In: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Vol. 3. Brachycera: Cyclorrhapha, excluding Calyptratae. Suricata 6*. African National Biodiversity Institute, Pretoria, pp. 1633–1656.
- Gaimari, S.D., Milonas, P. & Souliotis, C. (2007) Notes on the taxonomy, biology and distribution of *Neoleucopis kartliana* (Diptera: Chamaemyiidae). *Folia Heyrovskyana, Series A*, 15, 7–16.
- Greathead, D.J. (1995) The *Leucopis* spp. (Diptera: Chamaemyiidae) introduced for biological control of *Pineus* sp. (Homoptera: Adelgidae) in Hawaii: implications for biological control of *Pineus ?boernerii* in Africa. *The Entomologist*, 114, 83–90.
- Grubin, S.M., Ross, D.W. & Wallin, K.F. (2011) Prey suitability and phenology of *Leucopis* spp. (Diptera: Chamaemyiidae) associated with hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. *Environmental Entomology*, 40 (6), 1410–1416.
<https://doi.org/10.1603/EN11127>
- Haliday, A.H. (1833) Catalogue of Diptera occurring about Holywood in Downshire. *Entomological Magazine*, 1, 147–180.
- Harris, J.W.E. & Dawson, A.F. (1979) Predator release program for balsam woolly aphid *Adelges piceae* (Homoptera: Adelgidae) in British Columbia, Canada, 1960–1969. *Journal of the Entomological Society of British Columbia*, 76, 21–26.
- Havill, N.P., Gaimari, S.D. & Caccone, A. (2018) Cryptic east-west divergence and molecular diagnostics for two species of silver flies (Diptera: Chamaemyiidae: *Leucopis*) from North America being evaluated for biological control of hemlock woolly adelgid. *Biological Control*, 121, 23–29.
<https://doi.org/10.1016/j.biocontrol.2018.02.004>
- Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astrartes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 14812–14817.
<https://doi.org/10.1073/pnas.0406166101>
- Humble, L.M. (1994) Recovery of additional exotic predators of balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in British Columbia. *The Canadian Entomologist*, 126, 1101–1103.
<https://doi.org/10.4039/Ent1261101-4>
- Kohler, G.R., Stiefel, V.L., Wallin, K.F. & Ross, D.W. (2008) Predators associated with the hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. *Environmental Entomology*, 37, 494–504.
<https://doi.org/10.1093/ee/37.2.494>
- Krishnaswamy, S. & Chako, M.J. (1988) Population dynamics of *Adelges knucheli* and its predators in the north-western Himalayas. I. Host phase: Gallicola. *Journal of Biological Control*, 2, 92–96.
- Malloch, J.R. (1921) Forest insects in Illinois, I. The subfamily Ochthiphilinae (Diptera, Family Agromyzidae). *Bulletin of the Illinois Natural History Survey*, 13, 347–361.
<https://doi.org/10.21900/j.inhs.v13.338>
- Malloch, J.R. (1933) *Diptera of Patagonia and South Chile based mainly on material in the British Museum (Natural History). Part VI—Fascicle 4. Acalyptrata (Helomyzidae, Trypetidae, Sciomyzidae, Sapromyzidae, etc.* British Museum (Natural History), London, pp. 171–391, 7 pls.
- McAlpine, J.F. (1963) Relationships of *Cremifania* Czerny (Diptera: Chamaemyiidae) and description of a new species. *The Canadian Entomologist*, 95, 239–253.
<https://doi.org/10.4039/Ent95239-3>
- McAlpine, J.F. (1965) Chamaemyiidae. In: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H. & Coulson, J.R. (Eds.), *A catalog of the Diptera of America north of Mexico. USA Department of Agriculture, Agricultural Handbook 276*. Agricultural Research Service, U.S. Dept. of Agriculture, Washington, D.C., pp. 706–709.

- McAlpine, J.F. (1971) A revision of the subgenus *Neoleucopis* (Diptera: Chamaemyiidae). *The Canadian Entomologist*, 103, 1851–1874.
<https://doi.org/10.4039/Ent1031851-12>
- McAlpine, J.F. (1977) A remarkable new species of *Leucopis* from western Canada (Diptera: Chamaemyiidae). *Proceedings of the Entomological Society of Washington*, 79, 14–18.
- McAlpine, J.F. (1978) A new dipterous predator of balsam woolly aphid from Europe and Canada (Diptera: Chamaemyiidae). *Entomologica Germanica*, 4, 349–355.
<https://doi.org/10.1127/entom.germ/4/1978/349>
- McAlpine, J.F. & Tanasijtshuk, V.N. (1972) Identity of *Leucopis argenticollis* and description of a new species (Diptera: Chamaemyiidae). *The Canadian Entomologist*, 104, 1865–1875.
<https://doi.org/10.4039/Ent1041865-12>
- McLean, I.F.G. (1982) Three species of *Leucopis* Meigen (Diptera: Chamaemyiidae) new to Britain. *Entomologist's Record and Journal of Variation*, 94, 70–72.
- Meigen, J.W. (1830) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*. Sechster Theil. Schulz, Hamm, xi + 401 + [3] pp.
- Meijere, J.C.H. de (1928) Vierde supplement op de nieuwe namlijst van nederlandsche Diptera. *Tijdschrift voor Entomologie*, 71, 11–83. [in Dutch]
- Mills, N.J. (1990) Biological control of forest aphid pests in Africa. *Bulletin of Entomological Research*, 80, 31–36.
<https://doi.org/10.1017/S0007485300045880>
- Motley, K., Havill, N.P., Arsenault-Benoit, A.L., Mayfield, A.E., Ott, D.S., Ross, D., Whitmore, M.C. & Wallin, K.F. (2017) Feeding by *Leucopis argenticollis* and *Leucopis piniperda* (Diptera: Chamaemyiidae) from the western USA on *Adelges tsugae* (Hemiptera: Adelgidae) in the eastern USA. *Bulletin of Entomological Research*, 107, 699–704.
<https://doi.org/10.1017/S0007485317000219>
- Moulton, J.K. & Wiegmann, B.M. (2004) Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution*, 31, 363–378.
[https://doi.org/10.1016/S1055-7903\(03\)00284-7](https://doi.org/10.1016/S1055-7903(03)00284-7)
- Neidermeier, A.N., Ross, D.W., Havill, N.P. & Wallin, K.F. (2020) Temporal asynchrony of adult emergence between *Leucopis argenticollis* and *Leucopis piniperda* (Diptera: Chamaemyiidae), predators of the hemlock woolly adelgid (Hemiptera: Adelgidae), with implications for biological control. *Environmental Entomology*, 49 (4), 823–828.
<https://doi.org/10.1093/ee/nvaa049>
- Nguyen, L.-T., Schmidt, H.A., Haeseler, A. von & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
<https://doi.org/10.1093/molbev/msu300>
- Papp, L. (1979) Korhardéklegyek—Pajzstetülegyek—Lauxaniidae—Chamaemyiidae. *Fauna Hungariae*, 15 (4), 1–89. [in Hungarian]
- Papp, L. (1994) A new *Cremifania* species from Hungary (Diptera, Chamaemyiidae). *Annales Historico-Naturales Musei Nationalis Hungarici*, 86, 105–107.
- Papp, L. (2010) A new *Cremifania* species from Bulgaria (Diptera, Cremifaniidae), with a proposal for wing venation terms in higher Diptera. *Annales Historico-Naturales Musei Nationalis Hungarici*, 102, 193–204.
- Rao, V.P. (1965) *Final technical report covering the period May 2, 1960 to May 1, 1965. U.S. PL-480 Project: Survey for natural enemies of Adelges spp. attacking silver fir and spruce in the Himalayas*. Commonwealth Institute of Biological Control, India Station, Bangalore, 85 pp.
- Rao, V.P. & Ghani, M.A. (1972) Studies on predators of *Adelges* spp. in the Himalayas. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, England. *Miscellaneous Publication*, 3, 1–116.
- Raspi, A. (2008) Order Diptera, family Chamaemyiidae. *Arthropod Fauna of the UAE*, 1, 662–665.
- Ratzeburg, J.T.C. (1844) *Die Forst-Insekten oder Abbildung und Beschreibung der in den Wäldern Preussens und der Nachbarstaaten als schädlich oder nützlich bekannt gewordenen Insekten; in systematischer Folge und mit besonderer Rücksicht auf die Vertilgung der Schädlichen. Vol. 3. Die Ader-, Zwei-, Halb-, Netz- und Geradflügler*. Nicolai, Berlin, vii + 314 pp., 16 pls.
- Rondani C. (1848) Osservazioni sopra parecchie specie di esapodi afidicidi e sui loro nemici [part]. *Nuovi Annali delle Scienze Naturali e Rendiconto delle Sessioni della Società Agraria e dell'Accademia delle Scienze dell'Instituto di Bologna*, Serie 2, 8 [1847], 337–351, 432–448.
- Ross, D.W., Gaimari, S.D., Kohler, G.R., Wallin, K.F. & Grubin, S.M. (2011) Chamaemyiid predators of the hemlock woolly adelgid from the Pacific Northwest. In: Reardon, R. & Onken, B. (Eds.), *Implementation and Status of Biological Control of the Hemlock Woolly Adelgid. U.S. Forest Service, Publication FHTET-2011-04*. U.S. Forest Service, Morgantown, West Virginia, pp 97–106
- Sano, M., Tabuchi, K. & Ozaki, K. (2008) A holocyclic life cycle in a gall-forming adelgid, *Adelges japonicus* (Homoptera: Adelgidae). *Journal of Applied Entomology*, 132, 557–565.
<https://doi.org/10.1111/j.1439-0418.2008.01299.x>
- Sluss, T.P. & Foote, B.A. (1973) Biology and immature stages of *Leucopis pinicola* and *Chamaemyia polystigma* (Diptera: Chamaemyiidae). *The Canadian Entomologist*, 105, 1443–1452.

<https://doi.org/10.4039/Ent1051443-11>

- Talavera, G., Lukhtanov, V., Pierce, N.E. & Vila, R. (2021) DNA barcodes combined with multilocus data of representative taxa can generate reliable higher-level phylogenies. *Systematic Biology*, syab038. [published online]
<https://doi.org/10.1093/sysbio/syab038>
- Tanasijtshuk, V.N. (1958) New species of the genus *Leucopis* (Diptera, Chamaemyiidae) from Leningrad region. *Trudy Zoologicheskogo Instituta*, 24, 89–98. [in Russian]
- Tanasijtshuk, V.N. (1962) New and little-known species of the genus *Leucopis* (Diptera, Chamaemyiidae) from the European part of the USSR. *Entomologicheskoye Obozreniye*, 41, 220–229. [in Russian; English translation: (1962) *Entomological Review*, 41, 132–138]
- Tanasijtshuk, V.N. (1966) New species of the genus *Leucopis* (Diptera, Chamaemyiidae) from south-western Kazakhstan. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, 37, 233–236. [in Russian]
- Tanasijtshuk, V.N. (1968) Species of *Leucopis* (Diptera, Chamaemyiidae) from India. *Bulletin of Entomology, Madras*, 9, 6–12.
- Tanasijtshuk, V.N. (1986) [Silver-flies (Chamaemyiidae)]. *Fauna of the USSR. New Series 134. Dipterans. Vol. 14*. Zoological Institute of the Russian Academy of Sciences, Nauka Publishers, St Petersburg, 335 pp. [in Russian]
- Tanasijtshuk, V.N. (1997) A new Holarctic genus of Chamaemyiidae (Diptera). *International Journal of Dipterological Research*, 8 (2), 113–116.
- Tanasijtshuk, V.N. (2001) On two sister species of the genus *Anchioleucopis* Tanasijtshuk, 1997 (Diptera, Chamaemyiidae) from the Holarctic region. *Entomologicheskoye Obozreniye*, 80 (4), 901–907. [in Russian; English translation: (2001) *Entomological Review*, 81 (5), 542–547]
- Tanasijtshuk, V.N. (2002) Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). I. The redescription of Nearctic *Leucopis* published before 1965. *Zoosystematica Rossica*, 11, 193–207.
- Tanasijtshuk, V.N. (2003) Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). II. New species. *Zoosystematica Rossica*, 11, 375–396.
- Tanasijtshuk, V.N. (2005) Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). III. *L. annulipes* Zetterstedt and a new sibling species from the Nearctic. *Zoosystematica Rossica*, 13 (2), 233–238.
- Tanasijtshuk, V.N. (2006) Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). IV. New species. *Zoosystematica Rossica*, 14 (2), 281–288.
<https://doi.org/10.31610/zsr/2005.14.2.281>
- Thunes, K.H., Skartveit, J., Gjerde, I., Stary, J., Solhoy, T., Fjellberg, A., Kobro, S., Nakahara, S., zur Strassen, R., Vierbergen, G., Szadziowski, R., Hagan, D.V., Grogan Jr., W.L., Jonassen, T., Aakra, K., Anonby, J., Greve, L., Aukema, B., Heller, K., Michelsen, V., Haenni, J.-P., Emeljanov, A.F., Douwes, P., Berggren, K., Franzen, J., Disney, R.H.L., Prescher, S., Johanson, K.A., Mamaev, B., Podenas, S., Andersen, S., Gaimari, S.D., Nartshuk, E., Söli, G.E.E., Papp, L., Midtgaard, F., Andersen, A., Tschirnhaus, M. von, Bächli, G., Olsen, K.M., Olsvik, H., Foldvari, M., Raastad, J.E., Hansen, L.O. & Djursvoll, P. (2004) The arthropod community of Scots pine (*Pinus sylvestris* L.) canopies in Norway. *Entomologica Fennica*, 15, 65–90.
- Viggiani, G. & Mustica, L. (2008) Some notes on the biological control of insect pests in the island of Ischia. *Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri*, 62, 79–82.
- Wantuch, H.A., Havill, N.P., Hoebeke, E.R., Kuhar, T.P. & Salom, S.M. (2019) Predators associated with the pine bark adelgid (Hemiptera: Adelgidae), a native insect in Appalachian forests, United States of America, in its southern range. *The Canadian Entomologist*, 151 (1), 73–84.
<https://doi.org/10.4039/tce.2018.53>
- Wilson, F. (1938) Notes on the insect enemies of chermes with particular reference to *Pineus pini*, Koch, and *P. strobi*, Hartig. *Bulletin of Entomological Research*, 29, 373–389.
<https://doi.org/10.1017/S0007485300026286>
- Zetterstedt, J.W. (1848) *Diptera Scandinaviae disposita et descripta*. *Tomus septimus*. Officina Lundbergiana, Lundae [=Lund], pp. 2581–2934.
- Zetterstedt, J.W. (1855) *Diptera Scandinaviae disposita et descripta*. *Tomus duodecimus seu supplementum tertium, continens addenda, corrigenda & emedanda tomis undecim prioribus*. Officina Lundbergiana, Lundae [=Lund], pp. i–xx + 4547–4942.
- Zondag, R. & Nuttall, M.J. (1989) *Pineus laevis* (Maskell), pine twig chermes or pine woolly aphid (Homoptera: Adelgidae). In: Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P. (Eds.), *Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. CAB International Institute of Biological Control, Wallingford, Oxon, pp. 295–297.