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New *Macrocheles* species (Acari, Mesostigmata, Macrochelidae) associated with burying beetles (Silphidae, *Nicrophorus*) in North America

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Abstract

Burying beetles (Silphidae, *Nicrophorus*) are hosts to a broad diversity of mites (Acari), including several species of *Macrocheles* Latreille, 1829 (Mesostigmata, Macrochelidae). The macrochelid fauna associated with silphids primarily in North America was surveyed; in total, 1659 macrochelids representing seven species were collected from 112 *Nicrophorus* beetles representing nine host species. Three new species of *Macrocheles* were discovered during the survey and described as *Macrocheles willowae* **sp. n.**, *M. pratum* **sp. n.**, and *M. kaiju* **sp. n.** The barcode region of cytochrome oxidase subunit I (COI) was amplified from the three new described species, as well as *M. nataliae* and *M. praedafimetorum*, and analysed in a small phylogeny.

Keywords

Acari, carrion-feeding, COI, ecology, mite, phoresy

Introduction

Carrion-feeding beetles (Silphidae) are associated with a diverse assemblage of mites, nematodes, and fungi. *Nicrophorus* (Silphidae) species are large-bodied beetles, that breed and feed on decaying organic matter, most often vertebrate carcasses (Anderson and Peck 1985). There are at least 60 extant species of *Nicrophorus* worldwide, 22 of which occur in the New World (Sikes et al. 2008, Sikes et al. 2016). *Nicrophorus* beetles are unique amongst insects because most species provide biparental care and they bury small vertebrate carcasses in subterranean crypts (see Anderson and Peck (1985) for a summary of their life cycle). *Nicrophorus* beetles are associated with a broad diversity of mites that can occur at high prevalences and abundances, with at least 14 species of mites representing four families collected off 95% of beetles in a given population (Wilson and Knollenberg 1987). The symbiotic relationship between silphids and their associated mites are poorly understood; however, the relationship may be a blend of commensalism and mutualism, as some mite species actively prey on eggs of carrion-feeding flies that compete with *Nicrophorus* (Wilson and Knollenberg 1987).

The Macrochelidae (Mesostigmata) are a cosmopolitan family of predaceous mites with at least 480 described species from 20 genera, occurring in a wide variety of organic substrates where they feed on nematodes and other microinvertebrates (Krantz 1998, Lindquist et al. 2009, Emberson 2010). There are about 320 described species of *Macrocheles* Latreille, 1829 (Macrochelidae) worldwide (Emberson 2010), many of which are phoretic as adult females on insects, including nine species which are associated with silphids (*M. agilis*, *M. glaber*, *M. kurosai*, *M. lisae*, *M. merdarius*, *M. muscaedomesticae*, *M. nataliae*, *M. praedafimetorum*, *M. vespillo*) (Halliday 2000, Mašán 2003, Niogret et al. 2007, Perotti and Braig 2009). *Macrocheles* associated with silphids attach with their chelicerae to beetles dispersing to and from carcasses, and they generally feed on nematodes, insect eggs and larvae, and other invertebrates on carrion (Wilson and Knollenberg 1987, Schwarz et al. 1998). Macrochelids phoretic on burying beetles are often overlooked and unstudied, resulting in a scarcity of information about their life history and novel species that remain to be described. A recent survey of tortoise mites (Uropodina, *Uroobovella*) on *Nicrophorus* beetles (Knee et al. 2012) also uncovered three new species of *Macrocheles* associated with burying beetles. Herein, I propose and describe *Macrocheles willowae* sp. n., *M. pratum* sp. n., and *M. kaiju* sp. n., include a small phylogeny based on the barcode region of COI, and describe the diversity, abundance and host range of *Macrocheles* species found on *Nicrophorus* throughout this survey.

Methods

Biological collections

Silphids were collected by various researchers across eight countries and 21 provinces or states (see acknowledgments). In Canada, most silphids were collected as bycatch from xylophagous beetle trapping by W.K. Specimens from other countries were collected primarily in pitfall traps, and others were hand-collected. Beetle specimens preserved in ethanol were shipped to Carleton University, and upon receipt specimens were placed in 95% ethanol and stored at -20°C. Using a dissecting microscope, silphids were identified to species using keys from Anderson and Peck (1985). The presence, abundance, and attachment location of mesostigmatic mites was recorded. All mesostigmatic mites were removed and placed in a 0.5 ml microfuge tube with 95% ethanol and stored at -20°C for later identification and/or molecular analysis. Mites were slide-mounted in polyvinyl alcohol medium (6371A, BioQuip Products, Rancho Dominguez, California, United States of America (USA)) and cured on a slide warmer at 40°C for 3–4 days. Slide-mounted specimens were examined using a compound microscope (Leica DM 2500) with differential interference contrast illumination (DIC), and identified to species using the primary literature. Initial drawings of mites were made with pencil on paper using a camera lucida. Illustrations were later merged in Adobe Photoshop CS5 and redrawn in Adobe Illustrator CS5 using an Intuos 3 Graphics Tablet from WACOM Co., Ltd. (Saitama, Japan). Leg chaetotaxy is based on the system proposed by Evans (1963) and Evans and Till (1965). Idiosomal chaetotaxy follows the system of Lindquist and Evans (1965) as applied to macrochelids by Hyatt and Emberson (1988). Notation for glandular openings and poroids (proprioreceptors or lyrifissures) follows the system developed by Athias-Henriot (1969, 1971, 1975) and Johnston and Moraza (1991), as reviewed by Kazemi et al. (2014). Measurements were made from at least eight female specimens, all measurements are in micrometres (μm), and lengths presented with mean followed by the range in parenthesis. Type specimens are deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC), at Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada, and the Smithsonian Institution National Museum of Natural History.

Molecular methods

Genomic DNA was extracted from whole specimens for 24 hours using a DNeasy Tissue kit (Qiagen, Inc., Santa Clara, California, USA). Following extraction, mites were removed from the extraction buffer, vouchers were-slide mounted, and genomic DNA was purified following the DNeasy Tissue kit protocol. PCR amplifications were performed in a total volume of 25 μl, with 14.7 μl ddH2O, 2.5 μl 10× ExTaq buffer, 0.65 μl 25 mM MgCl2, 1.0 μl of each 10 μM primer, 2.0 μl 10 mM dNTPs, 0.15 μl ExTaq DNA polymerase, and 3 μl genomic DNA template. Primer pairs LCO1490 + HCO2198 (Folmer et al. 1994) were used to amplify a 689 bp fragment of the 5'–end of COI. PCR amplification was performed on an Eppendorf ep Gradient S Mastercycler (Eppendorf AG, Hamburg, Germany), using the following protocol: initial denaturation cycle at 94 °C for 3 min, followed by 45 cycles of 94 °C for 45 s, primer annealing at 45 °C for 45 s, 72 °C for 1 min, and a final extension at 72 °C for 5 min. Amplified products and negative controls were visualized on 1% agarose electrophoresis gels, and purified using pre-cast E-Gel CloneWell 0.8% SYBR Safe agarose gels (Invitrogen, Carlsbad, California, USA). Sequencing reactions followed the protocol of Knee et al. (2012), and sequencing was performed at the Agriculture and Agri-Food Canada, Eastern Cereal and Oilseed Research Centre Core Sequencing Facility (Ottawa, Ontario, Canada).

Sequence chromatograms were edited and contiguous sequences were assembled using Sequencher v5.3 (Gene Codes Corp., Ann Arbor, Michigan, USA). COI sequences were aligned manually in Mesquite v3.10 (Maddison and Maddison, 2016) according to the translated amino acid sequence. COI sequences from *Macrocheles subbadius* (MBIOE1677-13, MBIOE1699-13) generated by the Barcode of Life Data Systems (BOLD) were included in the phylogeny. COI sequences on GenBank from two Macronyssidae (Mesostigmata) species, *Ornithonyssus bacoti* and *O. sylviarum* (FM179677, KR103486), were used as outgroup sequences. Sequences generated during this study have been submitted to GenBank (Table 1).

Table 1. Collection information, host species records and mite abundance of *Macrocheles* (Macro.) mites collected from *Nicrophorus* (Nicro.) beetles, with GenBank accession numbers for COI.

Beetle number	Beetle species	Collection location	Coordinates	Collection date	*Macrocheles* species	Mite abundance	GenBank number
N002	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 2	45.895, -78.071	16.vi.08	*Macro. willowae* sp. n.	1	–
N003	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 2	45.895, -78.071	16.vi.08	*Macro. willowae* sp. n.	1	–
N005	*Nicro. orbicollis*	CAN, ON, Frontenac	44.447, -76.577	17.vi.08	*Macro. willowae* sp. n.	4	–
N006	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	17.vi.08	*Macro. willowae* sp. n.	4	–
N007	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	17.vi.08	*Macro. willowae* sp. n.	1	–
N008	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	17.vi.08	*Macro. willowae* sp. n.	1	–
N011	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	2	–
N012	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	2	–
N013	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	5	–
N014	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	7	–
N015	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	5	–
N017	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	1	–
N018	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	2	–
N019	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	2	–
N020	*Nicro. orbicollis*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	4	–
N021	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	1	–
N022	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	3	–
N023	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	2	–
N024	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	16.vi.08	*Macro. willowae* sp. n.	3	–
N026	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	01.vii.08	*Macro. willowae* sp. n.	5	–
N028	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	3	–
N029	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	4	–
N031	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	2	–
N036	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	1	–
N037	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	3	–
N039	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	1	–
N040	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	8	–
N042	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	3	–
N043	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	3	–
N044	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	3	–
N046	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	1	–
N047	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	17	–

Beetle number	Beetle species	Collection location	Coordinates	Collection date	*Macrocheles* species	Mite abun-dance	GenBank number
N048	*Nicro. orbicollis*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	30.vi.08	*Macro. willowae* sp. n.	5	–
N051	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	15.vii.08	*Macro. willowae* sp. n.	2	–
N052	*Nicro. orbicollis*	CAN, ON, Frontenac	44.447, -76.577	30.vii.08	*Macro. willowae* sp. n.	1	–
N055	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	30.vii.08	*Macro. willowae* sp. n.	3	–
N057	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	1	–
N058	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	2	–
N060	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	2	–
N061	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	5	–
N062	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	3	–
N068	*Nicro. defodiens*	CAN, ON, Algonquin P.P. 1	45.902, -77.605	29.vii.08	*Macro. willowae* sp. n.	9	–
N069	*Nicro. orbicollis*	CAN, ON, Charleston Lake	44.500, -76.072	12.viii.08	*Macro. willowae* sp. n.	1	–
N075	*Nicro. orbicollis*	CAN, ON, Frontenac	44.447, -76.577	26.viii.08	*Macro. willowae* sp. n.	1	–
N081	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. kaiju* sp. n.	4	MF192750
N081	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. willowae* sp. n.	9	MF192743
N086	*Nicro. orbicollis*	CAN, ON, Windsor, Elgin St.	42.261, -83.057	18.vi.2009	*Macro. willowae* sp. n.	1	–
N088	*Nicro. orbicollis*	CAN, ON, Hwy 132, Dacre	45.369, -76.988	25.vi.2009	*Macro. willowae* sp. n.	10	–
N089	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	25.vi.2009	*Macro. willowae* sp. n.	9	–
N104	*Nicro. defodiens*	CAN, BC, Prince George, nr. UNBC	53.904, -122.783	12.vi.2009	*Macro. willowae* sp. n.	1	–
N110	*Nicro. defodiens*	CAN, BC, Prince George, nr. UNBC	53.904, -122.783	12.vi.2009	*Macro. willowae* sp. n.	1	–
N113	*Nicro. defodiens*	CAN, BC, Prince George, nr. UNBC	53.904, -122.783	12.vi.2009	*Macro. willowae* sp. n.	4	MF192748
N114	*Nicro. orbicollis*	CAN, PEI, Wellington, Route 2	46.452, -63.949	06.vii.2009	*Macro. willowae* sp. n.	8	–
N115	*Nicro. orbicollis*	CAN, PEI, Wellington, Route 2	46.452, -63.949	06.vii.2009	*Macro. willowae* sp. n.	7	–
N116	*Nicro. orbicollis*	CAN, PEI, Wellington, Route 2	46.452, -63.949	06.vii.2009	*Macro. praedafime-torum*	1	MF192754
N116	*Nicro. orbicollis*	CAN, PEI, Wellington, Route 2	46.452, -63.949	06.vii.2009	*Macro. willowae* sp. n.	9	MF192747
N136	*Nicro. defodiens*	CAN, BC, Prince George, nr. UNBC	53.904, -122.783	12.vi.2009	*Macro. willowae* sp. n.	1	MF192749
N139	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	10.vii.2009	*Macro. willowae* sp. n.	12	–
N143	*Nicro. orbicollis*	CAN, ON, Hamilton, Site 4-7		07.vii.2009	*Macro. willowae* sp. n.	100	MF192744
N145	*Nicro. orbicollis*	CAN, ON, Hamilton, Site 4-7		07.vii.2009	*Macro. willowae* sp. n.	8	–
N147	*Nicro. orbicollis*	CAN, ON, Hamilton, Site 4-7		07.vii.2009	*Macro. willowae* sp. n.	10	–
N153	*Nicro. orbicollis*	CAN, NS, Dartmouth, Wright's Cove Rd.	44.694, -63.611	09.vii.2009	*Macro. willowae* sp. n.	4	–
N160	*Nicro. orbicollis*	CAN, ON, Waterloo	43.54, -80.211	07.vii.2009	*Macro. willowae* sp. n.	2	–
N161	*Nicro. orbicollis*	CAN, ON, Waterloo	43.54, -80.211	07.vii.2009	*Macro. willowae* sp. n.	8	–
N165	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	23.vii.2009	*Macro. willowae* sp. n.	17	–
N166	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	23.vii.2009	*Macro. willowae* sp. n.	8	–
N167	*Nicro. orbicollis*	CAN, NS, Glenmont, Black Hole Rd.	45.111, -64.296	17.vii.2009	*Macro. willowae* sp. n.	9	–
N168	*Nicro. orbicollis*	CAN, NS, Cold Brook, Hwy 101	45.079, -64.592	13.vii.2009	*Macro. willowae* sp. n.	10	MF192745
N169	*Nicro. orbicollis*	CAN, NS, Chipman	46.174, -65.899	08.vii.2009	*Macro. willowae* sp. n.	7	–
N174	*Nicro. orbicollis*	CAN, NS, Hantsport	45.099, -64.184	21.vii.2009	*Macro. willowae* sp. n.	6	–

Beetle number	Beetle species	Collection location	Coordinates	Collection date	*Macrocheles* species	Mite abun-dance	GenBank number
N178	*Nicro. orbicollis*	CAN, NS, East River off Hwy 329	44.583, -64.164	10.viii.2009	*Macro. willowae* sp. n.	4	–
N180	*Nicro. defodiens*	CAN, NS, Debert, Industrial Park	45.428, -63.429	05.viii.2009	*Macro. willowae* sp. n.	3	–
N181	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	06.viii.2009	*Macro. willowae* sp. n.	8	MF192746
N185	*Nicro. vespillo*	GER, Mooswald Forest, nr. Freiburg	48.0, 7.85	vi.2009	*Macro. nataliae*	4	–
N186	*Nicro. vespillo*	GER, Mooswald Forest, nr. Freiburg	48.0, 7.85	vi.2009	*Macro. nataliae*	7	MF192752
N187	*Nicro. vespillo*	GER, Mooswald Forest, nr. Freiburg	48.0, 7.85	vi.2009	*Macro. nataliae*	1	–
N188	*Nicro. vespillo*	GER, Mooswald Forest, nr. Freiburg	48.0, 7.85	vi.2009	*Macro. nataliae*	5	MF192753
N191	*Nicro. orbicollis*	USA, CT, Bethany	41.462, -72.961	16.vii.2009	*Macro. willowae* sp. n.	1	–
N192	*Nicro. orbicollis*	USA, CT, Bethany	41.462, -72.961	14.viii.2009	*Macro. willowae* sp. n.	5	–
N216	*Nicro. orbicollis*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	215	–
N218	*Nicro. orbicollis*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	135	–
N222	*Nicro. defodiens*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	30	–
N226	*Nicro. orbicollis*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	30	–
N228	*Nicro. orbicollis*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	97	–
N234	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	10	–
N235	*Nicro. guttula*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	7	–
N235x	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	04.vii.2002	*Macro. pratum* sp. n.	3	–
N236	*Nicro. obscurus*	CAN, AB, Onefour	49.121, -110.47	04.vii.2002	*Macro. pratum* sp. n.	5	–
N237	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	13	–
N238	*Nicro. obscurus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	5	–
N239	*Nicro. obscurus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	11	–
N240	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	13	–
N242	*Nicro. hybridus*	CAN, AB, Onefour	49.121, -110.47	18.vii.2002	*Macro. pratum* sp. n.	7	MF192751
N243	*Nicro. guttula*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	7	–
N244	*Nicro. guttula*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	7	–
N246	*Nicro. hybridus*	CAN, AB, Onefour	49.121, -110.47	18.vii.2002	*Macro. pratum* sp. n.	10	–
N274	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. glaber*	8	–
N275	*Nicro. obscurus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. glaber*	1	–
N295	*Nicro. carolinus*	USA, NE, Kearney Co.		05.vi.2009	*Macro. kaiju* sp. n.	1	–
N295	*Nicro. carolinus*	USA, NE, Kearney Co.		05.vi.2009	*Macro.* sp.	4	–
N298	*Nicro. carolinus*	USA, NE, Kearney Co.		05.vi.2009	*Macro. kaiju* sp. n.	2	–
N298	*Nicro. carolinus*	USA, NE, Kearney Co.		05.vi.2009	*Macro.* sp.	3	–
N303	*Nicro. pustulatus*	USA, NE, Kearney Co.		13.vii.2009	*Macro. pratum* sp. n.	3	–
N308	*Nicro. marginatus*	CAN, AB, Onefour	49.121, -110.47	17.vi.2003	*Macro. pratum* sp. n.	86	–
N329	*Nicro. orbicollis*	USA, NH		2009	*Macro. willowae* sp. n.	41	–
N330	*Nicro. orbicollis*	USA, NH		2009	*Macro. willowae* sp. n.	91	–
N331	*Nicro. orbicollis*	USA, CT, Bethany	41.462, -72.961	2009	*Macro. willowae* sp. n.	13	–
N332	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. kaiju* sp. n.	11	–
N333	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. kaiju* sp. n.	74	–

Beetle number	Beetle species	Collection location	Coordinates	Collection date	*Macrocheles* species	Mite abundance	GenBank number
N334	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. willowae* sp. n.	1	–
N334	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. kaiju* sp. n.	26	–
N334	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro*. sp.	1	–
N335	*Nicro. carolinus*	USA, FL, Highlands Co, Lake Placid	27.181, -81.352	10.iii.2009	*Macro. kaiju* sp. n.	45	–
N336	*Nicro. marginatus*	USA, NE, Kearney Co.		vi.2009	*Macro. pratum* sp. n.	9	–
N338	*Nicro. defodiens*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	8	–
N339	*Nicro. defodiens*	USA, NH, Durham	43.134, -70.926	07.vi.2009	*Macro. willowae* sp. n.	163	–
N346	*Nicro. orbicollis*	CAN, ON, Hwy 132, Dacre	45.369, -76.988	06.viii.2009	*Macro. willowae* sp. n.	6	–
N347	*Nicro. orbicollis*	CAN, ON, Carbine Rd.	45.33, -76.371	06.viii.2009	*Macro. willowae* sp. n.	16	–

Pairwise distances were calculated using neighbour-joining (NJ) analyses with the Kimura-2-parameter (K2P) model in PAUP* v4.0b10 (Swofford 2003). Phylogenetic reconstructions of the COI dataset was performed using Bayesian inference (BI) in MrBayes v3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Each specimen in the phylogeny is labeled with the mite species and the beetle number, followed by the host species and abbreviated state, province or country (Fig. 14).

MrModeltest v2.3 (Nylander 2004) was used to determine the best-fit model of molecular evolution for each molecular marker, which was determined to be GTR+I+G. Bayesian analysis was performed in MrBayes using the Markov Chain Monte Carlo (MCMC) method, two independent runs, with nucmodel = 4by4, N_{st} = 6, rates = invgamma, samplefreq = 1000, four chains = one cold and three heated. The COI dataset ran for 10 million generations, producing 19502 trees after a burn-in of 250 trees. The remaining trees in Mesquite, excluding the burn-in, were used to generate a majority-rule consensus tree displaying the posterior probability supports for each node. Bayesian analyses were performed using the on-line Computational Biology Service Unit at Cornell University, and at the Cyberinfrastructure for Phylogenetic Research (CIPRES) portal (Miller et al. 2010).

Results and discussion

Family Macrochelidae Vitzthum, 1930
Subfamily Macrochelinae

Genus *Macrocheles* Latreille, 1829

Type species. *Acarus marginatus* Hermann, 1804 (= *Acarus muscae domesticae* Scopoli, 1772), by original designation.

Macrocheles willowae **sp. n.**
http://zoobank.org/1085F03B-0DC9-4762-91E4-6FA1770E6965
Figs 1–4, 13A

Material examined. ***Type material.*** Holotype: female (CNC829414) on *Nicrophorus orbicollis* (N088, female) collected near Dacre, Ontario, Canada (45.369, -76.988), 25.vi.2009, coll: W. Knee.

Paratypes (26): Nine females (CNC829415–829423) with the same collection information as the holotype; 15 females (CNC829424–829438) on *N. defodiens* (N222, female), Durham, New Hampshire, USA (43.134, -70.926), 07.vi.2009, coll: W. Knee & M. Scott; female (CNC829439) on *N. defodiens* (N136, female), Prince George, near University of Northern British Columbia campus, British Columbia, Canada (53.904, -122.783), 12.vi.2009, coll: W. Knee & R. Dawson; female (CNC829440) on *N. orbicollis* (N143, male), Hamilton, Ontario, Canada, 7.vii.2009, coll: W. Knee.

Other material. 1241 mites examined from British Columbia, Nova Scotia, Ontario, Prince Edward Island, Connecticut, Florida, and New Hampshire on *N. carolinus, N. defodiens*, and *N. orbicollis* (Table 1).

Diagnosis female. As for *Macrocheles* (see Hyatt and Emberson 1988). All dorsal and ventral setae smooth and spinose, except *J5* barbed and slightly shorter than *Z5*. Seta *j1* simple with rounded tip, *j1* slightly longer than *z1*. Dorsal hexagonal setae (*j5, z5, j6*) nearly as long as marginal and submarginal setae (*R* and *UR*). Dorsal shield with moderate reticulations throughout, except smooth in dorsal hexagonal area and between *j4* setae, without well-defined procurved line, sigillary rami absent. Sternal shield more than twice as wide as long, punctures small, posterior margin concave. Well defined *linea media transversa* (l.m.t.) and *linea oblique anteriores* (l.o.a.), l.o.a. contacts l.m.t. *Linea arcuata* (l.arc.) well defined and contacts l.o.a. *Linea angulata* (l.ang.) and *linea oblique posteriore* (l.o.p.) well defined laterally but faint medially. *Area punctata laterale* (a.p.l.) well defined, but *area punctata posteriore* (a.p.p.) not well defined. Ventrianal shield longer than wide (ratio 1.3). Arthrodial brush as long as movable digit. Genu IV with six setae. Femur IV setae *ad2*, *pd1* prominent spikes with flattened forked tip.

Description female. ***Dorsal idiosoma*** (Fig 1). Dorsal shield 548 (526–572) long and 357 (344–372) (n=8) wide (level with *r3*), with 28 pairs of setae, all setae simple and spinose except *J5* is barbed. Seta *J5* 16 (15–18) shorter than *Z5* 24 (22–27). Seta *j1* simple with rounded tip, *j1* 18 (16–20) slightly longer than *z1* 16 (12–19). Marginal and submarginal setae simple, slightly longer 24 (23–25) than dorsal hexagonal setae 20 (15–22). Dorsal shield with moderate reticulations throughout, except smooth in dorsal hexagonal area and between *j4* setae, shield without well-defined procurved line, sigillary rami absent, and posterolateral margins narrowed slightly. Shield with 22 pairs of pore-like structures, of which six are secretory glands and 16 are non-secretory poroids.

Ventral idiosoma (Figs 2, 13A). Sternal shield more than twice as wide as long, medial length 91 (88–96), maximum width 213 (192–221) level with a.p.l., and minimum width 117 (115–124) posterior of *st1*. Sternal shield punctures small, posterior

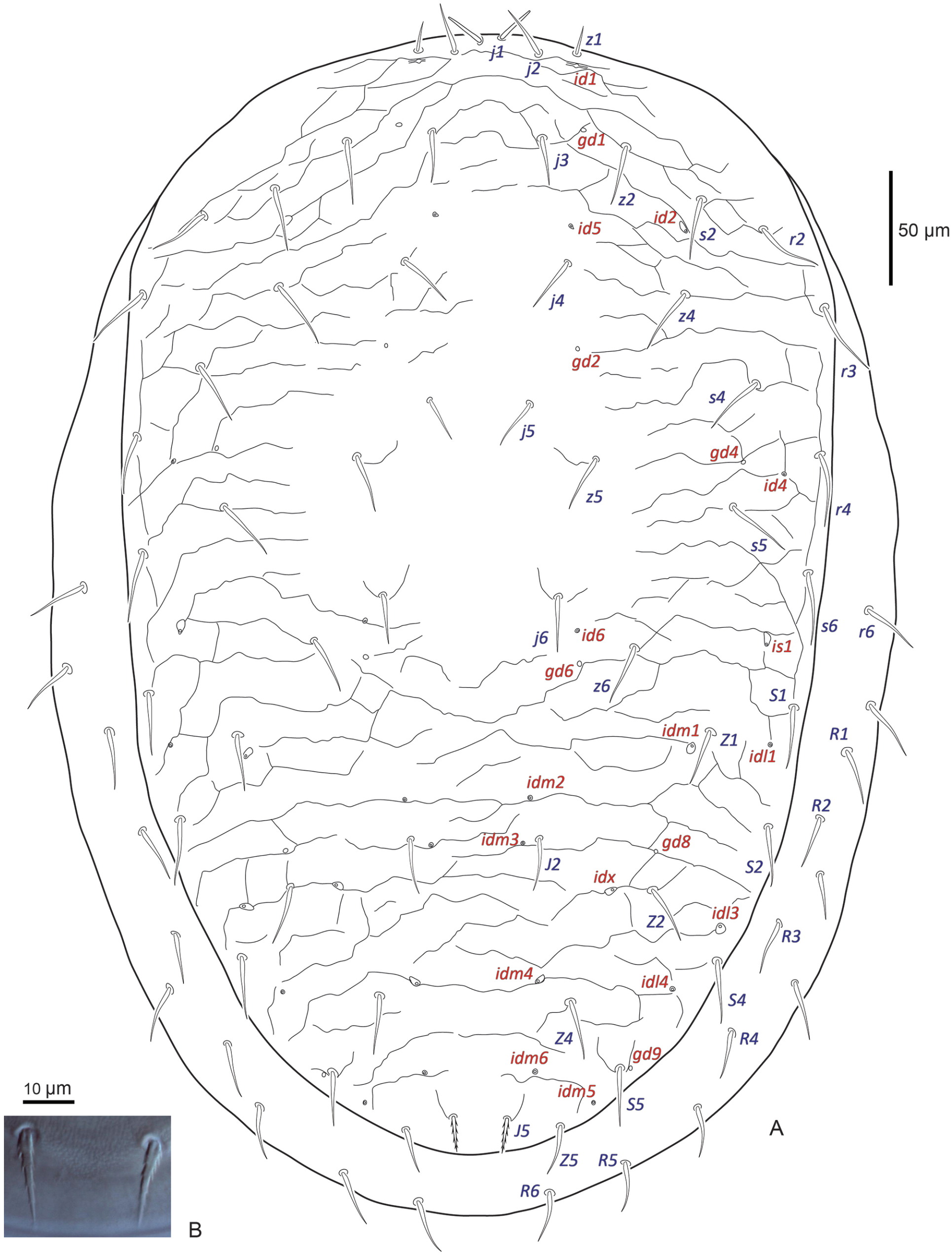

Figure 1. Female *Macrocheles willowae* sp. n. **A** dorsal idiosoma **B** seta *J5*.

margin concave. Setae *st1–3* 38 (33–43) simple and spinose, and two pairs of lyrifissures (*iv1*, *iv2*) on sternal shield. Pear-shaped metasternal shields well separated from sternal shield margin bearing lyrifissure *iv3* anteriorly and spinose seta *st4* 33 (30–35) posteriorly. Well defined l.m.t. and l.o.a., l.o.a. contacts l.m.t. Well defined l.arc. con-

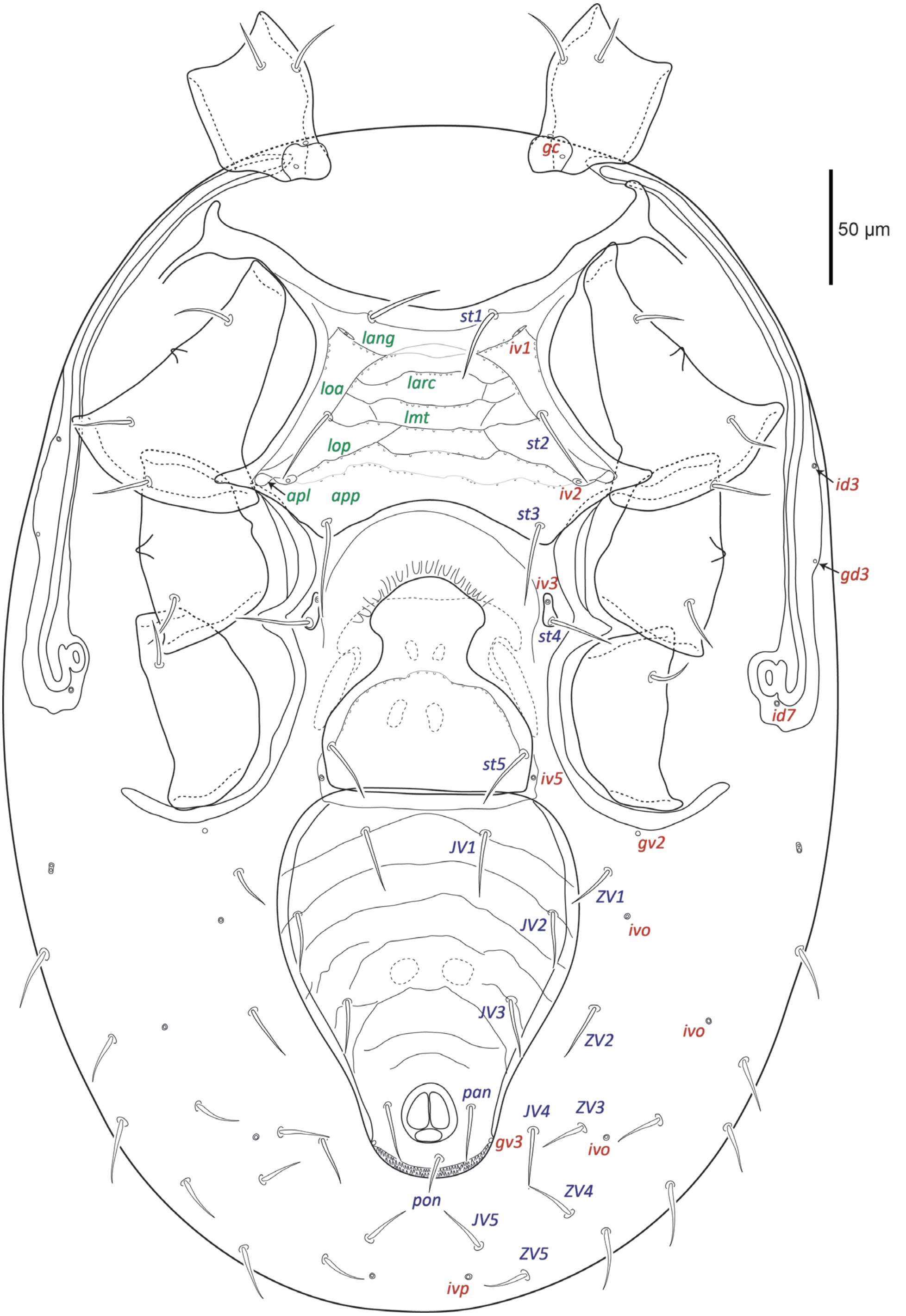

Figure 2. Female *Macrocheles willowae* sp. n. ventral idiosoma including coxae.

tacts l.o.a., l.ang. and l.o.p. well defined laterally but faint medially. Well defined a.p.l., a.p.p. not well defined. Genital shield length 149 (141–161), width 113 (104–120) level with *st5*. Genital shield truncate posteriorly and hyaline margin rounded anteriorly, spinose seta *st5* 32 (30–34) on shield, pair of lyrifissures *iv5* off shield near posterior margin. Transverse line on genital shield well defined laterally and faint medially, small punctures along transverse line. Peritrematal shield narrow, fused to dorsal shield near *r3*, peritreme extends beyond posterior margin of coxa I, two poroids (*id3*, *id7*) and one gland (*gd3*) on the shield. Ventrianal shield longer than wide (ratio 1.3); length 198 (187–204), width 153 (144–168) level with *JV2*. Ventrianal shield bearing several faint transverse lines, three pairs of simple spinose preanal setae *JV1–JV3* 26 (21–30), spinose paranal (*pan*) 27 (25–30) and postanal (*pon*) 18 (16–20) setae, narrow cribrum and a pair of glands (*gv3*) on shield margin posterior of the anal opening. Ventral opisthosomal setae in soft integument simple and spinose, *ZV1* 21 (17–29), *ZV2* 26 (22–29) as long or nearly as long as *JV* setae. Two pairs of glands (*gv2* and unknown paired-pore) and four pairs of poroids (*ivo*, *ivp*) in opisthosomal soft integument.

Gnathosoma (Fig. 3). Basis capitulum medial length excluding internal malae 114 (106–122), width 150 (143–157) posterior to *pc*. Subcapitular setae simple: *h1* 38 (28–48), *h2* 16 (13–19), *h3* 53 (44–67), and *pc* 19 (16–21). Palp chaetotaxy normal for genus (2–5–6–14–15), palp apotele three-tined, *al* setae on trochanter, femur and genu slightly spatulate. Corniculi pointed, length along lateral margin 42 (37–51), internal malae slender and smooth. Epistome tripartite with bifid central element bearing small fringe medially, lateral elements broad and flag-like distally, epistomatic margin finely serrate. Subcapitulum with seven rows, six of which have deutosternal denticles; the anterior most row with few (four) denticles laterally, and the second anterior most row with paired ridges without any denticles. Chelicerae robust, length of second cheliceral segment including fixed digit 140 (134–146), and movable digit 54 (52–58). Fixed digit bidentate with one large and one small tooth, moveable digit with bidentate tooth. Pilus dentilis and dorsal seta on fixed digit simple spikes, fixed digit with lyrifissure on each paraxial and antiaxial faces. Movable digit with narrow fringed arthrodial corona, and plumose arthrodial brush (50) almost as long as movable digit.

Legs (Fig. 4). Excluding ambulacra, lengths of leg I 420 (409–430), leg II 383 (357–402), leg III 338 (315–349), and leg IV 482 (469–489). As in all *Macrocheles*, ambulacra only present on legs II–IV, claws II–IV well developed. Pair of glands (*gc*) on coxa I. Setation of legs I–IV normal for Macrochelidae: coxae 2–2–2–1; trochanters 5–5–5–5; femora I (2–3/1,2/3–2) (as *al–ad/av, pd/pv–pl*), II (2–3/1,2/2–1), III (1–2/0,1/1–1), IV (1–2/1,1/0–1); genua I, II (2–3/1,2/1–2), III (1–2/1,2/0–1), IV (1–2/1,2/0–0); tibiae I (2–3/2,2/1–2), II (2–2/1,2/1–2), III, IV (1–1/1,2/1–1); tarsus I 20 setae plus numerous tapered setae distally, tarsi II–IV 18. Most leg setae simple, setiform, femur II *ad1*, III *pd1*, IV *ad2*, *pd1*, and genu II *ad3* prominent spike setae with flattened forked tip with two to four tines that can appear as a single tapered point viewed laterally. Tarsus II with four large distal spike setae with thickened conical base and rounded tip. Tarsi III, IV with four and three, respectively, distal setae

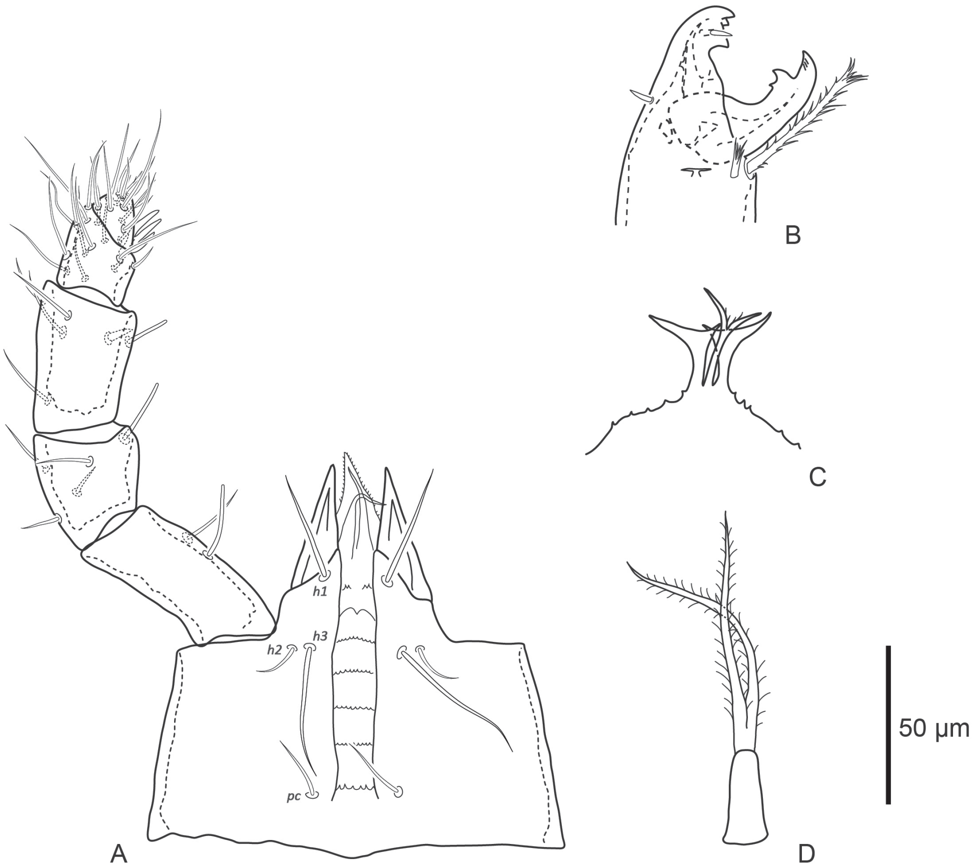

Figure 3. Female *Macrocheles willowae* sp. n. **A** subcapitulum and palp, ventral aspect **B** chelicera, antiaxial aspect **C** epistome **D** tritosternum.

with wide base and flexible filamentous tip. Genu and tibia IV with paired slight ridge anterolateral and posterolateral.

Male and immatures. Unknown.

Etymology. This species is named after my daughter Willow Knee. May it inspire her to notice the little creatures as well as the big.

Remarks. *Macrocheles willowae* sp. n. is most similar to *M. merdarius* (Berlese), *M. nemerdarius* Krantz and Whitaker, and *M. pratum* sp. n. *Macrocheles merdarius* is frequently found in litter, manure and compost worldwide, feeding on nematodes and eggs of insects (Krantz and Whitaker 1988). *Macrocheles merdarius* has been reported from small mammals, and female mites are often phoretic associates of dung beetles (Filipponi and Pegazzano 1963, Krantz and Whitaker 1988). Female *M. willowae* sp. n. differs from that of *M. merdarius* in the shape of the ventrianal shield, shape of the sternal shield, and length of the arthrodial brush. The anterior margin of the ventrianal shield is more truncated, and the widest part of the shield near *JV2* is more angular for *M. merdarius* than it is for *M. willowae* sp. n. The posterior margin of the sternal shield

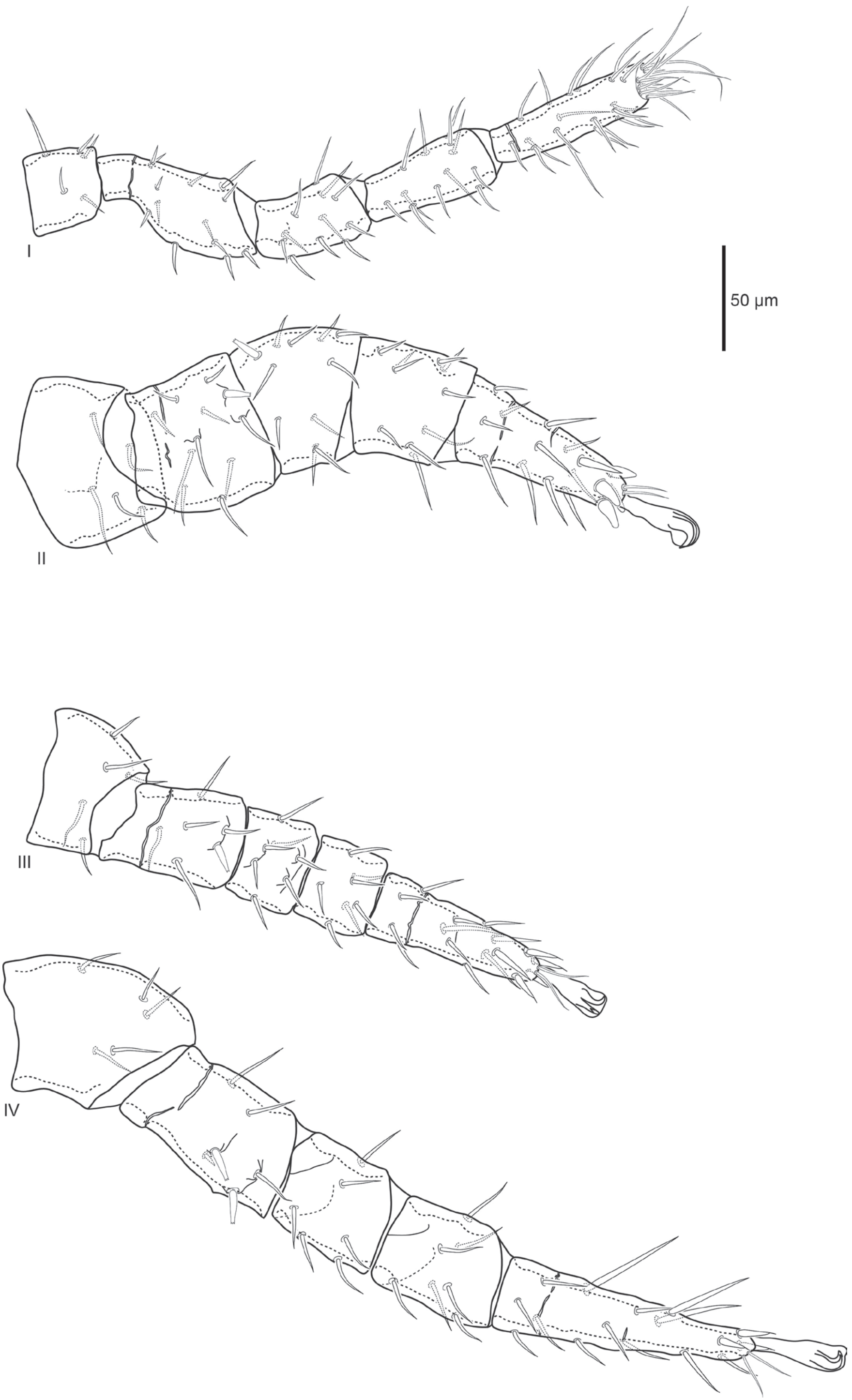

Figure 4. Female *Macrocheles willowae* sp. n. legs I–IV, coxae omitted; leg I anterolateral, II posterolateral, III dorsal, IV anterolateral.

is more concave for *M. willowae* sp. n. The arthrodial brush is almost as long as the movable digit for *M. willowae* sp. n., and for *M. merdarius* the brush is approximately half as long as the movable digit. Comparisons were made using the species description for *M. merdarius* and slide mounted material deposited in the CNC.

Macrocheles nemerdarius was described from the nest of a mouse, *Peromyscus* in Maryland and the nest of the eastern woodrat *Neotoma floridana* in Florida, USA, and this species is also phoretic on coprophilous beetles (Krantz and Whitaker 1988). Female *M. willowae* sp. n. differs from that of *M. nemerdarius* in having marginal or submarginal setae slightly longer than dorsal hexagonal setae, posterior margin of sternal shield more concave, *pon* seta smooth not weakly pilose, *j1* only slightly longer than *z1* not 1.5 times as long, and *J5* slightly shorter than *Z5* not half as long as *Z5*. Comparisons were made using the species description for *M. nemerdarius* and examination of the holotype specimen loaned from the National Museum of Natural History, Smithsonian Institution.

Female *M. willowae* sp. n. differs from that of *M. pratum* sp. n. in having marginal and submarginal setae slightly longer than dorsal hexagonal setae. Genu and tibia IV with slight ridge on anterolateral and posterolateral surfaces in *M. willowae* sp. n., while *M. pratum* sp. n. only has a ridge on the posterolateral surface. Seta *J5* is slightly shorter than *Z5* and more spinose in *M. willowae* sp. n., *J5* is less than half as long as *Z5* in *M. pratum* sp. n. Punctures on the sternal shield are smaller and less prominent in *M. willowae* sp. n. than in *M. pratum* sp. n. The ventrianal shield is longer than wide for both species, but the shield is slightly narrower in *M. pratum* sp. n., ratio of 1.4 compared to 1.3 for *M. willowae* sp. n.

In Krantz and Whitaker (1988), Dr. W. Yoder provided a short diagnosis and partial illustrations of the female and male of an undescribed and unnamed *Macrocheles* species collected from *Nicrophorus* beetles and three mammal species (*Tamiasciurus hudsonius*, American red squirrel in Michigan; *Tamias striatus*, eastern chipmunk in Maryland; and *Zapus hudsonius*, meadow jumping mouse in Prince Edward Island). This undescribed species was a common associate of *Nicrophorus* beetles, but it was also found frequently enough on live rodents to suggest an association with small mammals (Krantz and Whitaker 1988). Dr. W. Yoder reportedly intended to formally describe and illustrate this new species of *Macrocheles*; however, to date this species has not been described. *Macrocheles willowae* sp. n. is likely the same species that Dr. W. Yoder was intending to describe. Over several years, repeated attempts were made to contact Dr. W. Yoder about the status of the description, but contact was unsuccessful.

Macrocheles pratum **sp. n.**

http://zoobank.org/036A8E8D-9669-4524-89B4-4395BC71385A

Figs 5–8, 13B

Material examined. ***Type material.*** Holotype: female (CNC829441) on *Nicrophorus marginatus* (N336, female) collected in Kearney Co., Nebraska, USA, vi.2009, coll: W. Knee & W. Hoback.

Paratypes (11): eight females (CNC829442–829449) with the same collection information as the holotype; two females (CNC829450, 829451) on *N. hybridus* (N242, female), Onefour, Alberta, Canada, 18.vii.2002, coll: W. Knee & D. Johnson; female (CNC829452) on *N. guttula* (N235, female), Onefour, Alberta, 17.vi.2003, coll: W. Knee & D. Johnson.

Other material. 184 mites examined from Alberta and Nebraska on *Nicrophorus guttula*, *N. hybridus*, *N. marginatus*, *N. obscurus*, and *N. pustulatus* (Table 1).

Diagnosis female. All dorsal and ventral setae smooth and spinose, except *J5* barbed and much shorter than *Z5*. Seta *j1* simple with rounded tip, *j1* slightly longer than *z1*. Dorsal hexagonal setae slightly longer than marginal and submarginal setae. Dorsal shield with moderate reticulations throughout, except smooth in dorsal hexagonal area and between *j4* setae, without well-defined procurved line, sigillary rami absent. Sternal shield more than twice as wide as long, punctures moderate size, posterior margin concave. Well defined l.m.t. and l.o.a.; l.o.a. contacts l.m.t. Well defined l.arc. contacts l.o.a., l.ang. and l.o.p. well defined laterally but faint medially. Well defined a.p.l., but a.p.p. not well defined. Ventrianal shield longer than wide (ratio 1.4). Arthrodial brush as long as movable digit. Genu IV with six setae. Femur IV setae *ad2*, *pd1* prominent spikes with flattened forked tip.

Description female. ***Dorsal idiosoma*** (Fig. 5). Dorsal shield 520 (469–547) long and 358 (323–379) (n=8) wide (level with *r3*), with 28 pairs of setae, all setae simple and spinose except *J5* barbed. Seta *J5* 9 (8–10) half as long as *Z5* 22 (18–23). Seta *j1* simple with rounded tip, *j1* 20 (19–21) longer than *z1* 16 (13–18). Marginal and submarginal setae simple, shorter (19) than dorsal hexagonal setae 25 (24–28). Dorsal shield with moderate reticulations throughout, except smooth in dorsal hexagonal area and between *j4* setae, shield without well-defined procurved line, sigillary rami absent, and posterolateral margins narrowed slightly. Shield with 22 pairs of pore-like structures, of which six are secretory glands and 16 are non-secretory poroids.

Ventral idiosoma (Figs 6, 13B). Sternal shield more than twice as wide as long, medial length 92 (86–99), maximum width 217 (196–224) level with a.p.l., and minimum width 114 (110–119) posterior of *st1*. Sternal shield punctures moderate size, posterior margin concave. Setae *st1–3* 40 (35–45) simple and spinose, and two pairs of lyrifissures (*iv1*, *iv2*) on sternal shield. Pear-shaped metasternal shields well separated from sternal shield margin bearing lyrifissure *iv3* anteriorly and spinose seta *st4* 35 (33–39) posteriorly. Well defined l.m.t. and l.o.a., l.o.a. contacts l.m.t. Well defined l.arc. contacts l.o.a., l.ang. and l.o.p. well defined laterally but faint medially. Well defined a.p.l., a.p.p. not well defined. Genital shield length 151 (138–158), width 112 (99–122) level with *st5*. Genital shield truncate posteriorly and hyaline margin rounded anteriorly, spinose seta *st5* 32 (30–34) on shield, pair of lyrifissures *iv5* off shield near posterior margin. Transverse line on genital shield well defined laterally and faint medially, small punctures along transverse line. Peritrematal shield narrow, fused to dorsal shield near *r3*, peritreme extends beyond posterior margin of coxa I, two poroids (*id3*, *id7*) and one gland (*gd3*) on the shield. Ventrianal shield longer than wide (ratio 1.4); length 186 (168–194), width 135 (122–146) level with *JV2*. Ventrianal

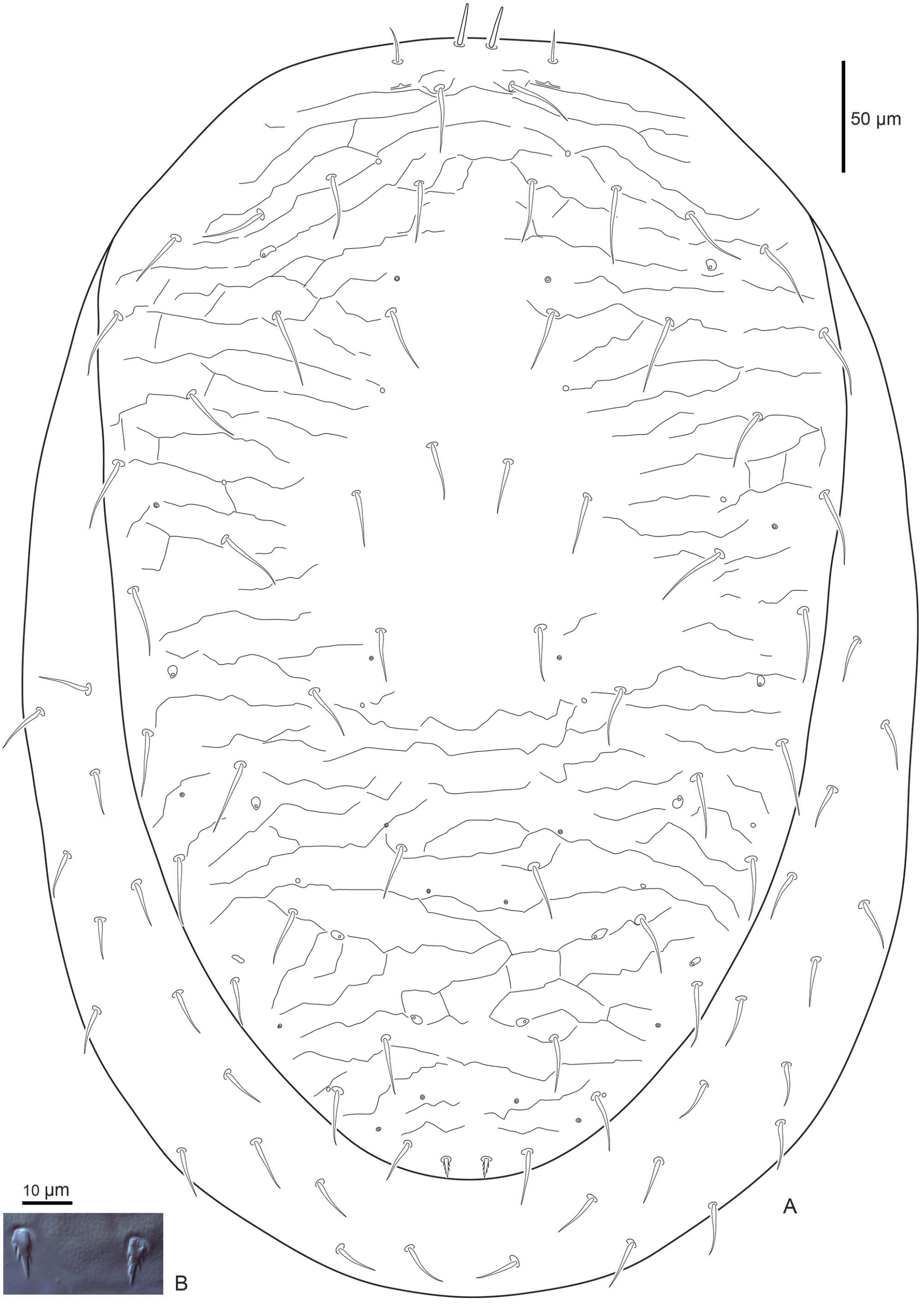

Figure 5. Female *Macrocheles pratum* sp. n. **A** dorsal idiosoma **B** seta *J5*.

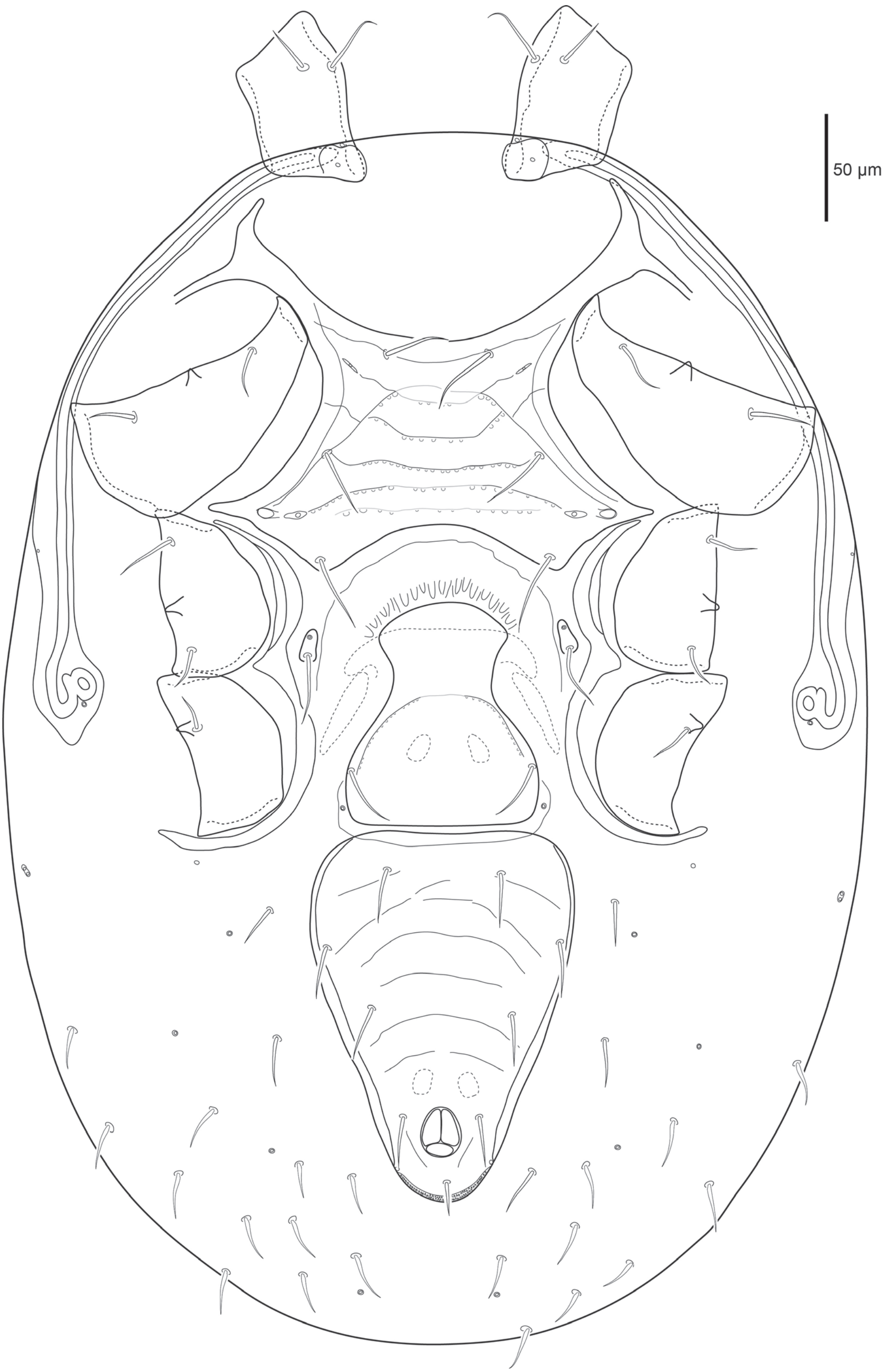

Figure 6. Female *Macrocheles pratum* sp. n. ventral idiosoma including coxae.

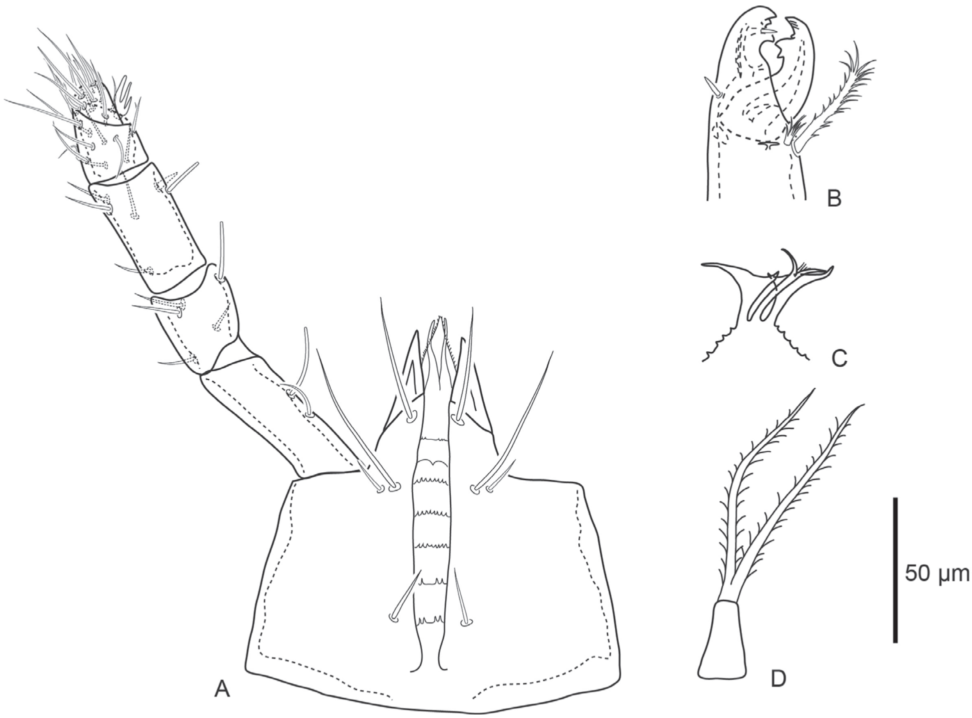

Figure 7. Female *Macrocheles pratum* sp. n. **A** subcapitulum and palp, ventral aspect **B** chelicera, antiaxial aspect **C** epistome **D** tritosternum.

shield bearing several faint transverse lines, three pairs of simple spinose preanal setae *JV1–JV3* 26 (21–29), spinose *pan* 25 (22–28) and *pon* 18 (15–19), narrow cribrum and a pair of glands (*gv3*) on shield margin posterior of the anal opening. Ventral opisthosomal setae in soft integument simple and spinose, *ZV1* 17 (13–23), *ZV2* 25 (21–27) as long or nearly as long as *JV* setae. Two pairs of glands (*gv2* and unknown paired-pore) and four pairs of poroids (*ivo*, *ivp*) in opisthosomal soft integument.

Gnathosoma (Fig. 7). Basis capitulum medial length excluding internal malae 115 (113–116), width 139 (134–143) posterior to *pc*. Subcapitular setae simple: *h1* 44 (41–48), *h2* 16 (13–18), *h3* 57 (51–62), and *pc* 20 (19–23). Palp chaetotaxy normal for genus (2–5–6–14–15), palp apotele three-tined, *al* setae on trochanter, femur and genu slightly spatulate. Corniculi pointed, maximum length 39 (35–45), internal malae slender and smooth. Epistome tripartite with bifid central element bearing small fringe medially, lateral elements broad and flag-like distally, epistomatic margin finely serrate. Subcapitulum with seven rows: six rows have deutosternal denticles, the anterior most, and two posterior most rows with few (four) denticles laterally; the second anterior most row with paired ridges without any denticles. Chelicerae robust, length of second cheliceral segment including fixed digit 135 (122–141), and movable digit 49 (45–52). Fixed digit bidentate with one large and one small tooth, movable digit with a bidentate tooth flanked by a small tooth distally. Pilus dentilis and dorsal seta on

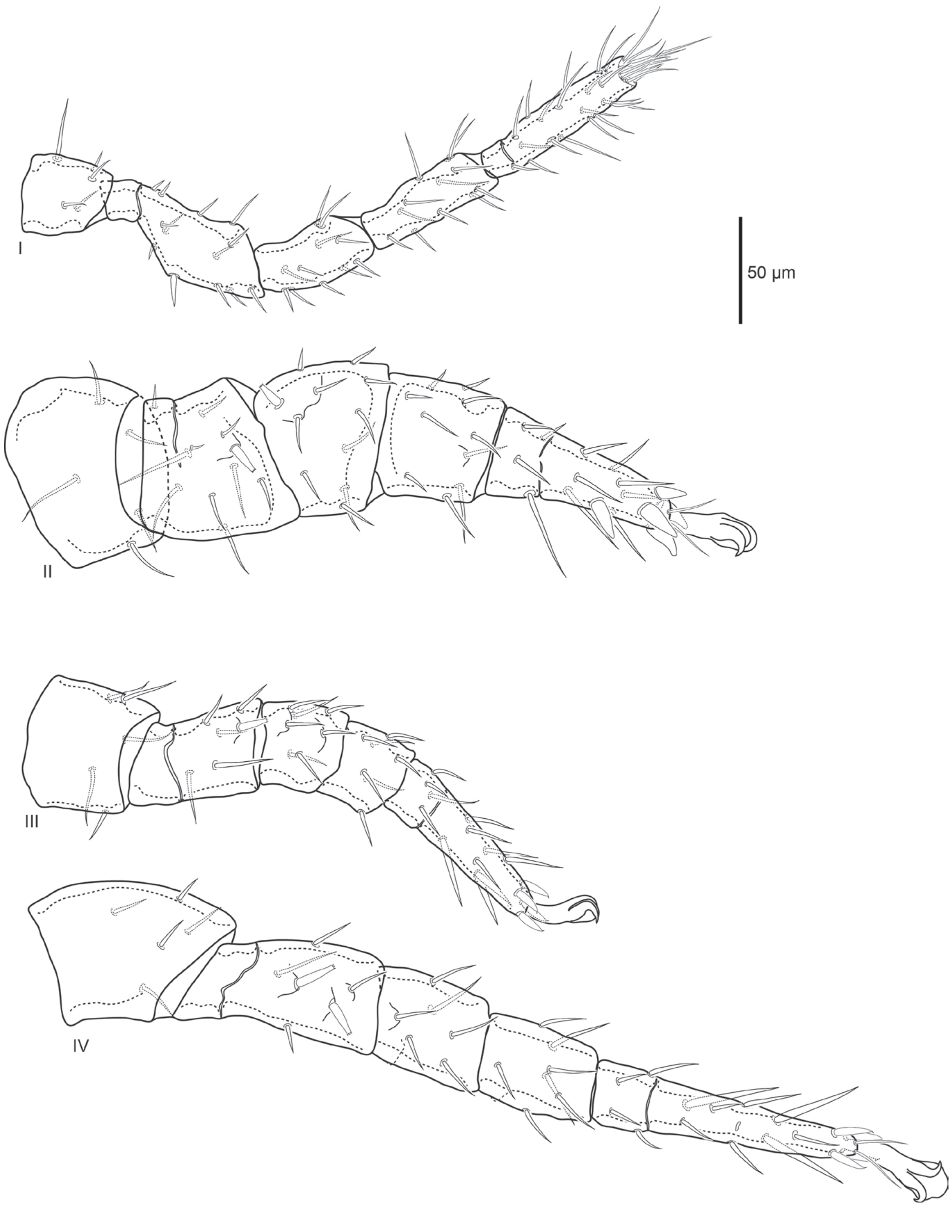

Figure 8. Female *Macrocheles pratum* sp. n. legs I–IV, coxae omitted; leg I anterolateral, II posterolateral, III posterolateral, IV femur dorsal, genu, tibia, tarsus anterolateral.

fixed digit simple spikes, fixed digit with lyrifissure on each paraxial and antiaxial faces. Movable digit with narrow fringed arthrodial corona, and plumose arthrodial brush (47) almost as long as movable digit.

Legs (Fig. 8). Excluding ambulacra, lengths of leg I 418 (409–432), leg II 390 (362–438), leg III 340 (319–358), and leg IV 474 (463–490). As in all *Macroche-*

les ambulacra only present on legs II–IV, claws II–IV well developed. Pair of glands (*gc*) on coxa I. Setation of legs I–IV normal for Macrochelidae: coxae 2–2–2–1; trochanters 5–5–5–5; femora I (2–3/1,2/3–2), II (2–3/1,2/2–1), III (1–2/0,1/1–1), IV (1–2/1,1/0–1); genua I, II (2–3/1,2/1–2), III (1–2/1,2/0–1), IV (1–2/1,2/0–0); tibiae I (2–3/2,2/1–2), II (2–2/1,2/1–2), III, IV (1–1/1,2/1–1); tarsus I 20 setae plus numerous tapered setae dorsoterminally, tarsi II–IV 18. Most leg setae simple, setiform, femur II *ad1*, III *pd1*, IV *ad2*, *pd1*, and genu II *ad3* prominent spike setae with flattened forked tip with two to four tines that can appear as a single tapered point viewed laterally. Tarsus II with four large distal, and one ventral, spike setae with thickened conical base and rounded tip. Tarsi III, IV with four distal spike setae with wide base and flexible filamentous tip. Genu and tibia IV with slight ridge posterolateral.

Male and immatures. Unknown.

Etymology. *Pratum* (Latin neuter noun) means "meadow". This species was only collected in Kearney County, Nebraska and Onefour, Alberta, which are in the prairies.

Remarks. The female of *Macrocheles pratum* sp. n. is most similar to those of *M. willowae* sp. n., *M. nemerdarius*, *M. spinipes* Berlese, and *M. grossipes* Berlese. *Macrocheles pratum* sp. n. differs from *M. willowae* sp. n. as outlined in the *M. willowae* sp. n. description.

Female *M. pratum* sp. n. differs from that of *M. nemerdarius* in having larger more prominent punctures on the sternal shield, the posterior margin of the sternal shield is more concave, *pon* seta is smooth not weakly pilose, *j1* is only slightly longer than *z1* not 1.5 times as long, *J5* is shorter and broader for *M. pratum* sp. n. (9) than for *M. nemerdarius* (13), and the ventrianal shield is narrower, length to width ratio of 1.4 for *M. pratum* sp. n. and 1.2 for *M. nemerdarius*. Measurements were made examining *M. nemerdarius* holotype specimen loaned from the National Museum of Natural History, Smithsonian Institution.

Macrocheles spinipes and *M. grossipes* are associated with coprophilous beetles (Krantz 1988). Female *M. pratum* sp. n. differs from those of *M. spinipes* and *M. grossipes* in having larger more prominent punctures and transverse lines on the sternal shield, the posterior margin of the sternal shield more concave, arthrodial brush nearly as long as movable digit and not half or three quarters as long as movable digit, setae *ad2* and *pd1* on femur IV are large spike-like setae with flattened forked tips with two to four tines, ventrianal shield tapers relatively more towards posterior starting anterior of *pan* setae, and ventrianal shield is narrower, length to width ratio of 1.4 for *M. pratum* sp. n. and 1.2 for *M. spinipes* and *M. grossipes*. Measurements were made examining *M. spinipes* and *M. grossipes* voucher material from the Oregon State University Arthropod Collection.

Macrocheles kaiju sp. n.

http://zoobank.org/1AFFAB07-D38F-429E-9F19-A76E2254787E

Figs 9–12, 13C

Material examined. ***Type material.*** Holotype: female (CNC829453) on *Nicrophorus carolinus* (N333, male) collected Highlands Co. Lake Placid, Florida, USA (27.181, -81.352), 10.iii.2009, coll: W. Knee & S. Peck.

Paratypes (28): 14 females (CNC CNC829454–829467) with the same collection information as the holotype; 13 females (CNC829468–829480) on *N. carolinus* (N334, female), Highlands Co. Lake Placid, Florida, USA (27.181, -81.352), 10.iii.2009, coll: W. Knee & S. Peck; female (CNC829481) on *N. carolinus* (N081), Highlands Co. Lake Placid, Florida, USA (27.181, -81.352), 10.iii.2009, coll: W. Knee & S. Peck.

Other material. 134 mites examined from Florida and Nebraska on *N. carolinus* (Table 1).

Diagnosis female. Dorsal setae smooth and spinose, except *r3*, *r4*, *s6*, *z6*, *S1–S5*, *Z1–Z5*, *J2* barbed distally, *J5* barbed, marginal and submarginal setae barbed distally. Seta *j1* smooth, spike, tapered distally with rounded tip, slightly longer than *z1*. Seta *J5* much shorter than *Z5*. Dorsal hexagonal setae as long as marginal and submarginal setae. Dorsal shield smooth medially with faint reticulations near shield margins, shield tapers from humeral region to posterior margin. Dorsal shield without well-defined procurved line, sigillary rami absent. Setae on sternal, genital and ventrianal shields, and *ZV1* smooth and spinose, other ventral setae in soft integument barbed distally. Sternal shield wider than long, punctures small, posterior margin slightly concave. Well defined l.m.t. and l.o.a.; l.o.a. contacts l.m.t. Well defined l.arc. contacts l.o.a., l.ang. and l.o.p. well defined laterally but faint medially. Well defined a.p.l., but a.p.p. not well defined. Ventrianal shield longer than wide (ratio 1.5), *pon* longer than *pan*, *pon* slightly spatulate. Arthrodial brush nearly as long as movable digit. Genu IV with six setae.

Description female. *Dorsal idiosoma* (Fig. 9). Dorsal shield 736 (647–812) long and 484 (421–547) (n=8) wide (level with *r3*), with 28 pairs of setae. Dorsal setae smooth and spinose, except *r3*, *r4*, *s6*, *z6*, *S1–S5*, *Z1–Z5*, *J2* barbed distally, *J5* barbed, marginal and submarginal setae barbed distally. Seta *J5* 22 (19–24) less than half as long as *Z5* 75 (65–83). Seta *j1* 29 (25–34) smooth, spike, tapered distally with rounded tip, slightly longer than *z1* 24 (20–32). Dorsal hexagonal setae 61 (50–71) smooth and spinose, as long as distally barbed marginal and submarginal setae (61). Dorsal shield smooth medially with faint reticulations near shield margins, shield tapers from humeral region to posterior margin. Dorsal shield without well-defined procurved line, sigillary rami absent. Dorsal shield fused to peritrematal shield near *r3* and anterior margin of shield wraps around onto ventral surface, *j1* on slight projection and typically on the venter, and *z1* occasionally expressed ventrally. Shield with 22 pairs of pore-like structures, of which six are secretory glands and 16 are non-secretory poroids.

Ventral idiosoma (Figs 10, 13C). Sternal shield wider than long, medial length 155 (145–163), maximum width 260 (224–288) level with a.p.l., and minimum width 115 (103–121) posterior of *st1*. Sternal shield punctures small, posterior margin slightly concave. Setae *st1–3* 75 (61–92) simple and spinose, and two pairs of lyrifissures (*iv1*, *iv2*) on sternal shield. Pear-shaped metasternal shields well separated from sternal shield margin bearing lyrifissure *iv3* anteriorly and spinose seta *st4* 80 (73–89) posteriorly. Well defined l.m.t. and l.o.a.; l.o.a. contacts l.m.t. Well defined l.arc. contacts l.o.a., l.ang. and l.o.p. well defined laterally but faint medially. Well defined a.p.l., a.p.p. not well defined. Genital shield length 196 (172–226), width 123 (109–141)

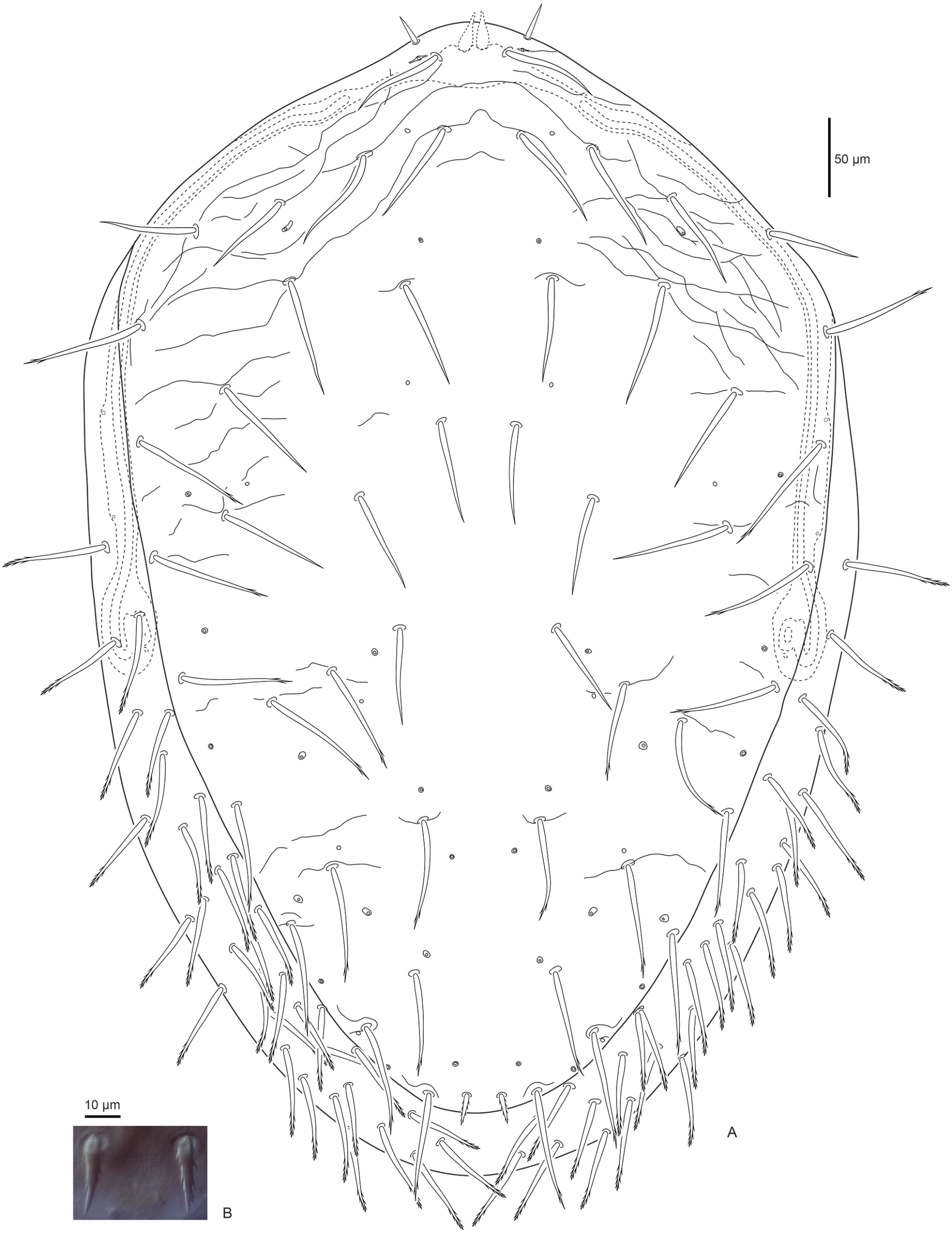

Figure 9. Female *Macrocheles kaiju* sp. n. **A** dorsal idiosoma **B** seta *J5*.

level with *st5*. Genital shield truncate posteriorly and hyaline margin rounded anteriorly, spinose seta *st5* 70 (65–74) on shield, pair of lyrifissures *iv5* off shield near posterior margin. Transverse line on genital shield well defined, and without punctures. Peritrematal shield narrow, fused to dorsal shield near *r3*, peritreme extends beyond

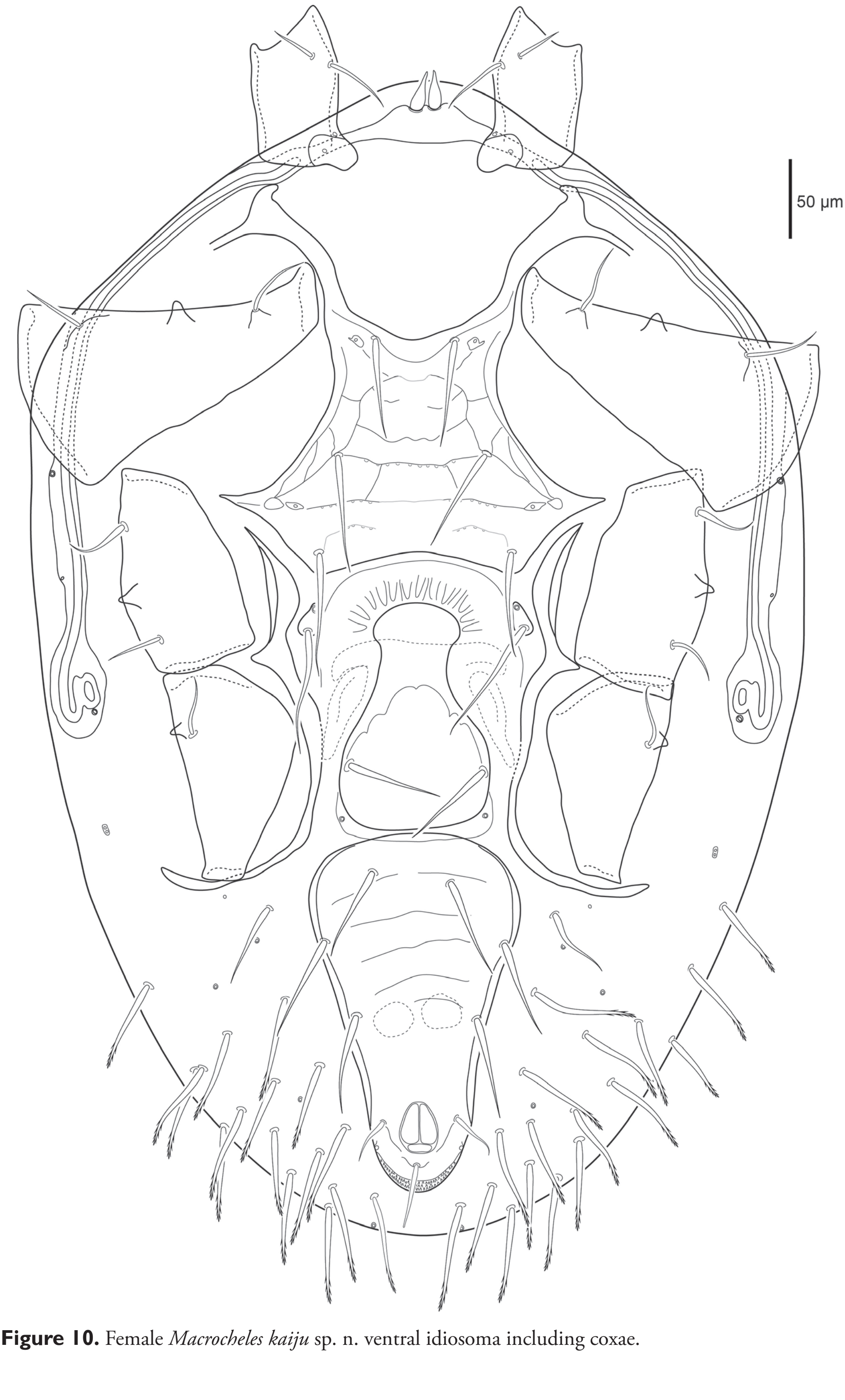

Figure 10. Female *Macrocheles kaiju* sp. n. ventral idiosoma including coxae.

posterior margin of coxa I, two poroids (*id3*, *id7*) and one gland (*gd3*) on the shield. Ventrianal shield longer than wide (ratio 1.5); length 230 (202–250), width 149 (135–160) anterior to *JV2*. Ventrianal shield bearing several faint transverse lines, three pairs of simple spinose preanal setae *JV1–JV3* 65 (64–75), spinose *pan* 37 (26–43) shorter than slightly spatulate *pon* 47 (40–54), narrow cribrum and a pair of glands (*gv3*) on shield margin posterior of the anal opening. Seta *ZV1* 55 (48–60) is simple, all other ventral opisthosomal setae in soft integument barbed distally, *ZV1* and *ZV2* 67 (58–75) as long or nearly as long as *JV* setae. Two pairs of glands (*gv2* and unknown paired-pore) and four pairs of poroids (*ivo*, *ivp*) in opisthosomal soft integument.

Gnathosoma (Fig. 11). Basis capitulum medial length excluding internal malae 159 (152–169), width 158 (153–170) posterior to *pc*. Subcapitular setae simple: *h1* 66 (61–70), *h2* 19 (17–21), *h3* 92 (85–98), and *pc* 25 (24–28). Palp chaetotaxy normal for genus (2–5–6–14–15), palp apotele three-tined, *al* setae on trochanter, femur and genu slightly spatulate. Corniculi pointed, maximum length 50 (45–60), internal malae thick and bristled. Epistome tripartite with bifid central element bearing small fringe medially, lateral elements broad and flag-like distally with irregular barbs, epistomatic margin finely serrate. Subcapitulum with seven rows, six of which have deutosternal denticles; the anterior most row with few (four) denticles laterally, and the second anterior most row with paired ridges without any denticles. Chelicerae robust, length of second cheliceral segment including fixed digit 184 (173–198), and movable digit 64 (60–67). Fixed digit bidentate with one large and one small tooth, movable digit with a bidentate tooth flanked by a small tooth distally. Pilus dentilis and dorsal seta on fixed digit simple spike, fixed digit with lyrifissure on each paraxial and antiaxial faces. Movable digit with narrow fringed arthrodial corona, and plumose arthrodial brush (57) almost as long as movable digit.

Legs (Fig. 12). Excluding ambulacra, lengths of leg I 512 (488–527), leg II 576 (525–622), leg III 482 (436–528), and leg IV 690 (628–737). Ambulacra only present on legs II–IV, claws II–IV well developed. Slight ridge on femur II anterolateral, not always easily visible. Slight ridge on femur IV dorsal, genu and tibia IV posterolateral. Pair of glands (*gc*) on coxa I. Setation of legs I–IV normal for Macrochelidae: coxae 2–2–2–1; trochanters 5–5–5–5; femora I (2–3/1,2/3–2), II (2–3/1,2/2–1), III (1–2/0,1/1–1), IV (1–2/1,1/0–1); genua I, II (2–3/1,2/1–2), III (1–2/1,2/0–1), IV (1–2/1,2/0–0); tibiae I (2–3/2,2/1–2), II (2–2/1,2/1–2), III, IV (1–1/1,2/1–1); tarsus I 20 setae plus numerous tapered setae dorsoterminally, tarsi II–IV 18. Setae on leg I are setiform and simple, setae on legs II–IV variable, most are setiform, others are variously modified. Femur II *ad1*, genu II *ad3*, and trochanter III with a prominent spike setae with flattened forked tip with two to four tines that can appear as a single tapered point viewed laterally. Tarsus II with 13 thick conical spike setae with either a rounded or filamentous tip; filamentous tip fragile and easily broken. Tarsi III, IV with four distal spike setae with wide base and flexible filamentous tip, tip easily broken. Long setae with small spatulate tip with or without barbs on femur IV *ad1, ad2, pd1*, genu IV *al, ad1, pd1, pd2*, tibia IV *al, pl*, and three on tarsus IV. Setae with small spatulate tip appear pointed when viewed laterally.

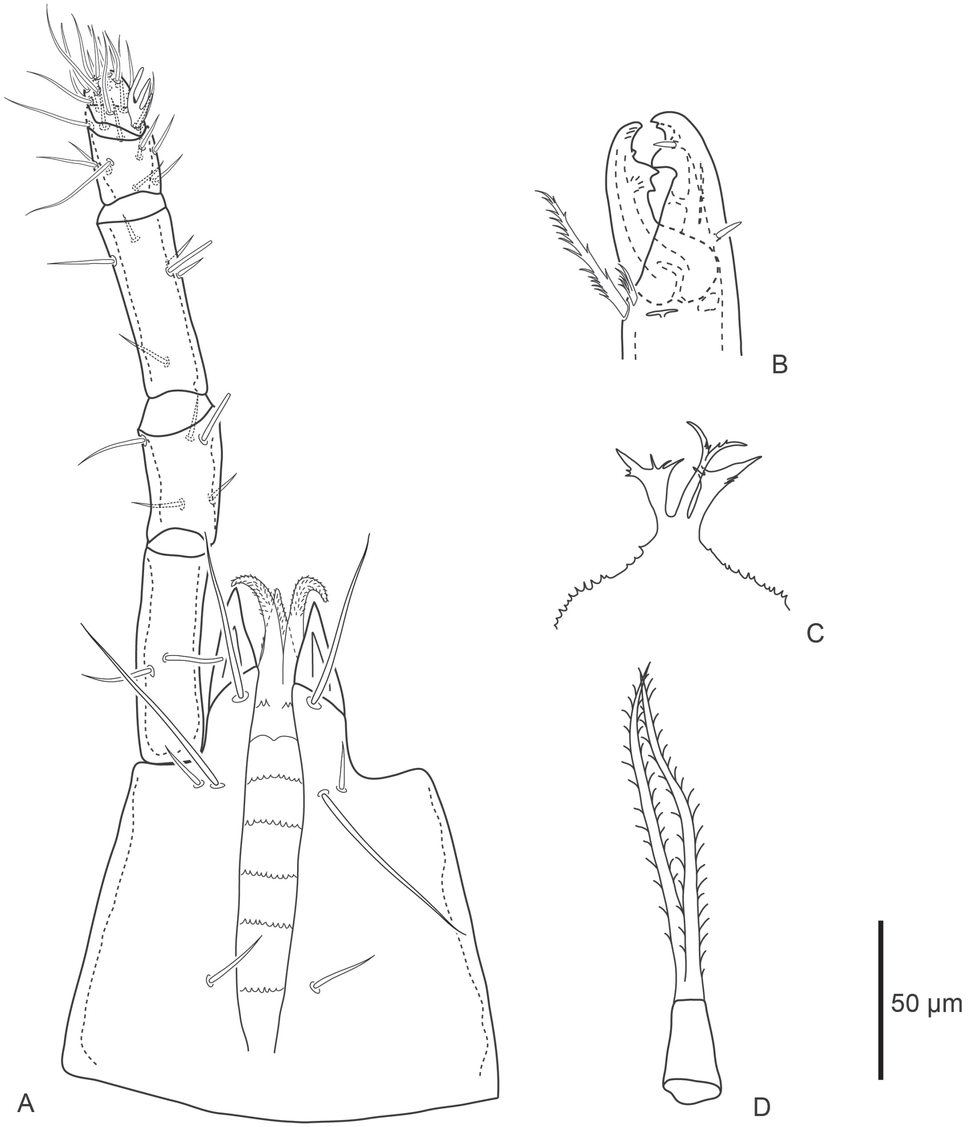

Figure 11. Female *Macrocheles kaiju* sp. n. **A** subcapitulum and palp, ventral aspect **B** chelicera, antiaxial aspect **C** epistome **D** tritosternum.

Male and immatures. Unknown.

Etymology. Kaiju, 怪獣, from Japanese means strange beast, and refers to giant monsters such as Godzilla or Mothra. Female *M. kaiju* sp. n. is relatively unique morphologically when compared to other *Macrocheles* species associated with beetles, it is relatively large, has a unique dorsal shield shape, and bears numerous setae with distinct forms.

Remarks. Female *M. kaiju* sp. n. is different from that of any other described *Macrocheles* species; however, it does fit the *Macrocheles* generic description (see Hy-

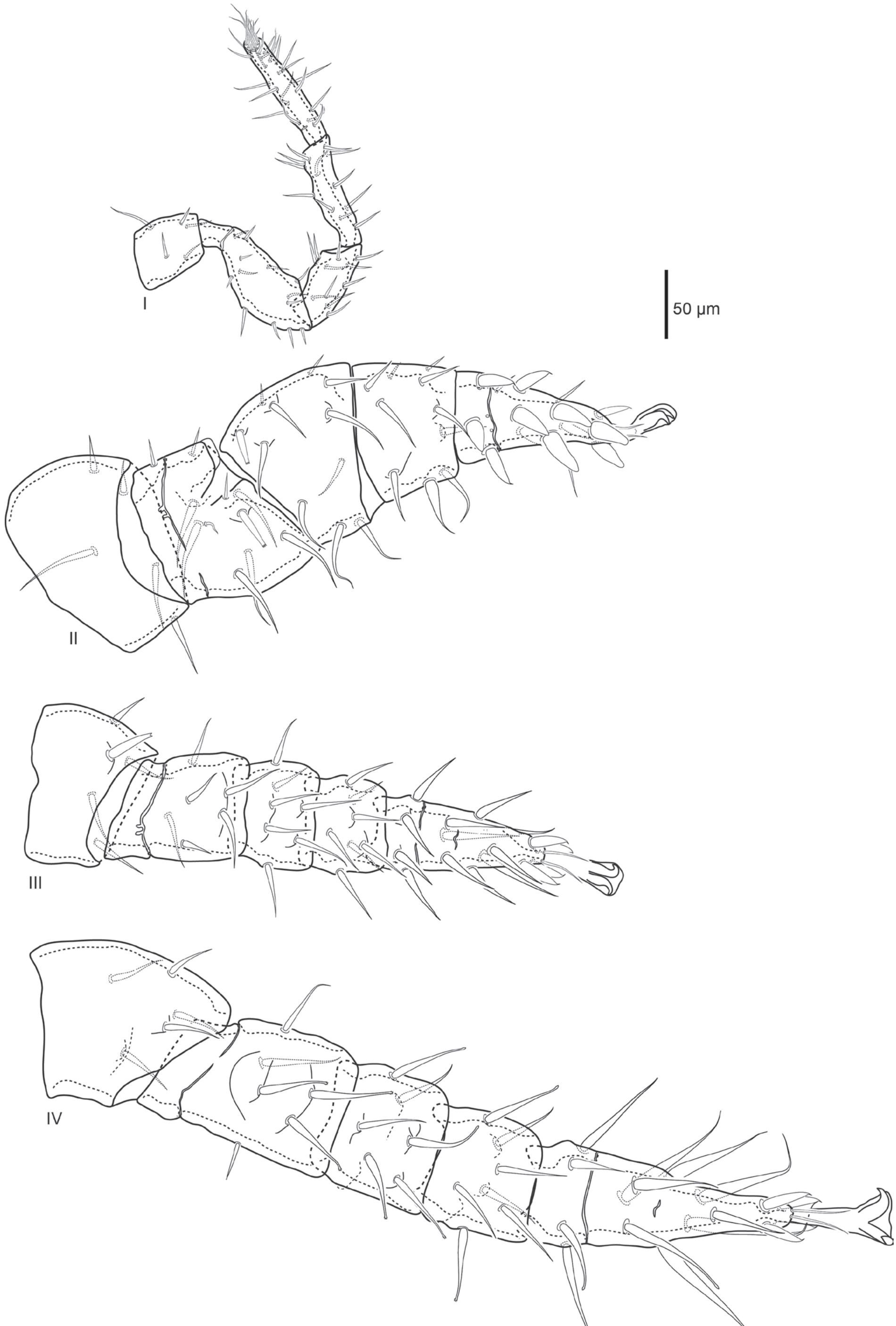

Figure 12. Female *Macrocheles kaiju* sp. n. legs I–IV, coxae omitted; leg I anterolateral, II posterolateral, III and IV dorsal.

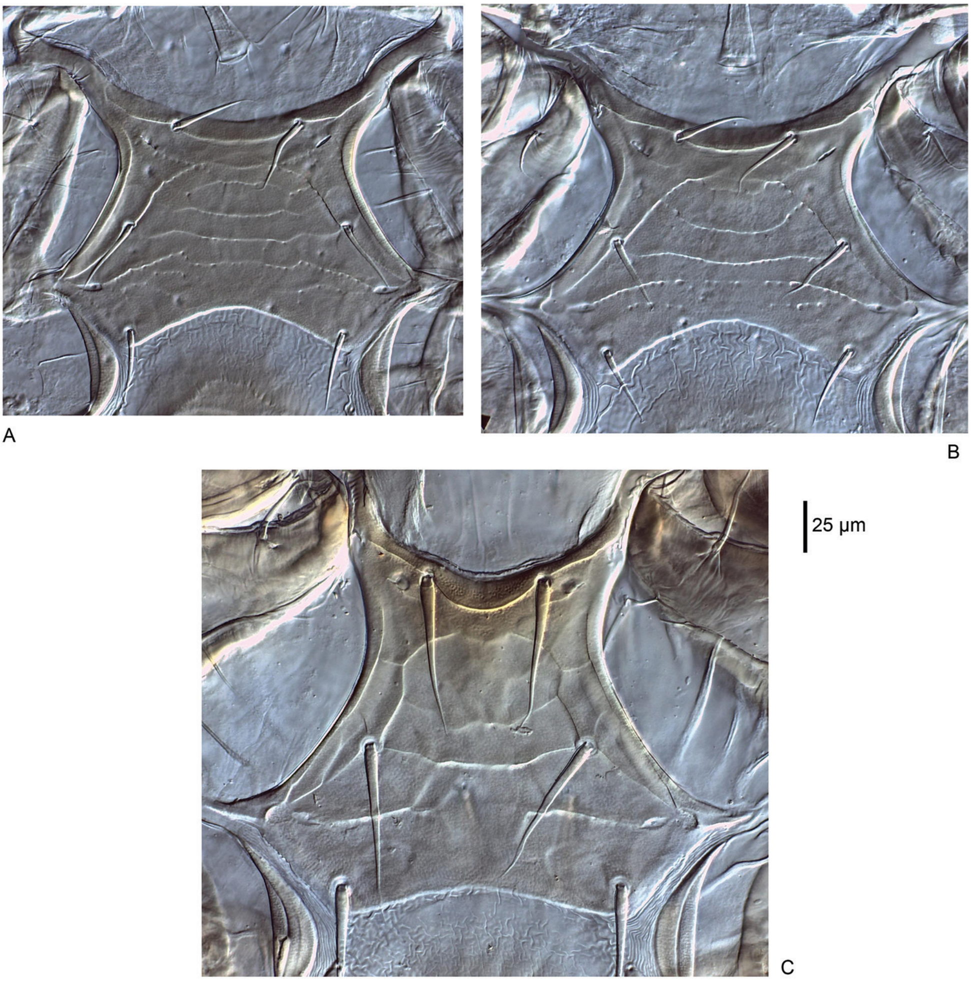

Figure 13. Sternal shield **A** *Macrocheles willowae* sp. n. **B** *M. pratum* sp. n. **C** *M. kaiju* sp. n.

att and Emberson 1988). Female *M. kaiju* sp. n. has two character states that are irregular for *Macrocheles* but somewhat similar to *Holostaspella* (Macrochelidae) species: the anterior margin of the dorsal shield wraps around onto the ventral surface such that *j1* is on a slight projection on the venter; and a slight ridge is present on femur II. *Holostaspella* species are characterised in part by females having a spur on femur II, and *j1* being on a tuberculate anterior extension of the dorsal shield but not wrapped around onto the venter. *Macrocheles kaiju* sp. n. differs from that of *Holostaspella* species in having weak ornamentation on the dorsal shield, its lateral regions without a series of depressions; *j1* is smooth and not pectinate, *j1* is on a slight projection and not a prominent tuberculate extension; sternal shield weakly ornamented and without strong median ridge; and metasternal shields small and always free of endopodal shields.

Phylogenetics

COI was amplified from 14 *Macrocheles* specimens representing six species, with 689 characters in total, 430 constant, 39 parsimony-uninformative, 220 parsimony-informative. NJ analysis (K2P) was performed on 14 ingroup *Macrocheles* specimens. Average intraspecific pairwise distance was low (1.2% ±1.4), and the maximum intraspecific divergence observed was for *M. willowae* sp. n. (2.8%). The higher than average intraspecific divergence for *M. willowae* sp. n. was due to the divergence between mites from different host species. Pairwise distance between *M. willowae* sp. n. mites from *N. defodiens* and those from *N. orbicollis* and *N. carolinus* was higher than average (5.2% ±0.1), while divergence among mites from *N. defodiens* and mites from *N. orbicollis* and *N. carolinus* was low, 0.1 and 0.6% respectively. Mean interspecific divergence was high (20% ±2.8), and the maximum divergence observed was between *M. nataliae* and *M. subbadius* (25%). The range of intra- (0.3–2.8%) and interspecific (15–25%) pairwise divergence did not overlap.

The majority rule consensus tree from the BI analysis of COI was well supported, with all nodes having high posterior probabilities, and eight nodes with 100% support (Fig. 14). *Macrocheles willowae* sp. n. was divided into two well supported clades, one with mites from *N. defodiens* and the other with mites from *N. orbicollis* and *N. carolinus*. *Macrocheles willowae* sp. n. did not appear to diverge based on geographic location (Fig. 14). *Macrocheles willowae* sp. n. mites from *N. defodiens* and those from *N. orbicollis* and *N. carolinus* were morphologically indistinguishable, despite the higher than average intraspecific divergence between these two well supported clades. The phylogenetic relationships between *Macrocheles* species, and the genetic structure of these newly described species, requires further analysis with better taxon sampling, specimens from more host species and localities, and additional molecular markers.

Distribution and biology

Seven species of macrochelids were collected from 112 *Nicrophorus* beetles representing nine species from three countries (Canada, USA, Germany) and 10 provinces or states (Table 1). *Nicrophorus carolinus* was associated with the most *Macrocheles* species (3), three host species had only two macrochelid species, and five had only one macrochelid species. Mites were usually found under the elytra, either clasping onto the integument near the prospiracle (68%) or on the ventral surface of the elytra (22%), and sometimes they were on the coxae (10%). Mites attached to the outer surface of the beetle could have been dislodged into the preservative.

A total of 1659 *Macrocheles* mites were collected from 112 beetles, *M. willowae* sp. n. (1268 mites on 86 beetles) was the most abundant, second most abundant was *M. pratum* sp. n. (196 mites on 15 beetles), *M. kaiju* sp. n. (163 mites on 7 beetles) was the third most abundant, and the four other species of *Macrocheles* collected were at

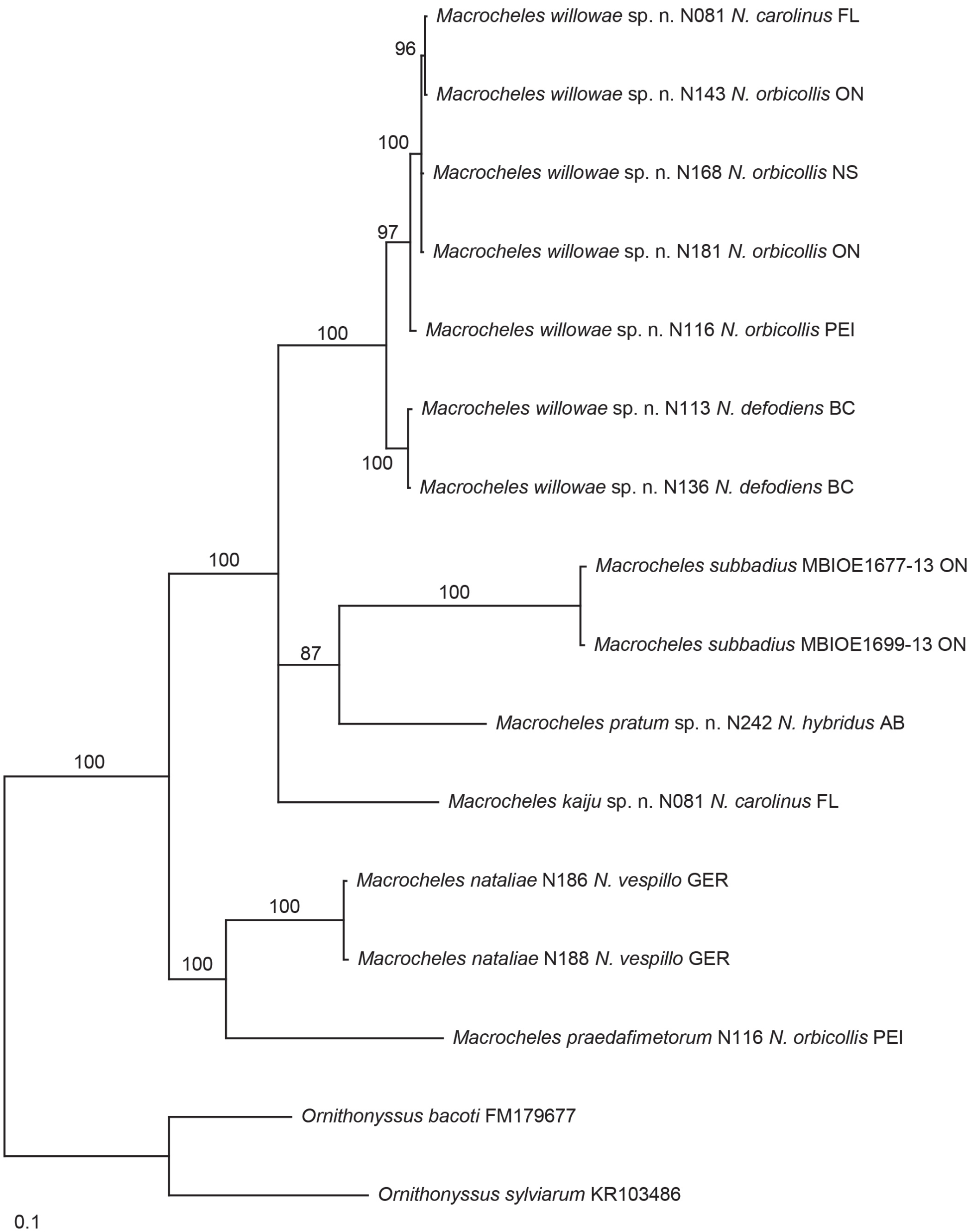

Figure 14. Majority rule consensus tree of 19502 trees generated by Bayesian MCMC analysis (10 million generations) of 689bp fragment of COI from 14 ingroup specimens representing six *Macrocheles* species, and two outgroup specimens representing two species, posterior probabilities >50% shown above branches.

low abundances (32 mites total on 10 beetles) (Table 1). *Macrocheles pratum* sp. n. was collected from five host species and had the greatest host range of all species collected. *Macrocheles willowae* sp. n. collected from three host species had the second broadest host range. *Macrocheles nataliae*, *M. praedafimetorum*, and *M. kaiju* sp. n. were each collected from a single host species.

The species with the greatest geographic range was *M. willowae* sp. n., collected from 22 sites, across seven provinces/states in Canada and USA. *Macrocheles pratum* sp. n. was collected from a single site in Alberta (Canada) and from another site in Nebraska (USA). *Macrocheles kaiju* sp. n. was collected from one site in Florida and another site in Nebraska, USA. The four other macrochelid species collected were each found in a single locale (Table 1).

COI sequences generated in this study were compared against those on GenBank and BOLD, and *M. willowae* sp. n. was the only species to have high level (100%) matches on BOLD. These matching sequences belonged to generic level identified specimens from Alberta, Ontario, Saskatchewan, Nova Scotia, and Florida. The species briefly diagnosed by Dr. W. Yoder was collected from three species of rodents in Maryland, Michigan and Prince Edward Island. Combined together, results from this study, BOLD and Dr. W. Yoder's findings, the geographic distribution of *M. willowae* sp. n. may cover 11 provinces or states in Canada and USA.

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RESEARCH ARTICLE

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Three new records of Nannosquillidae from Taiwan with notes on their ecology (Crustacea, Stomatopoda, Lysiosquilloidea)

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Abstract

The genus *Pullosquilla* Manning, 1978, including *P. litoralis*, *P. thomassini*, and *P. pardus,* has been found in Taiwan for the first time. All three species live in a subtidal sand flat north of the Bitou fishing port within the Kenting National Park, Taiwan. Adult specimens were examined, illustrated, and photographed. The habitat, which all three species share, is described. The implication of such closely related species sharing the same habitat is discussed.

Keywords

Kenting National Park, Nannosquillidae, new record, *Pullosquilla*, western Pacific

Introduction

Among the fourteen genera in the family of Nannosquillidae Manning, 1980, nine have been found in the Indo-West Pacific region (Ahyong 2001). However, only two genera, *Acanthosquilla* and *Bigelowina*, are currently known from Taiwan (Ahyong et al. 2008). Located near the center of Indo-West Pacific region, the number of taxa of stomatopod crustaceans found around Taiwan is surprisingly low (Yeh and Hsueh 2010). One possible explanation is that species with small adult size (e.g., smaller than 5 cm) or with deep burrows could have slipped through traditional collecting gears such as trawl nets or shrimp pots. Here, a detailed visual search was conducted on a subtidal sand flat and recorded, for the first time, three species of *Pullosquilla* Manning, 1978 from Taiwan.

Materials and methods

Surveys of sand-dwelling stomatopods were conducted in April 2014, November 2014, and June–July 2017. All specimens were collected in a sand flat north of the Bitou fishing port in the Kenting National Park, Pingtung County, Taiwan. The approximate GPS coordinates are 21°54.69'N, 120°50.76'E. The sampling site, between 5 to 7 m under water, has an undulating white sandy substrate. Specimens were found by visually locating their burrow entrances, usually a pair of circular holes 2–4 mm in diameter. Using a hand net to trawl 1–2 L of sand, the animal was sieved out on the spot. While sieving, special attention was given to avoid a sandy plume rising above the rim of the hand net; shaking the hand net horizontally for a few seconds at a time and looking for the animals above the remaining sand. Once found, individuals or pairs of animals were placed in 20 ml plastic vials with ambient seawater and brought back to laboratory for identification. Collected specimens were measured, photographed, and transferred to 75% alcohol for further analysis. Examined specimens in this study are deposited in National Museum of Nature Science (**NMNS**), Taichung City, Taiwan and National Chung Kung University (**NCKU**), Tainan City, Taiwan.

Morphological terminology and abbreviations follow Ahyong (2001). Total length (TL) was measured along the midline from apex of the rostral plate to the apices of the submedian teeth. Abbreviations include:

A1 antennule
A2 antenna
AS abdominal somite

Taxonomy

Pullosquilla litoralis (Michel & Manning, 1971)

Figs 1–3

Austrosquilla litoralis Michel & Manning, 1971: 237–239, fig. 1.
Pullosquilla litoralis: Manning 1978: 19–20; Ahyong 2001: 165–166, fig. 82.

Material examined. NMNS-7834-001, 1 female (TL 11.8 mm), April 2014. NCKU-0103-01, 1 male (TL 13.1 mm); NCKU-0103-02, 1 female (TL 8.8 mm), November 2014. NMNS-7834-002, 1 female (TL 15.7 mm); NMNS-7834-003, 1 male (TL 13.7 mm); NMNS-7834-004, 1 male (TL 18.0 mm), July 2017.

Figure 1. *Pullosquilla litoralis* Michel & Manning, 1971, male specimen from Taiwan. TL 18.0 mm, dorsal view, color in life.

Diagnosis. Cornea subglobular. Eyes extending to the end of the A1 peduncle. Rostral plate with acute apex; triangular-shaped, broader than long. Ocular scale fused along midline. Dorsal processes of A1 somite forming long triangular lobes directed anterolaterally (Fig. 2A).

Rostral claw dactylus with 10–12 teeth. Propodus occlusal margin pectinate, with four movable spines proximally. Distal end of ischium ventrally armed with a short spine (Fig. 2B). Basal segments of pereiopods 1–3 with short lateroventral spine. Mandibular palp absent; five epipods present.

AS6 without ventrolateral spine anterior to the uropod articulation (Fig. 2C). Telson with median semi-circular projection and submedian projection, acute in males greater than 13 mm but blunt in females. Posterior margin of telson with one pair of movable submedian teeth and 7–9 submedian denticles on either side of midline. Posterolateral margins of telson with two pairs of fixed primary teeth, of which lateral primary teeth are smaller than intermediate ones, and with one lateral and four intermediate denticles (Fig. 2D).

Uropodal protopod with single distal spine at inner margin above articulation of exopod; inner primary spine longer than outer. Outer margin of proximal uropodal exopod segment with three curved, movable spines, inner margin with 2–4 stiff setae. Exopod distal segment ovate and elongated. Endopod subtriangular and elongated (Fig. 2C, D).

Distribution. French Polynesia and Australia to the Western Indian Ocean (Ahyong 2001), and now Taiwan. Currently, Taiwan is the northernmost habitat known for *P. litoralis*.

Remarks. The specimens of *P. litoralis* from Taiwan agree well with the female holotype reported in Michel and Manning (1971) and other collections described in Manning (1978) and Ahyong (2001). In addition to sexual dimorphic coloration in their chromophores (Ahyong 2001), it was observed that the shape of submedian projections on the telson also differ between sexes. By comparing the adult male and female specimens with TL greater than 13 mm, it is noticeable that the posterior margin form blunt and short submedian projections in females, while males bear acute and long submedian projections, which protrude beyond the median lobe of the telson (Fig. 3).

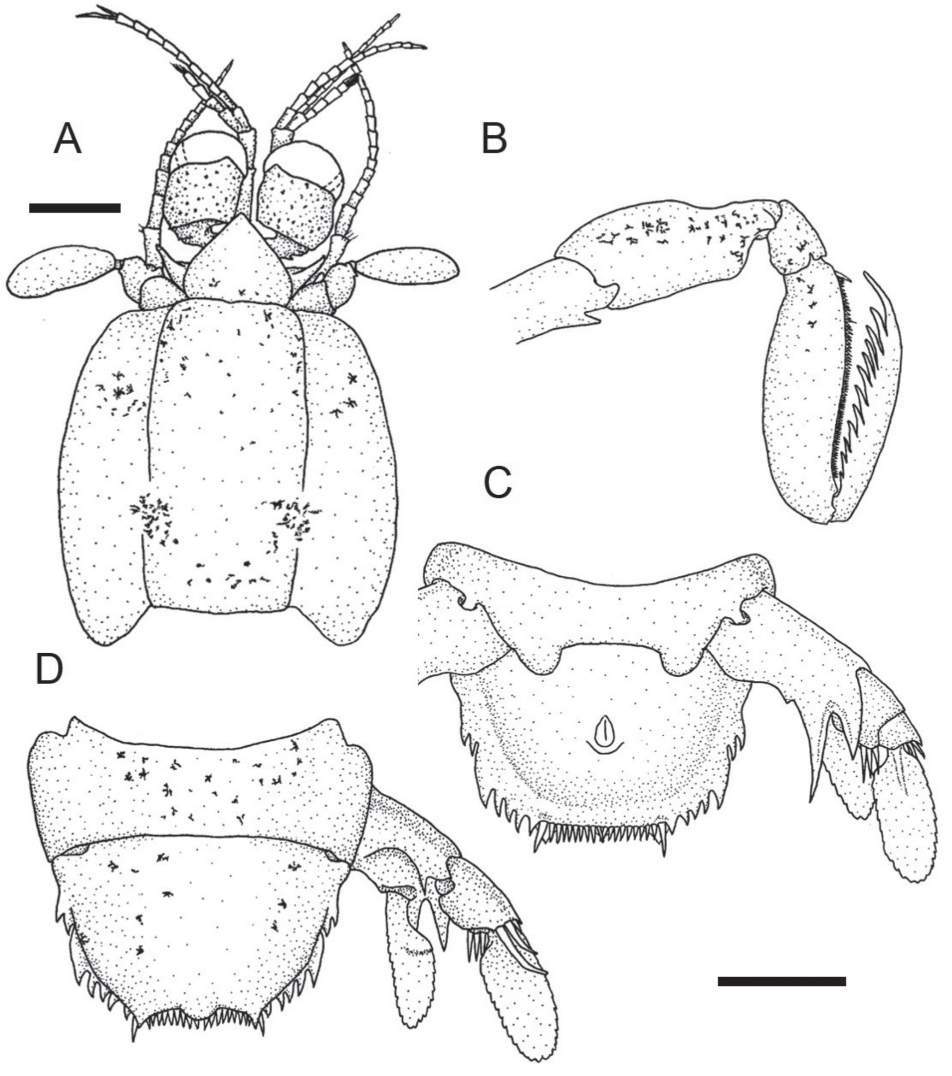

Figure 2. *Pullosquilla litoralis* Michel & Manning, 1971, male specimen from Taiwan, TL 18.0 mm: **A** cephalon, dorsal **B** raptorial claw, right lateral **C** telson and uropod, ventral **D** telson and uropod, dorsal. Scale bars: 1 mm.

Pullosquilla thomassini (Manning, 1978)

Figs 4–5

Pullosquilla thomassini Manning, 1978: 20–21, fig. 9; Manning 1980: 269–270; Ahyong 2001: 168–170, fig. 84.

Material examined. NMNS-7834-009, 1 female (TL 14.6 mm), June 2017. NMNS-7834-010, 1 male (TL 16.2 mm), July 2017.

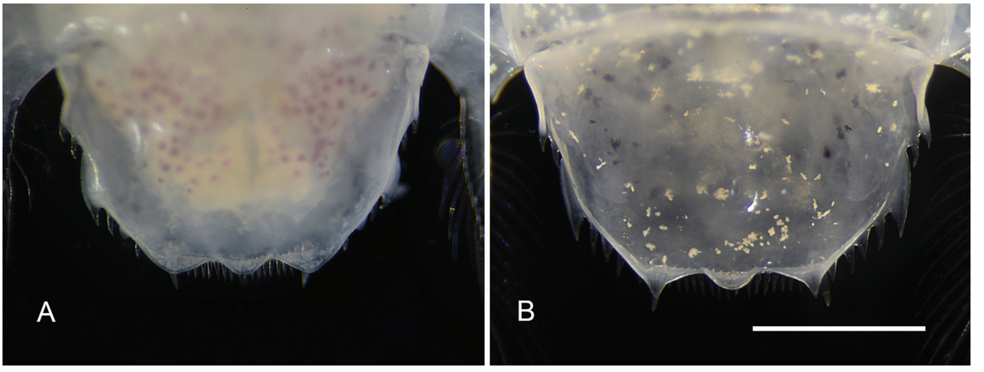

Figure 3. Morphology of telson in female and male *Pullosquilla litoralis* Michel & Manning, 1971: **A** female telson, dorsal view, TL 15.7 mm **B** male telson, dorsal view, TL 18.0 mm. Scale bar: 1 mm.

Figure 4. *Pullosquilla thomassini* Manning, 1978, female specimen from Taiwan. TL 14.6 mm, dorsal view, color in life.

Diagnosis. Cornea subglobular. Eyes reaching to the end of the A1 peduncle. Rostral plate triangular, longer than broad; apex depressed anteriorly. Dorsal processes of A1 somite forming sharp spines directed anterolaterally; with slightly sinuate margin. A2 protopod with blunt projection adjacent to basal rostral plate (Fig. 5A).

Rostral claw with 13–14 teeth on dactylus. Propodus pectinate; occlusal margin pectinate, and with 4 movable spines proximally. Distal end of ischium ventrally armed with slender spine (Fig. 5B). Basal segment of pereiopods 1–3 posteriorly with short spine. Mandibular palp absent; five epipods present.

AS6 with one ventrolateral spine at each lateral margin anterior to uropodal articulation; posterior margin on ventral surface with two spines directed posteriorly. Telson broader than long; dorsal surface smooth; mid-ventral surface covered with short spines. Lateral margin of telson with four broad and curved spines directed posteriorly, each ventro-medially flanked by slender spine. Posterior margin of telson depressed, forming a broad false eave with 21 posteriorly directed small spines, placed in row. Ventromedial telson margin with 12–13 submedian denticles either side of midline (Fig. 5C, D).

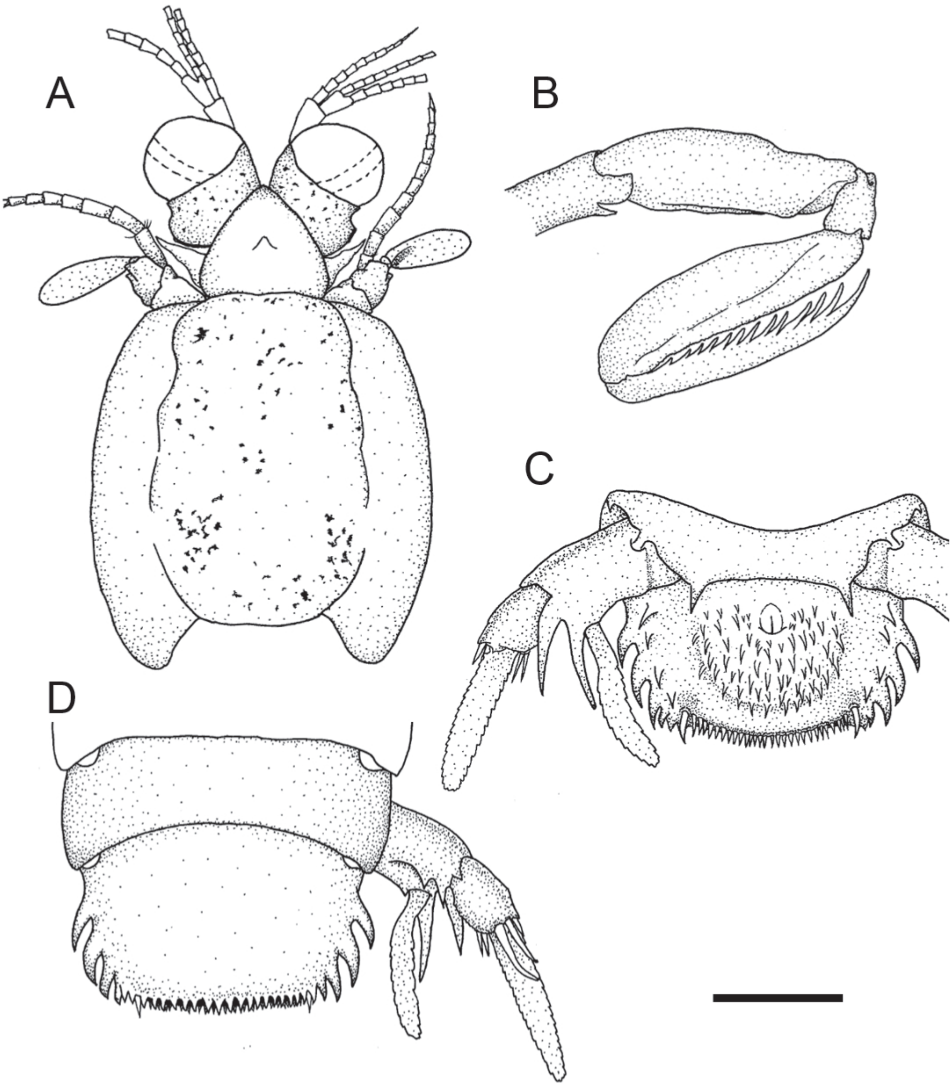

Figure 5. *Pullosquilla thomassini* Manning, 1978, female specimen from Taiwan, TL 14.6 mm: **A** cephalon, dorsal **B** raptorial claw, right lateral **C** telson and uropod, ventral **D** telson and uropod, dorsal. Scale bar: 1 mm.

Uropodal protopod with two distal spines above proximal exopod articulation; with two primary spines, inner spine longer than outer spine. Outer margin of uropodal exopod proximal segment with 3 movable spines, inner margin with 2–4 stiff setae. Distal segment of exopod and endopod slender and elongated (Fig. 5C, D).

Distribution. Based on Ahyong (2001), *P. thomassini* is widely distributed in the Indo-West Pacific region (Australia, French Polynesia to Ogasawara Island, Japan). These specimens are the first records of *P. thomassini* from Taiwan.

Remarks. The telson of *P. thomassini* is unique in the genus by bearing four strong spines on lateral margins, each flanked by a short spine on its inner ventral surface (Fig. 5C). Two specimens examined here, a female (TL 14.6 mm) and a male (TL 16.2 mm), agree well with the descriptions of *P. thomassini* by Manning (1978) and Ahyong (2001).

Pullosquilla pardus (Moosa, 1991)

Figs 6–7

Pullosquilla pardus Moosa, 1991: 184–185, fig. 8; Ahyong 2001: 165–168, fig. 83.

Material examined. NCKU-0102-01, 1 male (TL 12.3 mm); NCKU-0103-03, 1 male (TL 17.9 mm); NCKU-0103-04, 1 female (TL 13.1 mm), November 2014. NCKU-0104-01, 1 female (TL 19.7 mm); NCKU-0104-02, 1 female (TL 22.7 mm); NCKU-0104-03, 1 female (TL 21.9 mm); NCKU-0104-04, 1 male (TL N/A); NCKU-0104-05, 1 male (TL 23.1 mm); NMNS-7834-005, 1 male (TL 21.3 mm); NMNS-7834-006, 1 male (TL 20.4 mm); NMNS-7834-007, 1 female (TL 23.8 mm), June 2017. NCKU-0105-04, 1 female (TL N/A); NCKU-0105-05, 1 female (TL 24.0 mm); NCKU-0105-06, 1 female (TL 20.9 mm); NMNS-7834-008, 1 female (TL 25.3 mm); NCKU-0105-08, 1 female (TL 19.4 mm); NCKU-0105-09, 1 female (TL 23.2 mm); NCKU-0105-10, 1 female (TL 22.8 mm), July 2017.

Diagnosis. Cornea subglobular. Eyes reaching to end of A1 peduncle. Rostral plate cordiform, broader than long. Dorsal processes of A1 somite forming elongated triangular lobes directed anteriorly. A2 protopod with mesial and ventral papilla (Fig. 7A).

Raptorial claw dactylus with 12–13 teeth; propodus occlusal margin pectinate, proximally with 4 movable spines. Distal end of ischium armed with an anteroventrally-directed spine (Fig. 7B). Basal segment of pereiopods 1 and 2 each armed with inner and outer spines; basal segment of pereiopod 3 with outer spine only. Mandibular palp absent, five epipods present.

AS6 with ventrolateral spine anterior to uropodal articulation (Fig. 7C). Telson broader than long; dorsal surface posteriorly with one blunt subtriangular projection; lateral margins unarmed; posterior margin with a pair of movable submedian teeth and four pairs of fixed primary teeth. Margins between each primary tooth with denticle except for submedian margin, with 5–8 submedian denticles either side of midline (Fig. 7D).

Uropodal protopod with slender distal spine at inner margin above articulation of exopod. Outer margin of proximal uropodal exopod segment laterally armed with a short fixed spine; distally with4 straight movable spines directed posteriorly; medially with stiff seta. Exopod distal segment and endopod both ovate in shape (Fig. 7C, D).

Distribution. New Caledonia through Timor Sea to northwest shelf, Australia, and now Taiwan. This is the first record of *P. pardus* in the northern Hemisphere.

Figure 6. *Pullosquilla pardus* Moosa, 1991, male specimen from Taiwan. TL 20.4 mm, dorsal view, color in life.

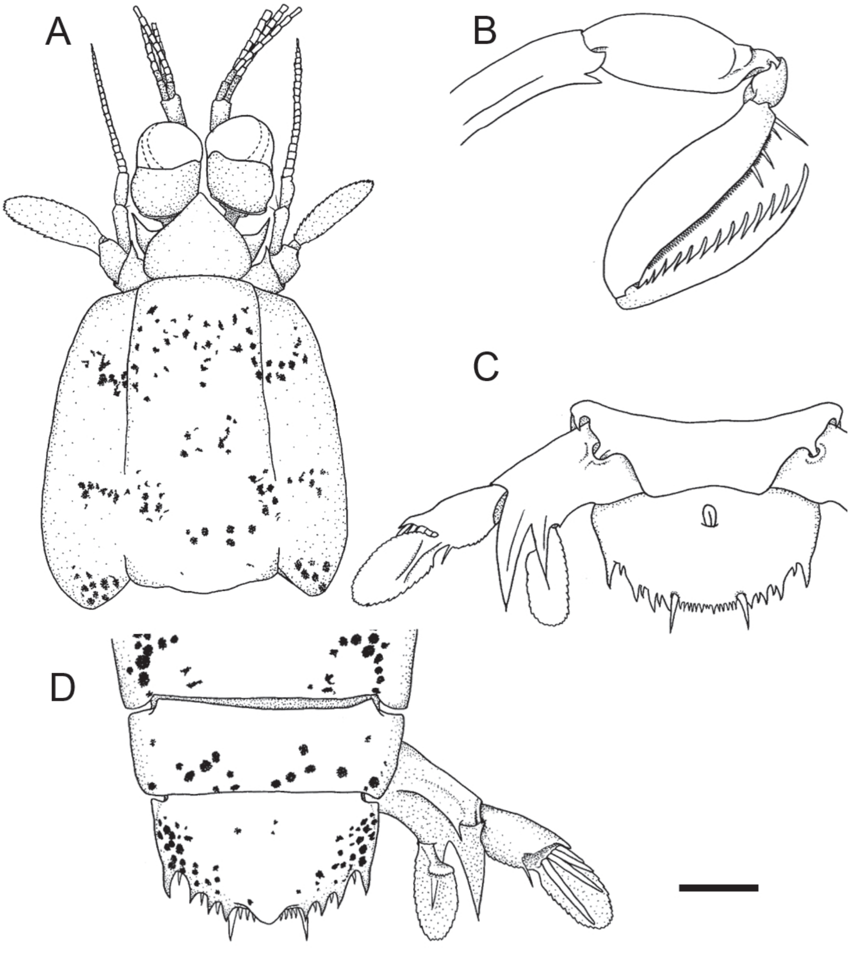

Figure 7. *Pullosquilla pardus* Moosa, 1991, male specimen from Taiwan, TL 21.3 mm: **A** cephalon, dorsal **B** raptorial claw, right lateral **C** telson and uropod, ventral **D** telson and uropod, dorsal. Scale bar 1 mm.

Remarks. According to Moosa (1991), *P. pardus* most closely resembles *P. malayensis* of the other *Pullosquilla* species (Moosa 1991). Specimens collected in this study agree well with the characteristics of *Pullosquilla pardus* reported in Moosa (1991) and Ahyong (2001). In addition to the differences described by Moosa (1991), the outer spine of the uropodal protopod in our specimens is always longer and stronger than the inner spine, unlike that in *P. malayensis,* which has a shorter and slenderer outer spine (Manning 1968).

Discussion

Pullosquilla is a genus of small sand burrowing stomatopods within the superfamily Lysiosquilloidea. Currently, *Pullosquilla* contains four species: *P. litoralis*, *P. thomassini*, *P. pardus,* and *P. malayensis* (Ahyong 2001). They grow into one of the smallest adults among spearing stomatopods and are named for their immature appearance (Manning 1978). Similar to many other Lysiosquilloidea, they often live in U-shaped burrows made of a mucus-sand mixture (pers. obs.; Caldwell 1991). However, within the Nannosquillidae, *Pullosquilla* is the only genus known to form long-term mated pairs sharing the same burrow (Jutte 1997; Wright 2013). As a result of this special monogamous life style, *P. litoralis* and *P. thomassini* has been systematically studied with respect to their pairing and biparental care behavior (Jutte 1997; Lindstrom 2003; Wright and Caldwell 2015).

Probably due to the scarcity of specimens, the pairing and breeding systems of *P. pardus* have rarely been studied. The only report regarding monogamous pairing of *P. pardus* is speculation on taxonomic samples collected from Timor Sea (Ahyong 2001). In the current study site, more than half of the burrows located belonged to *P. pardus.* Likewise, monogamous pairs were extracted from single U-shaped burrows, some of which were still caring for their donut-shaped egg clutch. Consequently, monogamous pair bonding and parental care in *P. pardus* is now confirmed.

In this study, only a tiny portion, approximately 150 m^2, of a relative large and continuous sandy bottom of more than ten hectares were surveyed. In such a small area, three of the four known *Pullosquilla* species, *P. thomassini*, *P. litoralis*, and *P. pardus*, were discovered. Although we failed to find *P. malayensis*, it is interesting to note that this is the first record of the sympatry of more than two *Pullosquilla* species. The previous records regarding the co-occurrence of *Pullosquilla* came from Tiahura, Moorea, Society Islands, and Tulear, Madagascar, where only *P. litoralis* and *P. thomassini* could be found from the surveyed reef complexes (Manning 1978). However, based on the time, depth, and location of collection it is highly possible that *P. malayensis* and *P. thomassini* coexist in Double Reefs, Guam (Ahyong and Erdmann 2003).

The study site is located slightly south of the famous Shell Beach Preservation Zone of the Kenting National Park. While it might appear to be a uniform continuous sandy substrate, there could be some unobserved factors that support the coexistence of these *Pullosquilla* species. One particular feature of the collection site, which is also the reason for its designation of the Shell Beach Preservation Zone, is the composition of the sand. From the slope of the Shell Beach, it is immediately obvious that the sand grains are very coarse. In conjunction with the nearshore currents, the sandy seabed rarely settles. As a result, there is hardly any coral or algae cover beyond the drop-offs of the nearshore reef flat. The lack of hiding places or food for relatively larger predators in this region could thus be favored by these small sand-dwelling stomatopods.

No research on *P. pardus* has been done beyond its taxonomic descriptions, probably due to few accessible localities were known for surveys. In Moosa (1991) and Ahyong (2001), among four records of the *P. pardus*, the holotype of *P. pardus* and one of the specimens from Australia were both collected at depth over 40 m, while only two other specimens were captured in sand at 6 m. Here, in this survey, more *P. pardus* were caught than *P. litoralis* and *P. thomassini* combined: of the 24 burrows, 17 belonged to *P. pardus* while only five and two burrows were occupied by *P. litoralis* and *P. thomassini,* respectively. Among them, two monogamous pairs were evacuated from two burrows, one of which was occupied by *P. pardus* and the other belonged to *P. litoralis*. No triples were found in any of the burrow. During the collection, *P. pardus* could easily be recognized by its panther-like color pattern and large body size, while other two species needed further examination. Although the sample sizes are too small to have any statistical significance, during the survey it was observed that *P. pardus* were evenly distributed throughout the subtidal region. They could be caught from near shore sandy substrate at approximately 3 m depth to the sandy plain at 7–9 m depth. On the other hand, the burrows occupied by *P. litoralis* were usually found on the sandy plain farther away from shore, at depths of 6 to 9 m. They were rarely observed on the near shore sandy substrate at 3-5 m depth. Although our sampling did not cover all seasons, it is suggested that the current location could be a good locality for a detailed study of the behavior of *P. pardus*. Except for the genus *Pullosquilla*, several burrows of larger stomatopods were also observed, potentially those of Lysiosquilloidea, on the same sand plain. However, proper collecting tools are required in order to retrieve these larger stomatopods for further examination and identification.

Stomatopod crustaceans are abundant worldwide throughout tropical and temperate waters, where they burrow in coral rock, coral rubble, or sandy benthic substrates (Ahyong et al. 2017). There were 29 genera, and 64 species of stomatopod crustaceans reported from Taiwan (Ahyong et al. 2008; Yeh and Hsueh 2010). In this study, by performing detailed hand surveys throughout the subtidal sand flat, we have successfully found new records from Taiwan, including an additional genus *Pullosquilla* and three more species of *Pullosquilla*. Since previous studies obtained specimens mainly by trawling, certain species were inevitably under-represented. For example, the records of Lysiosquilloidea were limited, presumably because larger species typically burrow too deeply while smaller species are too small to be caught in trawl nets. Overall, our findings not only expand the reported distribution of *Pullosquilla* stomatopods in the western Pacific Ocean but also contribute to the understanding of cohabitation and monogamous behaviors in genus *Pullosquilla*. Further studies comparing mating and breeding behaviors among these species will likely yield more insight into their unique monogamous system. Based on the diversity of stomatopods found in the Indo-West Pacific region, it is assumed that numerous stomatopod species are yet to be discovered from Taiwan.

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The geographical patterns of distribution of the genus *Teuthraustes* Simon, 1878 in Ecuador and description of three new species (Scorpiones, Chactidae)

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Abstract

Three new species of scorpions belonging to the genus *Teuthraustes* Simon, 1878 (Scorpiones: Chactidae) are described from the Amazonian and Pacific regions of Ecuador. The new descriptions raise to four the number of *Teuthraustes* species in Ecuadorian Amazonia and raise to two the number of species described from the Pacific region. The total number of species of *Teuthraustes* is now 27, including 15 in Ecuador. The geographical distribution of the genus in Ecuador is enlarged and its pattern of distribution in the country is also commented upon.

Keywords

Amazon, biodiversity, Ecuador, geographical distribution, new species, Pacific, scorpion, taxonomy, *Teuthraustes*

Introduction

The genus *Teuthraustes* was created by Simon (1878) based on a new species, *Teuthraustes atramentarius* Simon, 1878 collected in Ecuador by M. Deville of the Brussels Museum. Both the genus and species descriptions are extremely reduced and poorly diagnosed.

Between Simon's (1878) description and the revision of the genus by Kraepelin (1911), thirteen additional species were described or transferred to *Teuthraustes*. With the exceptions of *T. amazonicus* (Simon, 1880) and *T. glaber* Kraepelin, 1912, both described from Peru, all other species are known from Ecuador. Even if the taxonomic status of some Ecuadorian species is still uncertain, this remarkable concentration of species in Ecuador is realistic and can be explained by biogeographic models (Lourenço 1995a).

From the revision by Kraepelin (1911) until the monograph work of Mello-Leitão (1945) no new species of this genus were described. Subsequently, five new species were described from Venezuela, *T. carmelinae* Scorza, 1954, *T. adrianae* González-Sponga, 1975, *T. akananensis* González-Sponga, 1984, *T. maturaca* González-Sponga, 1991 and *T. reticulatus* González-Sponga, 1991, three from Brazil, *T. lisei* Lourenço, 1994, *T. braziliensis* Lourenço & Duhem, 2010 and *T. newaribe* Lourenço, Giupponi & Pedroso, 2011, one from Colombia, *T. guerdouxi* Lourenço, 1995 and one from Peru, *T. castiglii* Rossi, 2015 (Lourenço 1994a, 1995b, Lourenço and Duhem 2010, Lourenço et al. 2011, González-Sponga 1996, Rossi 2015). Almost all the species of *Teuthraustes*, so far described, were collected in the Andean mountains in Ecuador and Colombia, and in the Amazonian highlands of Venezuela and Brazil. These highlands are known as the 'Tepuys'. Exceptions remain however: *T. amazonicus* Simon, described from the region of Pebas, located on the banks of the Solimões River in Peruvian Amazonia, then later found in Brazilian and Colombian Amazonia, *T. glaber* Kraepelin and *T. castiglii* Rossi, both also described from the region of Pebas, Peru (to notice that the precise locality of *T. glaber* was originally indicated as only Peru, however in the personal notes by Simon the type specimen is indicated as from the region of Pebas), *T. braziliensis* Lourenço & Duhem, described from Brazilian Amazonia, *T. dubius* Borelli and *T. festae* Borelli, described from Morona-Santiago Province in Ecuador, *T. rosenbergi* Pocock, described from Guayas Province in Ecuador, and finally the three new species described in the present paper. In a recent publication by Brito and Borges (2015), an attempted checklist of the scorpions from Ecuador was proposed. This contribution is a compilation of previous works and no new species or locations were added neither to this fauna in general nor to the genus *Teuthraustes* in particular.

In the present paper, three new species of *Teuthraustes* are described from the lowlands of Ecuador: two from the Amazon region (Orellana and Sucumbíos Provinces; raising to four the number of *Teuthraustes* species in Ecuadorian Amazonia) and one from the rainforests of the Pacific Coast in Esmeraldas Province, this last species being the second record of a *Teuthraustes* species from the Pacific coastal region. The patterns of distribution presented by the species of the genus *Teuthraustes* in Ecuador are also discussed. This group remains, however, typical of highland formations of South America.

Geographical pattern of distribution of the genus *Teuthraustes*

The known geographical distribution of the genus *Teuthraustes* clearly indicates its endemic and disrupted nature. Of the 27 species known at present, nine are distributed in the Andean highlands of Ecuador. Another group of seven species has been described even more recently from a different highland site located between Brazil and Venezuela. This area clearly corresponds with the Imeri endemic centre which has been defined both for plants and for animals (Lourenço 2001, Prance 1982a, b). It is located in the 'Tepuys' region which lies mainly in Guayana, a floristic province that has been delineated botanically (Mori 1991). One species is known from the highlands of Colombia, 8 species are known from the lowlands of the Ecuadorian, Peruvian, Colombian and Brazilian Amazonia and 2 species are known from the Pacific coast region of Ecuador.

This outstanding concentration of *Teuthraustes* species in the Andean highlands and in the Imeri endemic centre may be similar to the 'explosive' pattern of speciation proposed by Gentry (1992) for plants of the genus *Gasteranthus*. According to Gentry (1992), it is probable that an entirely different evolutionary mode may be operating in these areas. The exceedingly dynamic speciation is perhaps mediated more by genetic transilience associated with genetic drift in small founder populations in a kaleidoscopically changing milieu, than by fine-tuned selection of the type generally suggested to be typical of lowland rain forest.

Several botanists (Gentry 1988, 1992) and entomologists (Erwin 1982, Wilson 1988) agree that tropical rainforests are the most species-rich ecosystems on earth. They also agree, on the basis of solid evidence, that the 'epicentre' of global biodiversity occurs in the tropical Andes, a region of the upper Amazonia which includes the North of Peru, Ecuador and the southern half of Colombia. This suggestion seems to be valid for plants, vertebrates and butterflies (Prance 1982a, b, Gentry 1992, Erwin 1982, Wilson 1988). The region is also one of the world's greatest sites of alpha-diversity on scorpions (Lourenço 1994b). Consequently, the very high concentration of *Teuthraustes* species in the Andean region could perhaps be no more than the consequence of the great ecological diversity there.

It is obvious that scorpion speciation and differentiation is by no means recent. As stated by Haffer (1982), the isolation of large populations due to Tertiary palaeogeographic changes undoubtedly played a major role in establishing the basic distributional and evolutionary patterns of the tropical floras and faunas at higher taxonomic levels of family and genera. At the same time, members of less 'plastic' groups with low evolutionary rates in the present flora and fauna survived relatively unchanged since Tertiary times. Since the Andes arose in the form of strings of growing islands from a marine geosynclinal basin, there was no pre-Andean continuous and widespread lowland fauna occupying what was later to become the Andes and their forelands. Consequently, Andean elements must have come from abroad. The 'Tepuys' region which includes the Imeri endemic centre, is located in the Precambrian Guiana Craton (or shield). From a geological point of view the 'Tepuys' are composed of sheer blocks of Precambrian sandstone and quartzite rocks. These 'mesas' are the remains of a huge sandstone plateau that once covered the granite basement complex between what is today the northern border of the Amazon Basin and the Orinoco, between the Atlantic coast and the Rio Negro (Lourenço and Duhem 2009).

Ecological, paleoclimatic, and palynologic data (Prance 1982b) indicate that the apparent 'stability' of present-day rainforests was interrupted by periods of climatic change through several dry/wet/dry episodes of the late Cenozoic period, and especially during more recent Pleistocene and Holocene epochs. During the earlier Quaternary

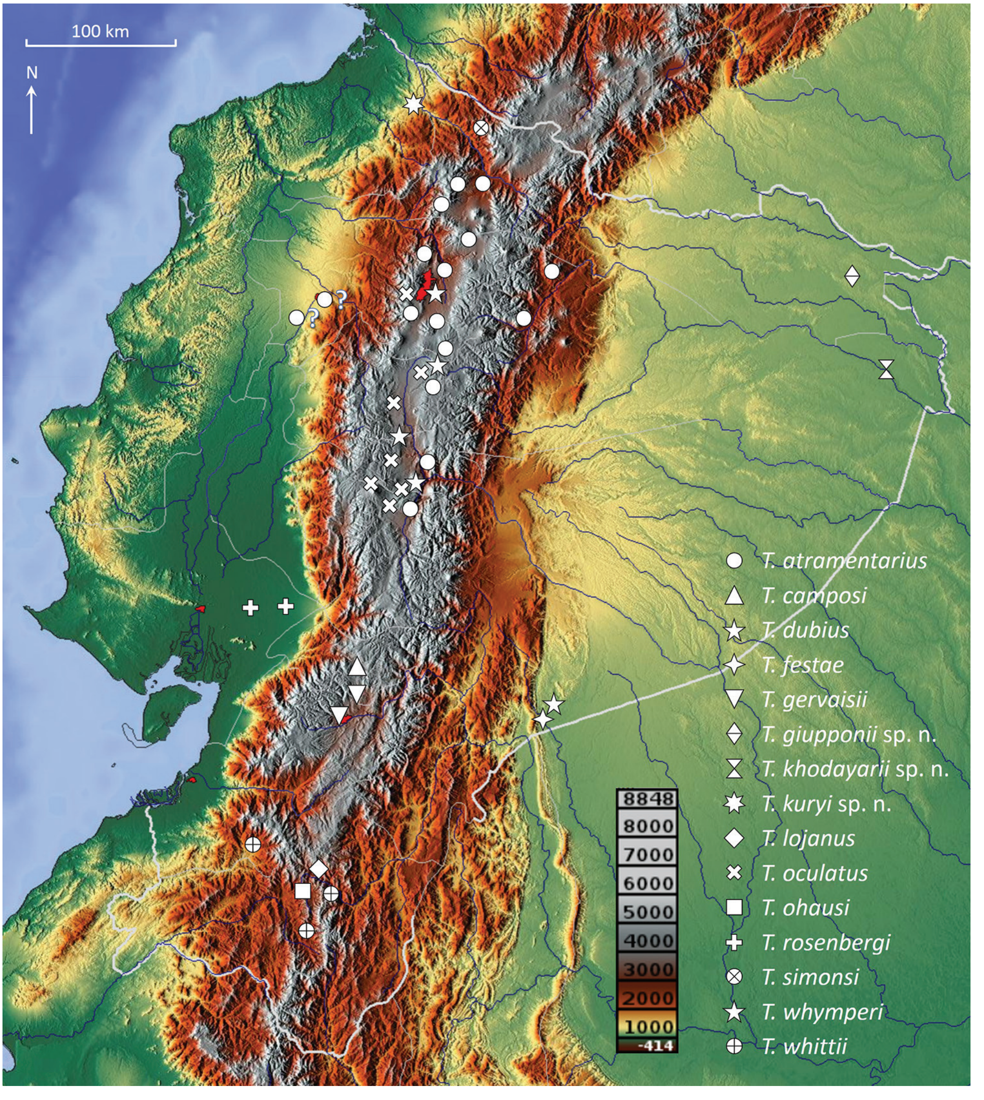

Figure 1. Topographic map of Ecuador showing the distribution of the known species of *Teuthraustes*.

period, temperate regions were glaciated. Cooler and drier conditions prevailed in the present tropical zones and reduced the rainforest to savannas or dry-forests except in localized regions where conditions of temperature and humidity allowed them to persist. During these glacial phases, more mesic species of scorpions, such as those of the genus *Teuthraustes*, and also of other mesic genera such as *Chactas* Gervais, 1844 and *Vachoniochactas* González-Sponga, 1978 probably experienced a more enlarged range of distribution than that observed today. With the return of the present interglacial phase these genera are again restricted to the highlands where mesic conditions prevail. Some species of the genera *Teuthraustes* and *Chactas*, however, probably evolved in and became adapted to the tropical forest when this one expanded and coalesced throughout the

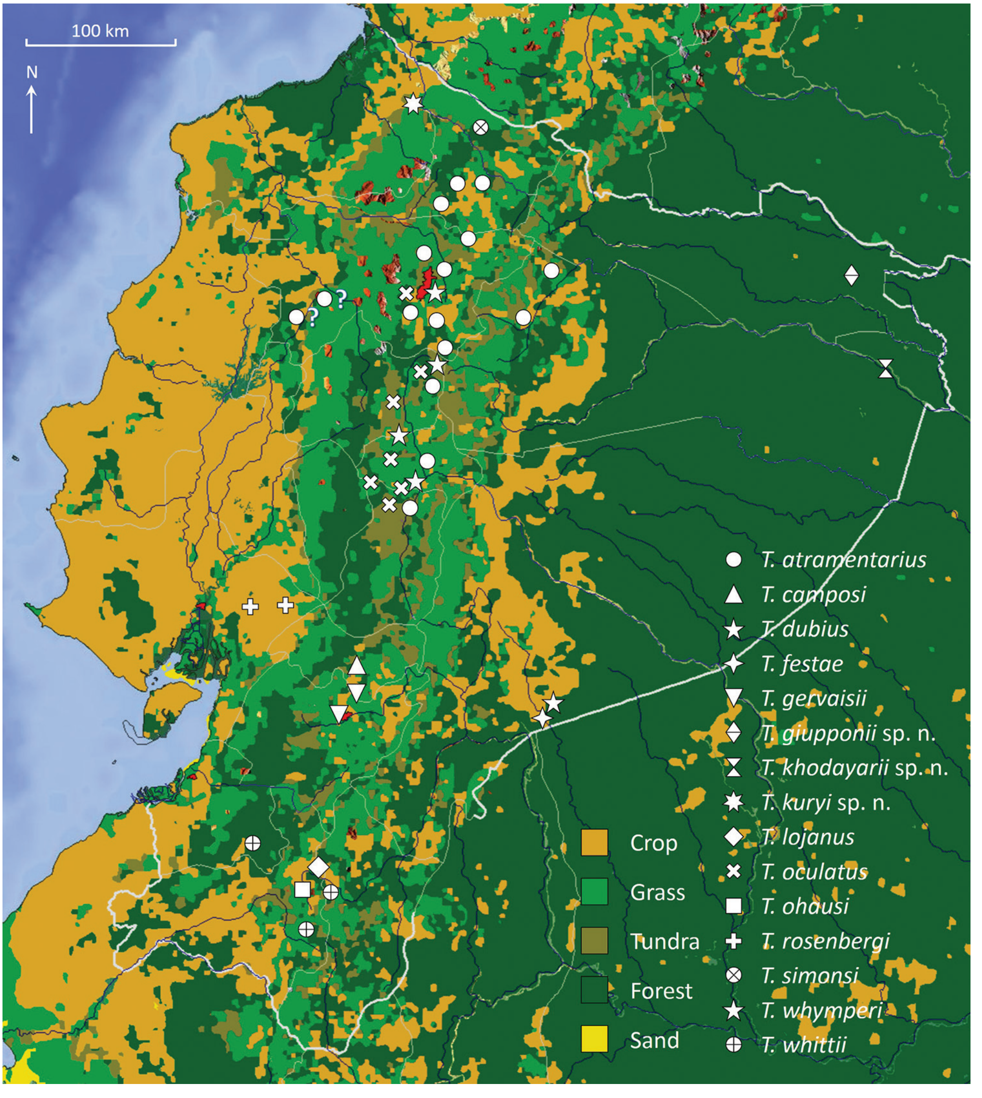

Figure 2. Vegetation map of Ecuador showing the distribution of the known species of *Teuthraustes*.

entire Neotropical lowlands (Lourenço 1995a, Lourenço et al. 2005). Consequently, one can expect new species of both genera still to be found in the lowlands of Amazonia.

Methods

Measurements and illustrations were made using a Wild M5 stereo-microscope with a drawing tube (*camera lucida*) and an ocular micrometre. Measurements follow those of Stahnke (1970) and are given in mm. Trichobothrial notations are those developed by Vachon (1974) and the morphological terminology mostly follows that of Hjelle (1990).

Taxonomic treatment

Family Chactidae Pocock, 1893
Genus *Teuthraustes* Simon, 1878
Composition of the genus *Teuthraustes*

Teuthraustes adrianae González-Sponga, 1975 – Venezuela (Amazonas)
Teuthraustes akananensis González-Sponga, 1984 – Venezuela (Amazonas)
Teuthraustes amazonicus (Simon, 1880) – Peru (Loreto), Brazil (Amazonas), Colombia (Amazonas)
Teuthraustes atramentarius Simon, 1878 – Ecuador (Chimborazo, Cotopaxi, Imbabura, Pichincha, Tungurahua)
Teuthraustes braziliensis Lourenço & Duhem, 2010 – Brazil (Amazonas)
Teuthraustes camposi (Mello-Leitão, 1939) – Ecuador (Cañar)
Teuthraustes carmelinae Scorza, 1954 – Venezuela (Amazonas)
Teuthraustes castiglii Rossi, 2015 – Peru (Loreto)
Teuthraustes dubius (Borelli, 1899) – Ecuador (Morona-Santiago)
Teuthraustes festae (Borelli, 1899) – Ecuador (Morona-Santiago)
Teuthraustes gervaisii (Pocock, 1893) – Ecuador (Azuay)
Teuthraustes giupponii sp. n. – Ecuador (Sucumbíos)
Teuthraustes glaber Kraepelin, 1912 – Peru (Loreto)
Teuthraustes guerdouxi Lourenço, 1995 – Colombia (Boyaca)
Teuthraustes khodayarii sp. n. – Ecuador (Orellana)
Teuthraustes kuryi sp. n. – Ecuador (Esmeraldas)
Teuthraustes lisei Lourenço, 1994 – Brazil (Amazonas)
Teuthraustes lojanus (Pocock, 1900) – Ecuador (Loja)
Teuthraustes maturaca González-Sponga, 1991 – Venezuela (Amazonas)
Teuthraustes newaribe Lourenço, Giupponi & Pedroso, 2011 – Brazil (Amazonas)
Teuthraustes oculatus Pocock, 1900 – Ecuador (Chimborazo, Cotopaxi, Tungurahua)
Teuthraustes ohausi Kraepelin, 1912 – Ecuador (Loja)
Teuthraustes reticulatus González-Sponga, 1991 – Venezuela (Amazonas)
Teuthraustes rosenbergi (Pocock, 1898) – Ecuador (Guayas)
Teuthraustes simonsi (Pocock, 1900) – Ecuador (Carchi)
Teuthraustes whymperi (Pocock, 1893) – Ecuador (Cotopaxi, Pichincha, Tungurahua)
Teuthraustes wittii (Kraepelin, 1896) – Ecuador (Loja)

Teuthraustes khodayarii sp. n.

http://zoobank.org/0F55C3BE-7744-4872-B55A-6B39F7960325
Fig 3–4, Table 1

Type material. Ecuador, Orellana Province (formerly Napo), Santa Maria de Huiririma 0°43'0"S, 75°37'0"W) VI/1976 (British expedition and local people), rainforest, under log. Pre-adult female holotype. Type material deposited in the Muséum national d'Histoire naturelle, Paris, France.

Etymology. The specific name honours Dr. Khosro Khodayari, founder, President and CEO of SynTech Research, Davis, California, USA, in recognition of his support for the study of scorpions.

Diagnosis. Moderate to small scorpion with 35.1 mm in total length. Colouration reddish brown to dark brown. Body and appendages very intensely granulated with a rather thin granulation. Pectines with 6–6 teeth in female. Fixed and movable fingers of chela with 5–5 rows of granules; extremities of fingers with 3 granules. Ventral carinae present on metasomal segments I to IV, but weak on I. Trichobothrial pattern of type C neobothriotaxic 'majorante'.

Description. Based on female holotype.

Colouration. General colouration basically reddish brown to dark brown. Prosoma: carapace reddish brown with a few paler spots; eyes blackish. Mesosoma: tergites reddish brown, with VII slightly paler with some yellow spots; venter and sternites reddish yellow; pectines and genital operculum with the same colour as sternites. Metasoma: segments reddish brown, with darker zones over carinae; vesicle reddish yellow with the tip of the aculeus dark red. Chelicerae: reddish yellow, with some diffuse variegated brown spots;

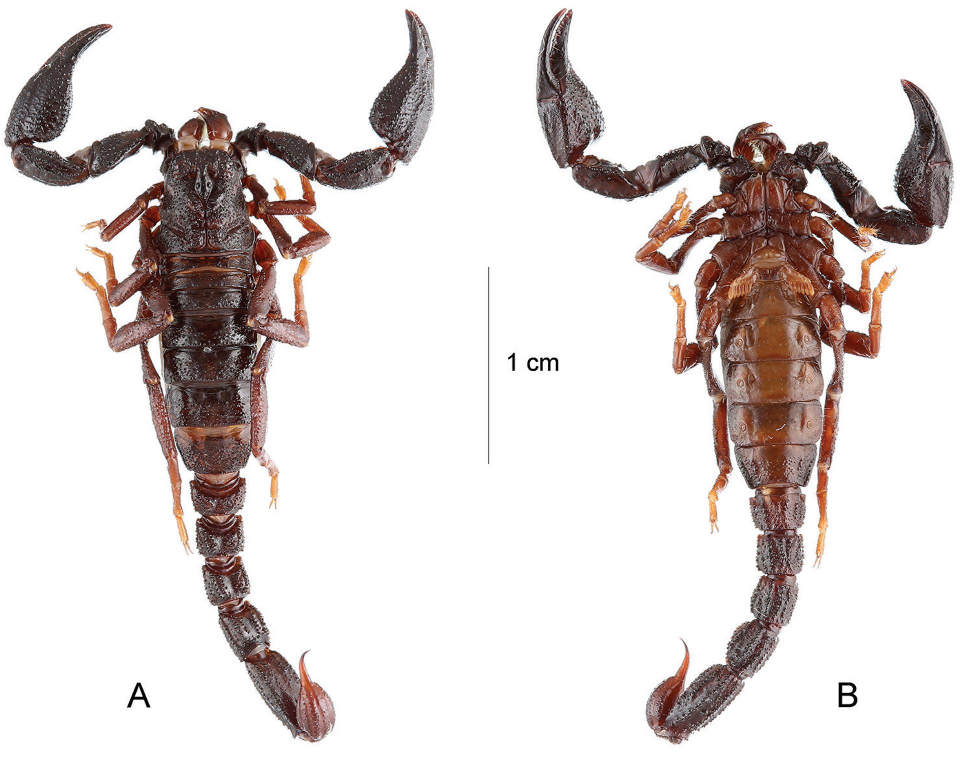

Figure 3. *Teuthraustes khodayarii* sp. n. female holotype.. Habitus, dorsal **A** and ventral **B** aspects.

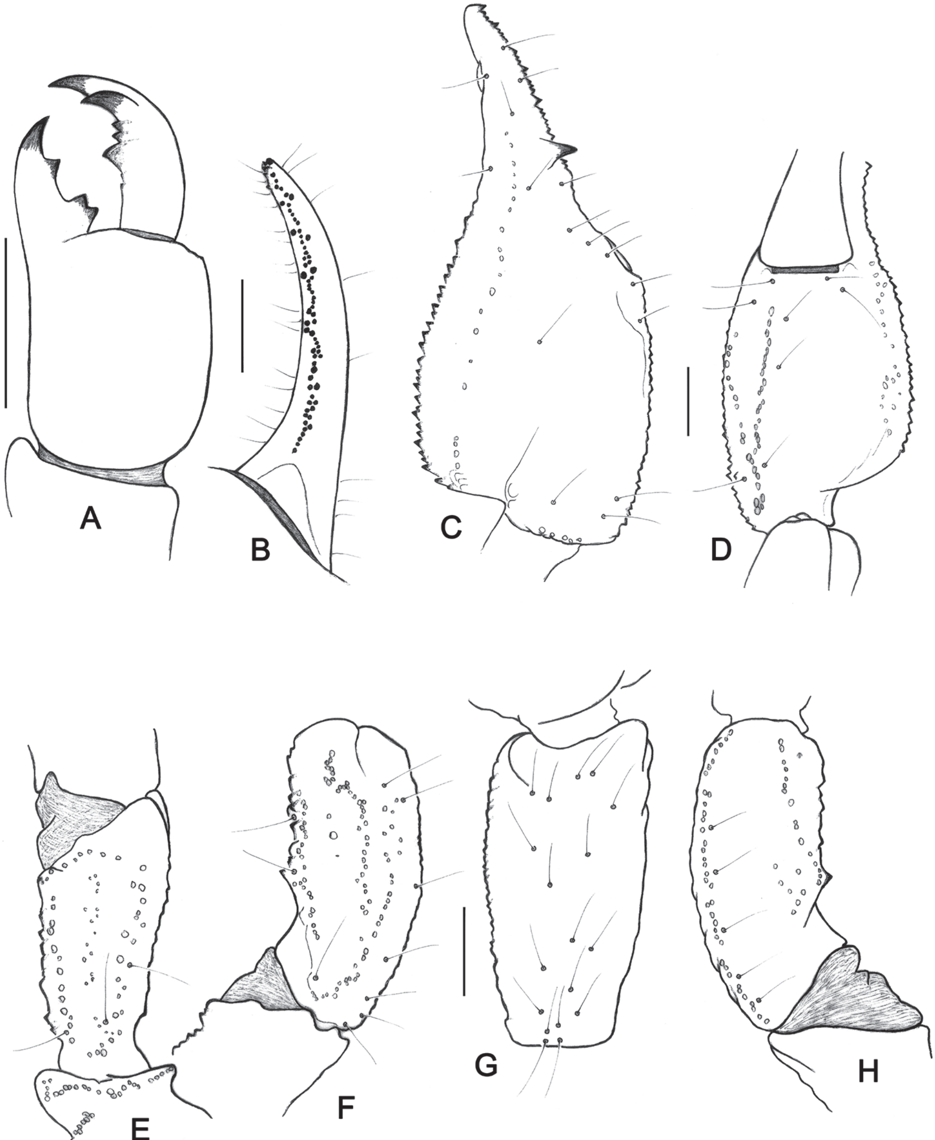

Figure 4. *Teuthraustes khodayarii* sp. n. Female holotype. **A** Chelicera, dorsal aspect **B** Disposition of the granulation over the dentate margins of pedipalp-chela movable finger **C–H** Trichobothrial pattern **C–D** Chela, dorso-external and ventral aspects **E** Femur, dorsal aspect **F–H** Patella, dorsal **F** external **G** and ventral **H** aspects. Scale bars 1 mm.v

fingers dark red with teeth reddish yellow. Pedipalps: dark brown with blackish carinae; cutting edges of fingers reddish. Legs: reddish yellow to reddish brown without spots.

Morphology. Prosoma: carapace intensely granulated, with a dense and thin granulation; furrows shallow; sternum pentagonal, wider than long. Mesosoma: tergites almost

Table 1. Morphometric values (in mm) of female holotypes of *T. khodayarii* sp. n., *T. giupponii* sp. n., *T. kuryi* sp. n., and *T. atramentarius* Simon, 1878.

	T. khodayarii	*T. giupponii*	*T. kuryi*	*T. atramentarius*
Total length	35.1	52.1	60.4	48.9
Carapace:				
length	5.3	7.1	8.0	7.1
anterior width	3.1	4.3	4.8	4.3
posterior width	5.4	8.0	8.6	7.3
Mesosoma length	11.1	15.5	16.2	14.8
Metasoma length	18.7	29.1	36.2	27.0
Metasomal segment I:				
length	1.9	3.0	3.6	2.7
width	3.0	4.0	4.9	3.8
Metasomal segment II:				
length	2.0	3.3	4.1	3.1
width	2.7	3.6	4.6	3.5
Metasomal segment III:				
length	2.2	3.6	4.6	3.3
width	2.5	3.6	4.5	3.5
Metasomal segment IV:				
length	2.7	4.3	5.6	4.0
width	2.3	3.4	4.3	3.3
Metasomal segment V:				
length	4.8	7.3	9.4	6.7
width	2.2	3.1	4.2	3.2
depth	2.0	2.7	3.6	2.8
Telson:				
length	5.1	7.6	8.9	7.2
width	2.0	3.5	4.3	3.3
depth	1.6	2.8	3.6	2.9
Pedipalp:				
femur length	3.8	4.7	5.7	4.8
femur width	1.3	2.1	2.4	1.9
patella length	3.7	5.6	6.1	5.3
patella width	1.8	2.5	2.8	2.9
chela length	8.1	11.2	11.1	10.7
chela width	2.9	4.0	5.1	3.7
chela depth	2.8	5.3	7.2	5.6
Movable finger length	4.6	6.3	5.9	5.8

acarinate, with a thin and dense granulation; sternites smooth and shiny, only VII with a few granulations; spiracles oval to rounded-shaped and conspicuous; pectinal tooth count 6–6, fulcra vestigial. Metasoma: segments I to III wider than long; metasomal tegument on segments I to IV with conspicuous granulations; segment V with spinoid granulations ventrally; carinae on segments I–V strongly developed; ventral present on all segments, less marked on I; telson with strongly marked granulations, only dorsal face smooth; aculeus shorter than vesicle. Chelicerae: dentition typical of the family Chactidae (Vachon 1963), and with dense setation ventrally and internally. Pedipalps: femur with dorsal internal, dorsal external and ventral internal carinae strongly marked; ventral external carina absent; dorsal, ventral and internal aspects with granulations; patella granulated with moderate carinae; chela very strongly granulated; internal aspect with conspicuous granules; dentate margins on movable and fixed fingers with 5–5 rows of granules; distal edge of fingers with three granules; trichobothriotaxy of type C; neobothriotaxic 'majorante' (Vachon 1974). Legs: tarsi with short setae disposed in a single line.

Morphometric values. Female holotype of *T. khodayarii* sp. n. Total length (in mm) including telson, 35.1. Carapace: length, 5.3; anterior width, 3.1; posterior width, 5.4. Mesosoma length 11.1. Metasomal segments. I: length, 1.9; width, 3.0; II: length, 2.0; width, 2.7; III: length, 2.2; width, 2.5; IV: length, 2.7; width, 2.3; V: length, 4.8; width, 2.2; depth, 2.0. Telson length, 5.1; vesicle: width, 2.0; depth, 1.6. Pedipalp: femur length, 3.8, width, 1.3; patella length, 3.7, width, 1.8; chela length, 8.1, width, 2.9, depth, 2.8; movable finger length, 4.6.

Relationships. The species can be distinguished from the others congeners in particular from *Teuthraustes atramentarius* Simon, which is also distributed in Ecuador, but exclusively in the high central Andes, by the following features: (i) a thin but very intense granulation over body and appendages, particularly marked on legs (ii) ocular tubercle much less pronounced, (iii) pectines are wider, (iv) pedipalpal chela are not bulk and elongated, (v) metasomal segments I to III wider than long.

Teuthraustes giupponii sp. n.

http://zoobank.org/64DE0CC3-8C83-4B2A-820F-50B6B4D8102D
Figs 5–6, Table 1

Type material. Ecuador, Sucumbíos Province (formerly Napo), Dureno/Cuyabeno, near lake Cuyabeno, Cuyabeno Wildlife Reserve (0°07'00"S, 75°50'00"W) VI/1976 (British expedition and local people), rain-forest, under stone. Female holotype. Type material deposited in the Muséum national d'Histoire naturelle, Paris, France.

Etymology. The specific name honours Dr. Alessandro Ponce de Leão Giupponi, Fundação Oswaldo Cruz, Rio de Janeiro, for his contributions to the study of scorpions.

Diagnosis. Moderate scorpions with 52.1 mm in total length. Colouration reddish to reddish yellow. Body and appendages weakly granulated, with minute punctation. Pectines small with 6–6 teeth in female. Fixed and movable fingers of chela with 5–5 rows of granules. Ventral carinae present on metasomal segments I to IV but inconspicuous on I. Trichobothrial pattern of type C neobothriotaxic 'majorante'.

Description. Based on female holotype.

Colouration. General colouration basically reddish to reddish yellow. Prosoma: carapace reddish; eyes blackish. Mesosoma: tergites reddish yellow, paler than carapace, with confluent yellowish strips; venter and sternites reddish yellow to yellow; pectines, genital operculum, and sternites yellow. Metasoma: segments reddish, with darker zones over carinae; vesicle reddish yellow with the tip of the aculeus dark red.

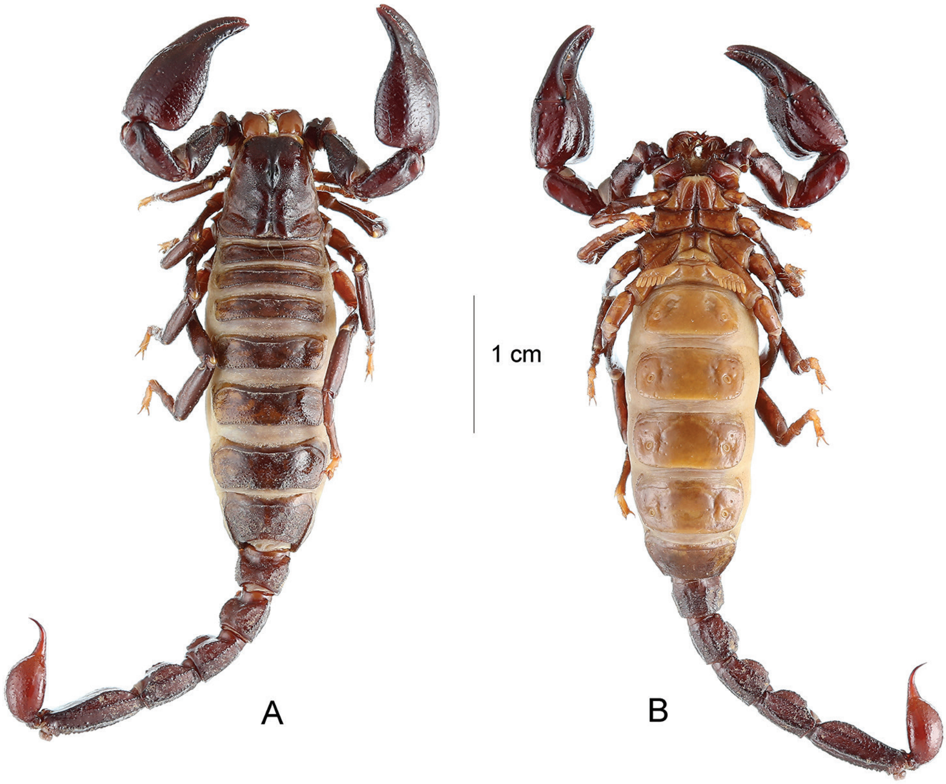

Figure 5. *Teuthraustes giupponii* sp. n. Female holotype. Habitus, dorsal **A** and ventral **B** aspects.

Chelicerae: yellow, with some diffuse variegated reddish spots at the base of fingers; fingers reddish yellow; teeth reddish. Pedipalps: dark reddish; carinae blackish. Legs: reddish yellow with pale spots.

Morphology. Prosoma: carapace acarinate, with dense minute granulations; lateral edges smooth; furrows shallow; sternum pentagonal, wider than long. Mesosoma: tergites acarinate, with a few granulations and some punctations; sternites, smooth and shiny; spiracles oval to rounded-shaped and conspicuous; VII acarinate with a few granules; pectinal tooth count 6–6, fulcra inconspicuous. Metasoma: segments I and II wider than long; metasomal tegument on segments I to IV with strong granulations; segment V with some spinoid granulations ventrally; carinae on segments I–V strongly developed; ventral present on segments I to IV; telson with a few ventral granulations, other faces almost smooth; aculeus shorter than vesicle. Chelicerae: dentition typical of the family Chactidae (Vachon 1963), and with dense setation ventrally and internally. Pedipalps: femur with dorsal internal, dorsal external and ventral internal carinae strongly marked; ventral external carina represented by a few granules; dorsal, ventral and internal aspects with thin granulations; patella smooth with weak carinae; chela smooth and almost acarinate; internal aspect with a few small granules; dentate margins on movable

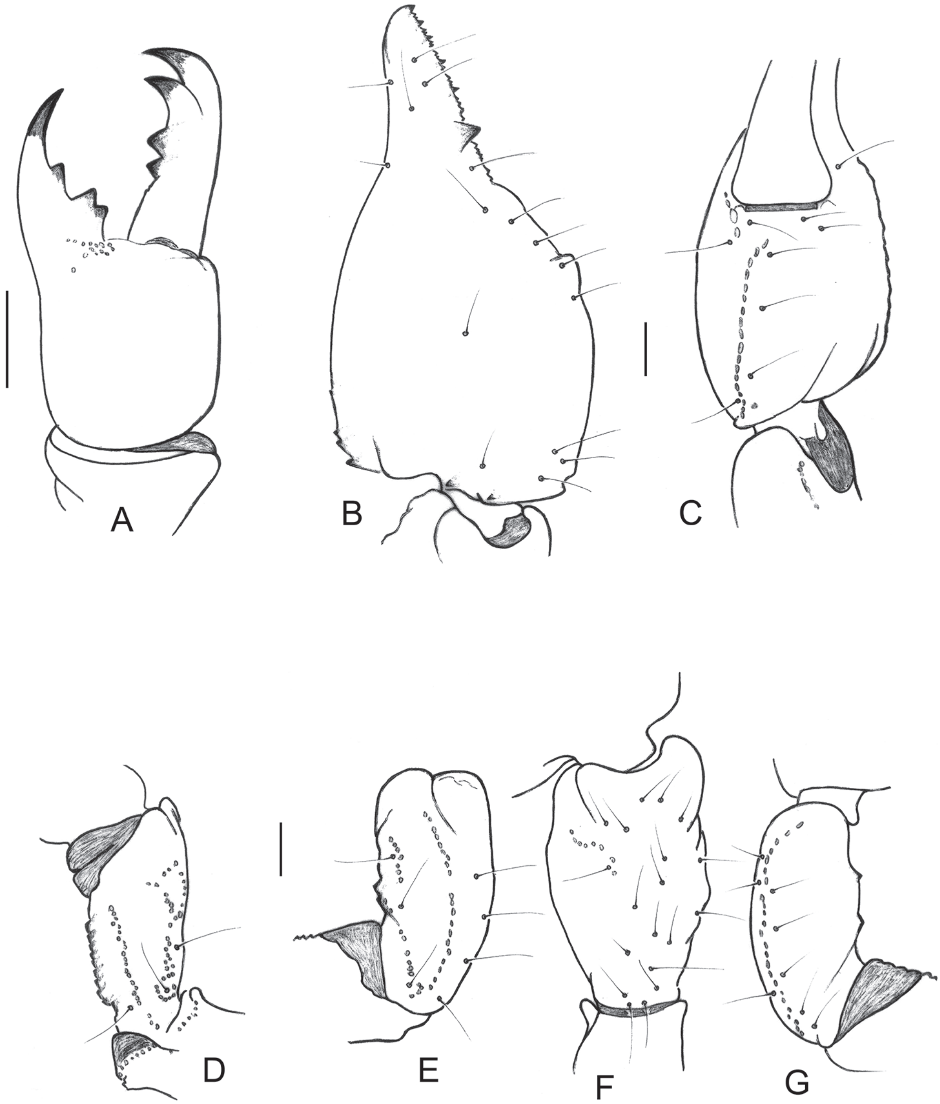

Figure 6. *Teuthraustes giupponii* sp. n. Female holotype. **A** Chelicera, dorsal aspect **B–G** Trichobothrial pattern **B–C** Chela, dorso-external and ventral aspects **D** Femur, dorsal aspect **E–G** Patella, dorsal **E** external **F** and ventral **G** aspects. Scale bars 1 mm.

and fixed fingers with 5–5 rows of granules; trichobothriotaxy of type C; neobothriotaxic 'majorante' (Vachon 1974). Legs: tarsi with short setae disposed in a single line.

Morphometric values. Female holotype of *T. giupponii* sp. n. Total length (in mm) including the telson, 52.1. Carapace: length, 7.5; anterior width, 4.3; posterior width, 8.0. Mesosoma length 15.5. Metasomal segments. I: length, 3.0; width, 4.0; II: length, 3.3; width, 3.6; III: length, 3.6; width, 3.6; IV: length, 4.3; width, 3.4; V:

length, 7.3; width, 3.1; depth, 2.7. Telson length, 7.6; vesicle: width, 3.5; depth, 2.8. Pedipalp: femur length, 4.7, width, 2.1; patella length, 5.6, width, 2.5; chela length, 11.2, width, 4.0, depth, 5.3; movable finger length, 6.3.

Relationships. The new species can be distinguished from other the congeners in particular from *Teuthraustes oculatus* Pocock, which is also distributed in Ecuador, but in the high central Andes, by the following features: (i) paler general colouration, reddish to reddish yellow, (ii) tergites and pedipalps weakly granulate to smooth, (iii) carapace with some thin granulations (iv) lateral eyes small and apart from each other, (v) anterior edge of carapace not straight, lobate, (vi) ventral carinae on metasomal segment I inconspicuous.

Teuthraustes kuryi **sp. n.**
http://zoobank.org/DB39E8D8-51EB-4784-AECF-43FC3BE4A923
Fig 7–8, Table 1

Type material. Ecuador, Esmeraldas Province (N00.88883, W078.53732), 873 m, in zone where rainforest was recently destroyed, under log, 17/III/2011 (A. Chagas, A. Giupponi, A. Kury, M. Vega). Female holotype and female paratype. Holotype deposited in the Museo de Zoologia, Pontificia Universidad Católica de Quito, Ecuador; paratype deposited in the Museu Nacional, Rio de Janeiro, Brazil.

Etymology. Specific name honours Prof. Adriano B. Kury, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil, for his important contribution to the study of arachnids.

Diagnosis. Moderate to large scorpions with 60–61 mm in total length. Colouration dark brown to blackish. Body and appendages strongly granulated. Pectines with 7–7 teeth in females. Pedipalps bulk with short fingers; fixed and movable fingers of chela with 5–6 rows of granules. Metasoma long and strong; ventral carinae strongly marked on metasomal segments I to IV. Trichobothrial pattern of type C neobothriotaxic 'majorante'.

Description. Based on female holotype and female paratype.

Colouration. General colouration basically dark brown to blackish. Prosoma: carapace dark brown; eyes blackish. Mesosoma: tergites reddish brown to dark brown, slightly paler than carapace; venter and sternites reddish brown to dark brown; pectines and genital operculum yellow. Metasoma: segments blackish brown, with darker zones over carinae; vesicle reddish brown with the base of the aculeus reddish yellow. Chelicerae: reddish yellow, with some diffuse variegated reddish spots at the base of the fingers; fingers dark reddish. Pedipalps dark brown to blackish; carinae blackish. Legs dark brown to blackish.

Morphology. Prosoma: carapace almost acarinate, but with dense strongly marked granulations on the entire surface, except on the zone of furrows; furrows deep; sternum pentagonal, wider than long. Mesosoma: tergites intensely granulated but less marked than carapace; sternites, smooth and shiny; spiracles oval-shaped and con-

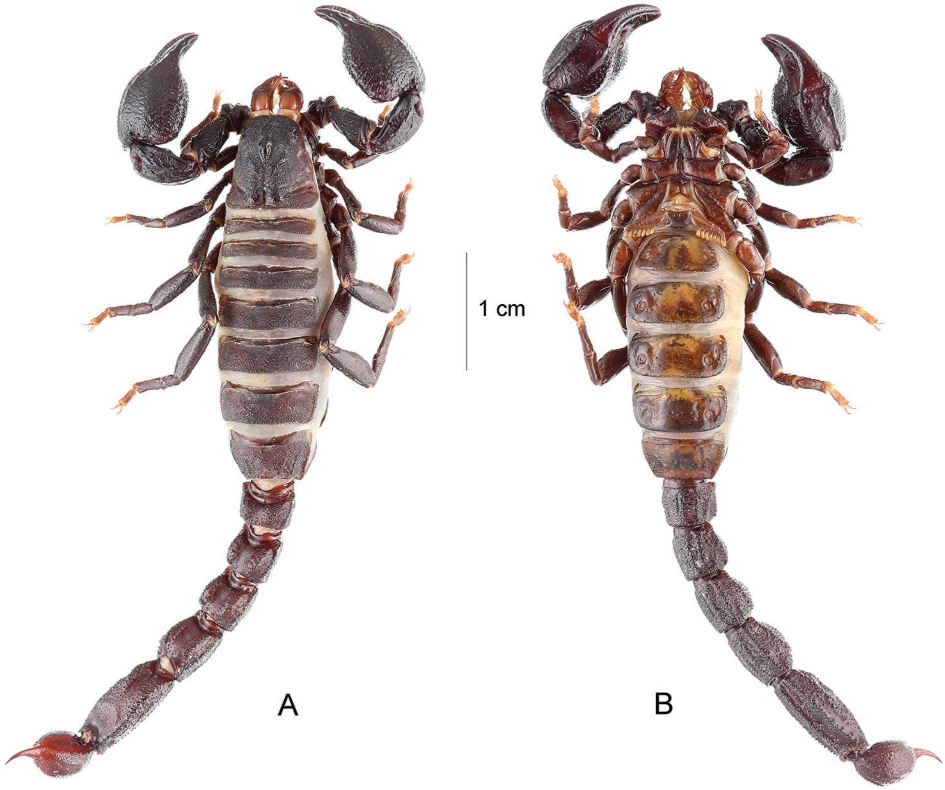

Figure 7. *Teuthraustes kuryi* sp. n. Female holotype. **A–B** Habitus, dorsal **A** and ventral **B** aspects.

spicuous; VII acarinate with granulations; pectinal tooth count 7–7 in both females, holotype and paratype, fulcra vestigial. Metasoma: segments I and II wider than long; metasomal tegument on segments I to IV strongly granulated including dorsal aspect; segment V with some spinoid granulations ventrally; carinae on segments I–V strongly developed; ventral present on all segments; telson strongly granulated; aculeus shorter than vesicle. Chelicerae: dentition typical of the family Chactidae (Vachon 1963), and with dense setation ventrally and internally. Pedipalps: femur with dorsal internal, dorsal external and ventral internal carinae strongly marked; ventral external carina vestigial; dorsal, ventral and internal aspects granulated; patella granulated with well-marked carinae; chela strongly granulated and with most carinae well-marked; dentate margins on movable and fixed fingers with 5–6 rows of granules; trichobothriotaxy of type C; neobothriotaxic 'majorante' (Vachon 1974). Legs: tarsi with short setae disposed in a single line.

Morphometric values. Female holotype of *T. kuryi* sp. n. Total length (in mm) including the telson, 60.4. Carapace: length, 8.0; anterior width, 4.8; posterior width, 8.6. Mesosoma length, 16.2. Metasomal segments. I: length, 3.6; width, 4.9; II: length, 4.1; width, 4.6; III: length, 4.6; width, 4.5; IV: length, 5.6; width, 4.3; V: length, 9.4;

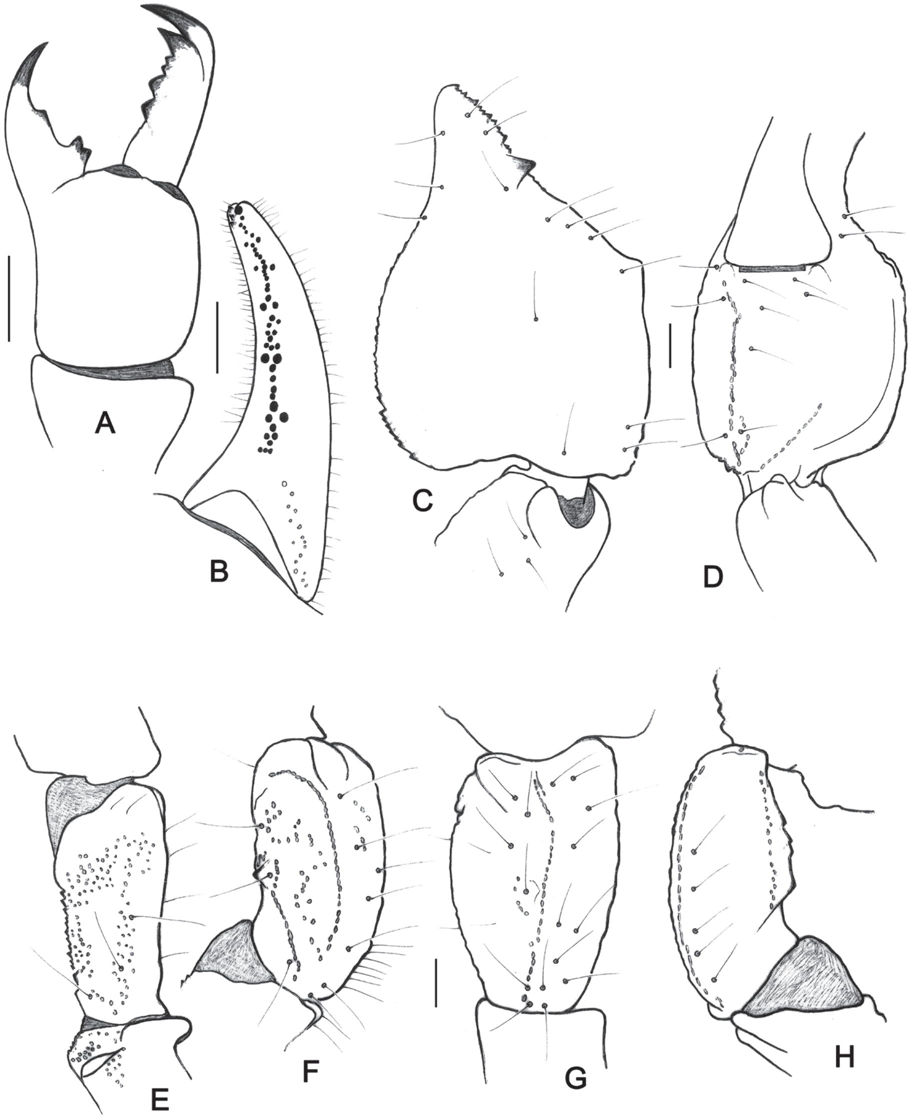

Figure 8. *Teuthraustes kuryi* sp. n. Female holotype. **A** Chelicera, dorsal aspect **B** Disposition of the granulation over the dentate margins of pedipalp-chela movable finger **C–H** Trichobothrial pattern **C–D** Chela, dorso-external and ventral aspects **E** Femur, dorsal aspect **F–H** Patella, dorsal **F** external **G** and ventral **H** aspects. Scale bars 1 mm.

width, 4.2; depth, 3.6. Telson length, 8.9; vesicle: width, 4.3; depth, 3.6. Pedipalp: femur length, 5.7, width, 2.4; patella length, 6.1, width, 2.8; chela length, 11.1, width, 5.1, depth, 7.2; movable finger length, 5.9.

Relationships. The new species can be distinguished from the others congeners in particular from *Teuthraustes atramentarius* Simon, which is also distributed in Ecuador,

Figure 9. Amazon region, Ecuador. Natural habitat of *Teuthraustes khodayarii* sp. n. and *Teuthraustes giupponii* sp. n. (photograph C. Benros-Ythier; E. Ythier in the photo).

but exclusively in the high central Andes, by the following features: (i) carapace, tergites, pedipalps, metasoma, and telson strongly granulated, (ii) metasomal segments I to V long and strong with well-marked ventral carinae, (iii) pedipalps bulk with short fingers on chela, (iv) ventral aspect with a darker pigmentation, reddish brown to dark brown.

Teuthraustes atramentarius Simon, 1878

The female holotype of *Teuthraustes atramentarius* was studied and its morphometric values (in mm) are presented in Table 1. The holotype is deposited in the Muséum national d'Histoire naturelle, Paris under the N° RS-0763 (Simon's N° 3019). In the catalogue of the scorpions of the World (Sissom 2000) the holotype is cited as deposited in the "Musée Royal d'Histoire naturelle de Belgique" in Brussels. This is, however, incorrect.

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Figure 10. Esmeraldas Province, Ecuador. Natural habitat of *Teuthraustes kuryi* sp. n. (photograph A. Chagas Júnior; A.B. Kury in the photo).

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RESEARCH ARTICLE

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New species of *Nipponoserica* and *Paraserica* from China (Coleoptera, Scarabaeidae, Sericini)

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Abstract

The species of the genera *Nipponoserica* Nomura, 1973 and *Paraserica* Reitter, 1896 from China are revised. The following eight new species are described from China: *Paraserica camillerii* Ahrens, Fabrizi, & Liu, **sp. n.**, *P. mupuensis* Ahrens, Fabrizi, & Liu, **sp. n.**, *P. wangi* Ahrens, Fabrizi, & Liu, **sp. n.**, *Nipponoserica alloshanghaiensis* Ahrens, Fabrizi, & Liu, **sp. n.**, *N. anjiensis* Ahrens, Fabrizi, & Liu, **sp. n.**, *N. jiankouensis* Ahrens, Fabrizi, & Liu, **sp. n.**, *N. henanensis* Ahrens, Fabrizi, & Liu, **sp. n.**, and *N. sericanioides* Ahrens, Fabrizi, & Liu, **sp. n.** A key to the species of the genera examined here and maps of the species distribution are provided. Habitus and male genitalia are illustrated.

Keywords

Beetles, chafers, China, new records, new species, *Nipponoserica*, *Paraserica*

Introduction

In the course of the revision of the Sericini of China a series of papers was published recently dealing mainly with the genera that possess a multi-lamellate antennal club (Ahrens et al. 2014a, b, c; Liu et al. 2014a, b, c, 2015; Liu et al. 2016). In continuation with this work, the results of the revision of the genera *Paraserica* Reitter, 1896 and *Nipponoserica* Nomura, 1973, both representing genera with a tri-lamellate antennal club, are presented here. So far, both groups are poorly known in China. While *Nipponoserica* is known only from four species, *Paraserica* is known from a single species from mainland China (Ahrens 2004b; Ahrens and Bezdek 2016). The examined material from different private and institutional collections contained a number of new species which are described herein. Furthermore, the material included numerous new and interesting locality records that are also given.

Materials and methods

The terminology and methods used for measurements, specimen dissections, and genital preparation follow Ahrens (2004a). Data from specimens examined are cited in the text with original label contents given in quotation marks, multiple labels are separated by a "/". Male genitalia were glued to a small pointed card attached to the specimen. Descriptions and illustrations of new taxa are based on the holotype or lectotype specimen, while the variation of other specimens is given separately. All descriptions and measurements were made under an Olympus SZX 12 microscope, and all genital and habitus illustrations were made with a digital camera (AxioCam HRc) attached to a stereo microscope (Zeiss Stereo Discovery V20) and Axio Version 4.8 software. The distribution maps were generated using Q-GIS 2.0.1 and Inscape software. Type specimens and other examined material are deposited in the following institutions or collections:

CPPB Coll. Petr Pacholátko, Brno, Czech Republic;
HBUM Museum of Hebei University, Baoding (Hebei Prov.), China;
IZAS Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
NUYS Northwest A & F University, Yangling (Shaanxi Prov.), China;
ZFMK Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany.

Systematics

Nipponoserica Nomura, 1973

Nipponoserica Nomura, 1973b: 120 (type species: *Serica similis* Lewis, 1895 – by original designation; Nomura 1973b); Ahrens 2005: 276.

Pseudomaladera Nikolajev, 1980: 40 [homonym] (type species: *Serica koltzei* Reitter, 1897 – by original designation; Nikolajev 1980).

Key to the Chinese Nipponoserica species (♂♂).

1 Dorsal surface shiny.. **3**
– Dorsal surface dull **2**
2 Parameres distinctly asymmetrical.............. ***N. elliptica* (Murayama, 1938)**
– Parameres symmetrical....................................... ***N. koltzei* (Reitter, 1897)**
3 Penultimate abdominal sternite with a deep longitudinal furrow **4**
– Penultimate abdominal sternite without a deep longitudinal furrow ....***N. sericanioides* Ahrens, Fabrizi, & Liu, sp. n.**
4 Distal portion of parameres symmetrical...**5**
– Distal portion of parameres asymmetrical .... ***N. jiankouensis* Ahrens, Fabrizi, & Liu, sp. n.**
5 Dorsomedial sinuation of apical phallobase as deep as wide. Basal lobes of parameres bent forward and directed mesodistally ..... ***N. sulciventris* Ahrens, 2004**
– Dorsomedial sinuation of apical phallobase distinctly deeper than wide......**6**
6 Parameres with a small external tooth before apex.......................................**7**
– Parameres without small external tooth before apex **8**
7 Sides of parameres convexly widened at middle .... ***N. shanghaiensis* Ahrens, 2004**
– Sides of parameres concave at middle.. .... ***N. anjiensis* Ahrens, Fabrizi, & Liu, sp. n.**
8 Each paramere with an internal short hook-like tooth.................................. .... ***N. alloshanghaiensis* Ahrens, Fabrizi, & Liu, sp. n.**
– Paramere unarmed, without an internal tooth...**9**
9 Parameres longer, distinctly longer than phallobase at apex wide.................. .... ***N. dahongshanica* Ahrens, 2005**
– Parameres short, only litter longer than phallobase at apex wide ....***N. henanensis* Ahrens, Fabrizi, & Liu, sp. n.**

Checklist of the genus *Nipponoserica* and its occurrence (corrected, from Ahrens and Bezdek 2016; abbreviations: HUB – Hubei, GAN – Gansu, GUI – Guizhou, HEI – Heibei, HEN – Henan, JIX – Jiangxi, SCH – Sichuan, SHA – Shaanxi, SHG – Shanghai, ZHE – Zheijang, XIZ – Xizang, FE – Russian Far East, SC – South Korea, JA – Japan, TAI – Taiwan, NARi – Nearctic region, imported):

Nipponoserica alloshanghaiensis Ahrens, Fabrizi, & Liu, sp. n. A: JIX
Nipponoserica anjiensis Ahrens, Fabrizi, & Liu, sp. n. A: SHA, ZHE
Nipponoserica babai Kobayashi, 1991a: 47 A: TAI
Nipponoserica chinensis Moser, 1915b: 144 (as *Serica*) [doubtful assignment] A: SHN
Nipponoserica daisensis Sawada, 1937: 24 (as *Serica*) A: JA
syn. *lewisi* Chapin, 1938: 68 (as *Serica*)
Nipponoserica dahongshanica Ahrens, 2005: 276 A: HUB
Nipponoserica elliptica Murayama, 1938: 17 (as *Serica*) A: SC JIX

Nipponoserica gomandana Nomura, 1976: 187 A: JA
Nipponoserica henanensis Ahrens, Fabrizi, & Liu, sp. n. A: HEN
Nipponoserica jiankouensis Ahrens, Fabrizi, & Liu, sp. n. A: GUI
Nipponoserica koltzei Reitter, 1897: 214 (as *Serica*) A: FE GAN HEI HEN SHA XIZ SC
syn *opacicarina* Kim & Kim, 2003a: 76
Nipponoserica kunitachiana Nomura, 1976b: 190 A: JA
Nipponoserica laferi Nikolajev, 1980: 41 (*Pseudomaladera*) A: FE
Nipponoserica peregrina Chapin, 1938: 68 (*Serica*) A: JA NARi
Nipponoserica pubiventris Nomura, 1976: 189 A: JA
Nipponoserica sericanioides Ahrens, Fabrizi, & Liu, sp. n. A: ZHE
Nipponoserica shanghaiensis Ahrens, 2004: 8 A: SHG
Nipponoserica similis Lewis, 1895c: 391 (as *Serica*) A: JA
syn *setiventris* Nomura, 1976: 188
Nipponoserica sulciventris Ahrens, 2004: 9 A: GAN HUB SCH SHA
Nipponoserica takeuchii Hirasawa, 1991: 171 [doubtful assignment] A: TAI

***Nipponoserica elliptica* (Murayama, 1938)**

Figures 2I–L, 4

Serica elliptica Murayama, 1938: 17; Kim and Lee 1991: 55, 60 (fig. 7a,b).
Nipponoserica elliptica: Nomura 1973: 139; Murayama 1954: 20.

Material examined. South Korea: 1 ♂ "27.06.2010 Beomeosa, Busan (Südkorea) leg. T. Kölkebeck" (ZFMK). **China:** 1 ♂ "Yiyang, Jiangxi, 16.V.1975, leg. Zhang Youwei" (IZAS), 1 ♂ "Yiyang, Jiangxi, 13.V.1975, leg. Zhang Youwei" (IZAS).

Redescription. Length: 9.6 mm, length of elytra: 7.6 mm, width: 5.1 mm. Body oblong, including legs dark brown, antenna yellowish brown, dorsal surface dull and glabrous.

Labroclypeus subtrapezoidal and wide, widest at base; lateral margins convex and strongly convergent, with weakly rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface flat and weakly shiny, finely and densely punctate, with a few short, erect setae anteriorly.

Frontoclypeal suture indistinctly incised and weakly curved medially; smooth area in front of eye 1.5 times as wide as long; ocular canthus short and triangular, finely and sparsely punctate with a short single terminal seta. Frons dull, with fine and moderately dense punctures, with a few long setae beside eyes. Eyes moderately large, ratio of diameter/interocular width: 0.7. Antenna with nine antennomeres; club with three antennomeres, 1.3 times as long as remaining antennomeres combined, weakly reflexed. Mentum elevated and flattened anteriorly. Labrum produced and deeply sinuate medially.

Pronotum transverse, widest at base, lateral margins moderately convex and convergent anteriorly; anterior angles weakly produced and blunt; posterior angles blunt, rounded at tip; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with moderately dense and fine punctures, glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals convex, with fine and sparse punctures concentrated along striae, glabrous; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a fine rim of microtrichomes (visible at 100× magnification).

Ventral surface dull, metasternum partly shiny, with moderately dense, large punctures, sparsely setose, only on metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow. Mesosternum between mesocoxae half as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/ metacoxa: 1/1.4. Pygidium dull, weakly convex, finely and moderately densely punctate, without smooth midline, glabrous except a few longer setae on apical half.

Legs slender, dull; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur dull, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/4.6; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at four-fifths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, sparsely finely punctate, with some longitudinal, superficial wrinkles; ventral margin finely serrate, with four fine nearly equidistant setae; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally and a fine longitudinal carina laterally; first metatarsomere slightly shorter than following two combined, slightly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical. Aedeagus: apical part of parameres asymmetrical, basal lobes symmetrical.

Remarks. We were unable to locate and examine the type material of this species; possibly the types are lost. Specimens were identified according to Kim and Lee (1991).

Distribution. The species was known only from South Korea (Ahrens and Bezdek 2016). Now it is recorded for the first time from China, Jiangxi province.

Nipponoserica koltzei **(Reitter, 1897)**

Figure 4

Serica koltzei Reitter, 1897: 214.

Nipponoserica koltzei: Nomura 1973: 139; Nikolajev 2002: 98; Ahrens 2004b: 7.

Pseudoserica koltzei: Nikolajev 1980: 40.
Nipponoserica opacicarina Kim & Kim, 2003: 76; syn by Ahrens 2007: 9.

Additional material examined. 2 ex. "China, W Henan, 9.VII.2006 Funiu Shan, 33°42'N, 112°15'E Shirenshan 1400–1900m, Jaroslav Turna leg. "(ZFMK), 17 ex. "China, W Henan, 6–7.VII.2006 Funiu Shan, 33°31'N, 111°56'E Baotianman, 1500–1750m, Jaroslav Turna leg." (ZFMK), 1 ex. "China-Shaanxi, SW Tsinling Mts., Taiping vill., 33°33'N, 106°43'E, June 2000, 1500–2000m, Siniaev & Plutenko leg." (CPPB), 1 ex. "China-Shaanxi, Tsinling Mts., Houzhenzi vill., 33°53'N, 107°49'E, June-Juli 2000, 1500m, Siniaev & Plutenko leg." (CPPB), 2 ex. "China, 1000–1300m, Shaanxi, Qinling mts., Xunyangba (6km E) 23.v.-13.vi.1998 J.H. Marshal leg." (CPPB), 1 ex. "China, W Henan, 7.–8.VII.2007, Funju Shan, N33°42', E112°15', Shirenshan, 1500m, leg. Jaroslav Turna" (ZFMK), 1 ♂ "Bayi, Xizang, No.255" (IZAS), 1 ♂ "Ha'erbin, 16.VI.1960" (IZAS), 3 ♂♂ "Getiaopa, Neixiang, Henan, 15.VII.1998, 600m, leg. Zhang Youwei" (IZAS).

Distribution. The species was known from South Korea, and Far East of Russia, as well as Gansu and Hubei provinces of China (Ahrens and Bezdek 2016). It is now recorded for the first time from Henan, Shaanxi, and Xizang provinces of China.

Nipponoserica sulciventris Ahrens, 2004

Figure 4

Nipponoserica sulciventris Ahrens, 2004b: 9.

Additional material examined. 2 ex. "China, W Hubei prov., Dashennogjia Nat. Res., Muyu, E slope, 2000 m, 12–15 Jun 1997, Bolm lgt." (CPPB), 2 ex. "China, N Sichuan, 5.–6.VI. Micang Shan, 1300–1400m, Daba, 32°40'N 106°55'E Jaroslav Turna leg., 2007" (ZFMK), 6 ex. "China, W Hubei, 21.–24.VI. Dashennongjia mts. 31.5N 110.3E, 2500–3000m Jaroslav Turna leg. 2001" (CPPB), 1 ♂ "Gansu, 7.IX.1980s" (HBUM).

Distribution. The species was known so far from Hubei, Shaanxi and Sichuan provinces of China (Ahrens and Bezdek 2016). It is now recorded for the first time also from Gansu province (China).

New taxa

Nipponoserica anjiensis Ahrens, Fabrizi, & Liu, sp. n.

http://zoobank.org/020469E7-21C6-4A89-9A97-9DFE89722C91
Figures 1A–D, 4

Type material examined. Holotype: ♂ "Mts. Longwangshan, Anji, Zhejiang, 12.V.1996, 450m, leg. Wu Hong/ LW-236" (IZAS). Paratypes: 1 ♂ "Wugong, Shaanxi, 2.VI.1974/ LW-085" (NUYS), 1 ♂ "Bayi, 29.VI.1982" (IZAS).

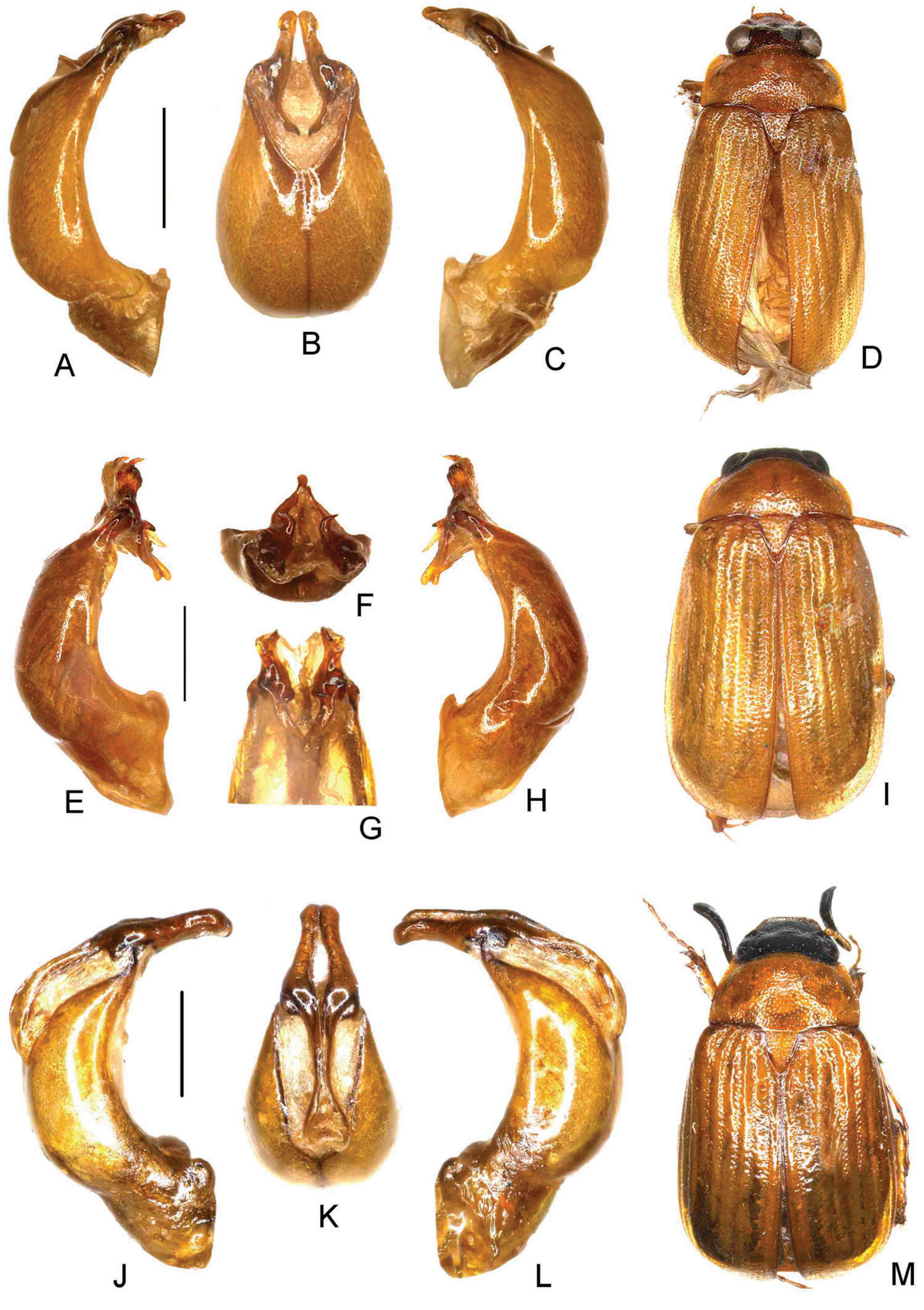

Figure 1. A–D *Nipponoserica anjiensis* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **E–I** *N. alloshanghaiensis* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **J–M** *N. henanensis* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **A, E, J** aedeagus, left side lateral view **C, H, L** aedeagus, right side lateral view **B, G, K** parameres, dorsal view **F** parameres, basidorsal view **D, I, M** habitus. Scale bar 0.5 mm. Habitus not to scale.

Diagnosis. *Nipponoserica anjiensis* sp. n. is very similar to *N. shanghaiensis* Ahrens in external appearance but differs in having distinctly shorter parameres. Sides of parameres concave at middle.

Description. Length: 8.5 mm, length of elytra: 6.4 mm, width: 3.8 mm. Body oblong, yellow, frons darker brown, antenna yellowish brown, dorsal surface entirely shiny and glabrous.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins weakly convex and moderately convergent with moderately rounded anterior angles, lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface weakly convex medially and shiny, finely and very densely punctate, distance between punctures less than their diameter, anteriorly with a few long, erect setae. Frontoclypeal suture feebly incised and medially weakly angled; smooth area in front of eye short, approximately 2.5 times as wide as long; ocular canthus moderately long and slender, finely and densely punctate with a short single terminal seta. Frons with fine and sparsely but regularly scattered punctures, with a few short setae beside the eyes. Eyes very large, ratio of diameter/interocular width: 0.94. Antenna with nine antennomeres; club with three antennomeres, almost 3 times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum slightly produced and deeply sinuate medially.

Pronotum wide and transverse, widest shortly before base, lateral margins weakly convex and weakly narrowed anteriorly; anterior angles moderately produced and blunt, posterior angles right angled but strongly rounded at tip; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with moderately dense and fine punctures, with microscopic setae in punctures, otherwise glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and dense punctures concentrated along striae, glabrous except for a few fine setae on penultimate lateral interval; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a very fine rim of short microtrichomes (visible at 100× magnification).

Ventral surface partly dull or shiny, with dense, large punctures, sparsely setose, only metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow. Mesosternum between mesocoxae almost as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/metacoxa: 1/1.3. Pygidium dull and weakly convex, finely and moderately densely punctate, without smooth midline, with sparse short setae and a few longer setae adjacent to apical margin.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/3.9; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at four-fifths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, impunctate but with some longitudinal, very superficial wrinkles; ventral margin finely serrate, with three fine setae, of which the two apical are more distant; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres dorsally with weak longitudinal impressions, ventrally with a strongly serrated ridge and a fine longitudinal carina laterally; first metatarsomere little longer than second, one third of its length longer than the upper tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical. Aedeagus: Parameres symmetrical, with asymmetrical basal lobes.

Etymology. The new species is named after the type locality Anji.

Variation. Length: 8.0–8.5 mm, length of elytra: 6.0–6.4 mm, width: 3.6–3.8 mm.

Nipponoserica alloshanghaiensis Ahrens, Fabrizi, & Liu, sp. n.

http://zoobank.org/142DDDCC-6FB5-456F-8163-DA1C60923E7B

Figures 1E–I, 4

Type material examined. Holotype: ♂ "Mts. Lushan, 10.V.1977, leg. Zhang Youwei" (IZAS). Paratypes: 3 ♀♀ "Mts. Lushan, 10.V.1977, leg. Zhang Youwei" (IZAS, ZFMK).

Diagnosis. *Nipponoserica alloshanghaiensis* sp. n. has distinctly longer parameres; each parameres has a sharp median tooth in the middle (at the level of its insertion to phallobase).

Description. Length: 7.8 mm, length of elytra: 6.4 mm, width: 4.6 mm. *Body* oblong, yellow, frons darker brown, antenna yellowish brown, dorsal surface moderately shiny and glabrous.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins weakly convex and moderately convergent with moderately rounded anterior angles, lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface weakly convex medially and shiny, finely and very densely punctate, distance between punctures less than their diameter, anteriorly with a few long, erect setae. Frontoclypeal suture feebly incised and medially weakly angled; smooth area in front of eye short, approximately 2.5 times as wide as long; ocular canthus moderately long and slender, finely and densely punctate with a short single terminal seta. Frons with fine and sparsely but regularly scattered punctures, with a few short setae beside eyes. Eyes large, ratio of diameter/interocular width: 0.83. Antenna with nine antennomeres; club with three antennomeres, three times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum slightly produced and deeply sinuate medially.

Pronotum wide and transverse, widest shortly before base, lateral margins weakly convex and weakly narrowed anteriorly; anterior angles moderately produced and blunt, posterior angles right angled but strongly rounded at tip; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with moderately dense and fine punctures, with microscopic setae in punctures, otherwise glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and dense punctures concentrated along striae, glabrous except for a few fine setae on penultimate lateral interval; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a very fine rim of short microtrichomes (visible at 100x magnification).

Ventral surface dull or shiny, with moderately dense, large punctures, sparsely setose, only metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow, apical margin of sternite tooth-like elevated beside furrow. Mesosternum between mesocoxae half as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/ metacoxa: 1/1.2. Pygidium dull, moderately convex, finely and moderately densely punctate, without smooth midline, with sparse short setae and a few longer setae adjacent to apical margin.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/4.5; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at four-fifths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, impunctate but with some longitudinal, very superficial wrinkles; ventral margin finely serrate, with three fine setae, of which the two apical are more distant; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres dorsally with weak longitudinal impressions, ventrally with a strongly serrated ridge and a fine longitudinal carina laterally; first metatarsomere little longer than second, one third of its length longer than the upper tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical.

Etymology. The name of the new species is combined from the Greek prefix *allo*- (other than) and the species name *shanghaiensis*, with reference to the very similar *Nipponoserica shanghaiensis* Ahrens.

Variation. Length: 7.8–8.8 mm, length of elytra: 6.4–7.1 mm, width: 4.6–4.9 mm. Female: Antennal club short, slightly shorter than remaining antennomeres combined; eyes small, ratio of diameter/interocular width: 0.58.

Nipponoserica henanensis **Ahrens, Fabrizi, & Liu, sp. n.**
http://zoobank.org/28D1A818-5DFE-48CD-A4E3-0F262AD42B83
Figures 1J–M, 4

Type material examined. Holotype: ♂ "China, W Henan, 15.V.–2.VI. Funiu Shan, Baotianman, pitfall traps, 33.5N 111.9E Jaroslav Turna leg., 2005" (ZFMK). Paratypes: 1 ♂, 3 ♀♀ "China, W Henan, 16.–18.V. Funiu Shan, 33°31'N 111°56'E Baotianman, pitfall traps, 1500–1750 m Jaroslav Turna leg., 2008" (ZFMK).

Diagnosis. *Nipponoserica henanensis* sp. n. has distinctly shorter and more robust parameres than *N. dahonshanica* Ahrens, which are distinctly shorter than their basal lobe.

Description. Length: 7.7 mm, length of elytra: 5.8 mm, width: 4.6 mm. *Body* oblong, yellow, frons blackish, labroclypeus and ventral surface dark brown, antenna yellowish brown, dorsal surface shiny and glabrous.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins straight and moderately convergent with weakly rounded anterior angles, lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin moderately but broadly sinuate medially; surface flat and shiny, finely and very densely punctate, with a few long, erect setae anteriorly. Frontoclypeal suture indistinctly incised and weakly curved medially; smooth area in front of eye twice as wide as long; ocular canthus moderately short and triangular, finely and densely punctate with a short single terminal seta. Frons with fine and dense punctures, with a few short setae beside eyes. Eyes small, ratio of diameter/interocular width: 0.52. Antenna with nine antennomeres; club with three antennomeres, 2.3 times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum produced and deeply sinuate medially.

Pronotum narrow, widest at base, lateral margins weakly convex and weakly narrowed anteriorly; anterior angles weakly produced but sharp; posterior angles blunt; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures concentrated along striae, glabrous except for a few short setae on odd intervals; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a fine rim of short microtrichomes (visible at 100× magnification).

Ventral surface dull, metasternum partly shiny, with moderately dense, large punctures, sparsely setose, only on metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow, apical margin of sternite tooth-like elevated beside furrow. Mesosternum between mesocoxae half as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/metacoxa: 1/1.35. Pygidium shiny, apical half dull, moderately convex, finely and moderately densely punctate, without smooth midline, with sparse short setae and a few longer setae adjacent to apical margin.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/4.2; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at five-sixths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, sparsely finely punctate, with some longitudinal, superficial wrinkles; ventral margin finely serrate, with three fine equidistant setae; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally and a fine longitudinal carina laterally; first metatarsomere distinctly longer than second, one third of its length longer than the upper tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical.

Etymology. The new species is named after its occurrence in the Henan province.

Variation. Length: 7.7–8.2 mm, length of elytra: 5.8–6.0 mm, width: 4.6–4.7 mm. Female: Antennal club short, slightly shorter than remaining antennomeres combined; eyes small, ratio of diameter/interocular width: 0.43.

Nipponoserica jiankouensis **Ahrens, Fabrizi, & Liu, sp.n.**

http://zoobank.org/249FAEC3-53AA-4771-ACE2-DE2C8514BB15
Figures 2A–D, 4

Type material examined. Holotype: ♂ "CH-Guizhou NE 27.V.–3.VI. 20km NW of Jiangkou, 1995 Fanjing Shan-Kuaichang E. Jendek & O. Sausa leg./ Coll. P. Pacholatko Invt. No./ CS11" (CPPB).

Diagnosis. *Nipponoserica jiankouensis* sp. n. has symmetrical basal lobes but an asymmetrical distal portion of parameres, with the right paramere being bent externally.

Description. Length: 7.8 mm, length of elytra: 5.6 mm, width: 4.1 mm. Body oblong, including legs dark yellow brown, frons and ventral surface dark brown, antenna yellowish brown, dorsal surface shiny and glabrous.

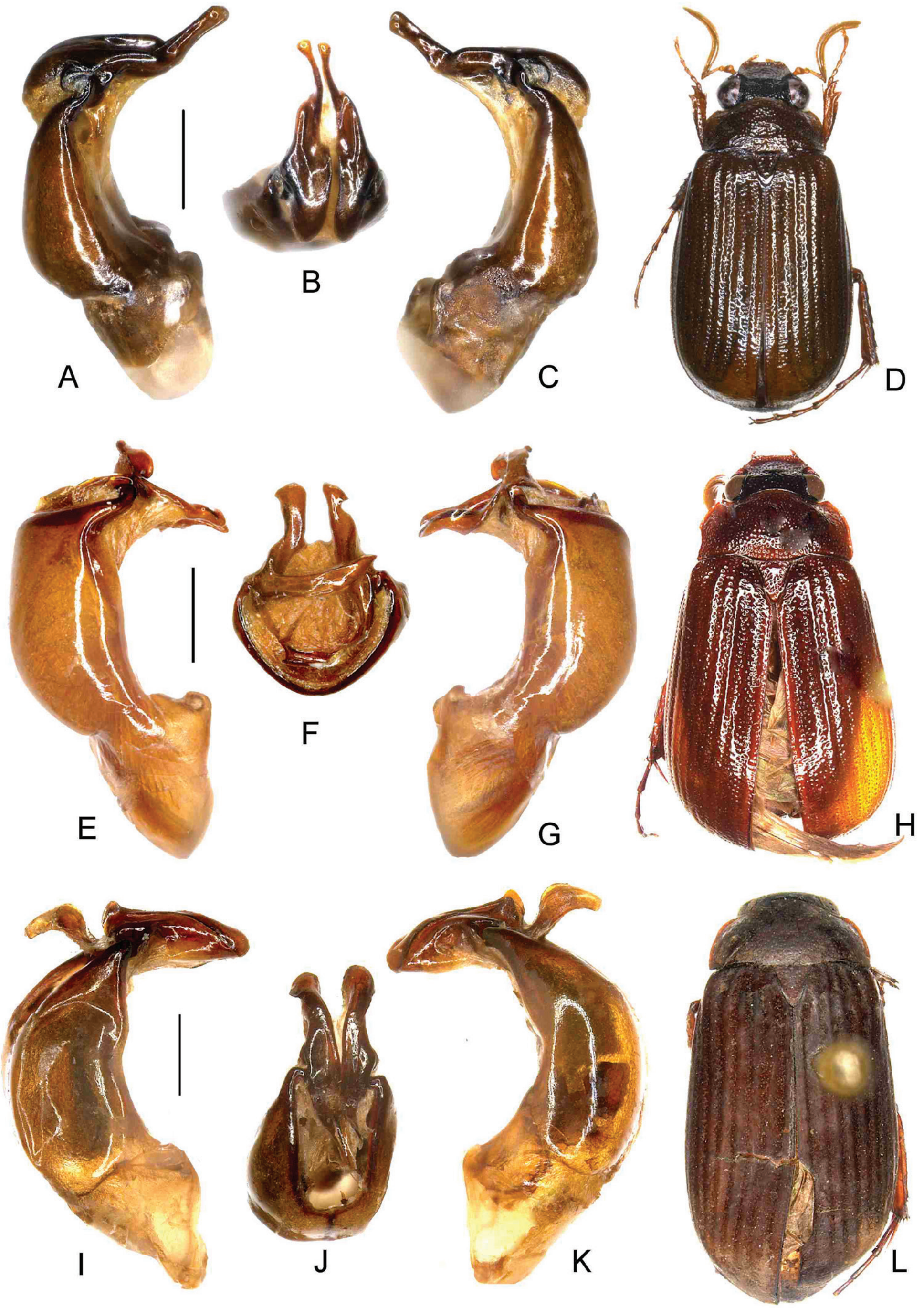

Figure 2. A–D *Nipponoserica jiankouensis* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **E–H** *N. sericanioides* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **I–L** *N. elliptica* (Murayama, 1938) (China: Yiyang, Jiangxi) **A, E, I** aedeagus, left side lateral view **C, G, K** aedeagus, right side lateral view **B, F, J** parameres, dorsal view **D, H, L** habitus. Scale bar 0.5 mm. Habitus not to scale.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins moderately convex and convergent, with moderately rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface flat and shiny, finely and densely punctate, with a few short, erect setae anteriorly. Frontoclypeal suture indistinctly incised and weakly curved medially; smooth area in front of eye twice as wide as long; ocular canthus moderately short and triangular, finely and densely punctate with a short single terminal seta. Frons with fine and dense punctures, with a few short setae beside eyes. Eyes moderately large, ratio of diameter/interocular width: 0.74. Antenna with nine antennomeres; club with three antennomeres, three times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum produced and deeply sinuate medially.

Pronotum transverse, widest at base, lateral margins straight and subparallel, in anterior quarter weakly convex and narrowed anteriorly; anterior angles weakly produced and blunt; posterior angles blunt, rounded at tip; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures concentrated along striae, glabrous except for a few short setae on odd intervals; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a very fine rim of short microtrichomes (visible at 100x magnification).

Ventral surface dull, metasternum partly shiny, with moderately dense, large punctures, sparsely setose, only on metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow, apical margin of sternite tooth-like elevated beside furrow. Mesosternum between mesocoxae half as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/metacoxa: 1/1.23. Pygidium completely dull, moderately convex, finely and moderately densely punctate, without smooth midline, with sparse short setae and a few longer setae on apical half.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/4.2; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at five-sixths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, sparsely finely punctate, with some longitudinal, superficial wrinkles; ventral margin finely serrate, with three fine setae of which the apical one is more distant; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally and a fine longitudinal carina laterally; first metatarsomere distinctly longer than second, nearly twice as long as dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical. Aedeagus: Apical part of parameres asymmetrical, basal lobes symmetrical. Female unknown.

Etymology. The new species is named after its occurrence in vicinity of Jiankou.

Nipponoserica sericanioides Ahrens, Fabrizi, & Liu, sp. n.

http://zoobank.org/8F661A6E-6995-40FF-85BE-6D2975C72A5E
Figures 2E–I, 4

Type material examined. Holotype: ♂ “Zheijang, Fengyangshan, Datianping, 2007-V-30/ LW-1242” (ZFMK). Paratypes: 1 ♂ “Zheijang, Fengyangshan, Datianping, 2007-V-30/ LW-1242bis” (IZAS).

Diagnosis. *Nipponoserica sericanioides* sp. n. bears strong asymmetrical parameres (both the basal and distal portions), which somewhat resembles the general morphology of species of *Sericania*.

Description. Length: 9.5 mm, length of elytra: 6.2 mm, width: 5.3 mm. *Body* oblong, including legs reddish brown, frons dark brown, antenna yellowish brown, dorsal surface shiny and glabrous.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins moderately convex and convergent, with moderately rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface slightly concave and shiny, finely and densely punctate, with a few short, erect setae anteriorly. Frontoclypeal suture indistinctly incised and weakly curved medially; smooth area in front of eye 1.5 times as wide as long; ocular canthus moderately short and triangular, finely and densely punctate with a short single terminal seta. Frons with fine and moderately dense punctures, with a few long setae beside eyes. Eyes small, ratio of diameter/interocular width: 0.6. Antenna with nine antennomeres; club with three antennomeres, 3 times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum produced and deeply sinuate medially.

Pronotum transverse, widest at base, lateral margins straight and slightly convergent, in anterior third convex and narrowed anteriorly; anterior angles weakly produced and blunt; posterior angles blunt, rounded at tip; anterior margin strongly and convexly produced medially with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, glabrous; anterior and lateral borders sparsely setaceous. Scutellum narrow and long, well pointed at apex, with fine and moderately dense punctures.

Elytra oblong, widest in posterior third, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures concentrated along striae, glabrous except for a few short setae on odd intervals; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous without rim of microtrichomes (visible at 100× magnification).

Ventral surface dull, metasternum partly shiny, with moderately dense, large punctures, sparsely setose, only on metasternal disc with a few longer setae. Metacoxa glabrous, laterally with a few fine setae. Abdominal sternites shiny, with fine, dense punctation, each with indistinct transversal row of coarse punctures bearing a short seta; penultimate sternite with a shallow and short median furrow, apical margin of sternite tooth-like elevated beside furrow. Mesosternum between mesocoxae half as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/metacoxa: 1/1.23. Pygidium shiny, at apex dull, moderately convex, finely and moderately densely punctate, without smooth midline, with sparse short setae and a few longer setae on apical half.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and serrate; dorsally serrated with short setae. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/3.9; dorsal margin sharply carinate, with one group of spines (basal group of spines reduced) at four-fifths of metatibial length, basally with a few single spines in punctures; external face beside dorsal margin longitudinally roof-like carinate, sparsely finely punctate, with some longitudinal, superficial wrinkles; ventral margin finely serrate, with three fine setae of which the apical one is more distant; medial face impunctate but superficially wrinkled; apex bluntly truncate interiorly near tarsal articulation. Tarsomeres glabrous and impunctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally and a fine longitudinal carina laterally; first metatarsomere distinctly longer than second, distinctly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical. The aedeagus has the apical part of the parameres asymmetrical, but the basal lobes are symmetrical (Fig. 2E–G). Female unknown.

Etymology. The name of the new species, according to its similarity to the species of the genus *Sericania*, is based on the genus name *Sericania* and the Greek suffix *-oides* (similar).

Variation. Length: 9.5–10.0 mm, length of elytra: 6.2–7.1 mm, width: 5.2–5.3 mm.

Paraserica Reitter, 1896

Paraserica Reitter, 1896: 183 (type species: *Serica grisea* Motschulsky, 1866 by monotypy)

Key to the species (♂♂).

1	Antennal club less than three times as long as remaining antennomeres combined	**2**
–	Antennal club four times as long as remaining antennomeres combined	***P. camillerii*** **Ahrens, Fabrizi, & Liu, sp. n.**
2	Species from Taiwan	***P. taiwana*** **Nomura & Kobayashi, 1979**
–	Species from Japan and mainland China	**3**
3	Antennal club more than twice as long as remaining antennomeres combined. Dorsomedial sinuation of apical phallobase as deep as wide	**4**
–	Antennal club twice as long as remaining antennomeres combined. Dorsomedial sinuation of apical phallobase distinctly deeper than wide	***P. mupuensis*** **Ahrens, Fabrizi, & Liu, sp. n.**
4	Apex of phallobase without lateral processes	***P. grisea*** **(Motschulsky, 1866)**
–	Apex of phallobase on each side bearing a lateral process	***P. wangi*** **Ahrens, Fabrizi, & Liu, sp. n.**

Paraserica grisea (Motschulsky, 1866)

Figure 5

Serica grisea Motschulsky, 1866: 171; Brenske 1897: 424, 1902: 48; Niijima and Kinoshita 1923: 15; Sawada 1937: 12.

Paraserica grisea: Reitter 1896: 183; Nakane and Baba 1960: 5; Nomura 1963: 125, 1966: 74, 1973: 124; Nakane 1972: 426; Ahrens 2004b: 7, 2007: 31.

Additional material examined. 1 ex. "Tsumbame-spa Myoko-Mts. Niigata-pref. 25.VII.1992 S. Tsuyuki leg." (ZFMK), 1 ex. "Japan Kioto" (ZFMK), 1 ex. "China: Shaanxi 21.-23.VI.1998 Quing Ling Shan mts., road Baoji-Taibai pass 35km S of Baoji O. Safranek & M. Trycna leg." (ZFMK), 1 ex. "China, W Hubei, 20.V. 5km S Lúcongpo 30.8N 110.25E Jaroslav Turna leg., 2004" (ZFMK), 4 ex. "China: Shaanxi prov., 21.–23. June 1998 Quing Ling Shan road Baoji-Tabai vill. pass. 40km S Baoji Zd. Jindra lgt." (ZFMK), 2 ex. "China, W Hubei, 3.V.–15.VII. Muyuping NW env. 31°27'N, 110°22'E, 1600m Jaroslav Turna leg., 2006" (ZFMK), 1 ♂, 1 ♀ "Mts. Tsukuba, 12.VII.1932" (IZAS).

Distribution. The species is distributed in Japan and newly recorded for the Chinese provinces of Hubei and Shaanxi.

Paraserica taiwana Nomura & Kobayashi, 1979

Paraserica taiwana Nomura & Kobayashi, 1979: 11.

Distribution. The species occurs in the central mountainous part (Nantou County) of Taiwan.

Remarks. Species is known (from Taiwan) only from female, thus the true identity of this species is uncertain yet. We had no chance yet to examine the holotype. Given its occurrence (Nantou County) in the central mountainous part of Taiwan which is characterised by a high endemism, it is highly improbable that this species does also occur in mainland China.

Paraserica camillerii Ahrens, Fabrizi, & Liu, sp. n.

http://zoobank.org/A1CC1553-CBC3-48B1-9359-3CF6F7729971
Figures 3A–D, 5

Type material examined. Holotype: "China: W Guizhou prov.; Leigongshan; Xijing; 29.v.-2.vi.1997; BOLM leg.; 1200–1900m/ 712 Sericini Asia sp." (CPPB). Paratypes: 3 ♀♀ "China, W Guizhou prov. Leigongshan, Xijing 29 May - 2 Jun 1997 1200–1900m, BOLM lgt." (CPPB, ZFMK), 1 ♂ "Mts. Leigongshan, Leishan, Guizhou, 2.VII.1988, 1700 m, leg. Zhang Xiaochun" (IZAS).

Diagnosis. *Paraserica camillerii* sp. n. has distinctly asymmetric parameres with large basal lobes.

Description. Length: 7.0 mm, length of elytra: 5.2 mm, width: 3.8 mm. *Body* including legs oblong, dark brown to grey-blackish, antenna yellowish brown, dorsal and ventral surface shiny and densely setose with double pilosity.

Labroclypeus subtrapezoidal and moderately wide, widest at base; lateral margins straight and moderately convergent, with moderately rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin nearly straight; surface flat and shiny, densely punctate, coarse punctures mixed with small ones; with long, dense, erect setae. Frontoclypeal suture indistinctly incised and weakly angled medially; smooth area in front of eye as wide as long; ocular canthus moderately short and narrow, finely and densely punctate, with a few setae. Frons with fine and dense punctures, with numerous short, adjacent setae and a few erect longer ones beside eyes and behind frontoclypeal suture. Eyes small, ratio of diameter/interocular width: 0.58. Antenna with nine antennomeres; club with three antennomeres, 4 times as long as remaining antennomeres combined, strongly reflexed. Mentum weakly elevated and flattened anteriorly. Labrum weakly produced and moderately sinuate medially.

Pronotum narrow, widest at base, lateral margins straight and subparallel in basal half, at middle moderately convex, again straight and strongly convergent in anterior half; anterior angles weakly produced but sharp; posterior angles right-angled; anterior margin straight, with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, with dense, double pilosity: numerous short setae bent backwards mixed with more sparse, long and erect setae; anterior and lateral borders densely setaceous. Scutellum narrow and long, with fine and dense punctures, with dense short setae.

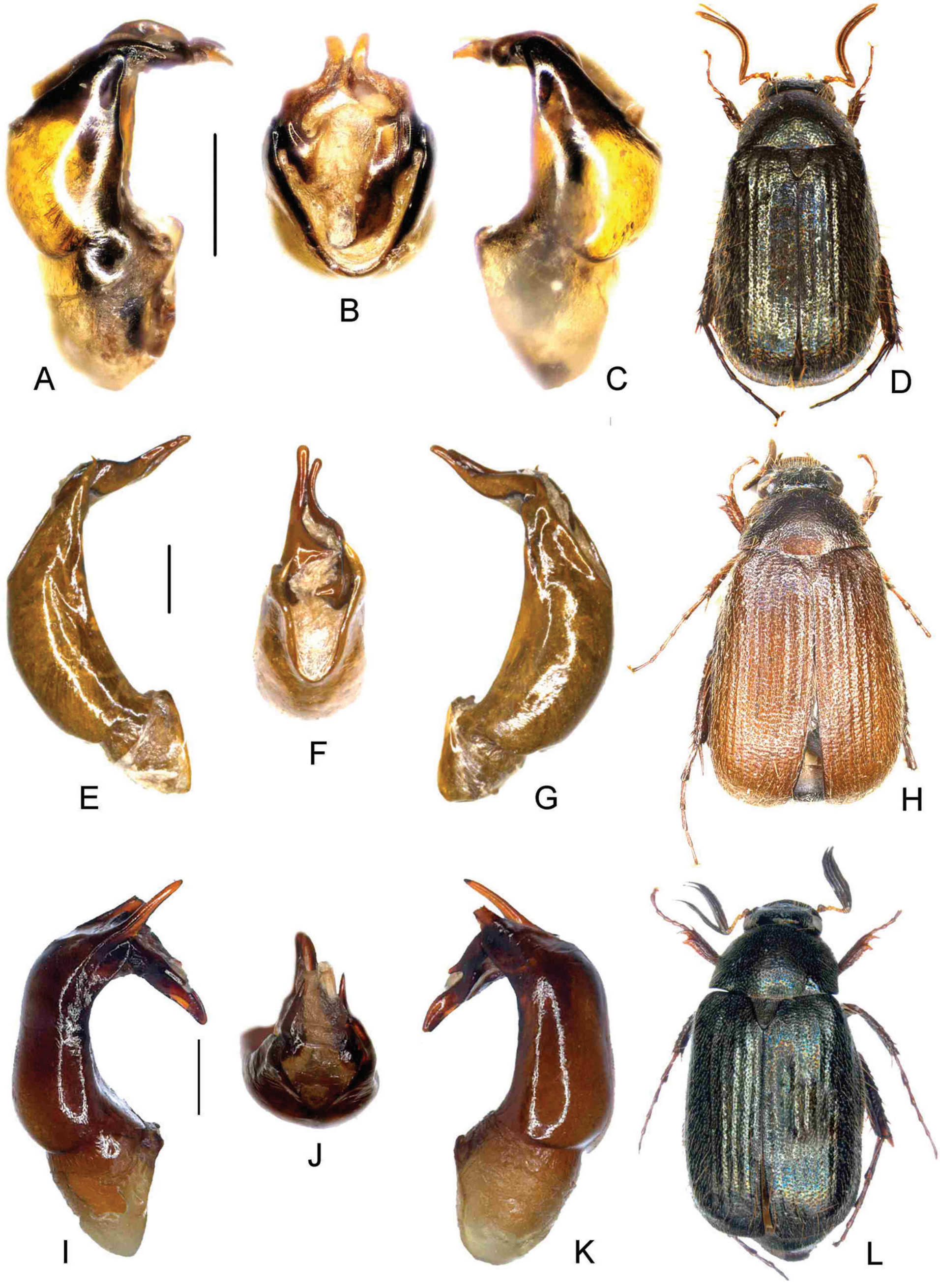

Figure 3. A–D *Paraserica camillerii* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **E–H** *P. mupuensis* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **I–L** *N. wangi* Ahrens, Fabrizi, & Liu, sp. n. (holotype) **A, E, I** aedeagus, left side lateral view **C, G, K** aedeagus, right side lateral view **B, F, J** parameres, dorsal view **D, H, L** habitus. Scale bar 0.5 mm. Habitus not to scale.

Elytra oblong, widest shortly behind middle, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures, densely setose as the pronotum, long erect setae only on odd intervals; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a fine rim of short microtrichomes (visible at 100× magnification).

Ventral surface shiny, with moderately dense, fine punctures, with dense short adjacent setae. Metacoxa completely finely setose as rest of ventral surface, laterally with a few longer setae. Abdominal sternites with fine, dense punctation and short fine pilosity, each sternite with a distinct transversal row of coarse punctures bearing a long seta; penultimate sternite simple. Mesosternum between mesocoxae as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/ metacoxa: 1/1.5. Pygidium basally shiny, apical half dull, moderately convex, finely and moderately densely punctate, without smooth midline, with dense, moderately long setae and a few longer setae adjacent to apical margin.

Legs slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate, shortly sparsely setose. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin straight with a few strong setae medially, ventrally weakly widened in apical half and smooth; dorsally serrated. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/3.8; dorsal margin sharply carinate, with two groups of spines, basal on shortly behind middle, apical one at four-fifths of metatibial length, basally with a few single spines; external face longitudinally convex, densely coarsely punctate, with dense short setae; ventral margin finely serrate, with four robust equidistant setae; medial face impunctate but coarsely punctate along the inner dorsal and ventral margin, punctures each bearing a fine seta; apex moderately truncate interiorly near tarsal articulation. Tarsomeres densely punctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally; first metatarsomere distinctly longer than second, one third of its length longer than the upper tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical.

Variation. Length: 7.0–8.1 mm, length of elytra: 5.2–5.6 mm, width: 3.8–4.1 mm. Female: Antennal club with three antennomeres, as long as remaining antennomeres combined; eyes as large as in male.

Etymology. This new species is dedicated to the Sicilian writer, Andrea Camillieri, whose books accompanied D.A.'s work on Chinese Sericini over all the years.

Paraserica mupuensis Ahrens, Fabrizi, & Liu, sp. n.

http://zoobank.org/E584DF19-12BF-4930-A0DF-8DE70D4BB5C6
Figures 3E–H, 5

Type material examined. Holotype: "China: Hunan; Mupu Mt. 1600m, Pingjiang VIII-2003, leg. Li et al." (ZFMK). Paratypes: 5 ♂♂, 15 ♀♀ "China: Hunan; Mupu Mt. 1600m, Pingjiang VIII-2003, leg. Li et al." (ZFMK), 1 ♂ "Jiugongshan Tongshan,

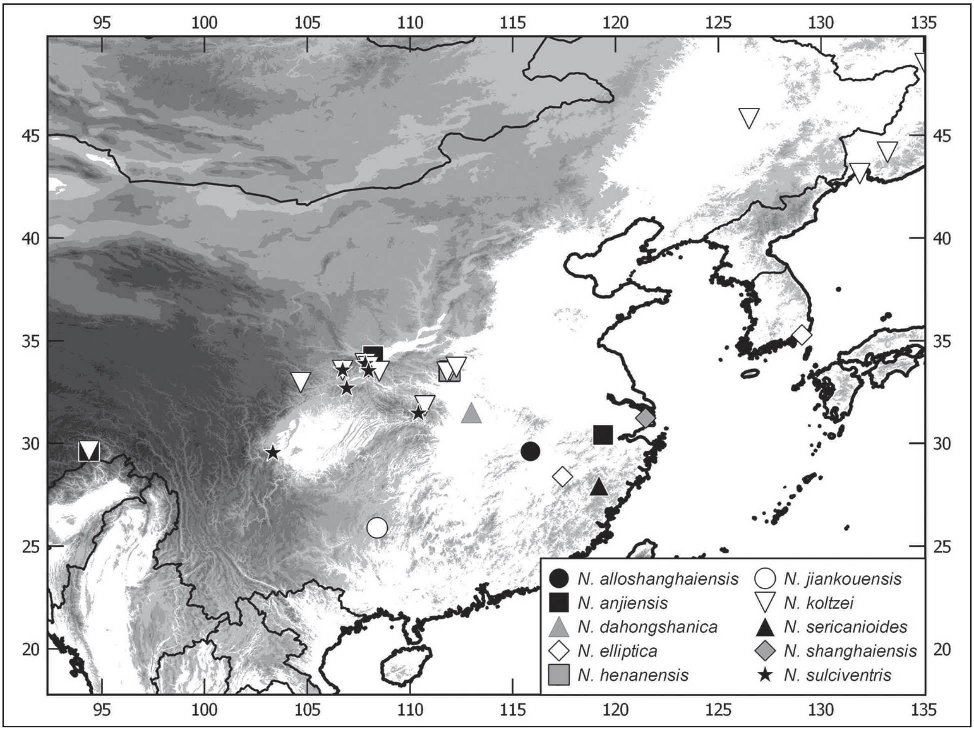

Figure 4. Distribution of Chinese *Nipponoserica* species (in case of *N. koltzei and N. elliptica* only material examined in this work is included).

S-Hubei, 1.V.2004, Leg Wen" (ZFMK), 4 ♂♂, 13 ♀♀ "China: Hubei, Dahongshan 1700m Shuizhou VI-2003 leg. Ying et al." (ZFMK, CPPB, IZAS), 1 ♂ "Mts. Tienmushan, 12.VI.1936, leg. O. Piel, Musee Heude" (IZAS).

Diagnosis. *Paraserica mupuensis* sp. n. has distinctly asymmetric parameres and the phallobase on each side of its apex with a narrow process.

Description. Length: 8.8 mm, length of elytra: 6.2 mm, width: 4.6 mm. *Body* oblong, head and pronotum including legs dark brown, elytra reddish brown, antenna yellowish brown, dorsal and ventral surface shiny and densely setose with partly double pilosity.

Labroclypeus subtrapezoidal and wide, widest at base; lateral margins straight and moderately convergent, with moderately rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface flat and moderately shiny, densely punctate, very coarse punctures mixed with small ones; with long, dense, erect setae. Frontoclypeal suture distinctly incised and weakly curved medially, slightly elevated; smooth area in front of eye 1.5 times as wide as long; ocular canthus moderately short and narrow, finely and densely punctate, with a 1–2 setae. Frons with fine and dense punctures, with numerous short, adjacent setae and a few erect longer ones beside eyes and behind frontoclypeal suture. Eyes small, ratio of diameter/interocular width: 0.64. Antenna with nine antennomeres; club with three antennomeres, 1.8 times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum weakly produced and moderately sinuate medially.

Pronotum narrow, widest at base, lateral margins straight and weakly convergent in basal half, weakly convex and moderately convergent in anterior half; anterior angles weakly produced but nearly blunt; posterior angles right-angled; anterior margin weakly convex, with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, with dense, double pilosity: numerous short setae bent backwards mixed with very sparse, long and erect setae, at disc pilosity partly abraded; anterior and lateral borders densely setaceous. Scutellum narrow and long, with fine and dense punctures, with dense short setae.

Elytra oblong, widest shortly behind middle, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures, densely setose with short adjacent setae as pronotum, long erect setae absent on elytra; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a broad rim of short microtrichomes (visible at 100× magnification).

Ventral surface shiny, with moderately dense, fine punctures, with dense short adjacent setae. Metacoxa completely finely setose as rest of ventral surface, laterally with a few longer setae. Abdominal sternites with fine, dense punctation and short fine pilosity, each sternite with a distinct transversal row of coarse punctures bearing a long seta; penultimate sternite simple. Mesosternum between mesocoxae as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/ metacoxa: 1/1.5. Pygidium shiny, in apical half strongly convex, finely and densely punctate, without smooth midline, with dense, moderately long setae and numerous longer setae adjacent to apical margin.

Legs moderately slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate, shortly sparsely setose. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin with a few strong setae medially, weakly widened in apical half and smooth ventrally; finely serrated dorsally. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/3.6; dorsal margin sharply carinate, with two groups of spines, basal on at three quarters of metatibial length, apical one shortly before apex, basally with a few single spines; external face beside dorsal margin longitudinally roof-like carinate, densely coarsely punctate, with dense short setae; ventral margin finely serrate, with six robust equidistant setae; medial face coarsely and densely punctate, punctures each bearing a fine seta; apex moderately truncate interiorly near tarsal articulation. Tarsomeres densely punctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally, dorsal punctures partly extended to longitudinal wrinkles; first metatarsomere distinctly longer than second, slightly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical.

Variation. Length: 7.8–8.8 mm, length of elytra: 5.8–6.6 mm, width: 4.2–5.0 mm.

Female: Antennal club with three antennomeres, as long as remaining antennomeres combined; eyes nearly as large as in male (ratio of diameter/interocular width: 0.55).

Etymology. The new species is named after the type locality in Mupu Mountain.

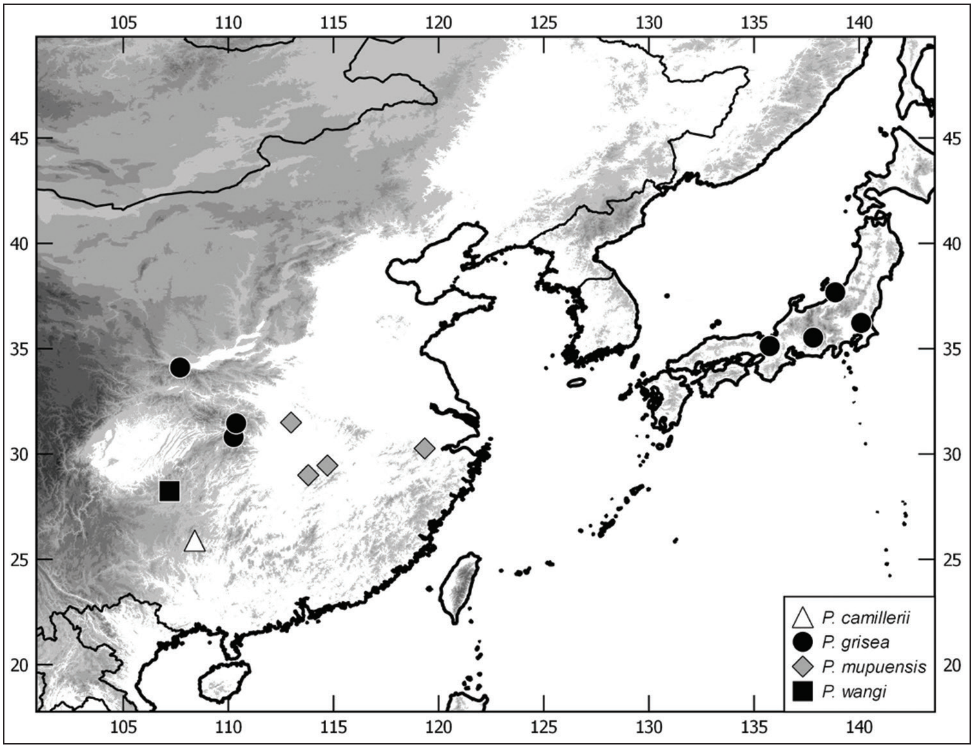

Figure 5. Distribution of Chinese *Paraserica* species (in case of *P. grisea* only material examined in this work is included).

***Paraserica wangi* Ahrens, Fabrizi, & Liu, sp. n.**
http://zoobank.org/9FFF2588-4633-4288-9E4A-66D641121519
Figures 3I–L, 5

Type material examined. Holotype: "Kuankuoshui Nature Reserve, Guizhou, 5.VI.2010, leg. Wang Zhiliang/ LW-355" (IZAS).

Diagnosis. *Paraserica wangi* has longer phallobasal processes and the median interior lobe is directed distally.

Description. Length: 8.3 mm, length of elytra: 5.8 mm, width: 4.3 mm. *Body* oblong, colour greyish-black, antenna yellowish brown, dorsal and ventral surface shiny and densely setose with partly double pilosity.

Labroclypeus subtrapezoidal and wide, widest at base; lateral margins straight and weakly convergent, with moderately rounded anterior angles; lateral border and ocular canthus producing a distinct blunt angle; margins weakly reflexed; anterior margin distinctly sinuate medially; surface flat and moderately shiny, densely punctate, very coarse punctures mixed with small ones; with long, dense, erect setae. Frontoclypeal suture distinctly incised and weakly curved medially, slightly elevated; smooth area in front of eye 1.5 times as wide as long; ocular canthus moderately short and narrow, finely and densely punctate, with a 1–2 setae. Frons with fine and dense punctures, with numerous short, adjacent setae and a few erect longer ones beside eyes and behind frontoclypeal suture. Eyes very small, ratio of diameter/interocular width: 0.46. Antenna with nine antennomeres; club with three antennomeres, 2.5 times as long as remaining antennomeres combined, strongly reflexed. Mentum elevated and flattened anteriorly. Labrum weakly produced and moderately sinuate medially.

Pronotum narrow, widest at base, lateral margins straight and subparallel in basal half, weakly convex and moderately convergent in anterior half; anterior angles weakly produced but nearly blunt; posterior angles right-angled; anterior margin weakly convex, with a distinct and broad marginal line; basal margin without marginal line; hypomeron distinctly margined at base; surface with dense and fine punctures, with dense, double pilosity: numerous short setae bent backwards mixed with sparse, long and erect setae; anterior and lateral borders densely setaceous. Scutellum narrow and long, with fine and dense punctures, with dense short setae.

Elytra oblong, widest at middle, striae distinctly impressed, finely and densely punctate; intervals weakly convex, with fine and sparse punctures, densely setose with short adjacent setae as pronotum, with numerous long erect setae on odd intervals; epipleural border robust, ending at strongly curved external apical angle; epipleura densely setaceous; apical border chitinous with a broad rim of short microtrichomes (visible at 100x magnification).

Ventral surface shiny, with moderately dense, fine punctures, with dense short adjacent setae. Metacoxa completely finely setose as rest of ventral surface, laterally with a few longer setae. Abdominal sternites with fine, dense punctation and short fine pilosity, each sternite with a distinct transversal row of coarse punctures bearing a long seta; penultimate sternite simple. Mesosternum between mesocoxae as wide as mesofemur, with irregularly scattered, strong setae. Ratio of length of metepisternum/metacoxa: 1/1.65. Pygidium shiny, beside apical margin dull, moderately convex, finely and densely punctate, without smooth midline, with dense, moderately long setae and numerous longer setae adjacent to apical margin.

Legs moderately slender, shiny; femora with two longitudinal rows of setae, finely and moderately densely punctate, shortly sparsely setose. Metafemur shiny, anterior margin acute, without a submarginal serrated line; posterior margin with a few strong setae medially, weakly widened in apical half and smooth ventrally; finely serrated dorsally. Metatibia slender and long, widest shortly before apex, ratio width/length: 1/3.6; dorsal margin sharply carinate, with two groups of spines, basal on at three quarters of metatibial length, apical one shortly before apex, basally with a few single spines; external face beside dorsal margin longitudinally roof-like carinate, densely coarsely punctate, with dense short setae; ventral margin finely serrate, with five robust equidistant setae; medial face coarsely and densely punctate, punctures each bearing a fine seta; apex moderately truncate interiorly near tarsal articulation. Tarsomeres densely punctate dorsally, with sparse, short setae ventrally; metatarsomeres with a strongly serrated ridge ventrally, dorsal punctures partly extended to longitudinal wrinkles; first metatarsomere distinctly longer than second, slightly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetrical. Female unknown.

Etymology. The new species is named after the collector of this species, Wang Zhiliang.

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RESEARCH ARTICLE

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Revision of the species of *Lytopylus* from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae)

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Abstract

Thirty two new species of *Lytopylus* (Agathidinae) are described with image plates for each species: *Lytopylus alejandromasisi* **sp. n.**, *Lytopylus alfredomainieri* **sp. n.**, *Lytopylus anamariamongeae* **sp. n.**, *Lytopylus angelagonzalezae* **sp. n.**, *Lytopylus cesarmorai* **sp. n.**, *Lytopylus eddysanchezi* **sp. n.**, *Lytopylus eliethcantillanoae* **sp. n.**, *Lytopylus ericchapmani* **sp. n.**, *Lytopylus gahyunae* **sp. n.**, *Lytopylus gisukae* **sp. n.**, *Lytopylus guillermopereirai* **sp. n.**, *Lytopylus gustavoindunii* **sp. n.**, *Lytopylus hartmanguidoi* **sp. n.**, *Lytopylus hernanbravoi* **sp. n.**, *Lytopylus hokwoni* **sp. n.**, *Lytopylus ivanniasandovalae* **sp. n.**, *Lytopylus johanvalerioi* **sp. n.**, *Lytopylus josecortesi* **sp. n.**, *Lytopylus luisgaritai* **sp. n.**, *Lytopylus mariamartachavarriae* **sp. n.**, *Lytopylus miguelviquezi* **sp. n.**, *Lytopylus motohasegawai* **sp. n.**, *Lytopylus okchunae* **sp. n.**, *Lytopylus pablocobbi* **sp. n.**, *Lytopylus robertofernandezi* **sp. n.**, *Lytopylus rogerblancoi* **sp. n.**, *Lytopylus salvadorlopezi* **sp. n.**, *Lytopylus sangyeoni* **sp. n.**, *Lytopylus sarahmeierottoae* **sp. n.**, *Lytopylus sergiobermudezi* **sp. n.**, *Lytopylus sigifredomarini* **sp. n.**, and *Lytopylus youngcheae* **sp. n.** A dichotomous key and a link to an electronic, interactive key are included. All specimens were reared from Lepidoptera larvae collected in Area de Conservación Guanacaste (ACG) and all are associated with ecological information including host caterpillar, collection date, eclosion date, caterpillar food plant, and locality. Neighbor-joining and maximum likelihood analyses of the barcode region of the mitochondrial cytochrome *c* oxidase subunit I gene (COI DNA barcode) were conducted to aid in species delimitation.

Keywords

Costa Rica, DNA barcoding, host use, parasitoid wasps, species limits, taxonomy

Introduction

Agathidinae contains approximately 1,200 described species (Yu et al. 2012), making it a moderately species-rich subfamily of Braconidae. All members of Agathidinae are koinobiont endoparasitoids of Lepidoptera larvae (Sharkey 2006) meaning that they are internal parasitoids that enter early instar host larvae and their hosts continue to develop before being consumed in the last instar or prepupal parasitoid stage. Over most of its history, *Lytopylus* was considered a junior synonym of *Bassus* Fabricius, *Microdus* Nees, or *Agathis* Latreille. Sharkey et al. (2016) removed the genus from synonymy and synonymized *Agathellina* Enderlein, 1920, *Ditropia* Enderlein, 1920, and *Austroearinus* Sharkey, 2006, under it, thereby including six species in the genus, i.e., *Lytopylus azygos* Viereck, 1905, *Agathellina columbiana* Enderlein, 1920, *Austroearinus chrysokeras* Sharkey, 2006, *Austroearinus melanopodes* Sharkey, 2006, *Bassus rufofemoratus* Muesebeck, 1927, *Ditropia strigata* Enderlein, 1920, *Lytopylus unicolor* (Schrottky, 1902). Only one species of *Lytopylus* has a published host association: *L. unicolor* (Shenefelt 1970) is a parasitoid of the potato tuber-worm *Phthorimaea operculella* (Zeller 1873) in the Gelechiidae.

Although this article appears to be the second taxonomic revision of *Lytopylus* Forster, 1862 from Area de Conservación Guanacaste (ACG), the revision by Sharkey et al. (2011) employed the name *Lytopylus* in error and later Sharkey et al. (2016) transferred all of species described under *Lytopylus* in that paper to *Aerophilus* Szépligeti, 1902.

This work focuses on specimens of *Lytopylus* reared from Lepidoptera larvae collected by Drs Janzen and Hallwachs and the team of ACG parataxonomists since 1978 in the ACG (Janzen et al. 2009, Janzen and Hallwachs 2011, 2016). All are associated with ecological information including host caterpillar, collection date, eclosion date, caterpillar food plant, and locality. COI mitochondrial DNA barcodes for most specimens are deposited in the Barcode of Life Datasystem (BOLD) (http://www.boldsystems.org) (Hebert et al. 2003) and are equally available at http://janzen.sas.upenn.edu. The sequence data are publicly available through the Public Data Portal of BOLD (http://www.boldsystems.org/index.php/Public_BINSearch?searchtype=records).

We include an image plate for each species, a traditional identification key and a digital web-based interactive key; both have illustrations of morphological characters (https://www.dropbox.com/s/j9xongce1qrav5j/Revised%20Lytopylus%20Interactive%20key.zip?dl=0). A diagnoses and descriptions are provided for thirty-two new species and one previously described species.

Methods

Species concepts

We use Mayr's (1969) biological species concept, i.e., a species consists of a group of natural populations that are reproductively isolated from other groups. Because insect taxonomists usually work with dead specimens, delimitation of insect species is based on methods that indirectly infer reproductive isolation rather than direct observation, i.e., similarity in morphological, molecular (COI DNA sequences), geography, and host use data if recorded.

Specimen information

Most specimens, and all holotypes, are deposited in the insect collection in the Biology Department of Utah State University (USU) Logan, Utah. Duplicates are in the Hymenoptera Institute Collection (HIC), Entomology Department, University of Kentucky and those from ACG will eventually be deposited in a major North American Museum. The detailed parasitoid specimen records are available by search of the individual specimen DHJPARxxxxxxx voucher codes on Janzen's database (http://janzen.sas.upenn.edu/caterpillars/database.lasso). Host caterpillars are uniquely identified by their own voucher code system, which is recognizable by YY-SRNP-XXXXX where "YY" is the two-digit year and "XXXXX" is a unique number within that year. Some of the host caterpillars are incompletely identified, but they also have unique names such as *Dichomeris* Janzen512, which is an interim name for *Dichomeris* species 512 as determined by a biodiversity specialist of the ACG team or a professional taxonomist who provides the proper genus epithet. These names will be updated in the database when the species is blessed with a formal scientific name, but the interim name, in this case *Dichomeris* Janzen512, will remain searchable in that database.

Morphological analysis

Morphological characters were recorded using the DELTA Editor (v. 1.02; Dallwitz et al. 1999). The DELTA Editor was used to enter the data for both interactive (web-based) and traditional printed keys (https://www.dropbox.com/s/j9xongce1qrav5j/Revised%20Lytopylus%20Interactive%20key.zip?dl=0). Images to illustrate the couplets were taken by a JVC digital camera fixed on microscopes and stacked with the program Automontage. Plates for each species were arranged using Adobe Photoshop Elements 12. The morphological terms mostly follow Sharkey and Wharton (1997) and are coordinated with the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010). The minimum number of characters necessary to distinguish a species from all other species in this study is included in a diagnosis for each species. Descriptions, based on the holotype of each species, were automatically generated using DELTA.

DNA extraction, PCR, and sequencing

271 COI DNA sequences were sourced from the BOLD database. DNA was extracted by the Centre for Biodiversity Genomics using a glass fibre protocol (Ivanova et al. 2006).

Extracts were resuspended in 30 µL $_{d}H_2O$, and a 658-bp region near the 5' terminus of the CO1 gene was amplified using standard insect primers LepF1 (5'-ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'-TAAACTTCTGGATGTCCAAAAAATCA-3') following the established protocols (Smith et al. 2008). If initial amplification failed, other amplifications were conducted following the established protocols using internal primer pairs, LepF1-C113R (130 bp) or LepF1-C_ANTMR1D (300 bp) and MLepF1-LepR1 (400 bp) to generate shorter overlapping sequences (Smith et al. 2008).

For the specimens which DNA sequences were not available in BOLD, DNA was extracted from individual legs at University of Kentucky (UKY) with Qiagen DNeasy Blood and Tissue Kit following the manufacturer's animal tissue protocol (Qiagen Inc., Chatsworth, California, USA).

COI was amplified from extracted DNA using the forward primer mlCOIintF (Leray et al. 2013) and reverse primer jgHCO2198 (Geller et al. 2013). Unique 9 bp tags, designed using Barcode Generator (available from http://comailab.genomecenter.ucdavis.edu/index.php/Barcode_generator) were attached to the primers so that each sequence could be traced to its parent specimen by the unique combination of tags. PCR was performed using Takara reagents consisted of 10X buffer, 2.5 µM nucleotides, 1 µM of each primer, 0.125 U Takara Ex Taq, 2 µL template DNA and enough $_{dd}H_2O$ for a total reaction volume of 25 µL. We followed the "touchdown" thermal cycling protocol for these primers as outlined in Leray et al. (2013).

COI PCR DNA products, in addition to those from BOLD, were sequenced on an Illumina MiSeq system at the UKY Genomics Core Laboratory.

DNA assembly and phylogenetic analysis

Individual directional reads were downloaded from BOLD (produced by Sanger sequencing) and were edited and assembled using Geneious Pro (v. 6.1.6; Drummond et al. 2010) with the default settings. Edited sequences were stored in the NEXUS file format. The three sequences produced by NGS at UKY were included in the file of edited sequences. NGS sequencing data was assembled using PEAR (Zhang et al. 2013) and demultiplexed using custom Phython scripts. Among all bidirectional reads from each specimen, the 1st and 2nd most numerous reads were manually retrieved from the output file. The sequences were then queried against the GenBank nucleotide library using NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and those that were highly similar to *Lytopylus* specimens were retained. Finally, three COI sequences were exported from the FASTQ file and added to the file of edited sequences. The multiple sequence alignment was assembled on the MAFFT server (http://www.ebi.ac.uk/Tools/msa/mafft/; v. 7; Katoh et al. 2013) using the default settings.

A NJ tree (Saitou and Nei 1987) was constructed by using PAUP* (v. 4.0β10; Swofford 2003) using the p-distance setting. ML analyses were performed using Garli (v. 2.01; Zwickl 2006). For ML, the data were partitioned by codon position for COI (three partitions). We applied the most complex model available (GTR+I+G; Rodriguez et al. 1990) to each partition as per recommendations of Huelsenbeck and Rannala (2004) for likelihood-based analyses. Garli applies separate parameter estimates to each partition. A 20-replicate ML analysis was performed using default settings. Additionally, a ML bootstrap analysis (minimum 500 replicates) was conducted to assess nodal support (Garli, default settings). The COI data set analyzed herein is available from the senior author upon request.

Host use

Besides the notes included here additional data can be accessed at http://janzen.sas.upenn.edu (Janzen et al. 2009).

Species delimitation

The NJ tree and the tree of highest log-likelihood from 20 ML search reps in Fig. 1 and Fig. 2 were based solely on COI. These trees were constructed solely to assist in the delimitation of species. Molecular species concepts were initially based on the NJ tree and were compared to the best ML tree with COI data. The 2% genetic distance cut-off, which has been a conventional threshold for species delimitation using COI barcodes (Jones et al. 2011) and has been used in the Barcode Index Numbers (BINs) (http://www.barcodinglife.org/index.php/Public_BarcodeIndexNumber_Home), was used to cluster putative species (Smith et al. 2013). Morphological and host use data were then employed to make final decisions when genetic distances between putative molecular species were near the 2% threshold or below it, as is necessary for other groups of insects (e.g., Janzen et al. 2017).

Results and discussion

Species delimitation

The NJ tree and the highest log-likelihood ML tree with COI data both suggest twenty-eight molecular species, and twenty-eight putative species were clustered using the 2% genetic distance cut-off.

Before running the molecular analyses I.K. and M.S. independently sorted the specimens to morphospecies and had error rates of 62% and 54% respectively based on our final species delimitations. All possible types of errors were discovered, i.e., clumping, splitting, and both clumping and splitting (mixing the members of two or more species). In contrast the molecular species concepts matched with our final species delimitations at 96.6%. The implications for previous taxonomic

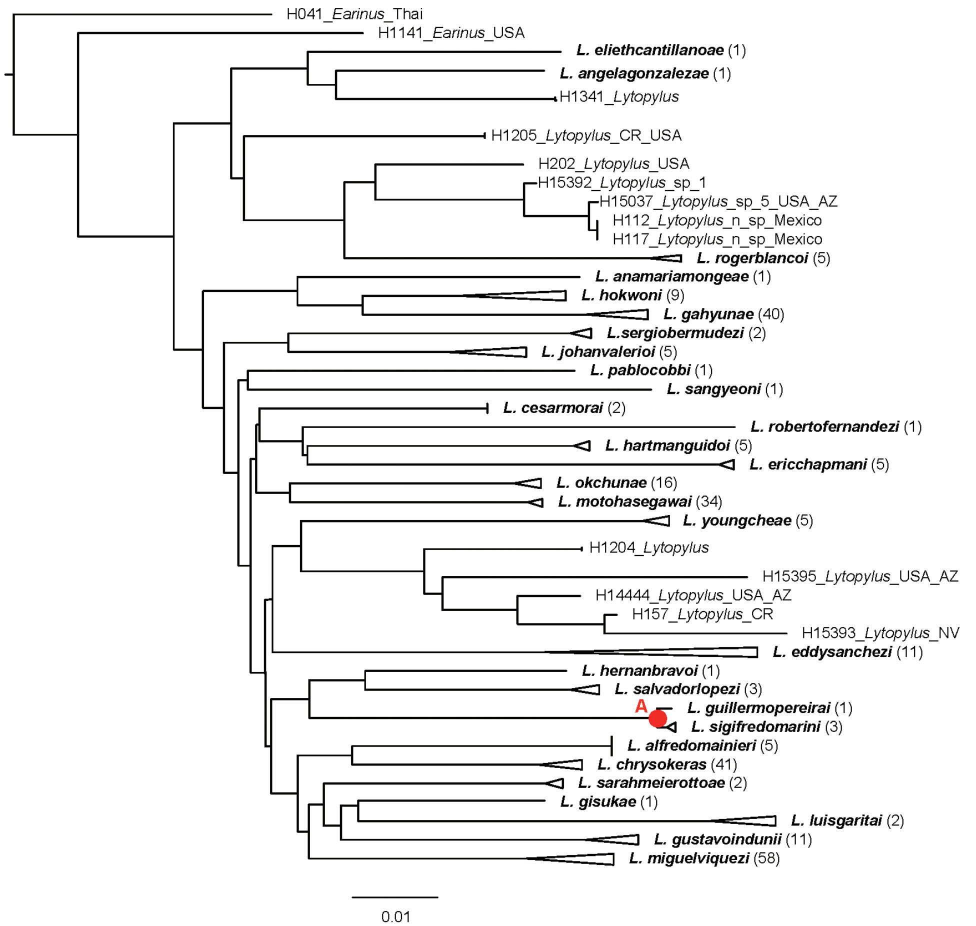


Figure 1. The NJ tree of the COI DNA barcode region for twenty-nine of the thirty-three *Lytopylus* species treated here. Triangles represent collapsed clades; their lengths (measured horizontally) represent the distance from the most basal node to the apex of the longest branch. The number of specimens in each triangle is given in parentheses following the species name. The node labeled with a red "**A**" is discussed in the text.

treatments of braconids (and other speciose small tropical insects) based solely on morphology are dire.

The sole incongruity between molecular species concepts and final species concepts concerned *L. sigifredomarini* and *L. guillermopereirai*. The genetic variation between these two species was 0.4%, and the ML tree grouped them together (Fig. 2, node A). We, however, delimited them as separate species because they are morphologically distinct in their strikingly different color patterns, and the NJ tree recovered these two species as monophylic sister taxa. (Fig. 1, node A). In addition, they attack different species of host caterpillars with different feeding niches.

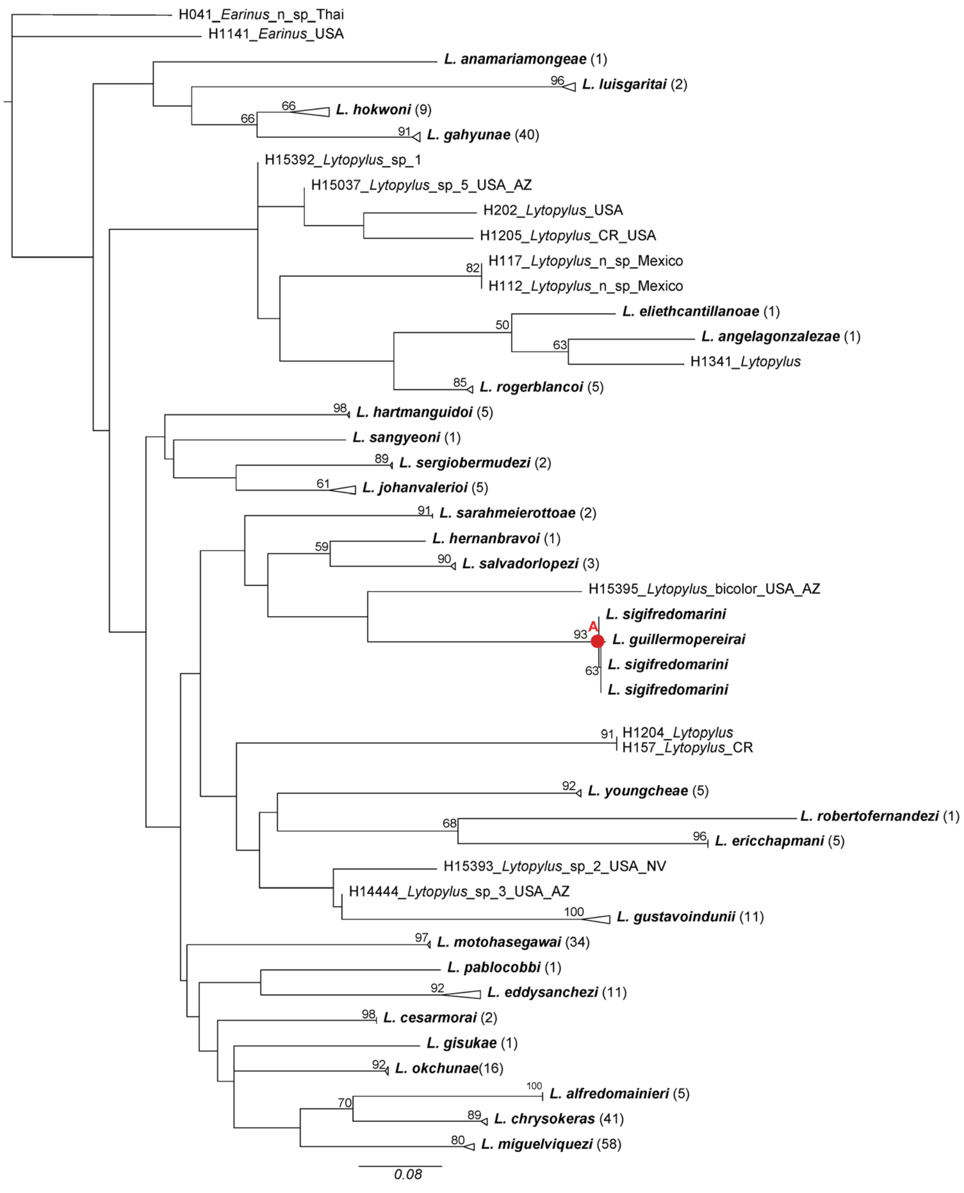


Figure 2. Tree of highest log-likelihood from 20 ML search reps of the COI data set. Terminals with bold-faced type indicate species described herein. ML bootstrap values appear above the branches. Triangles represent collapsed clades; their lengths (measured horizontally) represent the distance from the most basal node to the apex of the longest branch. The number of specimens in each triangle is given in parentheses following the species name. The node labeled with a red "A" is discussed in the text.

The four species (*L. alejandromasisi*, *L. ivanniasandovalae*, *L. josecortesi*, *L. mariamartachavarriae*) for which genetic data were not available were delimited using morphological and host data.

Systematics

Lytopylus Föster, 1862

Agathellina Enderlein, 1920. Type species: *Agathellina columbiana* Enderlein, 1920.
Ditropia Enderlein, 1920. Type species: *Ditropia strigata* Enderlein, 1920.
Austroearinus Sharkey, 2006. Type species: *Bassus rufofemoratus* Muesebeck, 1927.

Type species. *Lytopylus azygos* Viereck, 1905, by monotypy, first included species.

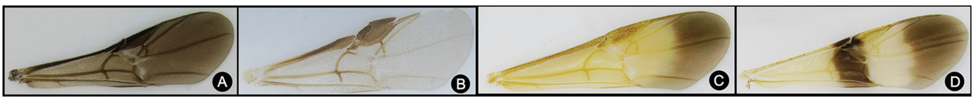
Diagnosis. *Lytopylus* can be distinguished from all other agathidine genera with the following combination of characters: tarsal claws simple with a basal lobe; mesoscutum unsculptured and notauli absent; fore wing vein (RS+Ma) not complete; vein CUb of hind wing weak or absent and never tubular; hind coxal cavities open; median tergite 3 smooth.

Distribution. Restricted to the New World, from the northeastern USA south to Argentina, primarily Neotropical.

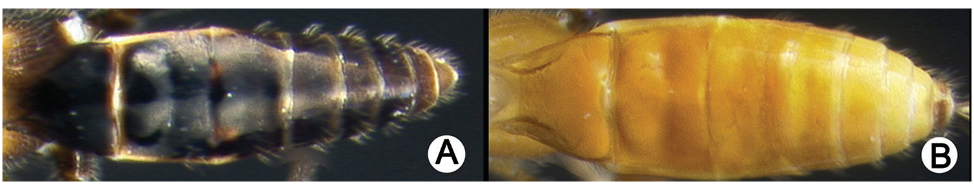
Species diversity. Including the thirty-two species described here, there are 39 described species of *Lytopylus*. Based on the diversity in the University of Kentucky Hymenoptera Institute Collection, there are hundreds more awaiting description.

Key to the species of *Lytopylus* of Area de Conservación Guanacaste, Costa Rica

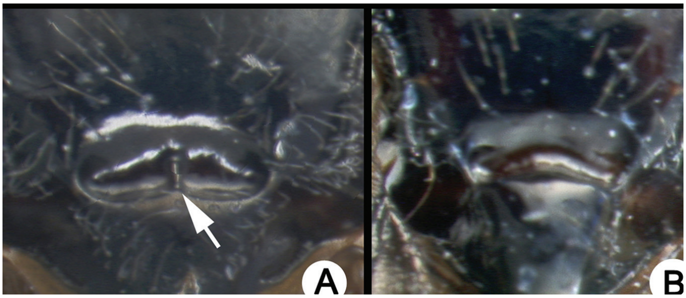
1 A. Fore wing mostly or entirely infuscated **2**
– B. Fore wing hyaline or with a slight yellow tinge **28**
– C. Fore wing with one apical black band **31**
– D. Fore wing with two black bands... **33**



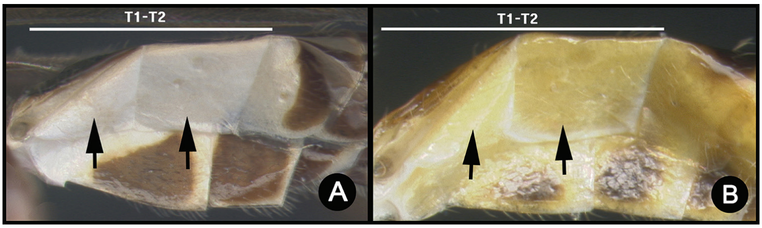
2(1) A. Median tergites mostly or entirely melanic (brown to black) **3**
– B. Median tergites entirely pale (yellow to orange) or mostly pale with posterior terga black.. **10**



3(2) A. Scutellar sulcus with at least one longitudinal carina................................**4**
– B. Scutellar sulcus lacking longitudinal carinae **6**

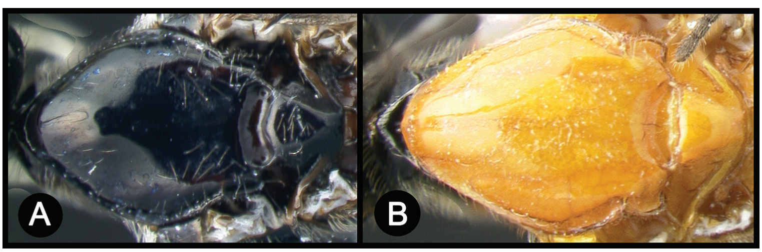


4(3) A. Lateral tergites one and two entirely white..........................***L. cesarmorai***
– B. Lateral tergites one and two mostly or entirely yellow.............................**5**

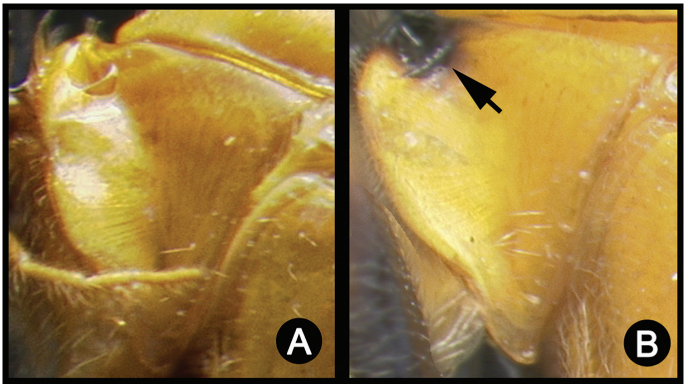


5(4) A. Hind femur mostly pale (yellow to orange) or black and pale with a similar percentage of each color..***L. motohasegawai*** ♂
– B. Hind femur mostly black, pale apically......................***L. miguelviquezi*** ♂

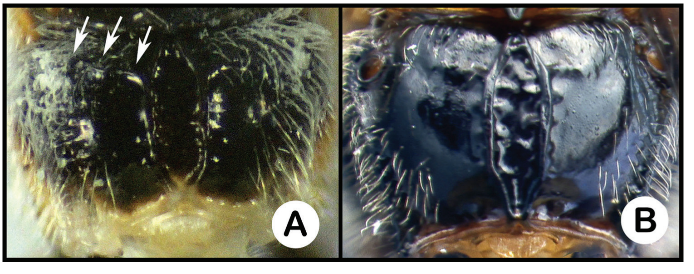
6(3) A. Mesoscutum mostly or entirely melanic (brown to black) ..***L. guillermopereirai***
– B. Mesoscutum mostly or entirely pale (yellow to orange) 7



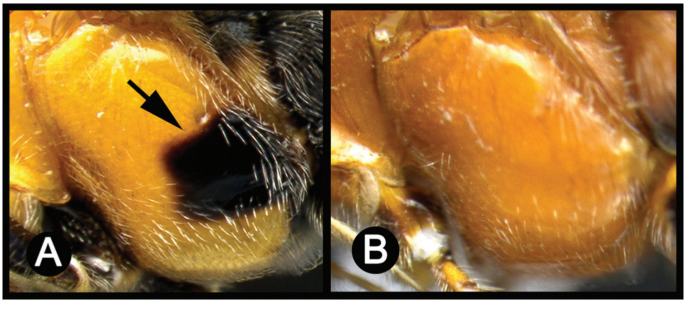
7(6) A. Pronotum entirely pale (yellow to orange) **8**
– B. Pronotum bicolored **9**



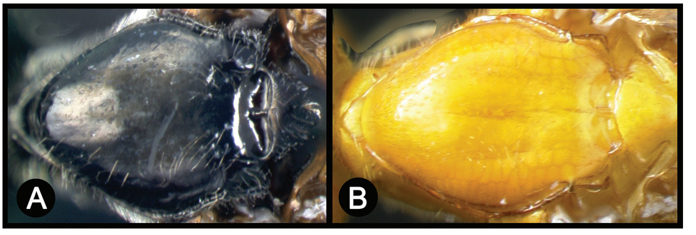
8(7) A. Anterior transverse carina of propodeum reaching the lateral margin........ ....***L. sarahmeierottoae***
– B. Anterior transverse carina of propodeum not reaching the lateral margin or absent .... ***L. salvadorlopezi***



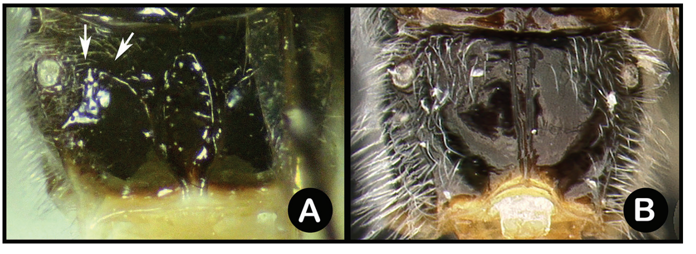
9(7) A. Mesopleuron bicolored... ***L. anamariamongeae***
– B. Mesopleuron entirely pale (yellow to orange) ....***L. luisgaritai***



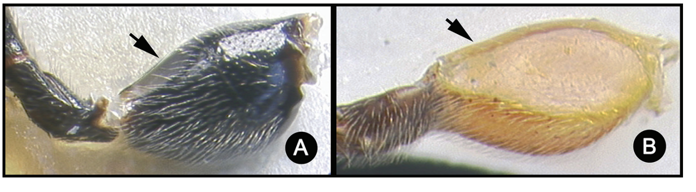
10(2) A. Mesoscutum mostly or entirely melanic **11**
– B. Mesoscutum mostly or entirely pale (yellow to orange) **18**



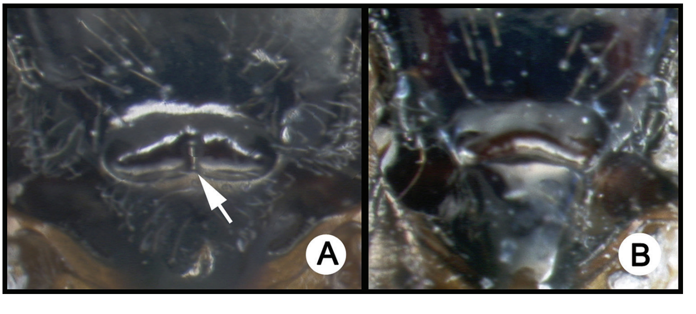
11(10) A. Anterior transverse carina of propodeum reaching the lateral margin.... **12**
– B. Anterior transverse carina of propodeum not reaching the lateral margin or absent **15**



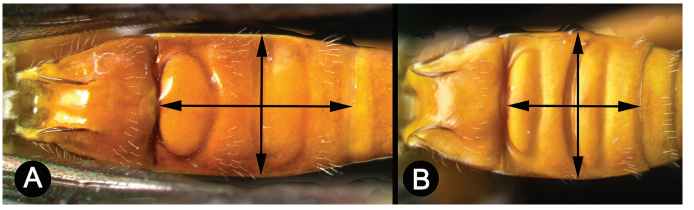
12(11) A. Hind coxa entirely black... ***L. hernanbravoi***
– B. Hind coxa mostly or entirely pale **13**



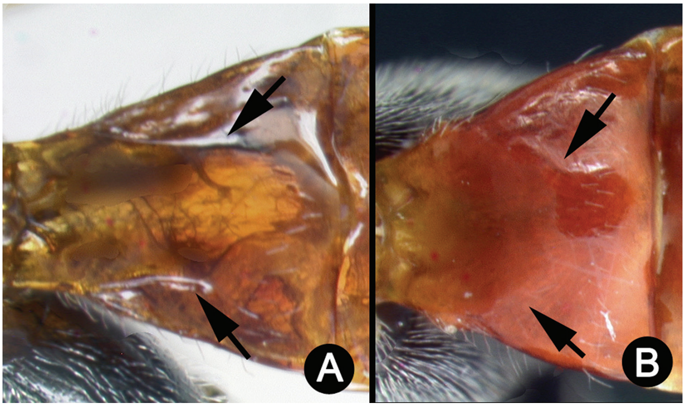
13(12) A. Scutellar sulcus with at least one longitudinal carina............................ **14**
– B. Scutellar sulcus lacking longitudinal carinae ....***L. sigifredomarini***



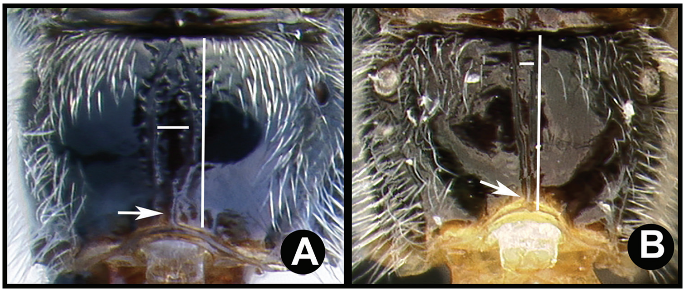
14(13) A. Median syntergite 2+3 1.4× longer than wide........................ ***L. gahyunae***
– B. Median syntergite 2+3 as long as wide..................................***L. sangyeoni***



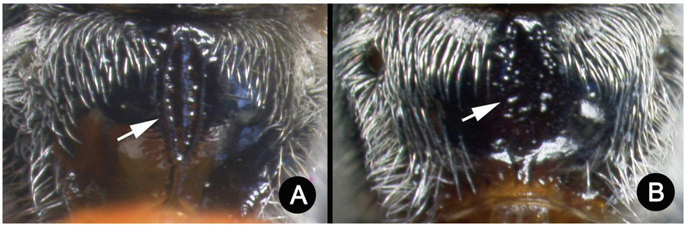
15(11) A. Lateral longitudinal carinae of median tergite 1 well-defined................**16**
– B. Lateral longitudinal carinae of median tergite 1 blunt **17**



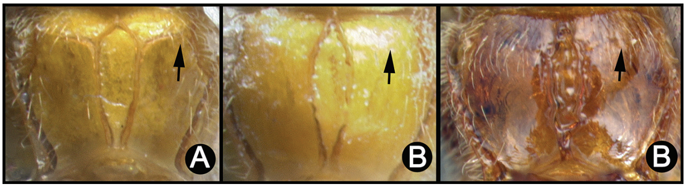
16(15) A. Median areola of propodeum spindle-shaped; median areola length 6× its width; median areola closed posteriorly.................................... ***L. josecortesi***
– B. Median areola of propodeum wide anteriorly narrow and not closed posteriorly; median areola length 11× its width.................***L. eliethcantillanoae***



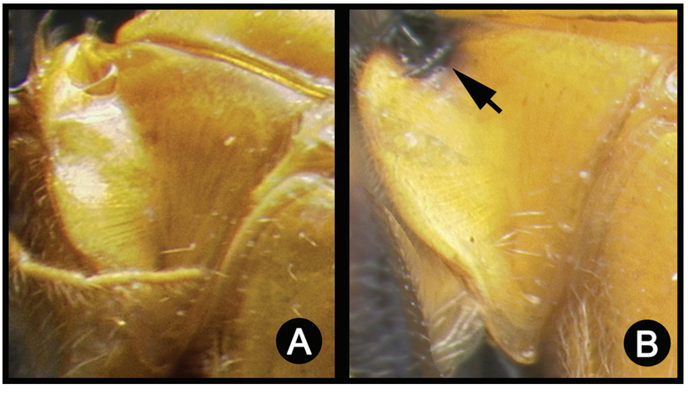
17(15) A. Median areola of propodeum with well-defined margins ..... ***L.rogerblancoi***
– B. Median areola of propodeum lacking well-defined margins .... ***L. angelagonzalezae***



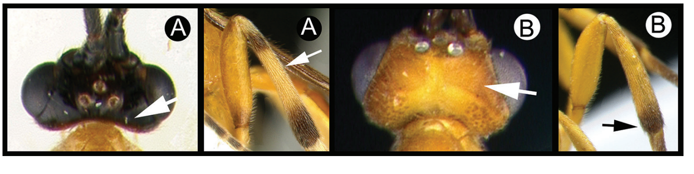
18(10) A. Anterior transverse carina of propodeum reaching the lateral margin.... **19**
– B. Anterior transverse carina of propodeum not reaching the lateral margin or absent **21**



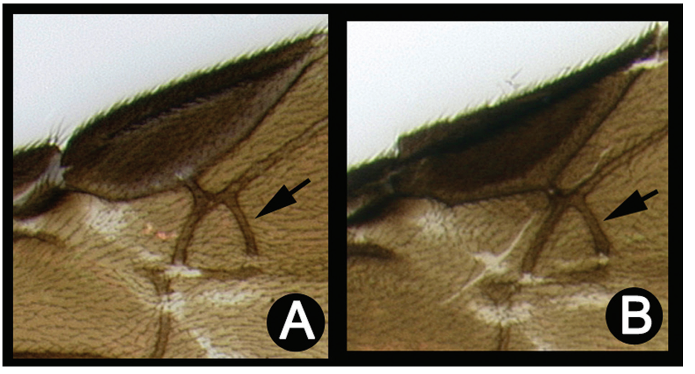
19(18) A. Pronotum entirely pale (yellow to orange) **20**
– B. Pronotum bicolored .... ***L. johanvalerioi***



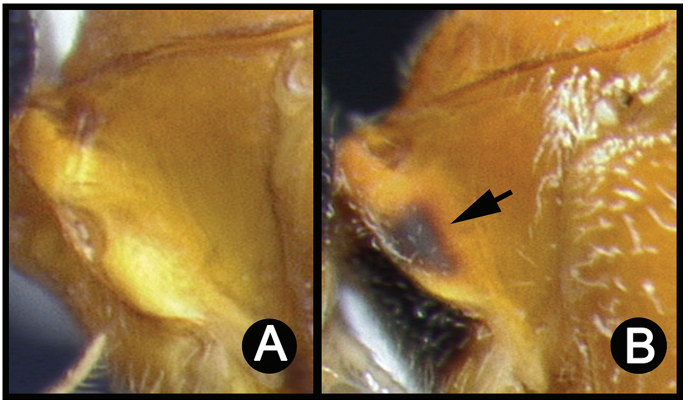
20(19) A. Vertex of head entirely melanic; hind tibia black basally and distally, yellow at mid-length .... ***L.alejandromasisi***
– B. Vertex of head mostly or entirely yellow; hind tibia pale basally, black apically .... ***L. chrysokeras***



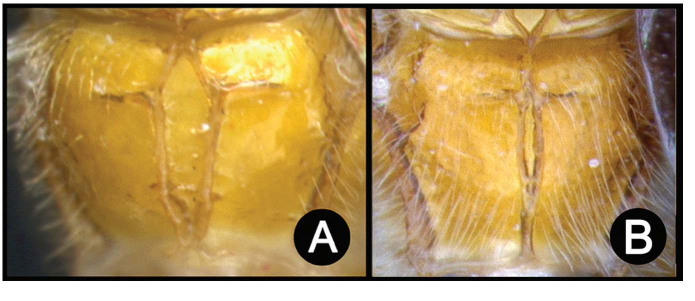
21(18) A. Fore wing second submarginal cell weakly quadrate **22**
– B. Fore wing second submarginal cell triangular **24**



22(21) A. Pronotum entirely pale (yellow to orange) **23**
– B. Pronotum bicolored .... ***L. pablocobbi***

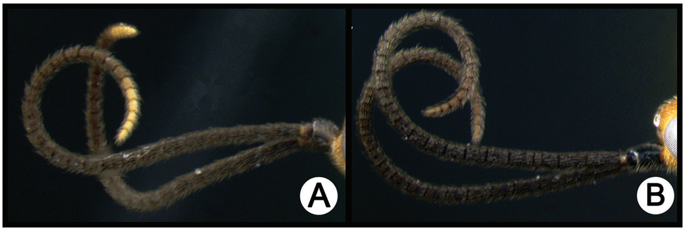


23(22) A. Median areola length 4× its width; median areola of propodeum kite-shaped .... ***L.motohasegawai*** ♀
– B. Median areola length 15× its width; median areola of propodeum spindle-shaped .... ***L. gisukae***



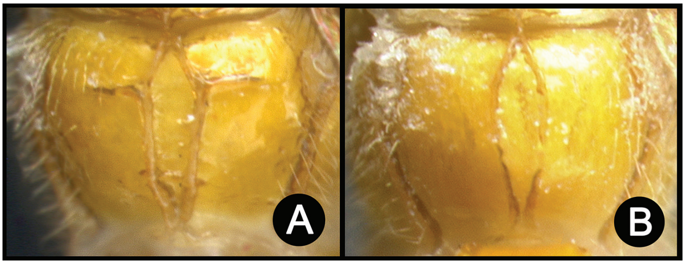
24(21) A. Apical flagellomeres usually bright yellow, always distinctly paler than subapical flagellomeres .... ***L. chrysokeras***

– B. Apical flagellomeres brown not distinctly paler than subapical flagellomeres **25**



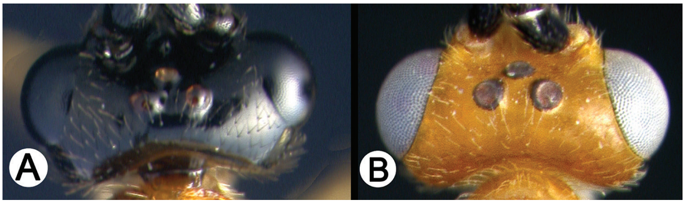
25(24) A. Median areola of propodeum kite-shaped................. ***L. miguelviquezi*** ♀

– B. Median areola of propodeum spindle-shaped **26**



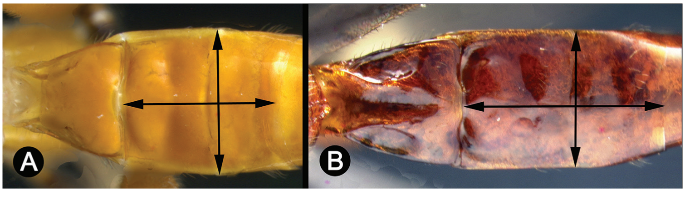
26(25) A. Vertex of head entirely melanic.. **27**

– B. Vertex of head mostly or entirely yellow .... ***L.gustavoindunii***

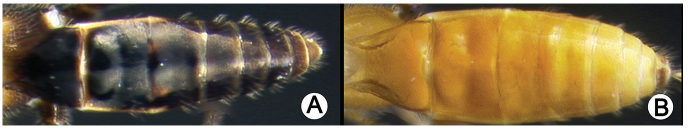


27(26) A. Median syntergite 2+3 1.1 times longer than wide ..... ***L. alfredomainieri***

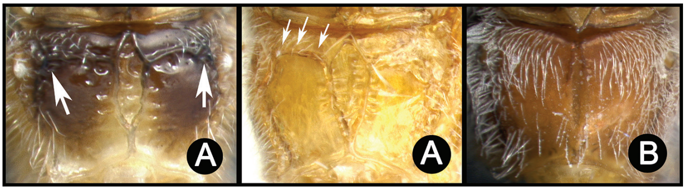
– B. Median syntergite 2+3 1.5 times longer than wide .... ***L. okchunae***



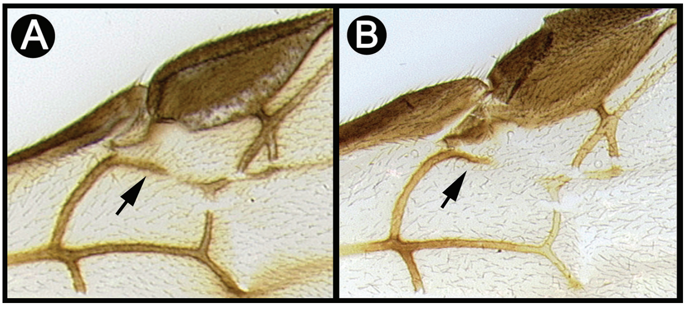
28(1) A. Median tergites mostly or entirely melanic (brown to black) ...*L. cesarmorai*
– B. Median tergites entirely pale (yellow to orange) or mostly pale with posterior terga black...**29**



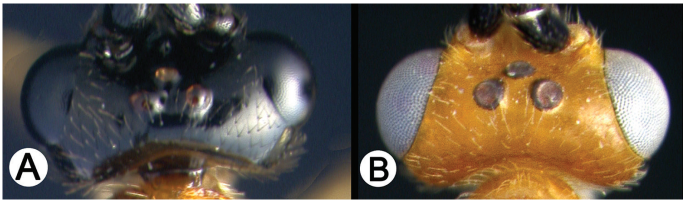
29(28) A. Anterior transverse carinae of propodeum reaching the lateral margin;..... median areola of propodeum kite-shaped...**30**
– B. Anterior transverse carinae of propodeum not reaching the lateral margin or absent; median areola of propodeum spindle-shaped ..... *L. ivanniasandovalae*



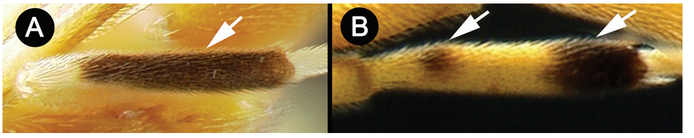
30(29) A. Fore wing RS+Ma tubular on more than half its length... *L. sergiobermudezi*
– B. Fore wing RS+Ma tubular on less than one third its length ....*L. mariamartachavarriae*



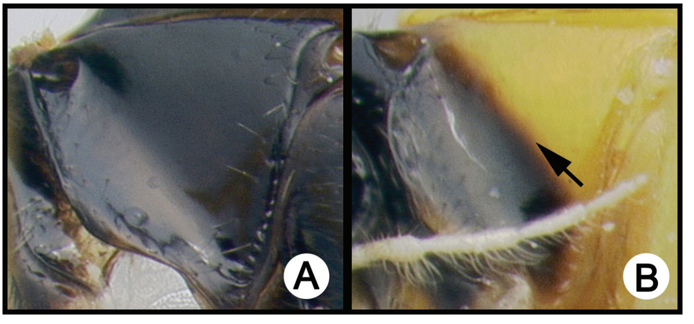
31(1) A. Vertex of head mostly or entirely melanic .... *L. youngcheae*
– B. Vertex of head mostly or entirely yellow **32**



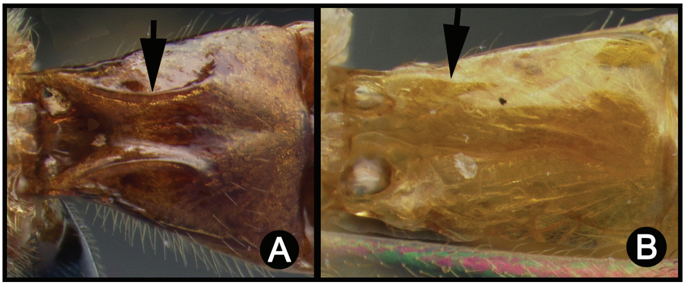
32(31) A. Mid tibia mostly black, yellow basally .... ***L. eddysanchezi***
– B. Mid tibia with a sub-basal black patch and black apically, yellow at mid-length and basally .... ***L. hartmanguidoi***



33(1) A. Pronotum entirely melanic **34**
– B. Pronotum bicolored .... ***L. ericchapmani***



34(33) A. Lateral longitudinal carinae of median tergite 1 well-defined..***L. hokwoni***
– B. Lateral longitudinal carinae of median tergite 1 blunt...***L. robertofernandezi***



Species descriptions

Lytopylus alejandromasisi Kang, sp. n.

http://zoobank.org/C27B1AC1-2924-4700-AB21-134B9882E3F2
Fig. 3

Diagnosis. Fore wing mostly infuscated; hind tibia black basally and distally, yellow at mid-length; pronotum entirely yellow; mesoscutum entirely pale; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely pale.

Description. Holotype: male. Body length 5.6 mm. Fore wing length 5.4 mm. Fore wing mostly infuscated. Scutellar sulcus with five longitudinal carinae. Median

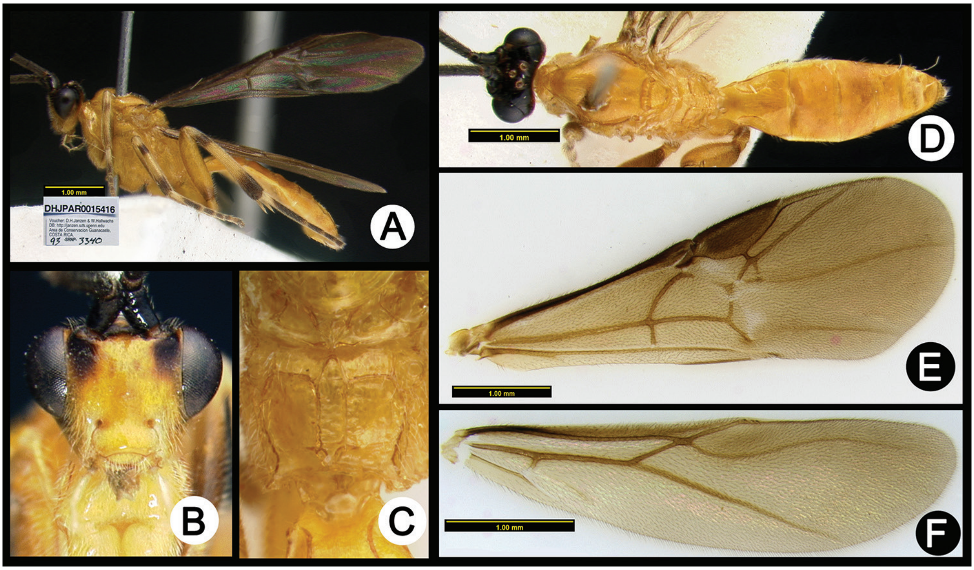


Figure 3. *Lytopylus alejandromasisi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.

Female. Unknown.

Etymology. *Lytopylus alejandromasisi* is named in honor of Alejandro Masis in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared one time from Gelechiidae "same as 93-SRNP-3345.1" feeding on very new leaves of *Bursera tomentosa* (Burseraceae) in ACG dry forest at 280 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Santa Rosa, Quebrada Duende, Area de Conservación Guanacaste 10.83663N -85.61144W 280m., gusaneros coll., host plant: Burseraceae *Bursera tomentosa*, host caterpillar: Gelechiidae, same as 93-SRNP-3345.1, coll. date: 7/7/1993, parasitoid eclosion date: 7/25/1993, DHJPAR0015416.

Lytopylus alfredomainieri Kang, sp. n.

http://zoobank.org/ED76E996-F310-4605-BB8D-F1EC579B21D9

Fig. 4

Diagnosis. Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely melanic; fore wing mostly infuscated; pronotum entirely pale

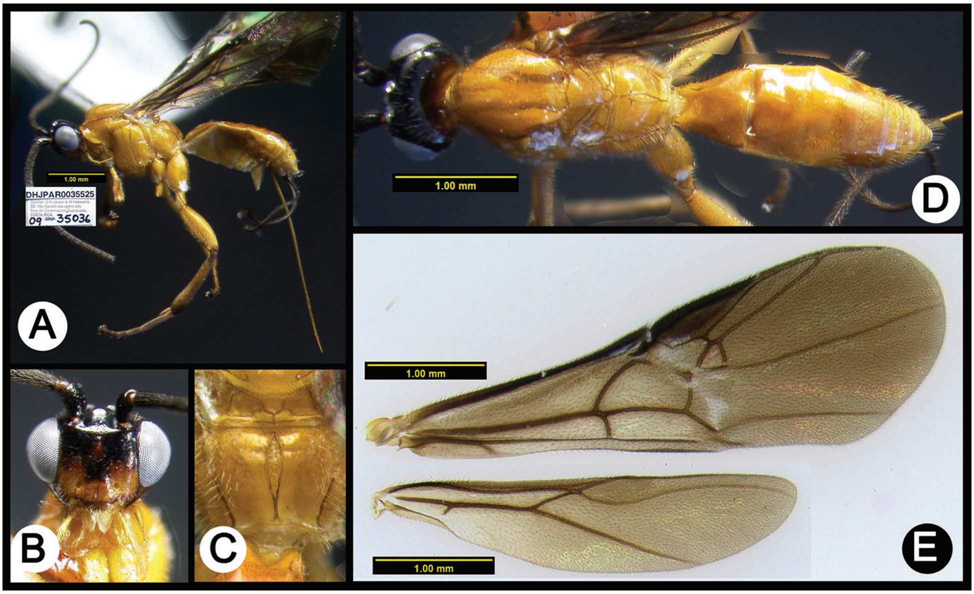


Figure 4. *Lytopylus alfredomainieri* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** wings.

(yellow to orange); fore tibia entirely pale (yellow to orange); mesoscutum entirely pale; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange); median syntergite 2+3 1.1 times longer than wide.

Description. Holotype: female. Body length 4.4 mm. Fore wing length 5.1 mm. Fore wing mostly infuscated. Pronotum entirely pale (yellow to orange). Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor about same length as body.

Males. Similar to holotype except for face. Face usually paler than holotype.

Etymology. *Lytopylus alfredomainieri* is named in honor of Alfredo Mainieri in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared five times from two species of *Olethreutes* (Olethreutinae, Tortricidae) leaf-tiers feeding on mature leaves of *Meliosma glabrata* (Sabiaceae) in ACG cloud forest edge at 1220 to 1276 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Cacao, Sendero Derrumbe, Area de Conservación Guanacaste 10.92918N -85.46426W 1220m., Manuel Pereira coll., food plant: Sabiaceae *Meliosma glabrata*, host caterpillar: Tortricidae, Olethreutinae, *Olethreutes* Janzen188, coll. date: 2/2/2009, parasitoid eclosion date: 3/19/2009, DHJPAR0035525. Paratypes: [the following have the same data as the holotype except as indicated] ♂, DHJPAR0035519. ♀, DHJPAR0035513. ♂, Sector

Pailas Gemelos, 10.76928N -85.34662W, 1276m., Jose Cortez coll., host caterpillar: *Olethreutes* Brown22, coll. date: 10/7/2009, parasitoid eclosion date: 11/2/2009, DHJPAR0038251. [same as previous except eclosion date] ♂, parasitoid eclosion date: 11/1/2009, DHJPAR0037861.

Lytopylus anamariamongeae Kang, sp. n.

http://zoobank.org/14F4C7B3-3857-4584-8CCA-3781096E338C
Fig. 5

Diagnosis. Fore wing mostly infuscated; pronotum mostly pale, anteriorly black; mesoscutum entirely pale (yellow to orange); mesopleuron mostly pale, posteroventrally black; scutellar sulcus lacking longitudinal carina; median tergites entirely melanic.

Description. Holotype: female. Body length 6.2 mm. Fore wing length 5.5 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor about same length as body.

Male. Unknown.

Etymology. *Lytopylus anamariamongeae* is named in honor of Ana Maria Monge in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared one time from *Antaeocerconota* Janzen433 (Depressariidae) a leaftier feeding on mature leaves of *Inga punctata* (Fabaceae) in ACG dry forest – rain forest ecotone at 540 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Tajo Angeles, Area de Conservación Guanacaste 10.86472N -85.41531W 540m., Gloria Sihezar coll., food plant: Fabaceae *Inga punctata*, host caterpillar: Depressariidae, Stenomatinae, *Antaeocerconota* Janzen433, coll. date: 11/29/2010, parasitoid eclosion date: 12/17/2010, DHJPAR0041571.

Lytopylus angelagonzalezae Kang, sp. n.

http://zoobank.org/53BD9379-0092-4255-A872-311C8795407F
Fig. 6

Diagnosis. Fore wing mostly infuscated; mesoscutum entirely melanic; median areola of propodeum lacking well-defined margins; anterior transverse carina of propodeum absent; median tergites entirely reddish orange; lateral longitudinal carinae of median tergite 1 blunt.

Description. Holotype: female. Body length 5.8 mm. Fore wing length 5.6 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Me-

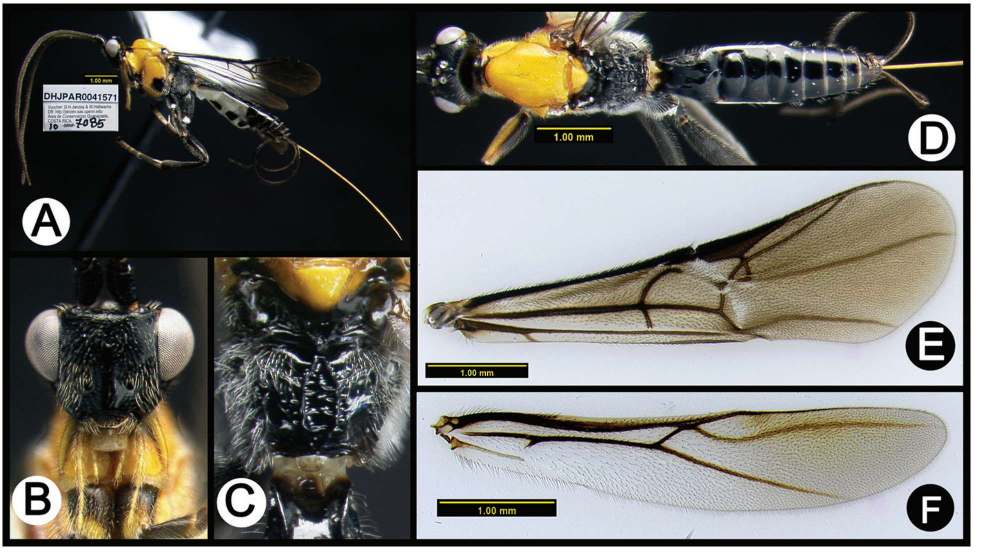


Figure 5. *Lytopylus anamariamongeae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

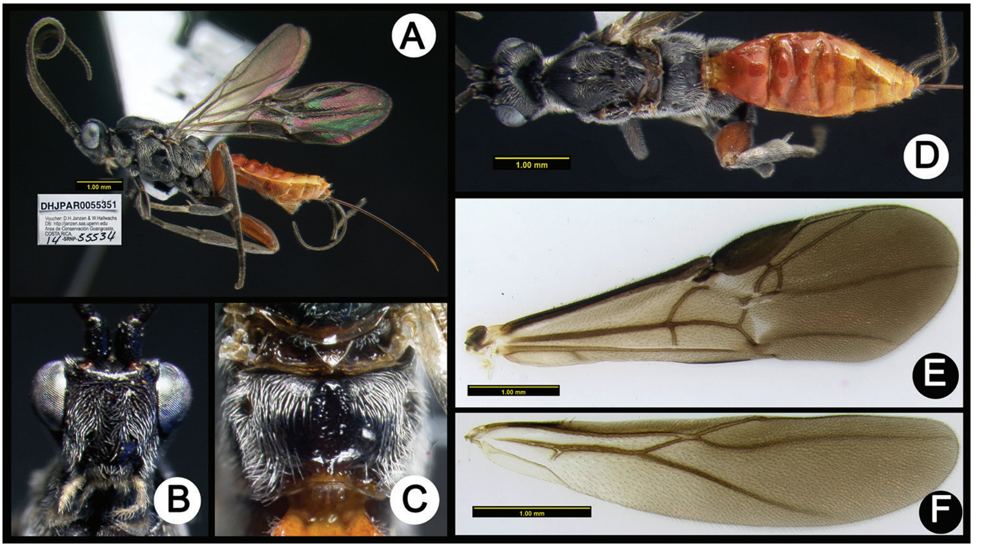


Figure 6. *Lytopylus angelagonzalezae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

dian areola of propodeum lacking well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 blunt. Median syntergite 2+3 as long as wide. Ovipositor length longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. *Lytopylus angelagonzalezae* is named in honor of Angela González Grau in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Anacampsis* Janzen353 (Anacampsinae, Gelechiidae) feeding on two species of Rutaceae in ACG dry forest – rain forest ecotone at 280 to 825 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Pailas, PL12, Area de Conservación Guanacaste 10.76248N -85.33689W 752m., Jose Cortez coll., food plant: Rutaceae *Zanthoxylum acuminatum*, host caterpillar: Gelechiidae, Anacampsinae, *Anacampsis* Janzen353, coll. date: 3/6/2014, parasitoid eclosion date: 4/9/2014, DHJPAR0055351.Paratype: [the following have the same data as the holotype except as indicated] ♀, Sector Del Oro, Puente Mena, 11.04562N -85.45742W 280m., Lucia Ríos coll., food plant: *Amyris pinnata*, coll. date: 4/1/2002, parasitoid eclosion date: 4/15/2002, DHJPAR0015430.

Lytopylus cesarmorai Kang, sp. n.

http://zoobank.org/5D2E689D-6076-4242-938B-73C772324EE1
Fig. 7

Diagnosis. Fore wing mostly infuscated; scutellar sulcus with one median longitudinal carina; median tergites entirely melanic; lateral tergites one and two entirely white.

Description. Holotype: female. Body length 5.7 mm. Fore wing length 5.4 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor slightly longer than body.

Male. Fore wing with a slight yellow tinge. Body color pattern similar to holotype, but slightly lighter.

Etymology. *Lytopylus cesarmorai* is named in honor of Cesar Mora in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Stenoma* BioLep82 (Depressariidae) feeding on mature leaves of *Apeiba membranacea* (Malvaceae) in ACG rain forest at 527 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Huerta, Area de Conservación Guanacaste 10.9305N -85.37223W 527m., Carolina Cano coll., food plant: Malvaceae *Apeiba membranacea*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma* BioLep82, coll. date: 1/11/2010, parasitoid eclosion date: 2/5/2010, DHJPAR0037960. Paratype: [the following have the same data as the holotype except as indicated] ♂, parasitoid eclosion date: 2/9/2010, DHJPAR0038304.

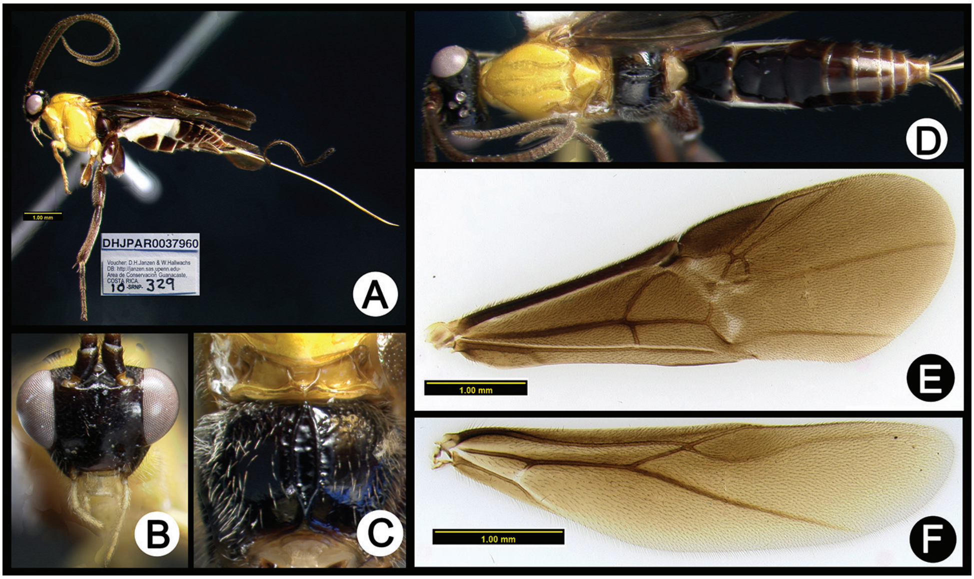


Figure 7. *Lytopylus cesarmorai* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

***Lytopylus chrysokeras* (Sharkey)**
Fig. 8

Austroearinus chrysokeras (Sharkey), (Sharkey 2006).
Lytopylus chrysokeras Sharkey, (Sharkey et al. 2016).

Diagnosis. Apical flagellomeres usually bright yellow, always distinctly paler than subapical flagellomeres; fore wing mostly infuscated; hind tibia black apically; mesoscutum entirely pale; median tergites entirely pale (yellow to orange).

Biology. Reared 48 times from seven species of dichomeridine Gelechiidae feeding on seven species of mature leaves of Malvaceae, Violaceae, Rubiaceae, Asteraceae, and Fabaceae growing in ACG rain forest at 240 to 645 m elevation.

Material. ♀: Costa Rica, Alajuela, Sector San Cristobal, Tajo Angeles, Area de Conservación Guanacaste 10.86472N -85.41531W 540m., Carolina Cano coll., food plant: Violaceae *Rinorea squamata*, host caterpillar: Gelechiidae, Dichomeridinae, gelJanzen01 Janzen485, coll. date: 6/10/2010, parasitoid eclosion date: 6/29/2010, DHJPAR0040492. [the following have the same data as previous except as indicated] ♂, parasitoid eclosion date: 6/26/2010, DHJPAR0040344. ♂, parasitoid eclosion date: 6/27/2010, DHJPAR0040476. ♂, parasitoid eclosion date: 6/30/2010, DHJPAR0040485. ♂, parasitoid eclosion date: 6/27/2010, DHJPAR0040487. ♀, Gloria Sihezar coll., coll. date: 6/15/2010, parasitoid eclosion date: 7/2/2010, DHJPAR0040473. ♀, Gloria Sihezar coll. food plant: Malvaceae *Mortoniodendron*

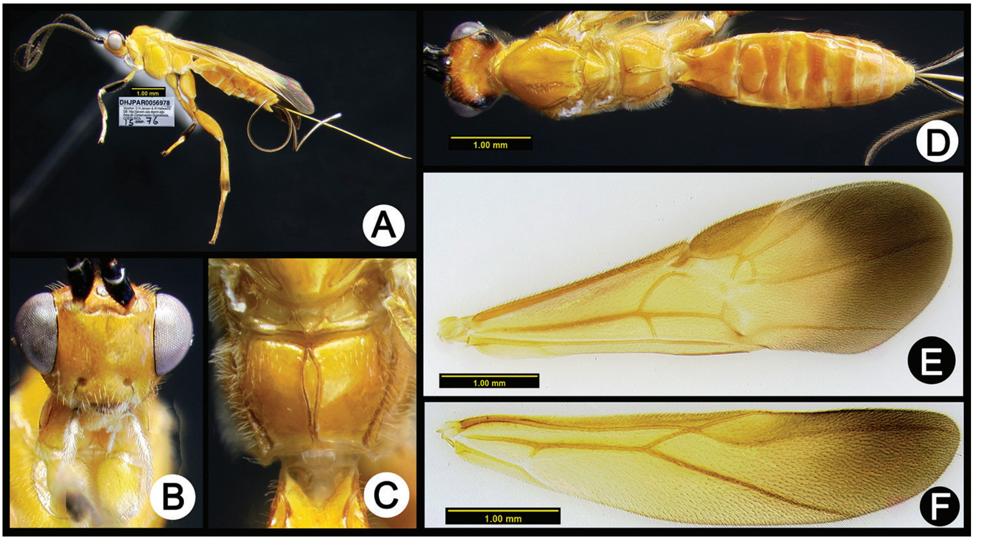


Figure 8. *Lytopylus chrysokeras*: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

costaricense, host caterpillar: gelJanzen01 Janzen356, coll. date: 7/8/2010, parasitoid eclosion date: 7/25/2010, DHJPAR0040505. ♀, Elda Araya coll., food plant: Malvaceae *Mortoniodendron costaricense*, host caterpillar: gelJanzen01 Janzen356, coll. date: 7/8/2010, parasitoid eclosion date: 7/23/2010, DHJPAR0040460. ♀, Osvaldo Espinoza coll., food plant: *Rinorea deflexiflora*, host caterpillar: gelJanzen01 Janzen179, coll. date: 6/4/2014, parasitoid eclosion date: 6/20/2014, DHJPAR0055352. ♂, Finca San Gabriel, 10.87766N -85.39343W 645m., Carolina Cano coll., food plant: Malvaceae *Mortoniodendron costaricense*, host caterpillar: gelJanzen01 Janzen356, coll. date: 11/16/2012, parasitoid eclosion date: 12/5/2012, DHJPAR0051373. [same as previous except coll. date and eclosion date] ♂, coll. date: 11/30/2012, parasitoid eclosion date: 12/21/2012, DHJPAR0051162. ♀, Gloria Sihezar coll., coll. date: 6/2/2012, parasitoid eclosion date: 6/28/2012, DHJPAR0049276. ♀, Elda Araya coll., coll. date: 10/11/2012, parasitoid eclosion date: 11/4/2012, DHJPAR0051364. [the following have the same data as the holotype except as indicated] ♂, Cementerio Viejo, 10.88111N -85.38889W 570m., Gloria Sihezar coll., food plant: Malvaceae *Mortoniodendron costaricense*, host caterpillar: gelJanzen01 Janzen356, coll. date: 7/30/2014, parasitoid eclosion date: 8/17/2014, DHJPAR0057739. ♂, Rio Blanco Abajo, 10.90037N -85.37254W 500m., food plant: Malvaceae *Mortoniodendron costaricense*, host caterpillar: gelJanzen01 Janzen356, coll. date: 6/29/2009, parasitoid eclosion date: 7/19/2009, DHJPAR0040070. ♀, Sector Rincon Rain Forest, Rio Francia Arriba, 10.89666N -85.29003W 400m., Jose Perez coll., food plant: Fabaceae *Dialium guianense*, host caterpillar: *Dichomeris* Janzen512, coll. date: 1/19/2011, parasitoid eclosion date: 2/7/2011, DHJPAR0042837. [same as previous except and eclosion date] ♀, parasitoid eclosion date: 2/10/2011, DHJPAR0042835. ♀, parasitoid eclosion date: 2/9/2011, DHJPAR0043002. ♀, Sector Rincon Rain Forest, Sendero Anonas, 10.90528N -85.27882W 405m., Jose Perez coll., food plant: Violaceae *Rinorea deflexiflora*, coll. date: 4/6/2012, parasitoid eclosion date: 5/1/2012, DHJPAR0049388. [same as previous except as indicated] ♂, food plant: *Rinorea hummelii*, coll. date: 2/12/2013, parasitoid eclosion date: 2/26/2013, DHJPAR0051817. ♀, Anabelle Cordoba coll., food plant: *Rinorea hummelii*, coll. date: 5/20/2014, parasitoid eclosion date: 6/6/2014, DHJPAR0055505. ♂, Anabelle Cordoba coll., coll. date: 5/20/2014, parasitoid eclosion date: 6/5/2014, DHJPAR0055528. [same as previous except as indicated] ♀, parasitoid eclosion date: 6/8/2014, DHJPAR0055522. ♂, parasitoid eclosion date: 6/7/2014, DHJPAR0055527. ♀, parasitoid eclosion date: 6/11/2014, DHJPAR0055353. ♂, coll. date: 5/23/2014, parasitoid eclosion date: 6/7/2014, DHJPAR0055543. ♂, coll. date: 5/23/2014, parasitoid eclosion date: 6/9/2014, DHJPAR0055490. ♂, coll. date: 5/23/2014, parasitoid eclosion date: 6/7/2014, DHJPAR0055507. ♀, coll. date: 5/30/2014, parasitoid eclosion date: 6/18/2014, DHJPAR0055513. ♀, coll. date: 6/2/2014, parasitoid eclosion date: 6/14/2014, DHJPAR0055504. ♀, Sector Rincon Rain Forest, Jacobo, 10.94076N -85.3177W 461m., Petrona Rios coll., food plant: *Rinorea deflexiflora*, host caterpillar: gelJanzen01 Janzen179, coll. date: 6/7/2014, parasitoid eclosion date: 6/23/2014, DHJPAR0055986. ♂, Sector Rincon Rain Forest, Conguera, 10.91589N -85.26631W 420m., Jose Perez coll., food plant: Asteraceae *Koanophyllon hylonoma*, host caterpillar: *Dichomeris* Janzen703, coll. date: 7/1/2009, parasitoid eclosion date: 7/22/2009, DHJPAR0040067. ♂, Guanacaste, Sector Pitilla, Ingas, 11.00311N -85.42041W 580m., Natalia Santamaria coll. food plant: *Rinorea deflexiflora*, host caterpillar: gelJanzen01 Janzen781, coll. date: 5/29/2004, parasitoid eclosion date: 6/21/2004, DHJPAR0015527. ♂, Guanacaste, Sector Pitilla, Sendero Trichoptera, 10.98571N -85.41869W 655m., Calixto Moraga coll. food plant: *Rinorea sylvatica*, coll. date: 10/8/2009, parasitoid eclosion date: 10/27/2009, DHJPAR0040065. ♂, Guanacaste, Sector Pitilla, Sendero Laguna, 10.9888N -85.42336W 680m., Roster Moraga coll., food plant: Rubiaceae *Chiococca alba*, coll. date: 1/8/2010, parasitoid eclosion date: 1/28/2010, DHJPAR0038356. ♂, Guanacaste, Sector Pitilla, Leonel, 10.99637N -85.40195W 510m., Dinia Martinez coll., food plant: *Rinorea sylvatica*, coll. date: 2/4/2010, parasitoid eclosion date: 2/22/2010, DHJPAR0039071. ♀, Guanacaste, Sector Pitilla, Sendero Orosilito, 10.98332N -85.43623W 900m., Freddy Quesada coll., food plant: Malpighiaceae *Hiraea reclinata*, host caterpillar: gelJanzen01 Janzen19, coll. date: 7/25/2013, parasitoid eclosion date: 8/15/2013, DHJPAR0052673. ♂, Guanacaste, Sector Del Oro, Quebrada Raiz, 11.02865N -85.48669W 280m., Elieth Cantillano coll. food plant: *Rinorea deflexiflora*, coll. date: 5/18/2010, parasitoid eclosion date: 6/3/2010, DHJPAR0040331. [same as previous except collector and eclosion date] ♂, Roster Moraga coll., parasitoid eclosion date: 6/1/2010, DHJPAR0040335. ♂, Roster Moraga coll., parasitoid eclosion date: 6/2/2010, DHJPAR0040503.

Lytopylus eddysanchezi **Kang, sp. n.**
http://zoobank.org/7BD05EB2-A120-4442-AABA-0D70E4AE0FB6
Fig. 9

Diagnosis. Vertex of head entirely yellow; fore wing with one black band; mid tibia mostly melanic, yellow basally.

Description. Holotype: female. Body length 6.0 mm. Fore wing length 5.5 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor about same length as body.

Males. Similar to holotype except for fore legs color. Fore legs usually less melanic.

Etymology. *Lytopylus eddysanchezi* is named in honor of Eddy Sánchez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared 11 times from one species leaf-tier in the Depressariidae, feeding on mature leaves of *Meliosma glabrata* (Sabiaceae) in ACG rain forest at 540 to 645 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Finca San Gabriel, Area de Conservación Guanacaste 10.87766N -85.39343W 645m., Gloria Sihezar coll., food plant: Sabiaceae *Meliosma glabrata*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen900, coll. date: 1/7/2015, parasitoid eclosion date: 2/7/2015, DHJPAR0056978. Paratypes: [the following have the same data

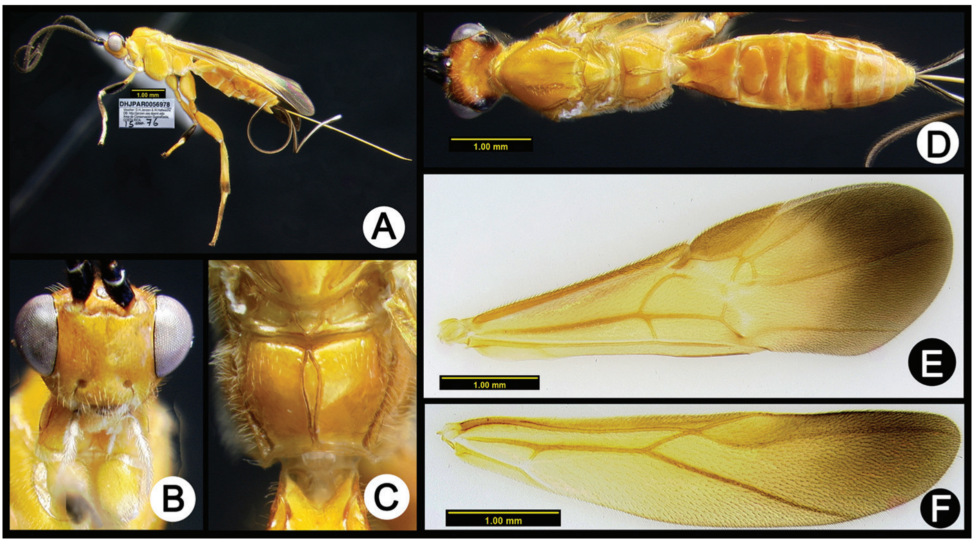


Figure 9. *Lytopylus eddysanchezi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

as the holotype except as indicated] ♂, Sendero Corredor, 10.87868N -85.38963W 620m., Elda Araya coll., coll. date: 11/7/2009, parasitoid eclosion date: 12/5/2009, DHJPAR0038240. ♂, Sendero Corredor, 10.87868N -85.38963W 620m., coll. date: 7/25/2013, parasitoid eclosion date: 8/17/2013, DHJPAR0052903. ♀, Tajo Angeles, 10.86472N -85.41531W 540m., coll. date: 9/20/2010, parasitoid eclosion date: 10/14/2010, DHJPAR0041600. ♂, Sendero Carmona, 10.87621N -85.38632W 670m., coll. date: 3/25/2012, parasitoid eclosion date: 4/18/2012, DHJPAR0049278. ♀, coll. date: 2/24/2014, parasitoid eclosion date: 3/31/2014, DHJPAR0055232. ♂, Elda Araya coll., coll. date: 11/26/2009, parasitoid eclosion date: 12/22/2009, DHJPAR0038208. [same as previous except as coll. date and eclosion date] ♀, coll. date: 11/30/2009, parasitoid eclosion date: 1/1/2010, DHJPAR0038180. ♂, coll. date: 11/30/2009, parasitoid eclosion date: 12/23/2009, DHJPAR0038231. ♂, coll. date: 11/30/2009, parasitoid eclosion date: 12/21/2009, DHJPAR0038225. ♂, coll. date: 12/16/2012, parasitoid eclosion date: 1/13/2013, DHJPAR0051357.

Lytopylus eliethcantillanoae Kang, sp. n.

http://zoobank.org/747FAD7E-4637-4F8E-8E35-93BCFD8D5739
Fig. 10

Diagnosis. Fore wing mostly infuscated; mesoscutum entirely melanic; anterior transverse carina of propodeum absent; median areola of propodeum narrow and not closed posteriorly; median areola length 11x its width, lateral longitudinal carinae of median tergite 1 well-defined; median tergites entirely reddish orange.

Description. Holotype: male. Body length 5.2 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Female. Unknown.

Etymology. *Lytopylus eliethcantillanoae* is named in honor of Elieth Cantillano in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared perhaps one time from elachJanzen01 Janzen873 (Depressariidae) feeding on *Malvaviscus arboreus* (Malvaceae) in ACG dry forest – rain forest ecotone at 840 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Santa Maria, Estacion Santa Maria, Area de Conservación Guanacaste 10.76448N -85.31161W 840m., Jose Cortez coll., food plant: Malvaceae *Malvaviscus arboreus*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen873, coll date: 4/26/2009, parasitoid eclosion date: 5/12/2009, DHJPAR0035345.

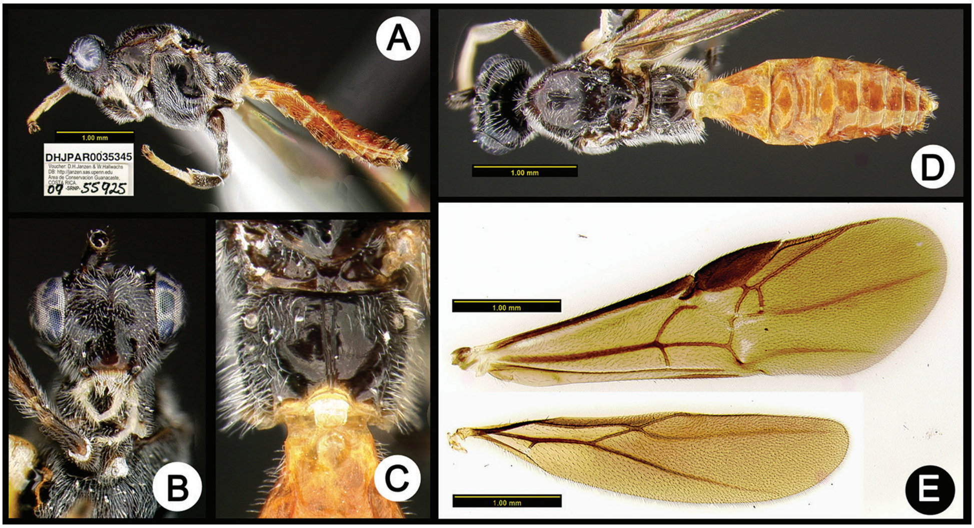


Figure 10. *Lytopylus eliethcantillanoae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** wings.

Lytopylus ericchapmani **Kang, sp. n.**
http://zoobank.org/A2C8DCE5-4DA5-4F79-94A2-1D7750C5AFDA
Fig. 11

Diagnosis. Fore wing with two black bands; pronotum anteriorly black and posteriorly pale.

Description. Holotype: female. Body length 5.8 mm. Fore wing length 5.7 mm. Fore wing with two black bands. Scutellar sulcus lacking longitudinal carina. Anterior transverse carina of propodeum absent. Median areola of propodeum with well-defined margins. Median areola of propodeum narrow. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.7 times longer than wide. Ovipositor slightly longer than body.

Male. Body color similar to holotype. Body length slightly shorter than holotype.

Etymology. Named in honor of Dr Eric G. Chapman, research analyst in the Department of Entomology at the University of Kentucky, for his kindly advice on molecular systematics and phylogenetics.

Biology. Reared five times but only from the leaf-tier *Stenoma adytodes* (Depressariidae) feeding on mature leaves of *Pouteria juruana* (Sapotaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 722 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Jardin Estrada, Area de Conservación Guanacaste 10.86546N -85.39694W 722m., Carolina Cano coll., food plant: Sapotaceae *Pouteria juruana*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma adytodes*, coll. date: 12/10/2013, parasitoid eclosion date: 1/12/2014, DHJPAR0054533. Paratypes: [the following have the same data as the hol-

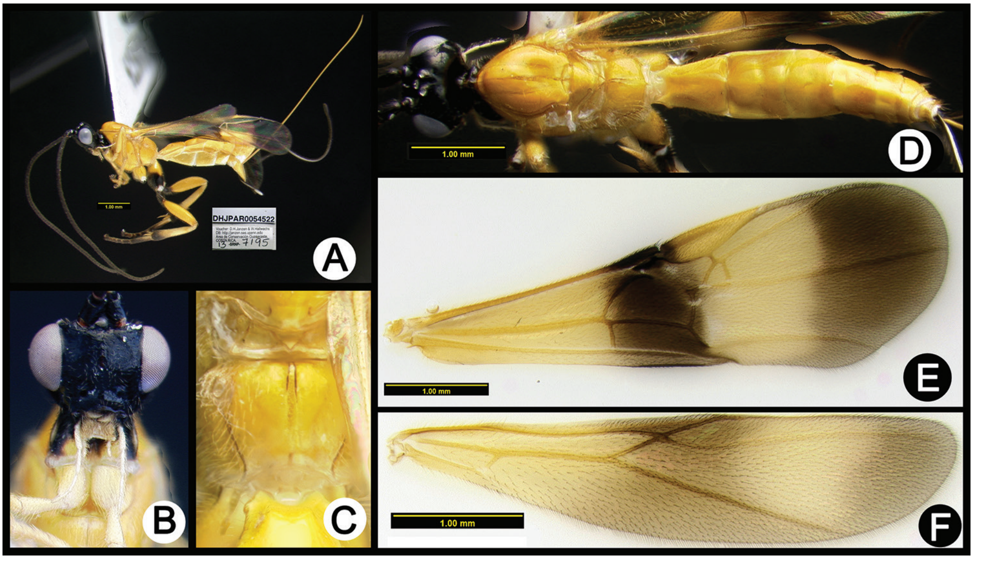


Figure 11. *Lytopylus ericchapmani* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

otype except as indicated] ♀, coll. date: 2/5/2013, parasitoid eclosion date: 1/4/2014, DHJPAR0054527. ♀, parasitoid eclosion date: 1/9/2014, DHJPAR0054522. ♀, parasitoid eclosion date: 1/7/2014, DHJPAR0055238. ♂, Elda Araya coll., coll. date: 12/5/2013, parasitoid eclosion date: 12/26/2013, DHJPAR0054526.

***Lytopylus gahyunae* Kang, sp. n.**
http://zoobank.org/34C499A2-CEC2-4D38-8D16-342D152B15B8
Fig. 12

Diagnosis. Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely melanic; scutellar sulcus with one median longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 1.4 times longer than wide.

Description. Holotype: female. Body length 7.1 mm. Fore wing length 6.4 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.4 times longer than wide. Ovipositor slightly longer than body.

Males. Similar to holotype.

Etymology. *Lytopylus gahyunae* is named in honor of Gahyun Park, wife of the first author.

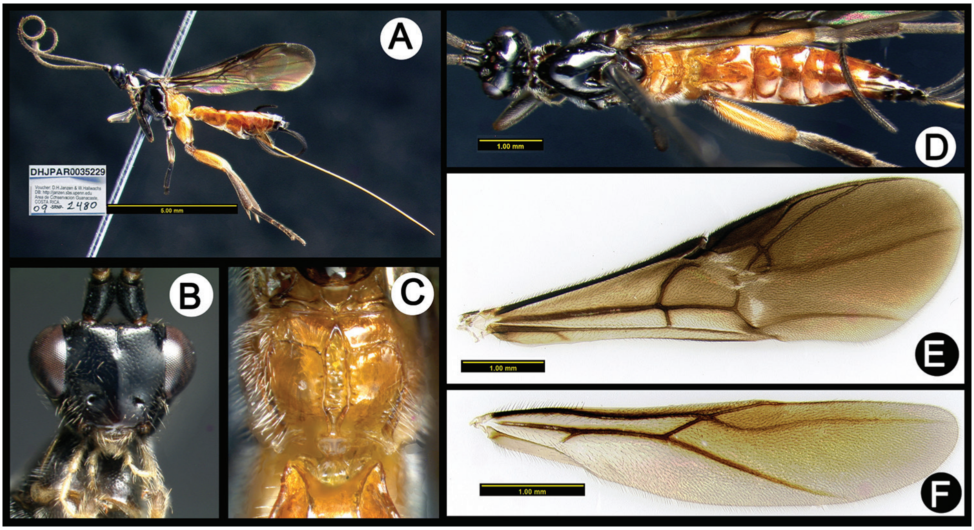


Figure 12. *Lytopylus gahyunae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Biology. Reared 43 times from six species of *Antaeotricha* (40) and *Stenoma* (2) (Depressariidae) feeding on mature leaves of 3 species of *Guarea* and 1 of *Trichilia* (Meliaceae) in ACG rain forest at 380 to 620 m elevation.

Type material. Holotype♀: Costa Rica, Alajuela, Sector San Cristobal, Rio Areno, Area de Conservación Guanacaste 10.91407N -85.38174W 460m., Osvaldo Espinoza coll., food plant: Meliaceae *Guarea bullata*, host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha* Janzen09, coll. date: 6/4/2009, parasitoid eclosion date: 6/26/2009, DHJPAR0035229. Paratypes: [the following have the same data as the holotype except as indicated] 2♀, coll. date: 6/4/2009, parasitoid eclosion date: 6/22/2009, DHJPAR0035298, DHJPAR0035294. ♀, parasitoid eclosion date: 6/23/2009, DHJPAR0036371. ♀, Elda Araya coll., food plant: *Guarea rhopalocarpa*, coll. date: 5/4/2009, parasitoid eclosion date: 6/21/2009, DHJPAR0035231. DHJPAR0035294. pes: [the following have the same data as the holotype except as indicated] 2odeum with well-defined ma8/27/2009, DHJPAR0036721. [same as previous except coll. date and eclosion date] ♀, coll. date: 9/13/2009, parasitoid eclosion date: 10/2/2009, DHJPAR0036686. ♂, Puente Palma, 10.9163N -85.37869W 460m., Carolina Cano coll., food plant: *Guarea kegelii*, coll. date: 11/10/2011, parasitoid eclosion date: 11/26/2011, DHJPAR0046956. ♀, Puente Palma, 10.9163N -85.37869W 460m., Gloria Sihezar coll., host caterpillar: *Antaeotricha* Janzen12, coll. date: 11/24/2012, parasitoid eclosion date: 12/27/2012, DHJPAR0051365. ♂, Tajo Angeles, 10.86472N -85.41531W 540m., Gloria Sihezar coll., food plant: *Guarea kegelii*, host caterpillar: Depressariinae, *Antaeotricha* Janzen07, coll. date: 9/24/2011, parasitoid eclosion date: 10/14/2011, DHJPAR0045788. [same as previous except coll. date and eclosion date] ♀, host caterpillar: Stenomatinae, coll. date: 11/6/2011, parasitoid eclosion date: 11/24/2011, DHJPAR0046745. ♀, host caterpillar: Stenomatinae, *Antaeotricha* Janzen09, coll. date: 11/22/2011, parasitoid eclosion date: 12/13/2011, DHJPAR0046744. ♀, Sendero Huerta, 10.9305N -85.37223W 527m., Gloria Sihezar coll., coll. date: 7/2/2012, parasitoid eclosion date: 7/27/2012, DHJPAR0049943. [same as previous except coll. date and eclosion date] ♀, 12/2/2012 12/24/2012, DHJPAR0051374. [same as previous except food plant, coll. date and eclosion date] 1♀, 1♂, food plant: *Guarea kegelii*, coll. date: 12/8/2012, parasitoid eclosion date: 1/1/2013, DHJPAR0051349, coll. date: 12/8/2012, parasitoid eclosion date: 12/31/2012, DHJPAR0051370. ♀, Elda Araya coll., host caterpillar: *Stenoma* Janzen144, coll. date: 7/21/2012, parasitoid eclosion date: 8/14/2012, DHJPAR0049649. [same as previous except food plant, coll. date and eclosion date] 2♀, food plant: *Guarea kegelii*, coll. date:12/23/2012, parasitoid eclosion date: 1/10/2012, DHJPAR0051360, coll. date: 12/23/2012, parasitoid eclosion date: 1/7/2013, DHJPAR0051371. ♀, Sendero Perdido, 10.8794N -85.38607W 620m., Carolina Cano coll., food plant: *Guarea kegelii*, coll. date: 10/9/2013, parasitoid eclosion date: 10/29/2013, DHJPAR0053649. [same as previous except coll. date and eclosion date] 2♂, 10/11/2013 10/26/2013, DHJPAR0053652, coll. date: 10/11/2013, parasitoid eclosion date: 10/29/2013, DHJPAR0053655. [same as previous except food plant, coll. date and eclosion date] ♀, food plant: *Trichilia adolfi*, coll. date: 10/9/2013, parasitoid eclosion date: 10/30/2013, DHJPAR0053654. ♂, Sendero Perdido, 10.8794N -85.38607W 620m., Gloria Sihezar coll., food plant: *Guarea kegelii*, 9/24/2013 10/9/2013, DHJPAR0053658. [same as previous except caterpillar, coll. date and eclosion date] ♂, host caterpillar: *Antaeotricha* Janzen07, 10/25/2013 11/22/2013, DHJPAR0054538. ♂, Sendero Perdido, 10.8794N -85.38607W 620m., Elda Araya coll., food plant: *Guarea kegelii*, coll. date: 1/9/2014, parasitoid eclosion date: 1/23/2014, DHJPAR0054515. [same as previous except coll. date and eclosion date] ♂, 1/9/2014 1/25/2014, DHJPAR0054517. ♀, Sendero Perdido, 10.8794N -85.38607W 620m., Elda Araya coll., food plant: *Guarea rhopalocarpa*, coll. date: 11/29/2013, parasitoid eclosion date: 12/29/2013, DHJPAR0054539. [same as previous except caterpillar and eclosion date] ♀, host caterpillar: *Antaeotricha thapsinopa*, parasitoid eclosion date: 12/31/2013, DHJPAR0054532. ♀, Sendero Perdido, 10.8794N -85.38607W 620m., Elda Araya coll., food plant: *Trichilia adolfi*, host caterpillar: *Antaeotricha* Janzen07, 2/1/2010 2/14/2010, DHJPAR0038910. ♀, Finca San Gabriel, 10.87766N -85.39343W 645m., Carolina Cano coll., food plant: *Guarea kegelii*, host caterpillar: *Antaeotricha* Janzen07, coll. date: 10/18/2013, parasitoid eclosion date: 11/2/2013, DHJPAR0054519. ♂, Finca San Gabriel, 10.87766N -85.39343W 645m., Carolina Cano coll., food plant: *Guarea rhopalocarpa*, host caterpillar: *Stenoma* Janzen144, coll. date: 8/11/2013, parasitoid eclosion date: 8/29/2013, DHJPAR0053645. ♀, Finca San Gabriel, 10.87766N -85.39343W 645m., Elda Araya coll., food plant: *Guarea kegelii*, coll. date: 1/6/2014, parasitoid eclosion date: 1/24/2014, DHJPAR0054511. ♂, Sendero Palo Alto, 10.88186N -85.38221W 570m., Carolina Cano coll., food plant: *Guarea rhopalocarpa*, coll. date: 9/12/2013, parasitoid eclosion date: 9/29/2013, DHJPAR0053618. [same as previous except eclosion date] ♂, parasitoid eclosion date: 10/2/2013, DHJPAR0053621. ♀, Cementerio Viejo, 10.88111N -85.38889W

570m., Carolina Cano coll., food plant: *Guarea kegelii*, coll. date: 9/10/2013, parasitoid eclosion date: 10/1/2013, DHJPAR0053611. [same as previous except eclosion date] ♂, parasitoid eclosion date: 9/30/2013, DHJPAR0053619. [same as previous except caterpillar, coll. date and eclosion date] ♀, host caterpillar: *Antaeotricha ribbei* 12/3/2013 12/21/2013, DHJPAR0054520. [same as previous except coll. date and eclosion date] ♀, 12/3/2013 12/21/2013, DHJPAR0054534. ♂, Sendero Corredor, 10.87868N -85.38963W 620m., Carolina Cano coll., food plant: *Trichilia adolfi*, host caterpillar: Depressariinae, *Antaeotricha* Janzen09, coll. date: 1/3/2014, parasitoid eclosion date: 1/25/2014, DHJPAR0054518. ♀, Rio Blanco Abajo, 10.90037N -85.37254W 500m., Elda Araya coll., coll. date: 8/11/2009, parasitoid eclosion date: 8/27/2009, DHJPAR0036722. ♂, Guanacaste, Sector Del Oro, Margarita, 11.03234N -85.43954W 380m., Lucia Ríos coll., host caterpillar: *Antaeotricha thapsinopa*, coll. date: 1/15/2005, parasitoid eclosion date: 2/1/2005, DHJPAR0015317.

Lytopylus gisukae **Kang, sp. n.**

http://zoobank.org/40757AA3-B52C-4733-AEF2-334C861F561F
Fig. 13

Diagnosis. Vertex of head mostly pale; fore wing mostly infuscated with a quadrate second submarginal cell; mesoscutum entirely pale (yellow to orange); median areola of propodeum length 15x its width; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange).

Description. Holotype: female. Body length 5.0 mm. Fore wing length 5.0 mm. Fore wing mostly infuscated with a quadrate second submarginal cell. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum length 15x its width with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. *Lytopylus gisukae* is named in honor of Gisuk Lee, mother-in-law of the first author.

Biology. Reared one time from *Antaeotricha* Janzen405 (Stenomatinae, Depressariidae) feeding on mature leaves of *Astrocaryum alatum* (Arecaceae) in ACG rain forest at 420 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector Rincon Rain Forest, Sendero Venado, Area de Conservación Guanacaste 10.89678N -85.27001W 420m., Pablo Umaña coll., food plant: Arecaceae *Astrocaryum alatum*, host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha* Janzen405, coll. date: 8/1/2011, parasitoid eclosion date: 9/11/2011, DHJPAR0048076.

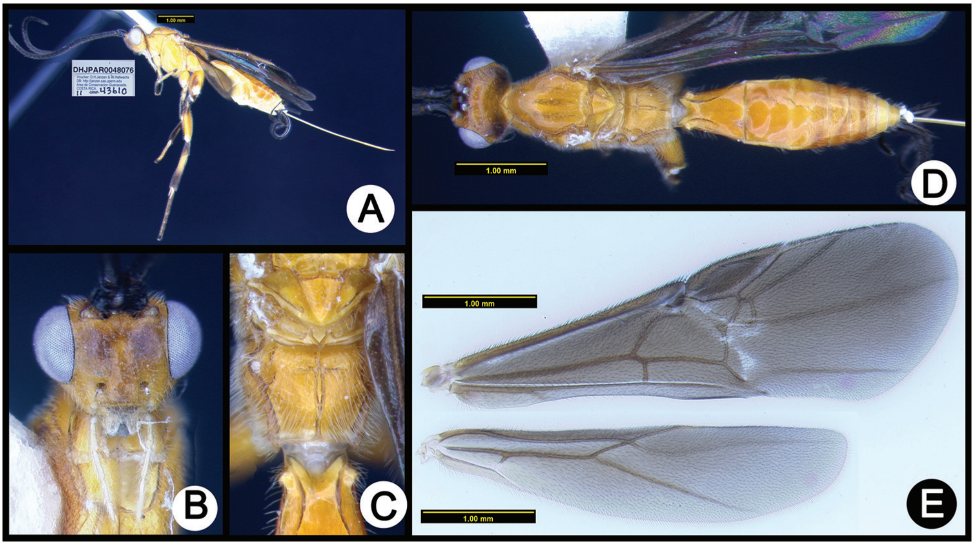


Figure 13. *Lytopylus gisukae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** wings.

Lytopylus guillermopereirai Kang, sp. n.

http://zoobank.org/FAC851A7-13CC-4DB7-AFDE-562014FE4D02

Fig. 14

Diagnosis. Fore wing mostly infuscated; mesoscutum entirely melanic; scutellar sulcus lacking longitudinal carina; median tergites entirely melanic.

Description. Holotype: female. Body length 5.4 mm. Fore wing length 4.5 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.3 times longer than wide.

Female. Unknown.

Etymology. *Lytopylus guillermopereirai* is named in honor of Guillermo Pereira in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared one time from elachJanzen01 Janzen726 (Depressariidae) feeding on *Sloanea faginea* (Elaeocarpaceae) in ACG rain forest at 645 m elevation.

Type material. Holotype ♂: Costa Rica, Alajuela, Sector San Cristobal, Finca San Gabriel, Area de Conservación Guanacaste 10.87766N -85.39343W 645m., Gloria Sihezar coll., food plant: Elaeocarpaceae *Sloanea faginea*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen726, coll. date: 2/24/2014, parasitoid eclosion date: 3/17/2014, DHJPAR0055234.

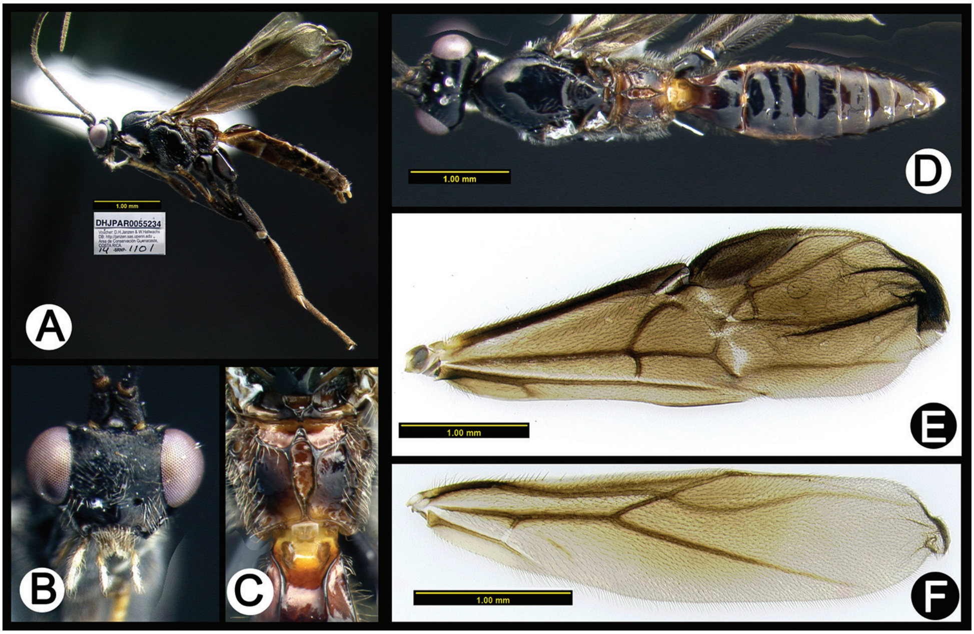


Figure 14. *Lytopylus guillermopereirai* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Lytopylus gustavoindunii Kang, sp. n.

http://zoobank.org/9008E51A-5E03-4E95-BCF1-E427306B35F9

Fig. 15

Diagnosis. Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely pale; fore wing mostly infuscated with a triangular second submarginal cell; mesoscutum entirely pale (yellow to orange); median areola spindle-shaped; anterior transverse carina of propodeum absent; median tergites entirely pale (yellow to orange).

Description. Holotype: female. Body length 4.8 mm. Fore wing length 4.5 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.3 times longer than wide. Ovipositor slightly longer than body.

Male. Unknown.

Etymology. *Lytopylus gustavoindunii* is named in honor of Gustavo Induni in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared 12 times from two species of palm-feeding (*Geonoma, Chamaedorea*) Depressariidae (*Stenoma* Janzen142 and *Stenoma* Janzen284) in the understory of ACG rain forest from 645-742 m elevation.

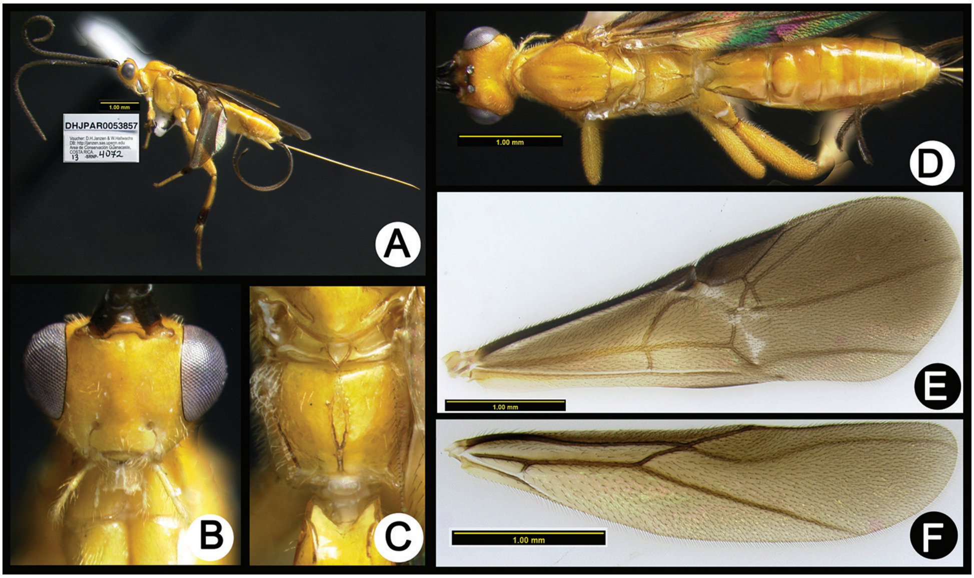


Figure 15. *Lytopylus gustavoindunii* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Perdido, Area de Conservación Guanacaste 10.8794N -85.38607W 620m., Elda Araya coll., food plant: Arecaceae *Geonoma ferruginea*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma* Janzen284, coll. date: 8/9/2013, parasitoid eclosion date: 8/28/2013, DHJPAR0053857. Paratypes: [the following have the same data as the holotype except as indicated] ♀, parasitoid eclosion date: 8/27/2013, DHJPAR0053648. ♀, parasitoid eclosion date: 8/31/2013, DHJPAR0053653. ♀, parasitoid eclosion date: 9/1/2013, DHJPAR0053646. ♀, Finca San Gabriel, 10.87766N -85.39343W 645m., host caterpillar: *Stenoma* Janzen142 coll. date: 11/16/2012, parasitoid eclosion date: 12/11/2012, DHJPAR0051369. [same as previous except eclosion date] ♀, parasitoid eclosion date: 12/20/2012, DHJPAR0051359. ♀, parasitoid eclosion date: 12/15/2012, DHJPAR0051372. ♀, Sendero Aguas Termales, geolocation unknown, food plant: *Chamaedorea tepejilote*, host caterpillar: *Stenoma* Janzen142, coll. date: 10/10/2010, parasitoid eclosion date: 10/29/2010, DHJPAR0041560.

Lytopylus hartmanguidoi **Kang, sp. n.**
http://zoobank.org/42792E91-4825-4562-93BE-7B2BB40A40FA
Fig. 16

Diagnosis. Fore wing with one black band; mid tibia black basally and distally, yellow at mid-length.

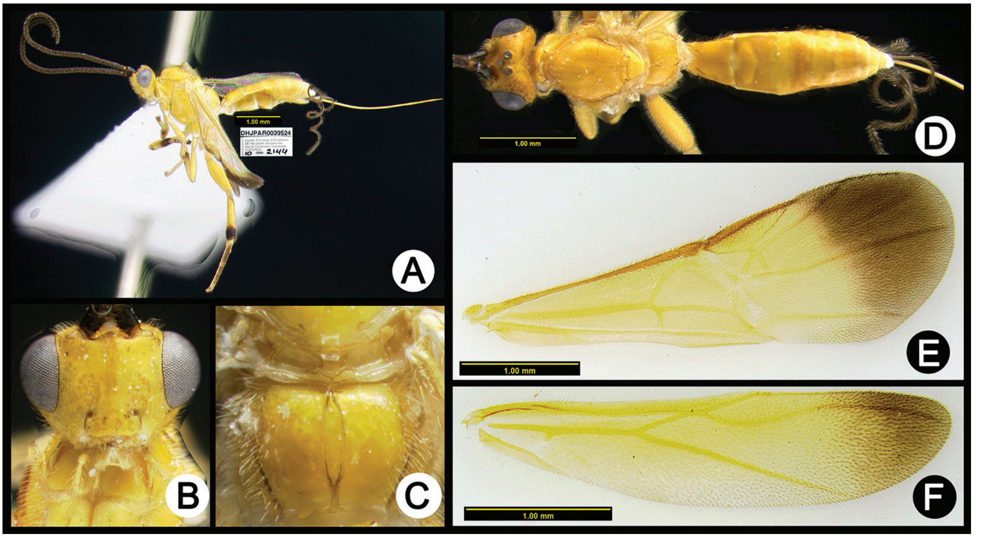


Figure 16. *Lytopylus hartmanguidoi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Description. Holotype: female. Body length 4.3 mm. Fore wing length 4.3 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.3 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. *Lytopylus hartmanguidoi* is named in honor of Hartman Guido in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared five times from three species leaf-tiers in the Depressariidae, feeding on mature leaves of *Hiraea reclinata (*Malpighiaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 540 m elevation.

Type material. Holotype ♀: Costa Rica, Area de Conservación Guanacaste, Alajuela, Sector San Cristobal, Tajo Angeles, 10.86472N -85.41531W 540m., Elda Araya coll., food plant: Malpighiaceae *Hiraea reclinata*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen392, coll. date: 4/27/2010, parasitoid eclosion date: 5/19/2010, DHJPAR0039524. Paratypes: [the following have the same data as the holotype except as indicated] ♀, Gloria Sihezar coll., host caterpillar: *Psilocorsis* Janzen369, coll. date: 4/20/2010, parasitoid eclosion date: 5/15/2010, DHJPAR0039513. ♀, Gloria Sihezar coll., parasitoid eclosion date: 6/4/2010, DHJPAR0039514. ♀, Gloria Sihezar host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha* Janzen126. 1/10/2011 2/6/2011, DHJPAR0042831. [same as previous except as coll. date and eclosion date] ♀, coll. date: 1/13/2011, parasitoid eclosion date: 2/8/2011, DHJPAR0042844.

Lytopylus hernanbravoi Kang, sp. n.

http://zoobank.org/028AF18F-E671-4FC7-9447-6EAD6AA30616

Fig. 17

Diagnosis. Fore wing mostly infuscated; hind coxa entirely black; mesoscutum entirely melanic; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely yellow.

Description. Holotype: male. Body length 6.0 mm. Fore wing length 6.7 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.

Female. Unknown.

Etymology. *Lytopylus hernanbravoi* is named in honor of Hernan Bravo in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared one time from *Anadasmus* Janzen08 (Depressariidae), a stenomine leaf-tier feeding on mature foliage of *Ocotea austinii* (Lauraceae) in ACG cloud forest at 1460 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Cacao, Sendero Cima, Area de Conservación Guanacaste 10.93328N -85.45729W 1460m., Harry Ramirez coll., food plant: Lauraceae *Ocotea austinii*, host caterpillar: Depressariidae, Stenomatinae, *Anadasmus* Janzen08, coll. date: 8/11/2008, parasitoid eclosion date: 9/6/2008, DHJPAR0028303.

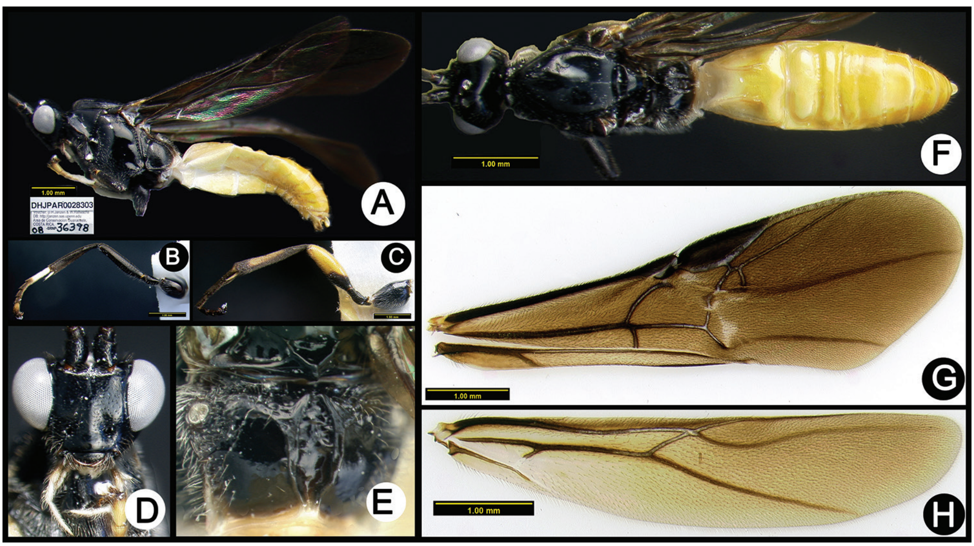


Figure 17. *Lytopylus hernanbravoi* holotype: **A** lateral habitus **B** mid leg **C** hind leg **D** anterior head **E** propodeum **F** dorsal habitus **G** fore wing **H** hind wing.

Lytopylus hokwoni **Kang, sp. n.**
http://zoobank.org/21D4210B-AFC4-4FF0-9AE9-360D26C6C940
Fig. 18

Diagnosis. Fore wing with two black bands; pronotum entirely melanic; lateral longitudinal carinae of median tergite 1 well-defined.

Description. Holotype: female. Body length 8.0 mm. Fore wing length 4.6 mm. Fore wing with two black bands. Scutellar sulcus with one median longitudinal carina. Anterior transverse carina of propodeum reaching the lateral margin. Median areola of propodeum with well-defined margins. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.6 times longer than wide. Ovipositor slightly longer than body.

Male. Mesoscutum bicolored. Mesopleuron pale.

Etymology. Named in honor of Hokwon Kang, father of the first author.

Biology. Reared nine times from seven species of stenomatine Depressariidae feeding as leaf-tiers on six species of plants in seven plant families at the intersection of the ACG dry forest and rain forest ecosystems at 280-640 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector El Hacha, Estacion Los Almendros, Area de Conservación Guanacaste 11.03226N -85.52776W 290m., Elieth Cantillano coll., food plant: Clusiaceae *Clusia rosea*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma* Janzen08, coll. date: 11/23/2011, parasitoid eclosion date: 12/10/2011, DHJPAR0048726. Paratypes: [the following have the same data as the holotype except as indicated] ♂, 290m., Lucia Ríos coll., coll. date: 9/19/2008, parasitoid eclosion date: 10/6/2008, DHJPAR0030605. ♀, Sendero Bejuquilla, 11.03004N -85.52699W 280m., food plant: Piperaceae *Peperomia angularis*, host caterpillar: Depressariidae, subfamily and species name unknown, coll. date: 1/11/2010, parasitoid eclosion date: 2/5/2010, DHJPAR0037940. ♀, Sendero Bejuquilla, 11.03004N -85.52699W 280m., Dunia Garcia coll., food plant: Hypericaceae *Vismia baccifera*, host caterpillar: *Cerconota recurvella*, coll. date: 10/26/2002, parasitoid eclosion date: 11/13/2002, DHJPAR0015414. ♀, Sector Cacao, Cuesta Caimito, 10.8908N -85.47192W 640m., Mariano Pereira coll., food plant: Hypericaceae *Vismia baccifera*, host caterpillar: *Cerconota recurvella*, coll. date: 5/16/2004, parasitoid eclosion date: 5/30/2004, DHJPAR0029302. ♀, Sector Cacao, Quebrada Otilio, 10.88996N -85.47966W 550m., Daniel Garcia coll., food plant: Fabaceae *Inga punctata*, host caterpillar: *Antaeotricha* Phillips01, coll. date: 9/24/2007, parasitoid eclosion date: 10/7/2007, DHJPAR0028279. ♀, Sector Pitilla, Cabrera, 11.00891N -85.40977W 500m., Calixto Moraga coll., food plant: Hypericaceae *Vismia baccifera*, host caterpillar: *Cerconota recurvella*, coll. date: 2/7/2007, parasitoid eclosion date: 2/14/2007, DHJPAR0017274. ♀, Alajuela, Sector Rincon Rain Forest, Sendero Tucan, 10.90424N -85.2712W 410m., Pablo Umaña Calderon coll., food plant: Melastomataceae *Miconia trinervia*, host caterpillar: elachJanzen01 Janzen211, coll. date: 4/7/2012, parasitoid eclosion date: 5/3/2012, DHJPAR0049051. ♀, Alajuela, Sector Rincon Rain Forest, Conguera, 10.91589N -85.26631W 420m., Jose

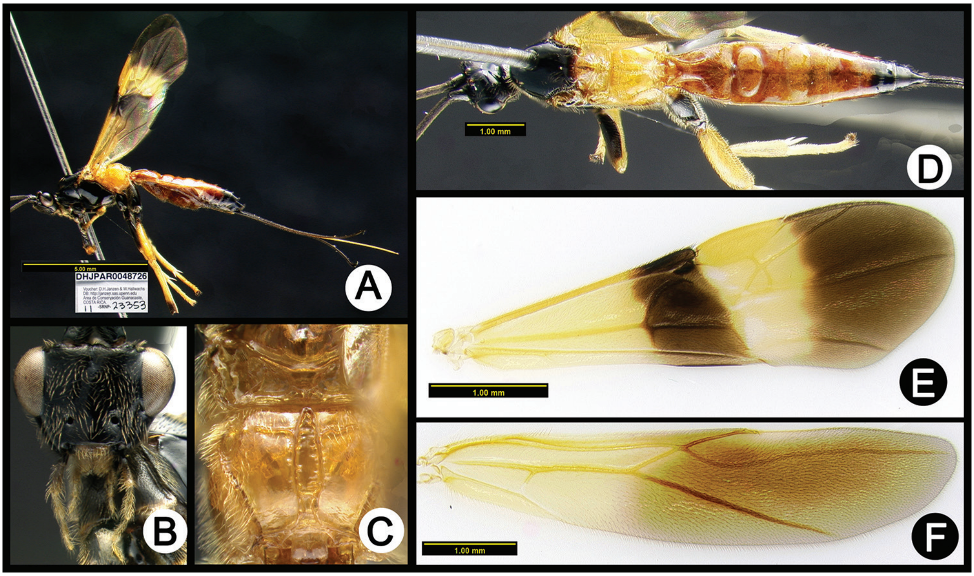


Figure 18. *Lytopylus hokwoni* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Perez coll., food plant: Malpighiaceae *Banisteriopsis elegans*, host caterpillar: *Antaeotricha* Janzen127, coll. date: 5/17/2012, parasitoid eclosion date: 6/7/2012, DHJPAR0048714.

Lytopylus ivanniasandovalae Kang, sp. n.

http://zoobank.org/11328F60-489F-41A1-B3FC-0F2EF21EAE40
Fig. 19

Diagnosis. Fore wing with a slight yellow tinge; anterior transverse carina of propodeum absent; median tergites entirely pale.

Description. Holotype: male. Body length 5.8 mm. Fore wing length 5.0 mm. Fore wing with a slight yellow tinge. Scutellar sulcus with four longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide.

Female. Unknown.

Etymology. *Lytopylus ivanniasandovalae* is named in honor of Ivannia Sandoval in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared one time from *Dichomerus* Janzen703 (Dichomeridinae, Gelechiidae) tying and feeding on mature leaves of *Neurolaena lobata* (Asteraceae) in ACG rain forest at 660 m elevation.

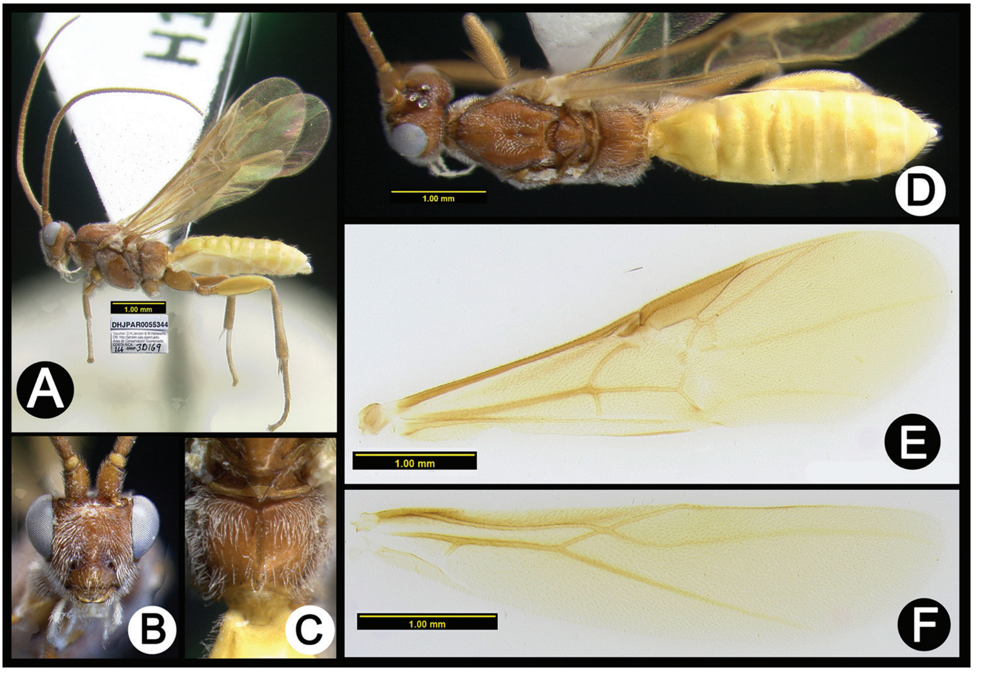


Figure 19. *Lytopylus ivanniasandovalae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Pitilla, Sendero Carica, Area de Conservación Guanacaste 10.99284N -85.42936W 660m., Calixto Moraga coll., food plant: Asteraceae *Neurolaena lobata*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris* Janzen703, coll. date: 1/25/2014, parasitoid eclosion date: 2/06/2014, DHJPAR0055344.

Lytopylus johanvalerioi Kang, sp. n.

http://zoobank.org/862254CE-7A11-4D65-B7A6-69A723E1392C
Fig. 20

Diagnosis. fore wing mostly infuscated; pronotum mostly yellow; mesoscutum mostly pale (yellow to orange); anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale posterior tergum black.

Description. Holotype: female. Body length 4.9 mm. Fore wing length 4.6 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 0.9 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

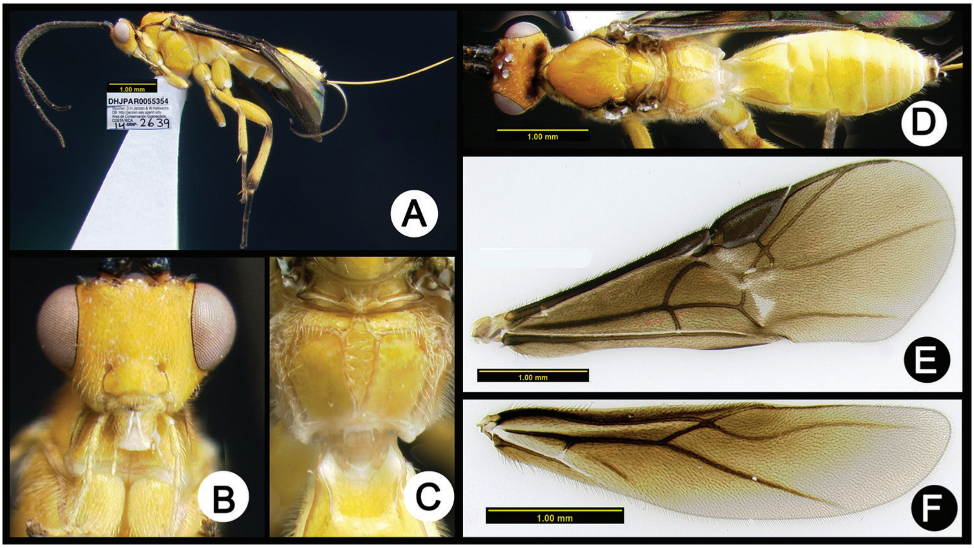


Figure 20. *Lytopylus johanvalerioi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Males. Occiput usually more melanic. Median tergites usually mostly pale with posterior terga black.

Etymology. *Lytopylus johanvalerioi* is named in honor of Johan Valerio in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared six times from two species of *Cerconota* leaf-tiers in the Depressariidae, feeding on mature leaves of three species of *Inga* (Fabaceae) in ACG rain forest at 540-645 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Huerta, Area de Conservación Guanacaste 10.9305N -85.37223W 527m., Gloria Sihezar coll., food plant: Fabaceae Inga oerstediana, host caterpillar: Depressariidae, Stenomatinae, Cerconota Janzen82, coll. date: 5/25/2014, parasitoid eclosion date: 6/7/2014, DHJPAR0055354. Paratypes: [the following have the same data as the holotype except as indicated] ♀, Brasilia, Moga, 11.01227N -85.34929W 320m., Duvalier Briceño coll., coll. date: 6/7/2012, parasitoid eclosion date: 6/19/2012, DHJPAR0049935. ♂, Guanacaste, Sector Pitilla, Estacion Quica, 10.99697N -85.39666W 470m., Ricardo Calero coll., food plant: Fabaceae Inga spectabilis, host caterpillar: Depressariidae, Stenomatinae, *Cerconota* Janzen216, coll. date: 5/25/2009, parasitoid eclosion date: 6/8/2009, DHJPAR0035498. [same as previous except coll. date and eclosion date] ♂, 5/27/2009 6/22/2009, DHJPAR0040066. ♂, Guanacaste, Sector Pitilla, Leonel, 10.99637N -85.40195W 510m., Mauricio Siezar coll., food plant: Inga spectabilis, host caterpillar: *Cerconota* Janzen216, coll. date: 6/15/2008, parasitoid eclosion date: 6/30/2008, DHJPAR0028298.

Lytopylus josecortesi **Kang, sp. n.**
http://zoobank.org/F15FE11D-1DE7-4A48-B4C5-0DCA61C97445
Fig. 21

Diagnosis. Fore wing mostly infuscated; mesoscutum entirely melanic; anterior transverse carina of propodeum absent; median areola of propodeum spindle-shape; lateral longitudinal carinae of median tergite 1 well-defined; median tergites entirely reddish orange.

Description. Holotype: female. Body length 5.2 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Median areola length 6x its width. Median areola closed posteriorly. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Similar to holotype.

Etymology. *Lytopylus josecortesi* is named in honor of José Cortés in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Dichomeris* Janzen703 (Dichomeridinae, Gelechiidae) feeding on mature leaves of *Neurolaena lobata* (Asteraceae) in ACG dry forest – rain forest ecotone at 620 m elevation.

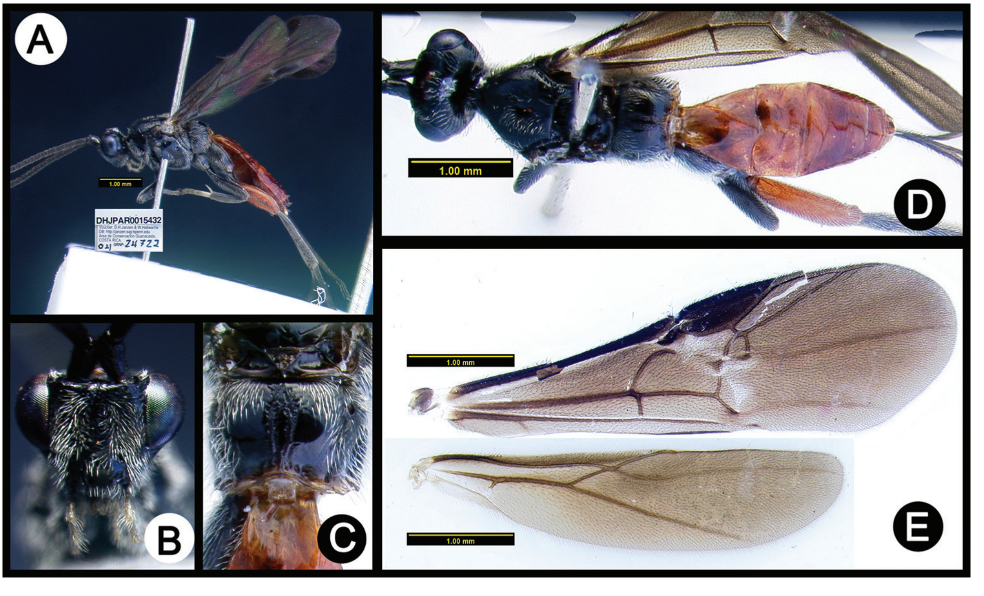


Figure 21. *Lytopylus josecortesi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Del Oro, Bosque Aguirre, Area de Conservación Guanacaste 11.0006N -85.438W 620m., Elieth Cantillano coll., food plant: Asteraceae *Neurolaena lobata*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris* Janzen703, coll. date: 9/21/2004, parasitoid eclosion date: 10/3/2004, DHJPAR0015432. Paratype: [the following have the same data as the holotype except as indicated] ♂, parasitoid eclosion date: 10/13/2004, DHJPAR0015431.

Lytopylus luisgaritai Kang, sp. n.

http://zoobank.org/EE7D1A31-9D2F-4B74-A6A6-C95012768953
Fig. 22

Diagnosis. Fore wing mostly infuscated; pronotum mostly pale, anteriorly melanic; mesoscutum entirely pale; mesopleuron entirely orange; scutellar sulcus lacking longitudinal carina; median tergites mostly melanic.

Description. Holotype: female. Body length 6.7 mm. Fore wing length 6.3 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

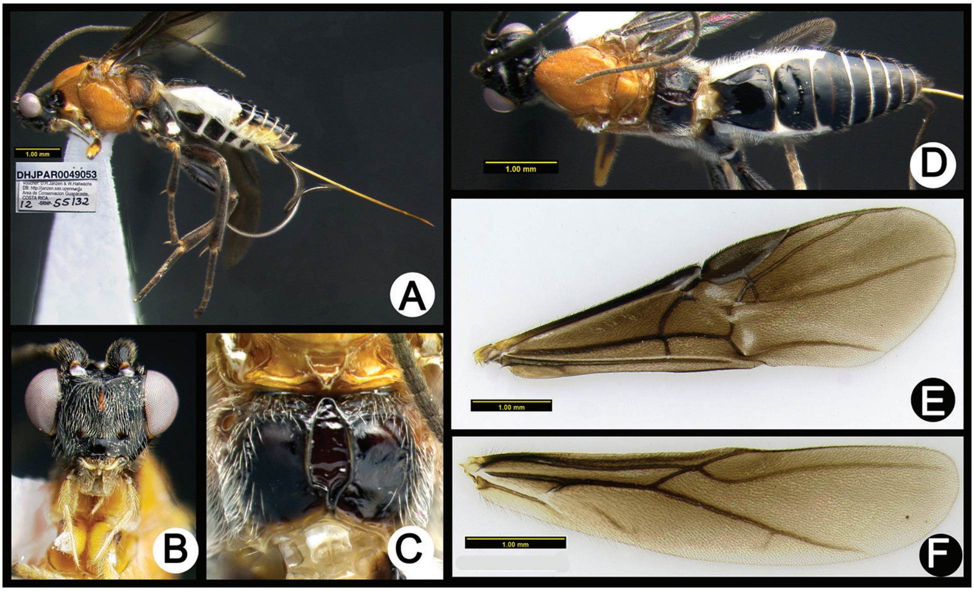


Figure 22. *Lytopylus luisgaritai* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Variation. Paratype propodeum mostly pale.

Etymology. *Lytopylus luisgaritai* is named in honor of Luis Garita in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Oecophora* Janzen52 (Oecophorinae, Oecophoridae) feeding on mature leaves of *Clethra lanata* (Clethraceae) in ACG dry forest at 733–740 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Mundo Nuevo, Camino Pozo Tres, Area de Conservación Guanacaste 10.77079N -85.37422W 733m., Jose Cortez coll., food plant: Clethraceae *Clethra lanata*, host caterpillar: Depressariidae, Oecophorinae, *Oecophora* Janzen52, coll. date: 1/22/2012, parasitoid eclosion date: 3/3/2012, DHJPAR0049053. Paratype: [the following have the same data as the holotype except as indicated] ♀, Cerro Gongora Pelado, 10.76307N -85.41332W 740m., coll. date: 1/18/2014, parasitoid eclosion date: 2/22/2014, DHJPAR0055239.

Lytopylus mariamartachavarriae Kang, sp. n.

http://zoobank.org/1691B66E-87CB-475D-AA54-0588AD1BCB13

Fig. 23

Diagnosis. Fore wing hyaline; fore wing RS+Ma tubular on less than one third its length; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely pale.

Description. Holotype: female. Body length 4.4 mm. Fore wing length 4.0 mm. Fore wing hyaline. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 0.9 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Similar to holotype, but median tergites mostly pale with three posterior terga melanic.

Etymology. *Lytopylus mariamartachavarriae* is named in honor of María Marta Chavarría in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared four times from *Dichomeris santarosensis* (Dichomeridinae, Gelechiidae) feeding on new leaves of *Quercus oleoides* (Fagaceae) in ACG dry forest at 305 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Santa Rosa, Arboles Via, Area de Conservación Guanacaste 10.86081N -85.60828W 305m., Daniel H. Janzen coll., food plant: Fagaceae *Quercus oleoides*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris santarosensis*, coll. date: 6/24/1982, eclosion date unknown, DHJPAR0015502. Paratypes: [the following have the same data as the holotype except as indicated] 2♀, 1♂, DHJPAR0015501, DHJPAR0015503, DHJPAR0015500.

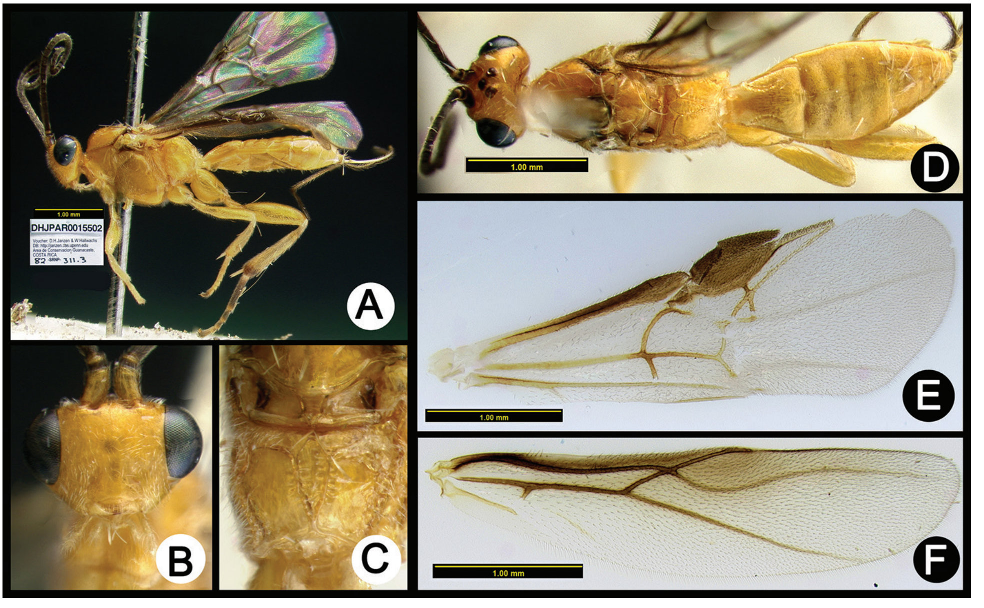


Figure 23. *Lytopylus mariamartachavarriae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

***Lytopylus miguelviquezi* Kang, sp. n.**
http://zoobank.org/1BE064F2-17DB-44CB-8B99-5A6F4224C7C1
Fig. 24, 25

Diagnosis. Apical flagellomeres brown not distinctly paler than subapical flagellomeres; fore wing mostly infuscated with a triangular second submarginal cell; fore tibia mostly melanic, yellow basally; hind tibia black basally and distally, yellow at mid-length; pronotum entirely pale (yellow to orange); mesoscutum entirely pale (yellow to orange); median areola of propodeum kite-shaped; anterior transverse carina of propodeum not reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 1.1 times longer than wide.

Description. Holotype: female. Body length 5.1 mm. Fore wing length 4.9 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Males. Body length usually shorter than holotype. Median tergites mostly melanic.

Variation. Female anterior head varies from mostly pale to mostly melanic.

Etymology. *Lytopylus miguelviquezi* is named in honor of Miguel Viquez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

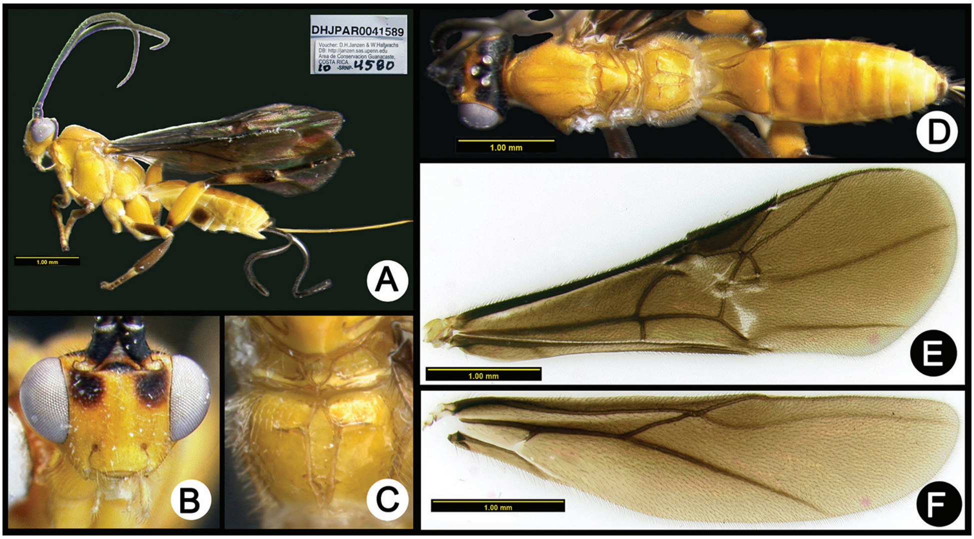


Figure 24. *Lytopylus miguelviquezi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Biology. Reared 58 times from the *Dichomeris designatella* complex (21), gelJanzen01 Janzen179 (13), and gelJanzen01 Janzen485 (16), all leaf tying dichomeridine Gelechiidae feeding on mature leaves of two species of *Erythroxylum* (Erythroxylaceae) and two species of *Rinorea* (Violaceae) in ACG rain forest-dry forest ecotone, and rain forest at 109 to 540 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Tajo Angeles, Area de Conservación Guanacaste 10.86472N -85.41531W 540m., Carolina Cano coll., food plant: Erythroxylaceae *Erythroxylum macrophyllum*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris* designatellaDHJ02, coll. date: 8/19/2010, parasitoid eclosion date: 9/8/2010, DHJPAR0041589. Paratypes: [the following have the same data as the holotype except as indicated] ♂, host caterpillar: *Dichomeris* designatellaDHJ03, coll. date: 1/25/2011, parasitoid eclosion date: 2/17/2011, DHJPAR0043147. ♀, coll. date: 7/8/2010, parasitoid eclosion date: 7/24/2010, DHJPAR0040341. ♀, coll. date: 7/8/2010, parasitoid eclosion date: 7/26/2010, DHJPAR0040347. ♀, food plant: Violaceae *Rinorea squamata*, host caterpillar: gelJanzen01 Janzen485, coll. date: 6/10/2010, parasitoid eclosion date: 6/26/2010, DHJPAR0040336. [same as previous except coll. date and eclosion date] ♀, coll. date: 10/15/2010, parasitoid eclosion date: 11/2/2010, DHJPAR0041566. ♂, coll. date: 10/15/2010, parasitoid eclosion date: 10/30/2010, DHJPAR0041570. ♂, coll. date: 10/15/2010, parasitoid eclosion date: 10/27/2010, DHJPAR0041565. ♂, coll. date: 10/20/2010, parasitoid eclosion date: 11/7/2010, DHJPAR0041567. ♂, coll. date: 11/7/2010, parasitoid eclosion date: 11/25/2010, DHJPAR0041555. ♂, coll. date: 11/7/2010, parasitoid eclosion date: 11/24/2010, DHJPAR0041553. ♀, Elda Araya coll., coll. date: 3/4/2010, parasitoid eclosion date: 4/6/2010, DHJPAR0038911.

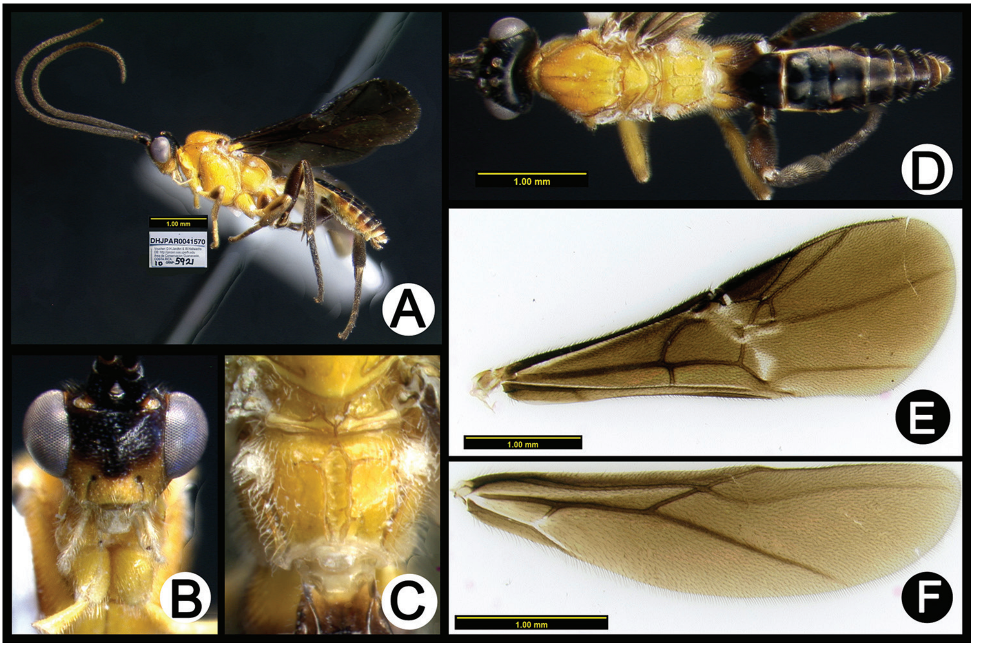


Figure 25. *Lytopylus miguelviquezi* male: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

[same as previous except coll. date and eclosion date] ♀, coll. date: 3/4/2010, parasitoid eclosion date: 3/21/2010, DHJPAR0038920. ♀, coll. date: 3/4/2010, parasitoid eclosion date: 3/26/2010, DHJPAR0038918. ♀, coll. date: 3/4/2010, parasitoid eclosion date: 3/25/2010, DHJPAR0038906. ♀, coll. date: 3/4/2010, parasitoid eclosion date: 3/26/2010, DHJPAR0038912. ♀, coll. date: 3/4/2010, parasitoid eclosion date: 3/26/2010, DHJPAR0038916. ♀, coll. date: 6/25/2010, parasitoid eclosion date: 7/11/2010, DHJPAR0040340. ♀, coll. date: 10/25/2010, parasitoid eclosion date: 11/14/2010, DHJPAR0041575. ♀, food plant: Violaceae *Rinorea squamata*, host caterpillar: gelJanzen01 Janzen485, coll. date: 3/7/2010, parasitoid eclosion date: 3/24/2010, DHJPAR0038909. [same as previous except coll. date and eclosion date] ♀, coll. date: 6/10/2010, parasitoid eclosion date: 6/30/2010, DHJPAR0040502. ♀, coll. date: 10/19/2010, parasitoid eclosion date: 11/10/2010, DHJPAR0041563. ♀, host caterpillar: gelJanzen01 Janzen179, 5/6/2011 6/23/2011, DHJPAR0045296. [same as previous except and eclosion date] ♂, 5/6/2011 6/22/2011, DHJPAR0045305. ♀, parasitoid eclosion date: 6/20/2011, DHJPAR0045373. ♀, parasitoid eclosion date: 6/22/2011, DHJPAR0045371. ♀, parasitoid eclosion date: 6/20/2011, DHJPAR0045276. ♀, parasitoid eclosion date: 6/19/2011, DHJPAR0045372. ♀, parasitoid eclosion date: 6/25/2011, DHJPAR0045369. ♀, parasitoid eclosion date: 6/22/2011, DHJPAR0045368. [same as previous except food plant and eclosion date] ♂, food plant: *Rinorea deflexiflora*, coll. date: 6/4/2014, parasitoid eclosion date: 6/17/2014, DHJPAR0055506. ♀, Gloria Sihezar coll., coll. date: 6/25/2010, parasitoid eclosion date: 7/20/2010, DHJPAR0040327. [same as previous except coll. date and eclosion date] ♀, coll. date: 7/8/2010, parasitoid eclosion date: 7/30/2010, DHJPAR0040332. ♀, coll. date: 11/1/2010, parasitoid eclosion date: 11/25/2010, DHJPAR0041561. ♂, host caterpillar: *Dichomeris* designatellaDHJ03, coll date: 7/26/2010, parasitoid eclosion date: 8/8/2010, DHJPAR0040330. [same as previous except eclosion date] ♂, parasitoid eclosion date: 8/13/2010, DHJPAR0040474. ♂, parasitoid eclosion date: 8/12/2010, DHJPAR0040459. ♂, parasitoid eclosion date: 8/11/2010, DHJPAR0040348. ♀, parasitoid eclosion date: 8/13/2010, DHJPAR0040342. ♂, parasitoid eclosion date: 8/13/2010, DHJPAR0040483. ♂, parasitoid eclosion date: 8/17/2010, DHJPAR0041588. ♀, host caterpillar: *Dichomeris* designatellaDHJ02, coll. date: 9/28/2010, parasitoid eclosion date: 10/25/2010, DHJPAR0041592. [same as previous except coll. date and eclosion date] ♀, coll. date: 3/14/2010, parasitoid eclosion date: 3/29/2010, DHJPAR0038917. [same as previous except as indicated] ♂, food plant: Violaceae *Rinorea squamata*, host caterpillar: gelJanzen01 Janzen485, coll. date: 5/24/2010, parasitoid eclosion date: 6/7/2010, DHJPAR0039509. [same as previous except coll. date and eclosion date] ♂, coll. date: 5/24/2010, parasitoid eclosion date: 6/7/2010, DHJPAR0039516. ♂, coll. date: 5/24/2010, parasitoid eclosion date: 6/8/2010, DHJPAR0039508. ♀, coll. date: 10/30/2010, parasitoid eclosion date: 11/27/2010, DHJPAR0041574. ♀, Gloria Sihezar coll., food plant: Erythroxylaceae *Erythroxylum havanense*, coll. date: 6/25/2010, parasitoid eclosion date: 7/10/2010, DHJPAR0040326. [same as previous except as indicated] ♀, food plant: *Erythroxylum macrophyllum*, host caterpillar: *Dichomeris* designatellaDHJ02, coll. date: 2/9/2011, parasitoid eclosion date: 3/1/2011, DHJPAR0042843. ♀, Osvaldo Espinoza coll., food plant: Violaceae *Rinorea squamata*, host caterpillar: gelJanzen01 Janzen179, coll. date: 2/9/2011, parasitoid eclosion date: 2/26/2011, DHJPAR0042842. ♂, Osvaldo Espinoza coll., coll. date: 8/29/2010, parasitoid eclosion date: 9/12/2010, DHJPAR0041597. ♀, Rio Blanco Abajo, 10.90037N -85.37254W 500m., Gloria Sihezar coll., food plant: Violaceae *Rinorea squamata*, host caterpillar: gelJanzen01 Janzen179, coll. date: 6/9/2011, parasitoid eclosion date: 6/24/2011, DHJPAR0045374. ♂, Sector Rincon Rain Forest, Sendero Anonas, 10.90528N -85.27882W 405m., Anabelle Cordoba coll., food plant: Violaceae *Rinorea hummelii*, host caterpillar: gelJanzen01 Janzen485, coll. date: 5/20/2014, parasitoid eclosion date: 6/10/2014, DHJPAR0055484. ♀, Sector Rincon Rain Forest, Quebrada Bambu, 10.9301N -85.25205W 109m., Cirilo Umaña coll., food plant: Violaceae *Rinorea deflexiflora*, host caterpillar: gelJanzen01 Janzen179, coll. date: 5/29/2014, parasitoid eclosion date: 6/10/2014, DHJPAR0055562. ♀, Guanacaste, Sector Del Oro, Quebrada Raiz, 11.02865N -85.48669W 280m., Roster Moraga coll., food plant: Violaceae *Rinorea deflexiflora*, host caterpillar: gelJanzen01 Janzen485, coll. date 6/3/2005, parasitoid eclosion date: 5/21/2005, DHJPAR0015528. ♀, Guanacaste, Sector Del Oro, Canyon Rio Mena, 10.99616N -85.45562W 560m., Lucia Ríos coll., coll. date: 3/26/2009, parasitoid eclosion date: 5/3/2009, DHJPAR0037860. ♂, Guanacaste, Sector Del Oro, Meteorologico, 11.00199N -85.46166W 590m., Lucia Ríos coll., coll. date: 9/3/2010, parasitoid closion date: 9/21/2010, DHJPAR0041949.

***Lytopylus motohasegawai* Kang, sp. n.**
http://zoobank.org/2F55247B-D2C7-4931-982F-7105C023953C
Fig. 26, 27

Diagnosis. Vertex of head entirely yellow; fore wing mostly infuscated with a quadrate second submarginal cell; mesoscutum mostly or entirely pale (yellow to orange); median areola of propodeum kite-shaped; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange).

Description. Holotype: female. Body length 4.9 mm. Fore wing length 4.9 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor longer than metasoma, but shorter than body.

Males. Vertical of head and occiput usually mostly melanic. Body length usually shorter than holotype. Median tergites mostly melanic.

Variation. Female occiput varies from entirely pale to mostly pale. Male hind femur color varies from mostly pale to black and pale with a similar percentage of each color.

Etymology. *Lytopylus motohasegawai* is named in honor of Motohiro Hasegawa in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared 36 times from gelJanzen01 Janzen28, a leaf-tier in the Gelechiidae feeding on mature leaves of two species of *Roupala* (Proteaceae) in ACG rain forest at 415 to 740 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Pitilla, Sendero Naciente, Area de Conservación Guanacaste 10.98705N -85.42816W 700m., Manuel Rios coll., food plant: Proteaceae *Roupala glaberrima*, host caterpillar: Gelechiidae, subfamily unknown, gelJanzen01 Janzen28, coll. date: 8/30/2010, parasitoid eclosion date: 9/23/2010, DHJPAR0041602. Paratypes: [the following have the same data as the holotype except as indicated] ♀, coll. date: 10/13/2010, parasitoid eclosion date: 11/1/2010, DHJPAR0041962. ♀, coll. date: 8/6/2011, parasitoid eclosion date: 9/10/2011, DHJPAR0048071. ♀, parasitoid eclosion date: 8/29/2011, DHJPAR0045318. ♂, parasitoid eclosion date: 9/8/2011, DHJPAR0048064. ♀, parasitoid eclosion date: 9/8/2011, DHJPAR0048068. ♀, Petrona Rios coll., parasitoid eclosion date: 8/31/2011, DHJPAR0048067. [same as previous except eclosion date] ♂, parasitoid eclosion date: 8/29/2011, DHJPAR0045364. ♂, Calixto Moraga coll., coll. date: 8/9/2011, parasitoid eclosion date: 8/29/2011, DHJPAR0045365. [same as previous except coll. date and eclosion date] ♀, coll. date: 1/17/2011, parasitoid eclosion date: 2/21/2011, DHJPAR0042463. ♀, Sendero Memos, 10.98171N -85.42785W 740m., Petrona Rios coll., coll. date: 8/8/2011, parasitoid eclosion date: 9/18/2011, DHJPAR0048065. [same as previous except eclosion date] ♀, parasitoid eclosion date: 9/9/2011, DHJPAR0048063. ♀, parsitoids eclosion date: 9/10/2011, DHJPAR0048066. ♀, Sendero Nacho, 10.98445N -85.42481W 710m.,

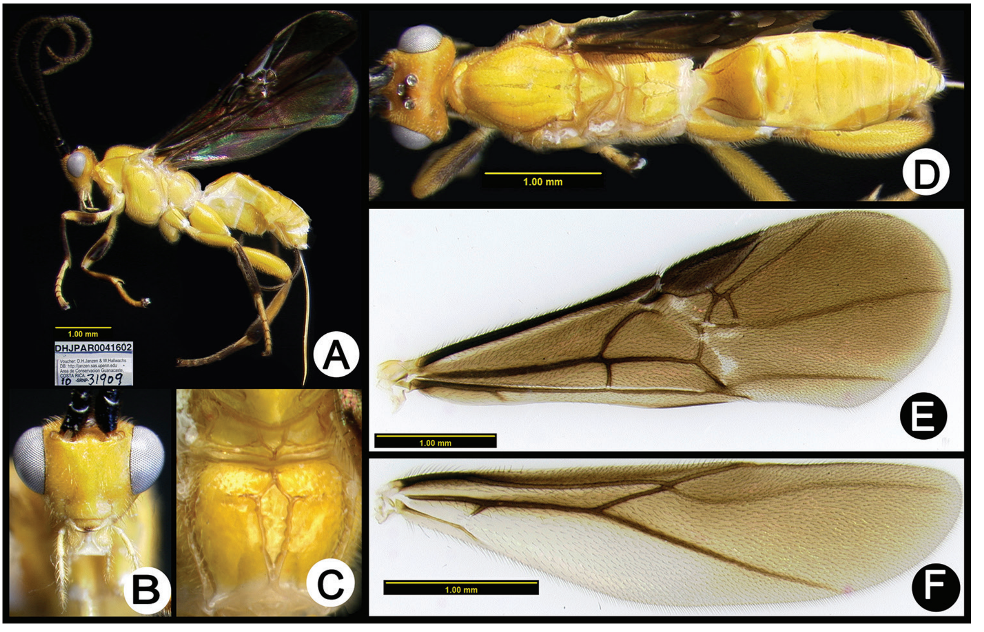


Figure 26. *Lytopylus motohasegawai,* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Petrona Rios coll., coll. date: 8/24/2010, parasitoid eclosion date: 10/1/2010, DHJPAR0041601. [same as previous except as indicated] ♀, Manuel Rios coll., coll. date: 9/27/2010, parasitoid eclosion date: 10/21/2010, DHJPAR0041203. [same as previous except eclosion date] ♂, parasitoid eclosion date: 11/2/2010, DHJPAR0041960. ♀, parasitoid eclosion date: 11/3/2010, DHJPAR0041963. ♂, parasitoid eclosion date: 10/28/2010, DHJPAR0041954. ♂, Manguera, 10.9959N -85.39842W 470m., Manuel Rios coll., coll. date: 1/4/2011, parasitoid eclosion date: 1/29/2011, DHJPAR0041577. [same as previous except as indicated] ♀, Ricardo Calero coll., coll. date: 7/15/2011, parasitoid eclosion date: 8/6/2011, DHJPAR0045330. [same as previous except eclosion date] ♀, parasitoid eclosion date: 9/12/2011, DHJPAR0048062. ♀, parasitoid eclosion date: 9/13/2011, DHJPAR0048061. ♀, parasitoid eclosion date: 9/13/2011, DHJPAR0048059. [same as previous except coll. date and eclosion date] ♀, coll. date: 9/11/2011 parasitoid eclosion date: 9/29/2011, DHJPAR0048060. ♂, coll. date: 9/18/2011 parasitoid eclosion date: 10/20/2011, DHJPAR0048073. ♀, coll. date: 9/18/2011 parasitoid eclosion date: 10/24/2011, DHJPAR0048072. ♀, Sendero Cuestona, 10.99455N -85.41461W 640m., Freddy Quesada coll., coll. date: 8/25/2011, parasitoid eclosion date: 9/14/2011, DHJPAR0048070. ♀, Alajuela, Sector San Cristobal, Tajo Angeles, 10.86472N -85.41531W 540m., Elda Araya coll., food plant: Proteaceae *Roupala montana*, coll. date: 10/9/2010, parasitoid eclosion date: 10/30/2010, DHJPAR0041573. [same as previous except coll. date and eclosion date] ♀, coll. date: 10/23/2010, parasitoid eclosion date: 11/12/2010, DHJPAR0041568. ♀, coll. date: 10/23/2010, parasitoid eclosion date: 12/3/2010,

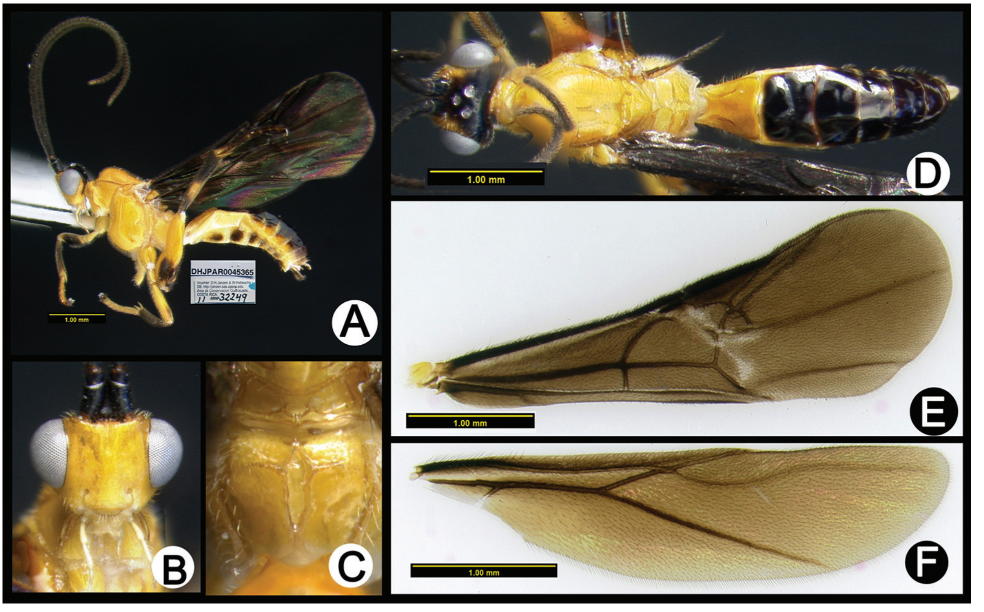


Figure 27. *Lytopylus motohasegawai* male: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

DHJPAR0041564. ♀, coll. date: 12/22/2010, parasitoid eclosion date: 1/28/2011, DHJPAR0041584. ♂, Sector Rincon Rain Forest, Jacobo, 10.94076N -85.3177W 461m, Edwin Apu coll., food plant: Proteaceae *Roupala glaberrima*, coll. date: 1/18/2014, parasitoid eclosion date: 2/6/2014, DHJPAR0054745. ♀, Estacion Caribe, 10.90187N -85.27495W 415m., Pablo Umaña Calderon coll., food plant: Proteaceae *Roupala montana*, coll. date: 7/31/2009, parasitoid eclosion date: 8/19/2009, DHJPAR0040071.

***Lytopylus okchunae* Kang, sp. n.**
http://zoobank.org/36FA08EB-98CC-45A1-828D-72542BE201E9
Fig. 28

Diagnosis. Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely melanic; fore wing mostly infuscated; mesoscutum entirely orange; anterior transverse carina of propodeum absent; median tergites entirely orange; median syntergite 2+3 1.5 times longer than wide.

Description. Holotype: female. Body length 6.8 mm. Fore wing length 6.3 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor about same length as body.

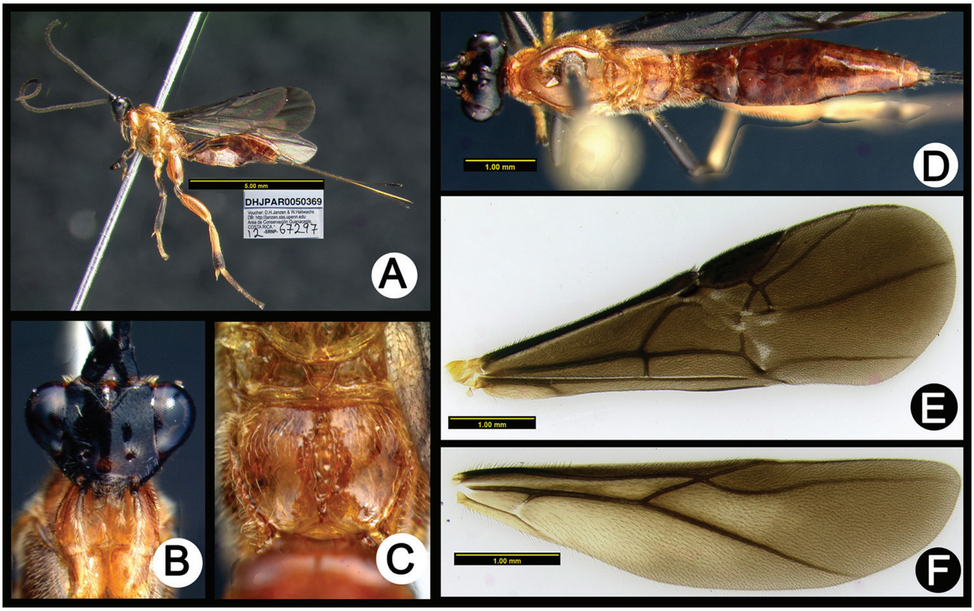


Figure 28. *Lytopylus okchunae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Males. Similar to holotype except for median tergite color. Median tergites usually mostly pale with posterior three terga melanic.

Etymology. *Lytopylus okchunae* is named in honor of Okchun Kim, grandmother of the first author.

Biology. Reared 18 times from three species of *Antaeotricha* (Depressariidae) leaf-webbers feeding on mature leaves of five species of broad-leafed monocots (Hylaeanthe, Renealmia, Hedychium, Pleiostachya, Calathea) in the Marantaceae and Zingiberaceae in ACG rain forest 96-575 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector Rincon Rain Forest, Palomo, Area de Conservación Guanacaste 10.96187N -85.28045W 96m., Cirilo Umaña coll., food plant: Marantaceae *Pleiostachya leiostachya*, host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha* Janzen224, coll. date: 2/20/2012 parasitoid eclosion date: 3/4/2012, DHJPAR0050369. Paratypes: [the following have the same data as the holotype except as indicated] ♀, Sendero Anonas, 10.90528N -85.27882W 405m., Jose Perez coll., food plant: Marantaceae *Hylaeanthe hoffmannii*, host caterpillar: *Antaeotricha* Janzen78, coll. date: 12/9/2010 parasitoid eclosion date: 1/2/2011, DHJPAR0041164. ♂, Anabelle Cordoba coll., food plant: Zingiberaceae *Renealmia cernua*, host caterpillar: *Antaeotricha* Janzen727, coll. date: 12/4/2012, parasitoid eclosion date: 12/23/2012, DHJPAR0051363. ♀, Quebrada Bambu, 10.9301N -85.25205W 109m., Cirilo Umaña coll. food plant: *Hylaeanthe hoffmannii*, host caterpillar: *Antaeotricha* Janzen78, coll. date: 10/29/2012, parasitoid eclosion date: 11/16/2012, DHJPAR0050939. [same as previous except coll. date and eclosion date]

♀, coll. date: 2/14/2013, parasitoid eclosion date: 3/24/2013, DHJPAR0051910. ♂, coll. date: 12/30/2014, parasitoid eclosion date: 1/16/2015, DHJPAR0057424. ♂, coll. date: 12/30/2014, parasitoid eclosion date: 1/14/2015, DHJPAR0056977. ♀, coll. date: 1/6/2015, parasitoid eclosion date: 1/20/2015, DHJPAR0056982. ♀, coll. date: 1/6/2015, parasitoid eclosion date: 1/20/2015, DHJPAR0056980. ♂, Finca Esmeralda, 10.93548N -85.25314W 123m., Cirilo Umaña coll., food plant: *Hylaeanthe hoffmannii*, host caterpillar: *Antaeotricha* Janzen78, coll. date: 1/6/2015, parasitoid eclosion date: 1/18/2015, DHJPAR0056981. ♀, Sector San Cristobal, Sendero Colegio, 10.89296N -85.3788W 520m., Carolina Cano coll. food plant: *Hylaeanthe hoffmannii*, host caterpillar: *Antaeotricha* Janzen78, coll. date: 9/30/2009, parasitoid eclosion date: 10/12/2009, DHJPAR0037191. ♀, Estacion San Gerardo, 10.88009N -85.38887W 575m., Gloria Sihezar coll. food plant: Zingiberaceae *Hedychium coronarium* (introduced), host caterpillar: *Antaeotricha* Janzen727, coll. date: 5/1/2014, parasitoid eclosion date: 5/16/2014, DHJPAR0055345. [same as previous except coll. date and eclosion date] ♀, coll. date: 5/1/2014, parasitoid eclosion date: 5/17/2014, DHJPAR0055355. ♀, coll. date: 5/1/2014, parasitoid eclosion date: 5/19/2014, DHJPAR0055984. ♀, Rio Blanco Abajo, 10.90037N -85.37254W 500m., Gloria Sihezar coll., food plant: Zingiberaceae *Hedychium coronarium* (introduced), host caterpillar: *Antaeotricha* Janzen727, coll. date: 5/9/2014, parasitoid eclosion date: 6/1/2014, DHJPAR0055819. ♀, Guanacaste, Sector Pitilla, Pasmompa, 11.01926N -85.40997W 440m., Manuel Rios coll., food plant: *Calathea marantifolia*, host caterpillar: *Antaeotricha* Janzen78, coll. date: 12/1/2005, parasitoid eclosion date: 12/16/2005, DHJPAR0015529.

Lytopylus pablocobbi Kang, sp. n.

http://zoobank.org/388474DC-9ED2-4C53-A0EA-46C8AA3EAFB4
Fig. 29

Diagnosis. Vertex of head entirely melanic; fore wing mostly infuscated; pronotum mostly orange, anteriorly black; mesoscutum entirely orange; anterior transverse carina of propodeum absent; median tergites entirely pale (yellow to orange); median syntergite 2+3 1.1 times longer than wide.

Description. Holotype: female. Body length 4.8 mm. Fore wing length 5.0 mm. Fore wing mostly infuscated. Pronotum bicolored. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. *Lytopylus pablocobbi* is named in honor of Pablo Cobb in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

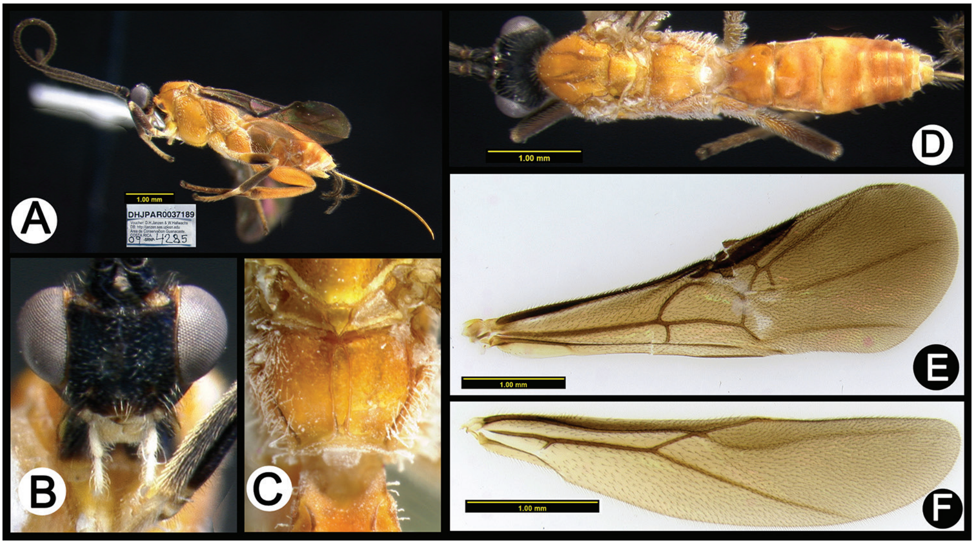


Figure 29. *Lytopylus pablocobbi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Biology. Reared one time from elachJanzen01 Janzen640 (Depressariidae), a stenomine leaf-tier feeding on mature foliage of *Bunchosia odorata* (Malpighiaceae) in ACG dry forest – rain forest ecotone at 722 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Jardin Estrada, Area de Conservación Guanacaste 10.86546N -85.39694W 722m., Gloria Sihezar coll., food plant: Malpighiaceae *Bunchosia odorata*, host caterpillar: Depressariidae, Stenomatinae, elachJanzen01 Janzen640, coll. date: 8/19/2009, parasitoid eclosion date: 9/16/2009, DHJPAR0037189.

Lytopylus robertofernandezi Kang, sp. n.

http://zoobank.org/E4012DEC-AAA8-4964-A1D2-F714C99EC057
Fig. 30

Diagnosis. Fore wing with two black bands; pronotum entirely black; lateral longitudinal carinae of median tergite 1 blunt.

Description. Holotype: male. Body length 7.6 mm. Fore wing length 6.7 mm. Fore wing with two black bands. Scutellar sulcus with two longitudinal carinae. Anterior transverse carina of propodeum absent. Median areola of propodeum lacking well-defined margins. Lateral longitudinal carinae of median tergite 1 blunt. Median syntergite 2+3 1.6 times longer than wide.

Female. Unknown.

Etymology. *Lytopylus robertofernandezi* is named in honor of Roberto Fernández in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

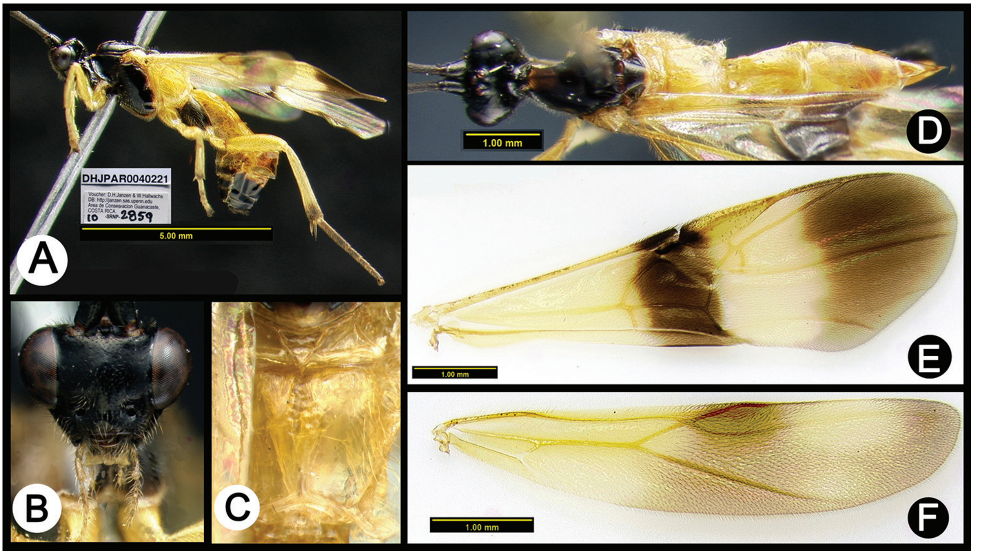


Figure 30. *Lytopylus robertofernandezi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Biology. Reared only one time and from the leaf-tier *Stenoma* Janzen687 (Depressariidae) feeding on mature leaves of *Pouteria exfoliata* (Sapotaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 540 m elevation.

Type material. Holotype ♂: Costa Rica, Alajuela, Sector San Cristobal, Tajo Angeles, Area de Conservación Guanacaste 10.86472N -85.41531W 540m., Carolina Cano coll., food plant: Sapotaceae *Pouteria exfoliata*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma* Janzen687, coll. date: 6/7/2010, parasitoid eclosion date: 6/23/2010, DHJPAR0040221.

***Lytopylus rogerblancoi* Kang, sp. n.**
http://zoobank.org/DE0D5410-134C-43BF-8A55-51B006AE8C76
Fig. 31

Diagnosis. Fore wing mostly infuscated; mesoscutum entirely black; median areola of propodeum with well-defined margins; anterior transverse carina of propodeum absent; median tergites entirely orange; lateral longitudinal carinae of median tergite 1 blunt.

Description. Holotype: female. Body length 6.0 mm. Fore wing length 6.4 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 blunt. Ovipositor longer than metasoma, but shorter than body. Median syntergite 2+3 0.9 times longer than wide.

Male. Similar to holotype.

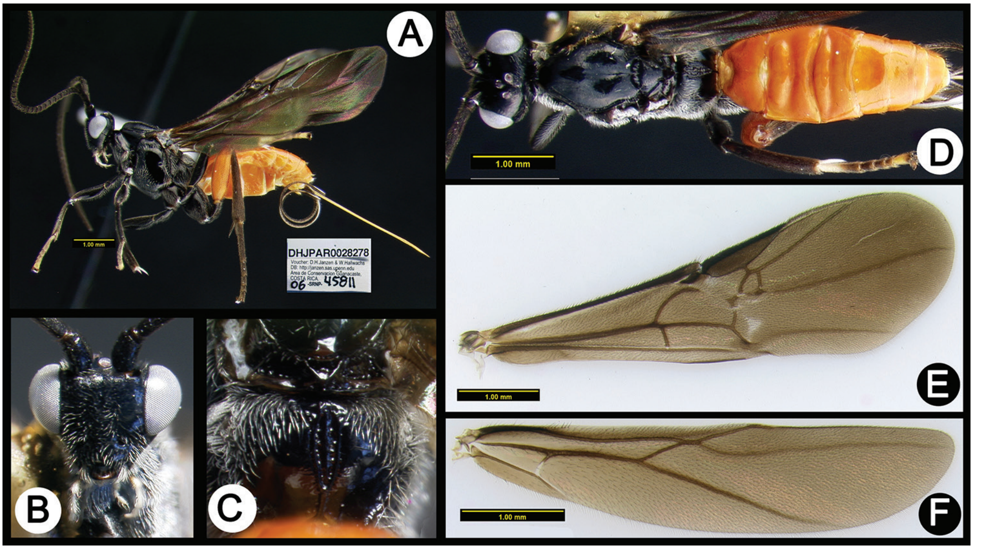


Figure 31. *Lytopylus rogerblancoi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Etymology. *Lytopylus rogerblancoi* is named in honor of Roger Blanco in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared eight times, one time from a waif pupa and seven times from gelJanzen01 Janzen356 (Dichomeridinae, Gelechiidae) feeding on mature leaves of *Hampea* and *Mortoniodendron* (Malvaceae) in ACG rainforest at 600 to 1180 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Finca San Gabriel, Area de Conservación Guanacaste 10.87766N -85.39343W 645m., Carolina Cano coll., food plant: Malvaceae *Mortoniodendron costaricense*, host caterpillar: Gelechiidae, Dichomeridinae, gelJanzen01 Janzen356, coll. date: 1/28/2010, parasitoid eclosion date: 2/25/2010, DHJPAR0038905. Paratypes: [the following have the same data as the holotype except as indicated] ♀, coll. date: 11/30/2012, parasitoid eclosion date: 1/1/2013, DHJPAR0051361. ♂, coll. date: 2/21/2013, parasitoid eclosion date: 3/18/2013, DHJPAR0051914. ♂, Jardin Estrada, 10.86546N -85.39694W 722m., Gloria Sihezar coll., coll. date: 12/10/2013, parasitoid eclosion date: 1/14/2014, DHJPAR0054536. ♂, Guanacaste, Sendero Segundo, 10.92679N -85.45332W 1180m., Manuel Pereira coll., food plant: Malvaceae *Hampea appendiculate*, coll. date: 7/30/2007, parasitoid eclosion date: 8/24/2007, DHJPAR0028281. ♂, Guanacaste, Sector Santa Maria, Sendero Canal, 10.76544N -85.28539W 799m., Mariano Pereira coll., food plant: Malvaceae *Mortoniodendron guatemalense*, coll. date: 7/23/2009, parasitoid eclosion date: 8/10/2009, DHJPAR0036354. ♀, Guanacaste, Sector Cacao, Gongora Bananal, 10.88919N -85.47609W 600m., Dunia Garcia coll., food plant unknown, host caterpillar: Gelechiidae, Dichomeridinae, species unknown, coll. date: 6/29/2006, parasitoid eclosion date: 7/24/2006, DHJPAR0028278.

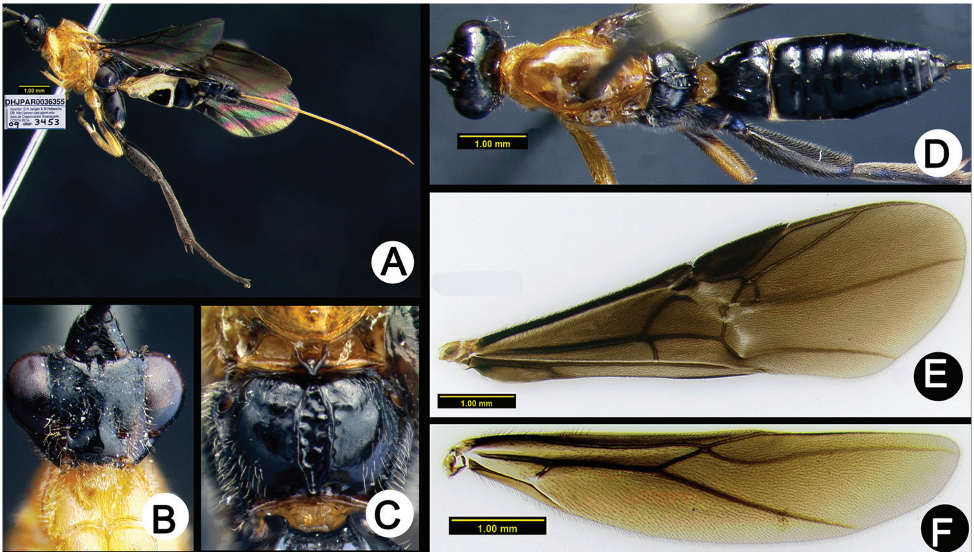


Figure 32. *Lytopylus salvadorlopezi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Lytopylus salvadorlopezi Kang, sp. n.

http://zoobank.org/6E529BF2-79C8-4B9C-9C3C-DC555133BCCD
Fig. 32

Diagnosis. Scutellar sulcus lacking longitudinal carina; fore wing mostly infuscated; anterior transverse carina of propodeum not reaching the lateral margin; median tergites mostly black.

Description. Holotype: female. Body length 7.5 mm. Fore wing length 7.3 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor length about same length as body.

Male. Unknown.

Etymology. *Lytopylus salvadorlopezi* is named in honor of Salvador López in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared five times from two species of leaf-tying *Stenoma* (Depressariidae) feeding on *Persea schiedeana* (Lauraceae) in ACG in the rain forest rain forest at 700 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Quebrada Cementerio, Area de Conservación Guanacaste 10.87124N -85.38749W 700m., Osvaldo Espinoza coll., food plant: Lauraceae *Persea schiedeana*, host caterpillar: Depressariidae, Stenomatinae, *Stenoma* Janzen06, coll. date: 7/6/2009, parasitoid eclosion date: 8/6/2009, DHJPAR0036355. Paratypes: [the following have the same data

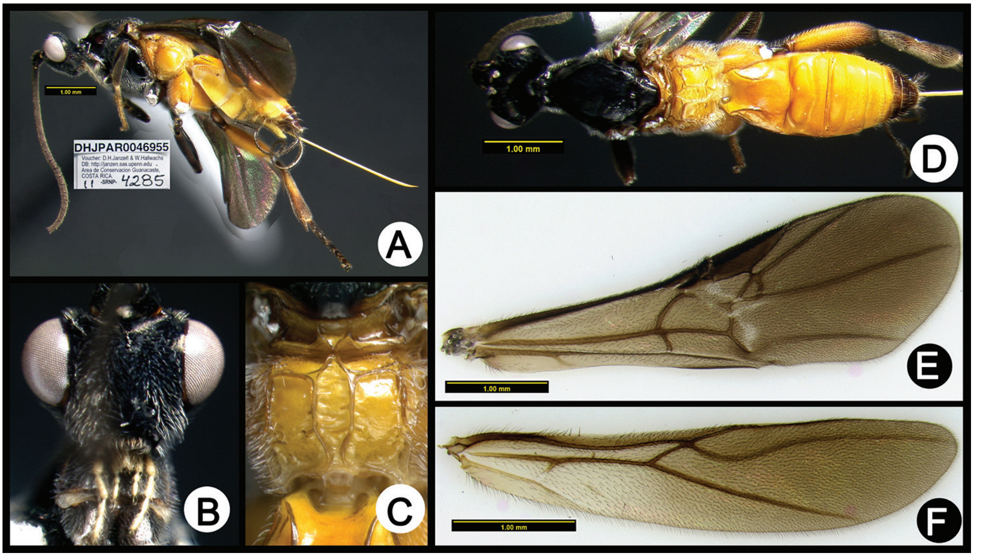


Figure 33. *Lytopylus sangyeoni* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

as the holotype except as indicated] ♀, parasitoid eclosion date: 8/15/2009, DHJPAR0036345. ♀, host caterpillar: *Stenoma* Janzen12, coll. date: 11/19/2009, parasitoid eclosion date: 12/18/2009, DHJPAR0037949.

Lytopylus sangyeoni Kang, sp. n.

http://zoobank.org/571E1D60-DF10-4EB9-B070-8291838382F7
Fig. 33

Diagnosis. Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely black; scutellar sulcus with one median longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 as long as wide.

Description. Holotype: female. Body length 5.5 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. Named in honor of Sangyeon Park, father-in-law of the first author.

Biology. Reared one time from elachJanzen01 Janzen847 (Depressariidae) as a leaf-tier feeding on mature leaves of *Senegalia tenuifolia* (Fabaceae) in ACG rain forest at 527 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Huerta, Area de Conservación Guanacaste 10.9305N -85.37223W 527m., Carolina Cano coll., food plant: Fabaceae *Senegalia tenuifolia*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen847, coll. date: 11/4/2011, parasitoid eclosion date: 11/21/2011, DHJPAR0046955.

Lytopylus sarahmeierottoae Kang, sp. n.

http://zoobank.org/8A0864DC-0480-4A42-9052-2E32B869093B
Fig. 34

Diagnosis. Fore wing mostly infuscated; pronotum entirely pale; mesoscutum entirely pale; scutellar sulcus lacking longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly melanic, anteriorly white.

Description. Holotype: female. Body length 5.1 mm. Fore wing length 4.8 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor slightly longer than body.

Male. Unknown.

Etymology. Named in honor of Sarah Meierotto, graduate student in the Department of Entomology at the University of Kentucky, for her assistance.

Biology. Reared four times from *Cerconota* Janzen82 (Stenomatinae, Depressariidae) feeding on mature leaves of *Inga micheliana* (Fabaceae) in ACG rain forest at 730 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Vivero, Area de Conservación Guanacaste 10.86739N -85.38744W 730m., Elda Araya coll., food plant: Fabaceae *Inga micheliana*, host caterpillar: Depressariidae, Stenomatinae, *Cerconota* Janzen82, coll. date: 12/20/2014, parasitoid eclosion date: 1/13/2015, DHJPAR0056993. Paratypes: [the following have the same data as the holotype except as indicated] 2♀, parasitoid eclosion date: 1/10/2015, DHJPAR0056984, DHJPAR0056991. ♀, parasitoid eclosion date: 1/17/2015, DHJPAR0056992.

Lytopylus sergiobermudezi Kang, sp. n.

http://zoobank.org/93CB5271-223B-4600-8D35-75486F6BA0C5
Fig. 35

Diagnosis. Fore wing hyaline; fore wing RS+Ma tubular on more than half its length; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black.

Description. Holotype: male. Body length 3.9 mm. Fore wing length 3.6 mm. Fore wing hyaline. Fore wing RS+Ma more complete. Scutellar sulcus with four

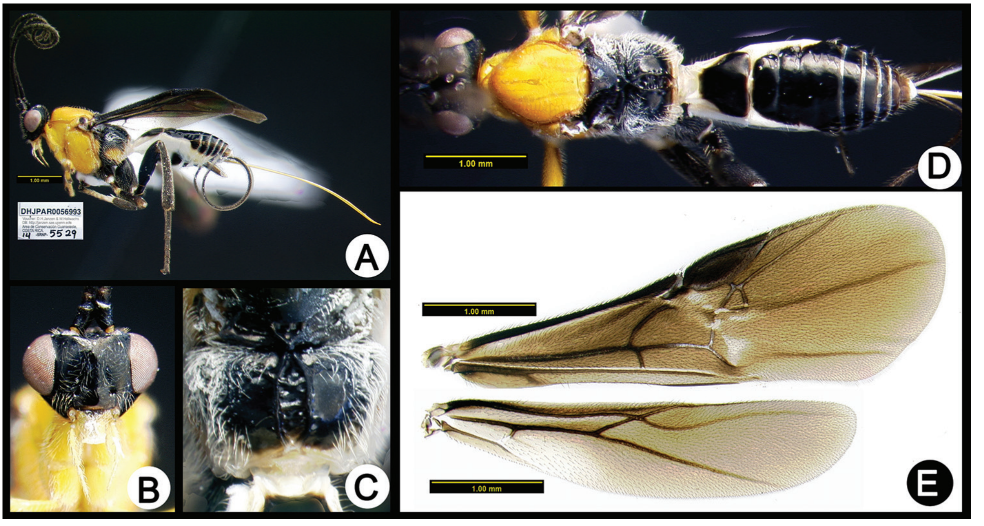


Figure 34. *Lytopylus sarahmeierottoae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** wings.

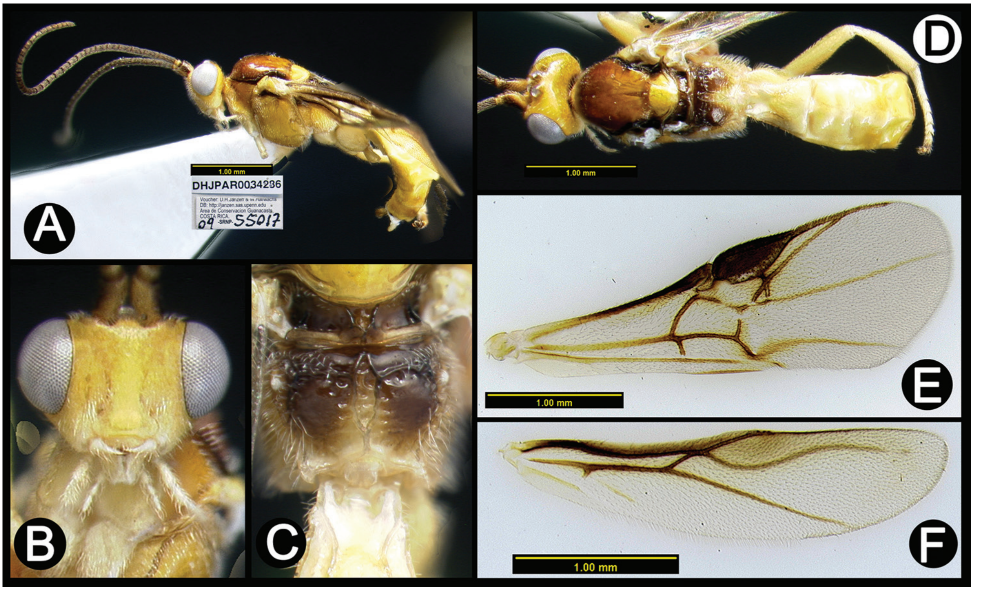


Figure 35. *Lytopylus sergiobermudezi* holotype: **A** lateral habitus, B. anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.

Female. Unknown.

Variation. Male mesoscutum varies from less melanic to mostly pale. Male propodeum varies bicolored to entirely pale.

Etymology. *Lytopylus sergiobermudezi* is named in honor of Sergio Bermúdez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Dichomerus santarosensis* (Dichomeridinae, Gelechiidae) leaf-tier feeding on new foliage of *Quercus oleioides* (Fagaceae) in ACG dry forest at 420 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Mundo Nuevo, Punta Plancha, Area de Conservación Guanacaste 10.7416N -85.42734W 420m., Mariano Pereira coll., food plant: Fagaceae *Quercus oleoides*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris santarosensis*, coll. date: 1/5/2009, parasitoid eclosion date: 1/19/2009, DHJPAR0034286. Paratype: [the following has the same data as the holotype except as indicated] DHJPAR0030601.

Lytopylus sigifredomarini Kang, sp. n.

http://zoobank.org/5E10353D-E093-4A12-886F-C92596DEE86E
Fig. 36

Diagnosis. Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely black; scutellar sulcus lacking longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin.

Description. Holotype: male. Body length 5.2 mm. Fore wing length 4.8 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide.

Female. Unknown.

Etymology. *Lytopylus sigifredomarini* is named in honor of Sigifredo Marín in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared three times from *Antaeotricha* Janzen224 (Stenomatinae, Depressariidae) feeding on mature leaves of *Hirtella media* (Chrysobalanaceae) in ACG rain forest at 410 to 620 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Del Oro, Tangelo, Area de Conservación Guanacaste 11.01823N -85.45024W 410m., Elieth Cantillano coll., food plant: Chrysobalanaceae *Hirtella triandra*, host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha* Janzen224, coll. date: 1/6/2011, parasitoid eclosion date: 1/31/2011, DHJPAR0042545. Paratypes: [the following have the same data as the holotype except as indicated] ♂, Bosque Aguirre, 11.0006N -85.438W 620m., Roster Moraga coll., coll. date: 5/7/2010, parasitoid eclosion date: 5/31/2010, DHJ-

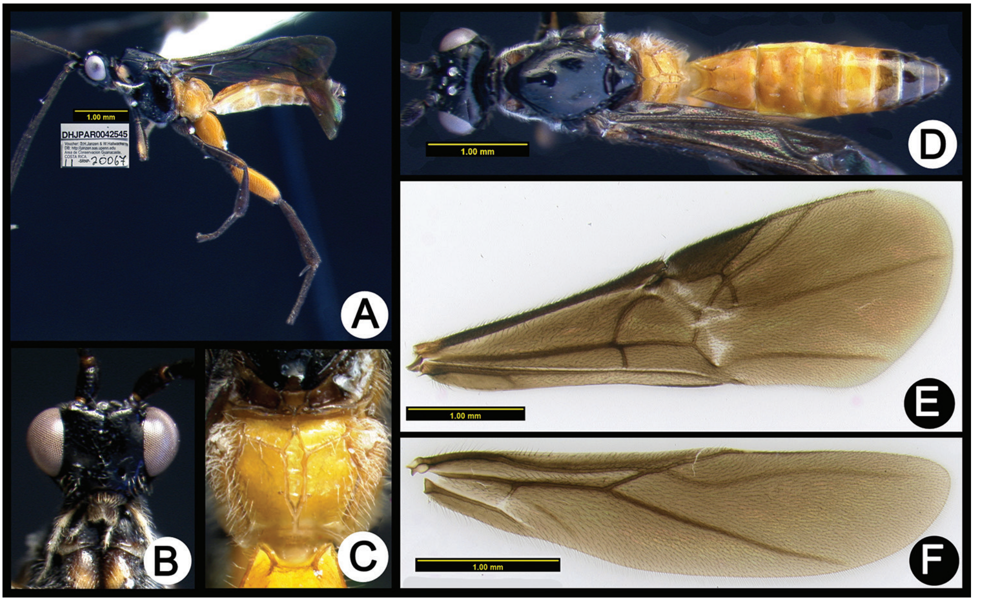


Figure 36. *Lytopylus sigifredomarini* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

PAR0040328. ♂, Sector Pitilla, Coneja, 11.01525N -85.39766W 415m., Dinia Martinez coll., food plant: *Hirtella media*, coll. date: 5/6/2013, parasitoid eclosion date: 5/27/2013, DHJPAR0052899.

Lytopylus youngcheae Kang, sp. n.

http://zoobank.org/6890246F-A78D-4AA9-AE26-F4322390B5DE
Fig. 37

Diagnosis. Fore wing with one black band; vertex of head entirely melanic.

Description. Holotype: female. Body length 8.9 mm. Fore wing length 8.1 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Anterior transverse carina of propodeum not reaching the lateral margin. Median areola of propodeum with well-defined margins. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor slightly longer than body.

Males. Body length usually shorter than holotype. Hind femur varies from mostly pale to mostly melanic.

Etymology. Named in honor of Youngche Choi, mother of the first author.

Biology. Reared five times from two species of stenomatine Depressariidae leaf-tiers feeding on mature leaves of *Calophyllum brasiliense* (Calophyllaceae) in ACG rain forest at 540 to 740 m elevation.

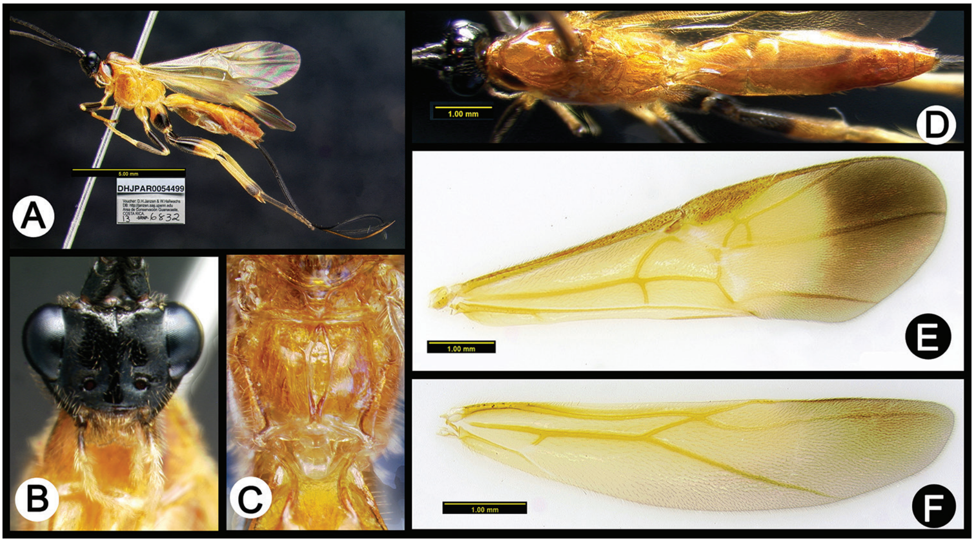


Figure 37. *Lytopylus youngcheae* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Cementerio Viejo, Area de Conservación Guanacaste 10.88111N -85.38889W 570m., Carolina Cano coll., food plant: Calophyllaceae *Calophyllum brasiliense*, host caterpillar: Depressariidae, Stenomatinae, *Cerconota* Janzen140, coll. date: 11/27/2013, parasitoid eclosion date: 12/31/2013, DHJPAR0054499. Paratypes: [the following have the same data as the holotype except as indicated] ♀, Guanacaste, Sector Pitilla, Sendero Memos, 10.98171N -85.42785W 740m., Elieth Cantillano coll., coll. date: 4/27/2007 parasitoid eclosion date: 5/27/2007, DHJPAR0021132. ♂, Finca San Gabriel, 10.87766N -85.39343W 645m., host caterpillar: *Antaeotricha* Janzen134, coll. date: 4/1/2013, parasitoid eclosion date: 4/30/2013, DHJPAR0052197. ♀, Tajo Angeles, 10.86472N -85.41531W 540m., Elda Araya coll., host caterpillar: *Antaeotricha* Janzen134, coll. date: 12/31/2010, parasitoid eclosion date: 1/24/2011, DHJPAR0041586. [same as previous except as eclosion date] ♂, parasitoid eclosion date:1/25/2011, DHJPAR0041585.

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Supplementary material 1

Interactive key, DELTA data matrix, and images for the revision of the species of *Lytopylus* from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae)

Authors: Ilgoo Kang, Eric G. Chapman, Daniel H. Janzen, Winnie Hallwachs, Tanya Dapkey, Smith M. Alex, Michael J. Sharkey

Data type: interactive key

Link: https://doi.org/10.3897/zookeys.721.20287.suppl1