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UNIVERSITY OF CALIFORNIA RIVERSIDE

Unraveling Diversity: A Systematic Study of the Sub-Saharan African Ant Parasitoid Genus *Tutucharis* (Hymenoptera: Eucharitidae)

A Thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science

in

Entomology

by

Alejandra Rocha

December 2024

Thesis Committee:

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Committee Chairperson

University of California, Riverside

Acknowledgements

I would like to express my heartfelt gratitude to Dr. John M. Heraty for providing me with this invaluable opportunity and believing in my potential. His guidance and support have been instrumental in shaping my research journey, and I am truly thankful for the knowledge he has generously shared with me.

To my esteemed committee members—Dr. Mark Hoddle, Dr. Richard Stouthamer, and Dr. Christiane Weirauch—thank you for your time, valuable insights, and thoughtful feedback.

A special thanks to Krissy Dominguez for her help with sequencing and bioinformatics. Her assistance and the time she spent helping me are deeply appreciated.

I would also like to extend my appreciation to the members of both the Heraty and Weirauch labs. Their encouragement and camaraderie have been pivotal in my academic experience, and their collective expertise has been a constant source of inspiration.

I am sincerely thankful to all the museums that supplied the material for my research, and I greatly appreciate the effort and dedication of the collectors who ventured into the field to gather them

Quiero expresar mi más profunda gratitud a mis padres por su apoyo incondicional a lo largo de mi tesis. Su fe en mí y su apoyo constante han sido invaluables. No podría haber completado esto sin ustedes.

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Dedication

This thesis is dedicated to my son, Fabrizio. Thank you for your unwavering patience and understanding as I worked tirelessly on this thesis. Your support has been my greatest motivation. May this work inspire you to pursue your own dreams and aspirations.

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Chapter 1: A Revision of the Palaeotropical Ant Parasitoid Genus

Ancylotropus (Hymenoptera: Eucharitidae)

Alejandra Rocha

1. Abstract

The genus Ancylotropus Cameron includes six valid species and numerous undescribed species from sub-Saharan Africa. Among the described species, four are from Southeast Asia, including Ancylotropus cariniscutis Cameron, A. keralensis Girish Kumar and Narendran, A. manipurensis (Clausen), and A. montanus (Girault), while two are from Madagascar, A. ivondroi (Risbec) and A. seyrigi (Risbec). Previous molecular analyses have not recovered the monophyly of Ancylotropus, although they are consistently nested within the Schizaspidia clade. We used molecular and morphological analyses to determine the monophyly of species currently assigned to the genus Ancylotropus. The monophyly of Ancylotropus was never recovered. Three distinct clades of 'Ancylotropus' are recognized: the African Tutucharis n. gen. and Madagascan Ancylotropus are monophyletic, but form paraphyletic groups leading to a monophyletic Southeast Asian clade that includes a few new species of Ancylotropus from Africa, A. montanus, the Asian Ancylotropus and all but one of the other genera in the Schizaspidia clade. With the recognition of *Tutucharis*, there are now seven genera within the Schizaspidia clade, including Eucharissa Westwood, Pogonocharis Heraty, Saccharissa Kirby, Schizaspidia Westwood, *Thoracanthoides* Girault, and *Ancylotropus*, with the latter further partitioned into four species groups. The sub-saharan African taxa previously classified under Ancylotropus fall into two distinct groups: one now recognized as a new genus, *Tutucharis*, and another, the *Ancylotropus neotropus* group from sub-Saharan

Africa (four undescribed species) that groups with the Asian *Ancylotropus*. Based on morphological characteristics, *Tutucharis* is recognized as a distinct new genus, encompassing 11 new species.

Any new generic or species names in this thesis are not considered as available for the scientific record.

2. Introduction

With over 27,000 described species across 50 families, the superfamily Chalcidoidea stands as potentially one of the most diverse superfamilies within the order Hymenoptera (Heraty et al., 2013; Cruaud et al., 2024). Economically and ecologically, they hold significant importance, serving both as crucial biological control agents and potential pests. Within this superfamily, Eucharitidae (Hymenoptera: Chalcidoidea) are comprised of 65 genera and 527 species categorized into four subfamilies: Akapalinae, Eucharitinae, Oraseminae, and Gollumiellinae (UCD Community, 2023).

All members of this family act as internal or external parasitoids targeting the immature stages of ants (Clausen, 1940; Zhang et al., 2022). Adult females deposit their eggs onto or into various plant structures (Heraty, 2002). The first larval instar, termed a planidium, is cylindrical, highly sclerotized, possesses distinct terga, and exhibits considerable mobility. These planidia utilize worker ants of the host species as vectors to infiltrate ant nests. Within the nest, they first attack the ant larvae, and then complete their development while attached

externally to the ventral thoracic region of the ant pupae (Heraty et al., 2017; Zhang et al., 2022).

The genus *Ancylotropus* Cameron as defined by Heraty (2002) includes six valid species found in Madagascar and southeast Asia, although numerous undescribed species were recognized in sub-Saharan Africa. Heraty (2002) placed the genus within the Schizaspidia clade, a group of 11 genera, which together with the Chalcura and Kapala clades are all considered to be parasitoids of poneromorph ants (Ectatomminae and Ponerinae) (Murray et al., 2013, but see Zhang et al., 2022). Among the described species, four described species originate from Southeast Asia, including *Ancylotropus cariniscutis* Cameron, *A. keralensis* Girish Kumar and Narendran, *A. manipurensis* (Clausen), and *A. montanus* (Girault), while two are from Madagascar, *A. ivondroi* (Risbec) and *A. seyrigi* (Risbec) (Heraty, 2002). None of the African species have been described. Heraty (2002) argued in support of the monophyly of *Ancylotropus*, although monophyly was not recovered in any of his morphological analyses, however he recognized the great diversity of forms within the genus.

Based on subsequent molecular analyses, the monophyly of *Ancylotropus* has never been recovered, although they are always nested within the Schizaspidia clade (Heraty et al., 2004; Murray et al., 2013; Zhang et al., 2022). Using the most inclusive sampling of *Ancylotropus*, Murray et al. (2013) recognized three unrelated clades represented by taxa from Africa, Madagascar and southeast Asia. One morphologically distinctive species, *A. montanus* from

southeast Asia, has not yet been included in any of these molecular studies. Herein we are focused on circumscribing and placing the large number of undescribed African species.

Biological information for Ancylotropus, including Tutucharis, is sparse. A single host is known for one of the African *Tutucharis* species, in which two specimens were extracted from cocoons of Odontomachus troglodytes Santischi (Heraty, 2002). This aligns with the hosts of all other members of the Schizaspidia clade attacking genera of the ant subfamily Ponerinae (Heraty, 2002; Murray et al. 2013; Heraty et al., 2015). The biology and oviposition behavior are known for only a few species of Asian Ancylotropus. Ancylotropus manipurensis is known to deposit clusters of around 1000 eggs under the outer bud scales of *Flemingia* (Fabaceae), which hatch within 2–3 weeks (Clausen, 1928). The highly active planidia attach themselves to any object near them (Clausen, 1928). Clausen tried placing the planidia on the mature larvae of *Camponotus* (Formicinae), which then fed on the host but did not develop beyond the first instar. This led Narendran and Sheela (1995) to mistakenly assume that *Camponotus* was the known host. Given its placement in the Schizaspidia clade, Camponotus is not a likely host, and thus we have no ant host records for the Asian or Madagascan species of Ancylotropus.

Ancylotropus montanus scatter eggs on the underside of leaves of Sandoricum (Meliaceae) and Premna (Verbenaceae) (Ishii, 1932). The freshly deposited eggs are white with a short stalk as found in most Eucharitidae. Larvae

hatched within one week, and the first instar was described by Ishii (1932). A previously undescribed species from South Africa (described herein) was associated (not observed directly) with oviposition into the skin of mature berries of *Psychotria capensis* (Eckl.) Vatke (Rubiaceae), in which clusters of 60–80 stalked eggs were deposited (Heraty, 2002). The first-instar larvae are morphologically similar to other members of the Schizaspidia clade and are described herein.

The focus of this study was to assess the monophyly of species currently assigned to the genus *Ancylotropus* using molecular and morphological methods. A comprehensive review is undertaken of the African species, with descriptions of unknown species, assignment to genera, and descriptions of their known biology. Three distinct clades of *'Ancylotropus'* are recognized, with the African *Tutucharis* **n. gen.** and Madagascan *Ancylotropus* as distinct paraphyletic groups leading to a monophyletic southeast Asian clade that includes a few other new species of *Ancylotropus* from Africa, *A. montanus*, and the Asian *Ancylotropus*. With the recognition of *Tutucharis*, there are now seven genera within the Schizaspidia clade including *Eucharissa* Westwood, *Pogonocharis* Heraty, *Saccharissa* Kirby, *Schizaspidia* Westwood, *Thoracanthoides* Girault, *Tutucharis*, and *Ancylotropus*, which is further partitioned into four species groups. A key to the genera of the Schizaspidia clade is provided.

3. Material and Methods

3.1 Specimens

Material was examined from the following collections: American Entomological Institute, Gainesville, FL, United States (AEIC); American Museum of Natural History, New York, NY, United States (AMNH); Natural History Museum, London, United Kingdom (BMNH); Bishop Museum, Honolulu, HI, United States (BPBM); California Academy of Sciences, San Francisco, CA, United States (CASC); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON, Canada (CNC); University of Kentucky, Department of Entomology, Hymenoptera Institute Collection, Lexington, KY, United States (HIC); Natural History Museum of Los Angeles, Los Angeles, CA, United States (LACM); National Museum of Natural History, Paris, France (MNHN); National Museum, Prague, Czechia (NMPC); Royal Museum for Central Africa, Tervuren, Belgium (RMCA); Royal Ontario Museum, Toronto, Canada (ROME); Iziko South African Museum, Cape Town, South Africa (SAMC); University of California, Riverside, Entomology Research Museum, Riverside, CA, United States (UCRC); Smithsonian National Museum of Natural History, Washington, DC, United States (USNM); Danish Natural History Museum, Copenhagen, Denmark (ZMUC). Collection acronyms largely adhere to Evenhuis (2020).

Material examined information is recorded in a FileMaker Pro Advanced version 17 database maintained at UC Riverside. Barcodes and identification numbers are assigned to all specimens, and molecular vouchers receive an

additional DNA reference number (Dxxxx). Material examined data is in the following order: country, elevation, coordinates (if in italics coordinates were estimated using Google Earth), collection date (DAY.MONTH.YEAR), collector; data within brackets provide details on sex, deposition location (specimen identification number), and D# (if applicable). Specimen locations are visualized using Simplemappr (Fig. 1).

3.2 Images and Illustrations

Images of pinned specimens were captured using a Leica Z16 APO automontage microscope and a Leica DFC 450C 5-megapixel camera system. Images were stacked using Zerene Stacker version 1.04 to achieve an extended depth of field. Illustrations of antennae and planidia were captured using a camera lucida on a Leica M10 stereoscope and a Leica DMRB compound microscope, respectively. All images and illustrations were enhanced using Adobe Photoshop version 25.9.1 and the Camera Raw plug-in.

3.3 Terminology

Specimens used in the taxonomic descriptions and phylogenetic analyses were primarily identified using Heraty (2002), with details on sculpture from Harris (1979) and Eady (1968). Morphological terms for adults and planidia follow Heraty (2002) and Heraty et al. (in press). For a complete list of terms and abbreviations see Table 2.

3.4 Measurements

Measurements were taken using an ocular micrometer with a Zeiss Stemi SV6 light microscope, with a 1.6x objective lens and a 10x eyepiece. All measurement ranges were obtained from at least 5 different specimens of each sex unless otherwise stated.

3.5 Molecular Methods

Molecular analyses include a total of 74 terminal taxa. Forty-five outgroup taxa were chosen based on previously published phylogenetic data from Carmichael (2006) and Murray et al. (2013). Newly sequenced dry museum specimens were prepared for non-destructive DNA extraction. Under sterile conditions point-mounted museum specimens were placed under a microscope; using forceps, the hind right leg (including the femur, trochanter, tibia, and tarsus) was removed, then placed inside a vial for extraction. Non-destructive full-body extractions were performed on specimens preserved in 95% ethanol. Where available, sequences referenced in Carmichael (2006) and Murray et al. (2013) were used (Table 3).

Specimens were extracted using the DNeasy® blood and tissue kit manufactured by Qiagen (Valencia, CA, USA) following the Heraty et al. (2013) protocol. The PCR product was purified with DNA Clean & Concentrator[™] -5 kits by Zymo Research (Irvine, CA, USA) and PCR product concentrations were determined using Nanodrop 2000c (Thermo Scientific[™]). The Sanger

sequencing dataset includes four gene regions: two nuclear ribosomal (28S D2, and 28S D3-5) and two mitochondrial cytochrome oxidase regions (COI NJ and COII) (Murray et al., 2013). Each gene was PCR amplified individually. Samples for Sanger sequencing were sent to Retrogen Inc. (San Diego, CA, USA) for sequencing on an Applied Biosystems 3730xl DNA Analyzer. Chromatograms were inspected for base calling errors and edited in Mesquite v.3.31 (Maddison & Maddison, 2017b) using Chromaseq v.1.2 with the PHRE/PHRAP plug-in (Green, 2009; Maddison & Maddison, 2017a). Protein sequences were translated to amino acids in Mesquite to search for errors or stop codons. Primers used in this study follow those used in Murray et al. (2013), for list see Table 1.

3.6 Phylogenetic Analyses

Each gene region was aligned using the MAFFT v7.3 online server (Katoh, 2013), with the E–INS–i algorithmic model and default settings. Nuclear and mitochondrial gene regions were concatenated in SEQUENCEMATRIX v1.7.8 (Vaiddya et al., 2011). Phylogenetic analyses were performed using Maximum likelihood, Parsimony and Successive Approximation Character Weighting (SAW) methods.

Maximum likelihood (ML) analyses were performed using RAxML v8.2.9 (Stamatakis, 2014) online through the CIPRES portal (Miller et al., 2010) with 1000 bootstraps and four gene partitions: 28S D2, 28S D3-5, COI NJ, and COII.

The best likelihood tree was visualized using Fig tree v1.4.0 (Rambaut, 2012) and rooted with *Pseudometagea*.

Parsimony analyses (PA) were performed using PAUP*4.0b10 (Swofford, 2003) using 10,000 random addition heuristic searches with a tree save limit of 9000, and tree bisection reconnection (TBR) branch swapping. Gaps were treated as missing. Successive approximation character weighting (SAW) was applied to the resulting trees using the maximum value of the rescaled consistency index and a base weight of 1000 without a tree save limit, with the resulting tree rescaled to unity character weights and compared in length with the most-parsimonious trees (Carpenter, 1988; Heraty, 2002). Resulting trees from the PA and SAW analyses were visualized using a majority rule consensus tree. Bootstrap support was evaluated with 1000 random replicates and two random addition searches per replicate and a save tree limit of 100.

4. Results

4.1 Phylogenetic analysis

Maximum Likelihood (Fig. 2), parsimony (Fig. 3), and Successive Approximations Weighting (Fig. 4) analyses of the Sanger sequencing dataset produce slightly different tree topologies. The parsimony analysis produced a large set of trees (4288 trees of 1690 steps). The SAW analysis reduced the number of trees to 16, but of one step longer (1691 steps). While the SAW results do not offer the most parsimonious tree solution, the relationships within

Tutucharis are more highly resolved. All analyses support the monophyly of the poneromorph clade with three monophyletic groups: the Chalcura, Kapala, and Schizaspidia clades, as proposed by Murray et al. (2013). Additional genera of Eucharitini were not included that would objectively test the monophyly of the poneromorph clade as this was not the aim of this study. All analyses indicate that Ancylotropus sensu lato are not monophyletic. Sub-Saharan African taxa previously classified under Ancylotropus fall into two distinct groups: one that we now recognize as a new genus, *Tutucharis*, and another, the *Ancylotropus neotropus* group (4 undescribed species) that groups within the Asian Ancylotropus clade. In parsimony analyses, the Madagascan Ancylotropus are consistently sister to *Tutucharis* and never sister to the Asian clade, whereas in the Likelihood analyses they are sister to the rest of the Schizaspidia clade. The other species groups of Ancylotropus are not treated further here as a better sampling of molecular data is necessary to more accurately assess their placement. Tutucharis is never sister to the Asian clade excluding the A. ivondroi species group. Based on both morphological characteristics, we recognize *Tutucharis* as a distinct new genus, encompassing 11 new species.

4.2 Key to the genera of the Schizaspidia clade and description of the genus *Tutucharis*

Key to genera of the Schizaspidia clade

- Posterior margin of first gastral tergite with two widely spaced incisions separating a broad median panel, gaster triquetrous. Antennal flagellomeres cylindrical or slightly serrate
 2
- Posterior margin of gastral tergite with one or two closely-spaced incisions
 (often difficult to discern the two) with incisions longer than width of median
 panel, gaster bivalved. Antennal flagellomeres cylindrical to pectinate 4

- Supraclypeal area and most of lower face transversely carinate. Apex of mesoscutellum with projection much longer than broad and truncate or emarginate apically *Ancylotropus neotropus* group (subsaharan Africa)

- Mesoscutellum with truncate or forked process (no lateral reference for origin). Frenal carina absent laterally and dorsally. Axillular sulcus usually absent, but if present weakly indicated. Protibial spur curved and bifid 6

- Antenna with 9–10 flagellomeres; basal flagellomere long or short. Upper prepectus quadrate and separated from tegula by greater than tegula length. Mesoscutellar disc variously scultured; if longitudinally carinate, then carinae crossed by numerous transverse ridges and tines of fork long 8
- **8 (7)** Occiput and face including frons smooth. Antennal flagellum of both sexes cylindrical; basal flagellomere more than 5x as long as broad. Mesosoma shallow rugose-areolate dorsally. *Ancylotropus ivondroi* group (Madagascar)

- Occiput circularly striate; frons sculptured, often vertically carinate. Antennal flagellum cylindrical to serrate, but males usually with pectinate flagellum after basal flagellomere; basal flagellomere at most 4x as long as broad.
 Mesosoma strongly sculptured but usually smooth or roughly carinate 9

Tutucharis Rocha gen. n.

Type Species. Tutucharis fabrizioi Rocha

Diagnosis. Recognized by apex of frenum prolonged into a short, rounded or squared, unforked projection; axillula laterally flattened and triangular, dorsally margined by a distinct axillular carina extending to base of projection and ventrally by a distinct frenal arm; gaster triquetrous; antennal flagellomeres elongate and cylindrical or weakly serrate in both sexes, except one species with

pectinate antenna in male; antennal flagellum 9–10 segmented, anellus absent; prepectus fused to pronotum.

Description. Both sexes known. Body length, 3.4–3.6 mm. Color of head, mesosoma, coxa and petiole ranging from black to dark green, blue, and purple; antenna light brown; metasoma brown; legs beyond coxa pale yellowish brown; wings hyaline; fore wing venation light brown.

Head. In frontal view subtriangular, cheeks broadly rounded; eyes rounded and bare; median ocellus slightly anterior to lateral ocelli or inline. Face excluding eyes with covering of fine, long setae; parascrobal area smooth, vertically carinate, or punctate, lower face smooth, horizontally carinate, or punctate; scrobal depression deeply impressed and smooth; occiput circularly carinate, dorsal margin rounded. Clypeus smooth, anteclypeus present, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 7–9 long digits. Maxillary complex large (not reduced).

Antenna. Female antenna with 11–12 segments; scape 2–3X as long as broad; anellus absent. Flagellum of female with 9–10 flagellomeres, F1L:F1W 3X longer than apical width and only flared apically, flagellomeres progressively decreasing in length, terminal flagellomere as long as broad; MPS dense on all flagellomeres. Flagellum of male with 10 flagellomeres, basal flagellomere 4X longer than broad, longer than scape; flagellomeres progressively decreasing in length and width, terminal flagellomere 4X as long as broad; MPS not apparent.

Mesosoma. Pronotum abutting mesoscutum, no overlap of sclerites.

Mesoscutum with anterior margin reflected, and with anterior margin strongly or weakly bilobed in dorsal view; lateral margin over spiracle rounded, posterolaterally evenly rounded or swollen and extending over spiracle and tegula, without an upturned lower margin over the spiracle or tegula; dorsum coarsely rugose-areolate, with sparse long setae; notauli shallow or deeply impressed; transscutal articulation present and transverse. Scutoscutellar sulcus transverse, meeting transscutal articulation medially; lateral axillar lobe broad; axillular carina present, axillula. Frenal carina distinct. Apex of frenum produced into a truncate projection that has a sharp lateral carina that barely reaches past the base of the proojection. Metanotum with narrow flange laterally, only slightly overlapping propodeum. Propodeal disc flat and evenly sculptured; propodeum laterad to postspiracular furrow weakly expanded, spiracle circular; metepimeral groove weakly indicated. Femoral groove shallow; mesepimeron evenly sculptured, transepimeral sulcus absent; acropleuron grooved for reception of upper corner of prepectus; mesepisternum with anteromedial margin abutting posterior margin of prepectus; ventral margin of mesepisternum wedge-shaped and extending vertically anterior to mid coxa. Prepectus fused with pronotum and in the same plane; dorsal third of prepectus narrowly triangular, about 2X as long as median width of projection, apex narrowly separated from tegula; pronotal spine absent; spiracle narrowly enclosed. Hind coxa semiglobose or globose; mid coxa without lateral groove or carina; hind tibia with 1 or 2 spurs. Fore wing

venation distinct; stigmal vein stout and linear; postmarginal vein several times longer than broad, but only about 2X as long as stigmal vein; pilosity dense and with a marginal fringe. Hind wing venation complete; fringe present. *Metasoma*. Petiole of female elongate, 1.2-1.5X as long as hind coxa; petiole subcylindrical. Gastral terga smooth or micropunctate and bare or with few scattered setae; gaster triquetrous, middle panel broad and bordered by deep incisions; tergal scar absent; cerci present. Hypopygium with few or several long setae on each side of midline.

Etymology. Named in honor of Desmond Tutu, a Nobel Peace Prize laureate known for his work as an apartheid and human-rights activist and winner of the Nobel Peace Prize.

Distribution. African (Uganda, Angola, Cameroon, Central African Republic, Republic of The Congo, Democratic Republic of The Congo, Ghana, Guinea, Kenya, Malawi, Nigeria, South Africa, Tanzania, Uganda, Zambia, Zimbabwe). **Biology.** Little is known about the biology of *Tutucharis*. The host is known for *Tutucharis troglodytes*, in which two specimens were extracted from cocoons of *Odontomachus troglodytes* (Heraty, 2002). *Tutucharis leoi* was associated (not observed directly) with oviposition into the skin of mature berries of *Psychotria capensis* (Rubiaceae), in which clusters of 60–80 stalked eggs were deposited (Heraty, 2002).

4.3 Key and description to the species of *Tutucharis*

Key to species of *Tutucharis*

1	Male 2
_	Female 11
2 (1)	Head and mesoscutum with long erect (strait) setae (Fig. 6C) 3
_	Head and mesoscutum with short recumbent (curved) setae (Fig. 21B–D)
3 (2)	Weakly sculptured mesosoma (Fig.16B–C); labrum with 9 long digits; axillula smooth (Fig. 16C)
_	Strongly sculptured mesosoma (Fig. 6B); labrum with 8 long digits; axillula mostly smooth, but if sculptured then weakly (Fig. 6C)
4 (3)	Antennal flagellomeres pectinate (Fig. 24H) [female unknown]

_	Antennal flagellomeres cylindrical with apex serrate (Fig. 24G) or truncate
	(Fig. 24Q) 5
5 (4)	Antennal flagellomeres with apex serrate (Fig. 24G) 6
_	Antennal flagellomeres with apex truncate (Fig. 24Q)
6 (5)	Vertex with large orbicular impression on either side of median ocellus
	(Fig. 8B–C); labrum with 6 digits; scutellar-axillar complex short and wide
	(Fig. 8B); frenal projection about as long as wide and broadly tapered
	apically (Fig. 8B) Tutucharis biimpressa
-	Vertex without orbicular impressions and evenly rounded (Fig. 22C–D);
	labrum with 8 digits; scutellar-axillar complex long and narrow (Fig. 22B);
	frenal projection 2.0-2.1X as long as wide and rounded apically (Fig. 22B)
	[female unknown] Tutucharis troglodytes
7 (5)	Parascrobal area strongly sculptured and vertically carinate (Fig. 21D):
	gena micropunctate
-	Parascrobal area mostly smooth or carinate only dorsally (Fig. 10D);
	gena smooth or micropunctate 9

- **8(7)** Head subcircular in frontal view (Fig. 13D); labrum with 7 digits *Tutucharis leoi*

11 (2) Mesosoma smooth dorsally (Fig. 15B) Tutucharis longiseta
 Mesosoma sculptured dorsally (Fig. 19B) 12
12 (11) Vertex with large orbicular impression on either side of median ocellus (Fig. 7C) <i>Tutucharis biimpressa</i>
 Vertex without large orbicular impressions on either side of median ocellus (Fig. 6A–D)
13 (12) Head and mesosoma dorsally punctate with hairs (Fig. 17B)
 Head and mesosoma variably sculptured, but not punctate with hairs (Fig. 9B)
14 (13) Head and mesosoma black and non-metallic (Fig. 9A–D)
 Head and mesosoma variably colored but not black and metallic 15

4.4 Species descriptions

Tutucharis ashlae n. sp.

(Figs 5–6, 24A–B)

Diagnosis. Distinguished from other *Tutucharis* by the 12–segmented pilose antenna; female with conspicuous rugae and multiporous plate sensilla; male lacking conspicuous rugae; head and mesosoma covered in long erect setae;

dorsally rectangular mesoscutum, anteriorly carinate and mostly smooth posteriorly with few scattered puctures; axilla laterally carinate, lateral panel of axilla with deep pit; mesoscutellar disc areolate with or without posterior shallow impression; axillula mostly smooth, axillular carina and frenal line well defined; head, mesosoma, coxa, and petiole blue, green, or purple metallic, gaster light brown; femora light brown to pale yellow.

Female. Length, 4.0 mm. Antenna with scape pale yellow, pedicel light brown, flagellum dark brown. Head, mesosoma, petiole, and coxa blue metallic with purple and green reflections. Femora light brown; tibia and tarsi pale yellow. Gaster light brown. Wings hyaline; venation light brown.

Head 1.5X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus slightly anterior to lateral ocellus. Face smooth with a few long erect setae; vertex micropunctate, parascrobal area mooth, lower face micropunctate; scrobal depression deeply impressed and smooth; occiputsmooth. Clypeus with few erect setae, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 7 long digits. Maxillary complex large. *Antenna* with 12 segments; scape 3.9X as long as broad with flange on ventral surface, reaching median ocellus; anellus absent. Antenna pilose. Flagellum with 10 flagellomeres, F1L:F1W 8X much longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; many multiporous plate sensilla present.

Mesosoma. Longer than broad with long erect setae. Frenal process rounded and slightly longer than broad, with weak longitudinal carina and sharp lateral margin; axillular carina well defined, axillula smooth. Coxa smooth with few erect setae; femora smooth with long scattered setae; tibia and tarsus pilose. Fore wing 2.3X as long as broad; stigmal vein about 3.7X as long as broad and perpendicular to wing margin; entire wing except basal area setose, posterior marginal fringe present. Hind wing entirely setose, posterior marginal fringe present.

Metasoma. Petiole of female 0.6X as long as hind coxa; subcircular and longitudinally carinate. Gastral tergum mostly bare and mostly smooth, except second gastral tergum micro punctate. Hypopygium surrounded by long erect setae.

Male. Length, 3.6–3.7 mm. Head, mesosoma, coxa, and petiole either green metallic with yellow reflections or purple metallic with green reflections, femora pale yellow. Antenna light brown and pilose; scape F1L:F1W 6.5–6.6X longer than wide, reaching median ocellus, flagellum with 10 segments. Labrum with 8 long digits. Gaster smooth and bare.

Etymology. Named in honor of my friend, Ashley Bui.

Genetic Data. Two specimens (D4533, D4660) were sequenced for the following gene regions: 28S D2, 28S D3-5, COI NJ, and COII. For D4532 only 28S D2 and 28S D3-5 were available.

Distribution. African (Tanzania).

Material Examined. Holotype: Tanzania: Tanga: West Usambara, Zigi hiuse, 462m, 5°05'60"S, 38°39'8"E, 2-3.ii.2015, P. Janšta & S. Straka, T15 [♀, UCRCENT00595229, D4532], deposited in NMPC. **Paratypes: Tanzania:** Tanga: East Usambbara Zigi house, 462m, 5°05'60"S, 38°39'8"E, 2-3.ii.2015, P. Janšta & J. Straka, light [♂, UCRC: UCRCENT00435942, D4660]. West Usambara, Zigi hiuse, 462m, 5°05'60"S, 38°39'8"E, 2-3.ii.2015, P. Janšta & S. Straka, T15 [♂, UCRC: UCRENT00485385, D4533].

Tutucharis biimpressa n. sp.

(Figs 7–8, 24C)

Diagnosis. Distinguished from other species of *Tutucharis* by the large orbicular impression on either side of the median ocellus; median ocellus surrounded by carina and pushed forward into the scrobal depression; head subcircular in frontal view; female mesoscutum strigate; male mesoscutum areolate-rugose; male with 12 segmented serrate antenna [female antennae broken apically]; notaulus conspicuous; frenal projection as long as wide and tapered. Female with head, mesosoma, coxae and petiole green-blue metallic with gold-green reflections; gaster and femora dark brown. Male with head, mesosoma, coxae and petiole black metallic with green reflections; gaster and femora dark brown. Male with head, mesosoma, coxae and petiole black metallic with green reflections; gaster and femora dark brown. Female with head, mesosoma, coxae and petiole green-blue metallic brown, flagellum dark brown. Female with head, mesosoma, coxae and petiole green-blue metallic with gold-green reflections, gaster and femora dark brown, femora brown, flagellum dark brown. Female with head, mesosoma, coxae and petiole green-blue metallic with gold-green reflections, gaster and femora dark brown, femora brown; tibia and tarsi pale yellow. Wings hyaline; venation light brown.
Head 1.5X as broad as high. In frontal view rhomboidal; eyes rounded and bare. Face with recumbent, short setae, vertex bare; parascrobal area smooth; scrobal depression deeply impressed, smooth, and narrow; occiput circularly carinate, dorsal margin not rounded. Clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 9 long digits. Maxillary complex large. *Antenna* broken apically; scape 4.3X as long as broad with flange on ventral surface, not reaching median ocellus; anellus absent. Antenna with few short setae, F1L:F1W 3.1X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; multiporous plate sensilla

present.

Mesosoma. About as long as broad covered in recumbent setae. Axillae rugose; scutoscutellar suture broadly carinate, meeting transscutal articulation medially; mesoscutellar disc areolate-rugose; frenal process tapered and as long as broad, with weak longitudinal carina and sharp lateral margin; axillular carina well defined, axillua rugose. Coxa smooth with few recumbent setae; femora smooth with long recumbent setae; tibia and tarsus setose. Fore wing 2.1X as long as broad; stigmal vein about 5X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Both with posterior marginal fringe.

Metasoma. Petiole of female 0.6X as long as hind coxa; petiole subcircular and rugose. Gastral terga smooth and bare. Hypopygium surrounded by long erect setae.

Male. Length, 3.9–4.1 mm. head, mesosoma, coxae and petiole black metallic with green reflections, gaster and femora dark brown. Flagellum light brown and setose; scape light brown, F1L:F1W 1.7–1.9X longer than apical width and serrate, not reaching median ocellus, flagellum with 10 segments. Labrum with 6 long digits. Axillula rugose. Gaster smooth and bare.

Etymology. The name is derived from the Latin prefix 'bi-' meaning 'two,' and 'impressa,' referring to the two distinct impressions on the vertex of the head on either side of the median ocellus.

Genetic Data. No molecular data available.

Distribution. African (Democratic Republic of the Congo, Kenya).

Material Examined. Holotype: Kenya: Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 4-11.vii.2000, R. Copeland, MT [♀, UCRCENT00485572], deposited in UCRC. Paratypes: Democratic Republic of the Congo: Rutshuru, 1°11'8"S, 29°26'49"E, 13.viii.1937, Miss Prophylactique [♂, RMCA: UCRCENT00416953]. Kenya: Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 31.vii-4.viii.1999, R. Copeland, MT [♂, UCRC: UCRCENT00496100].

Tutucharis fabrizioi n. sp.

(Figs 9–10, 24D–E)

Diagnosis. Distinguished from other species of *Tutucharis* by the apically swollen mesoscutal midlobe and mesoscutal lateral lobe with large circular puncture, and notaulus and transscutal articulation distinct and deeply impressed; axilla carinate, carina reaching mesoscutellum, lateral panel of axilla with deep pit; mesoscutellum finely areolate with scattered recumbent setae and posterior shallow impression; axillula shagreened, axillular carina and frenal line well defined. Female and male with head, mesosoma, coxae and petiole black; gaster reddish brown; femur pale yellow.

Female. Length, 4.3–4.5 mm. Antenna with scape pale yellow, pedicel and flagellum dark brown. Head, mesosoma, and petiole black metallic. Coxa dark brown to black, femora pale yellow; tibia and tarsi pale yellow. Gaster reddish brown. Wings hyaline; venation reddish brown.

Head 1.4–1.5X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus slightly anterior to lateral ocellus. Face and vertex with covering of recumbent, short setae; parascrobal area micropunctate with scattered setae, lower face micropunctate; scrobal depression deeply impressed and smooth; occiput circularly carinate, dorsal margin rounded. Clypeus with few short, scattered setae, clypeal margin transverse with scattered setae. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 10 long digits. Maxillary complex large. *Antenna* with 12 segments; scape 3.6X as long as broad with flange on ventral surface, reaching median ocellus; anellus absent. Antenna pilose. Flagellum with

10 flagellomeres, F1L:F1W 4.4X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; multiporous plate sensillum present.

Mesosoma. Longer than broad with scattered recumbent setae. Mesoscutum transversely carinate anteriorly, posteriorly smooth; mesoscutal midlobe swollen apically; notaulus distict, deeply furrowed and carinate. Axillae transversely carinate or completely smooth; scutoscutellar suture broadly carinate, meeting transscutal articulation medially; mesoscutellar disc rugose or foveolate; frenal process broadly rounded and as long as broad, with weak longitudinal carina and sharp lateral margin; axillular carina well defined. Coxa shallowly rugose with few erect setae; femora smooth with long scattered setae; tibia and tarsus pilose. Fore wing 2.6–2.7X as long as broad; stigmal vein about 3X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose.

Metasoma. Petiole of female 1.0–1.1X as long as hind coxa; swollen medially and laterally rugose. Gastral terga smooth and bare, except second gastral tergum micro punctate; gaster triquetrous; cerci present. Hypopygium surrounded by long erect setae.

Male. Length, 3.6 mm. Head black to very dark brown, mesosoma black, coxa brown and distally yellow, femora yellow, petiole not examined. Antenna yellow and pilose; scape F1L:F1W 1.5–1.8X longer than apical width and only slightly broader apically, not reaching median ocellus, flagellum incomplete. Labrum with

7 long digits. Mesoscutal midlobe rugose, mesoscutal lateral lobe mostly smooth with central pit. Mesoscutellar disc with scattered punctures. Axillula carinate. Without gaster.

Etymology. Named in honor of my son, Fabrizio Rocha.

Genetic Data. Two specimens were sequenced for the following gene regions: 28S D2, 28S D3-5, COI NJ, and COII.

Distribution. African (Democratic Republic of the Congo, Uganda).

Material Examined. Holotype: Uganda: Kibale National Park, Kanyawara, Makerere University Biological Field Station, 1523m, 0°33'50"N, 30°21'42"E, 4-26.viii.2008, S. van Noort, primary mid-altitude rainforest, YPT, UG08-KF8-Y07 [♀, SAM-HYM00084157; D5987], deposited in SAMC. **Paratypes: Democratic Republic of the Congo:** Rutshuru, 1°11'8"S, 29°26'49"E, 13.viii.1937, Miss Prophylactique [♂, RMCA: UCRCENT00416952]. Rutshuru, 1°11'8"S, 29°26'49"E, iii.1938, J. Ghesquiere [♀, RMCA: UCRCENT00416969]. **Uganda:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 1523m, 0°33'50"N, 30°21'42"E, 4-26.viii.2008, S. van Noort, primary mid-altitude rainforest, YPT, UG08-KF8-Y07 [♀, SAMC: SAM-HYM00084155; D5686].

Tutucharis krissae n. sp.

(Figs 11, 24H)

Diagnosis. Distinguished from other *Tutucharis* by the 10-segmented pectinate antennal flagellum; scrobal depression deeply impressed; face with strong

longitudinal carina; well defined scrobal sulcus; medial and lateral ocelli aligned; shallow notaulus and scutoscutellar suture; frenal process 1.5X longer than wide. Head, mesosoma, and petiole metallic green, coxa and gaster brown; femora pale yellow.

Female. Unknown.

Male. Length, 4.1 mm. Antenna with scape, pedicel and flagellum yellow. Head, mesosoma, and petiole metallic green. Coxa brown, femora, tibia and tarsus pale yellow. Gaster brown. Wings hyaline; venation brown, posterior margin of wing with fringe.

Head 1.6X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus and lateral ocellus aligned. Face and vertex with scattered setae; longitudinally carinate parascrobal area and lower face; scrobal depression deeply impressed and smooth; occiput circularly carinate, dorsal margin rounded. Clypeus smooth and bare, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 8 long digits. Maxillary complex large. *Antenna* with 12 segments; scape 5X as long as broad, reaching median ocellus; anellus absent. Antenna pilose. Flagellum with 10 flagellomeres, flagellomeres pectinate with notch progressively decreasing in length.

Mesosoma. Longer than broad and mostly bare. Mesoscutum transversely carinate-rugose; lateral lobes with lateral cluster of setae, notaulus shallow and carinate. Axillae rugose; scutoscutellar suture broadly carinate; mesoscutellar

disc rugose; frenal process rounded and 1.6X as long as broad, with longitudinal carina and sharp lateral margin; axillula rugose, axillular carina well defined. Coxa smooth with long erect setae; femora smooth with long scattered setae; tibia and tarsus pilose. Fore wing 2.1X as long as broad; stigmal vein about 5X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Both with posterior marginal fringe. *Metasoma.* Petiole 1.2X as long as hind coxa; swollen ventrally and entirely rugose. Gastral tergum smooth and bare, except second gastral terga micropunctate.

Note. The pectinate antenna more closely resembles similar forms in the Chalcura clade, especially in the genus *Chalcura* Kirby.

Etymology. Named in honor of my friend, Krissy Dominguez.

Genetic Data. No genetic data available.

Distribution. African (Zambia).

Material Examined. Holotype: Zambia: Ndola, 12°59'20"S, 28°38'59"E, 24.i.1954, C.B. Cottrell [♂, UCRCENT00416484], deposited in NMPC.

Tutucharis leoi n. sp.

(Figs 12–14, 24I)

Diagnosis. Distinguished from other species of *Tutucharis* by the dense covering of long recumbent setae on head and mesosoma; head in frontal view

subcircular; vertex of head rugose; apex of frenal projection broadly squared or almost squared and as long as wide.

Female. Length, 3.4–4.0 mm. Antenna with scape and pedicel yellow, flagellum dark brown. Head, mesosoma, coxae and petiole green metallic with yellow reflections or purple metallic with blue or gold reflections, gaster dark brown; femur yellow or light brown.; tibia and tarsi pale yellow. Wings hyaline; venation light brown.

Head 1.5–1.6X as broad as high; eyes rounded and bare; median ocellus slightly anterior to lateral ocellus. Face and vertex with covering of recumbent, short setae; parascrobal area smooth, lower face laterally rugose and micro punctate; scrobal depression narrow, deeply impressed and smooth; occiput circularly carinate, dorsal margin rounded. Clypeus smooth with few short, scattered setae, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 8 long digits. Maxillary complex large.

Antenna with 12 segments; scape 3.3–3.4X as long as broad with flange on ventral surface, not reaching median ocellus; anellus absent. Antenna sparsely pilose. Flagellum with 10 flagellomeres, F1L:F1W 4.3–4.2X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; many multiporous plate sensillum present.

Mesosoma. Longer than broad with scattered recumbent setae. Mesoscutum transversely carinate to areolate; mesoscutal midlobe slightly swollen apically;

notaulus inconspicuous. Axillae transversely carinate; scutoscutellar suture broadly carinate, meeting transscutal articulation medially; mesoscutellar disc rugose and apically swollen; frenal process broadly squared and as long as broad, rugose and a sharp lateral margin; axillular carina well defined; axillula rugose. Coxa shallowly smooth with recumbent setae; femora smooth with long scattered setae; tibia and tarsus pilose. Fore wing 2.1–2.4X as long as broad; stigmal vein about 4.7–4.8X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Posterior marginal fringe present.

Metasoma. Petiole of female 1.1X as long as hind coxa; subcircular and strongly laterally rugose. Gastral terga smooth and bare, except second gastral tergum micro punctate; gaster triquetrous; cerci present. Hypopygium surrounded by long erect setae.

Male. Length, 3.9–4.7 mm. Head, mesosoma, coxae and petiole green metallic with yellow reflections or purple metallic with blue or gold reflections, gaster dark brown; femur yellow or light brown. Antenna with 12 equal segments, yellow and pilose; scape F1L:F1W 1.4–2.1X longer than apical width and only slightly broader apically, not reaching median ocellus. Labrum with 7 long digits. Mesosoma rugose. Mesoscutellar disc apically swollen.

Description of planidium. Morphology and setal pattern typical of other members of the Schizaspidia clade (Fig. 15). Body composed of 12 segments. Tergopleural line separating pleural and dorsal tergites present, tergites I and II

fused ventrally; tergites I and II with five pairs of setae, tergite III with one pair of setae, tergite IV with two pairs of setae, tergite V with one pair of setae; tergite VI with one long pair of setae; tergites IX and XI with long processes on posterolateral margin; caudal cerci minute and not exceeding apical spines of tergite XI.

Biology. *Tutucharis leoi* was associated (not observed directly) with oviposition into the skin of mature berries of *Psychotria capensis* (Eckl.) Vatke (Rubiaceae), in which clusters of 60–80 stalked eggs were deposited (Heraty, 2002).

Etymology. Named in honor of my nephew, Leo Rogriguez.

Genetic Data. Two specimens were sequenced for the following gene regions: 28S D2, 28S D3-5, COI NJ, and COII.

Distribution. African (South Africa).

Material Examined. Holotype: South Africa: Mpumulanga: Umhalazi Nature Reserve, 10 m.m, 28°57'27"S, 31°46'25"E, 5.ii.1998, J.Heraty, coastal forest, H98/047 [♀, UCRCENT00485387, 7053], deposited in SAMC. Paratypes: South Africa: Mpumulanga: Umlalazi N.R., 10m, 28°57'20"S, 31°46'2"E, 2.ii.1998, J.Heraty, coastal forest, H98-045 [♂, UCRC: UCRCENT00103372, SAMC: UCRCENT00485391]; Giants Castle, 1 km E camp, 1900m, 29°16'0"S, 29°30'0"E, 1.ii.1998, J. Heraty, H98-044 [♂, UCRC: UCRCENT00092223]. Giants Castle, 1 km E of Camp, 26°16'0"S, 29°30'0"E, 1.ii.1998, Montane forest [♂, UCRC: UCRCENT00092222]; Umhalazi N. R., 10m, 28°57'27"S, 31°46'25"E, 2.ii.1998, J. Heraty, coastal forest [♂, UCRC: UCRCENT00485388]. Umhalazi N.

R., 10m, 28°57'27"S, 31°46'25"E, 5.ii.1998, J. Heraty, coastal forest, H98047 [♂, UCRC: UCRCENT00560621]. Umhalazi Nature Reserve, 10 m.m, 28°57'27"S, 31°46'25"E, 5.ii.1998, J.Heraty, coastal forest, H98/047 [5 ♂, UCRC: UCRCENT00485389, UCRCENT00485390, UCRCENT00485392–94]. East Mtunzini, Umlalazi Res., 28°59'9"S, 31°44'8"E, xi.1979, R. Miller [♀, USNM: UCRCENT00426060].

Tutucharis longiseta n. sp.

(Figs 15–16, 24J–K)

Diagnosis. Distinguished from other species of *Tutucharis* by the dense long setae that cover the 10-segmented antennal flagellum of males and females;m weakly sculptured mesoscutum and the presence of long, erect setae on the head, most of the mesosoma, and legs; female with mesoscutellum lightly umbilicate; male shallow punctate and mostly smooth, both with smooth lateral lobes. Female with head, mesosoma, coxae and petiole dark bluish-purple or blue with green reflections; male with head, mesosoma, coxae and petiole dark green; female femora mostly dark brown with apex pale yellow; male femora pale yellow.

Female. Length, 5.0–5.7 mm. Antenna with scape and pedicel pale yellow, flagellum reddish brown. Head, mesosoma, coxa and petiole dark blue with green or purple reflections. Femora mostly dark brown with apex pale yellow;

tibia and tarsi pale yellow. Gaster dark brown. Wings hyaline; venation pale brown.

Head 1.4–1.5X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus slightly anterior to lateral ocelli. Face and vertex with covering of fine, long setae; parascrobal area smooth, lower face smooth; scrobal depression deeply impressed and smooth; occiput circularly carinate, dorsal margin rounded. Clypeus smooth, clypeal margin transverse with scattered setae. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 10 long digits. Maxillary complex large.

Antenna with 12 segments; scape 3.5–3.8X as long as broad, reaching median ocellus; anellus absent. Flagellum with 10 flagellomeres; F1L:F1W 6.5–6.7X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length.

Mesosoma. Slightly longer than broad and covered with long erect setae. Mesoscutum transversely carinate anteriorly, posteriorly smooth with sparse shallow punctures; side lobes laterally broadly rounded in dorsal view; reticulate laterally and smooth dorsally; notauli complete and shallow foveate. Axillae with irregular sculpture; scutoscutellar sulcus broadly foveate, meeting transscutal articulation medially; mesoscutellar disc shallowly umbilicate; frenal process broadly rounded and slightly longer than broad, with weak longitudinal carina, with sharp lateral margin; axillular carina well defined. Coxae smooth with a few

erect setae; fore and mid femora smooth, hind femora with irregular punctures and scattered setae; tibiae pilose. Fore wing 2.5–2.9X as long as broad; stigmal vein about 4.2–4.5X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Fore and hind with distinct marginal fringe. *Metasoma.* Petiole of female 1.1–1.6X as long as hind coxa; petiole subcylindrical with longitudinal striations. Gastral terga with scattered erect setae. Hypopygium with 3 long setae on each side of midline.

Male. Length, 3.9–4.7 mm. Head, mesosoma, coxa and petiole green with yellow reflections; antenna light brown; femora pale yellow. Antenna pilose, setal bases distinct; scape F1L:F1W 4.1–4.4X longer than apical width and only slightly broader apically, reaching median ocellus; 10 flagellomeres, cylindrical, progressively decreasing in length. Labrum with 9 digits. Mesoscutum mostly smooth posteriorly; notauli complete but weakly indicated. Mesoscutellar disc smooth with scattered punctures. Petiole 3.8–4.1X as long as broad and 2.1–2.3X as long as hind coxa, petiole subcylindrical. Gastral tergites smooth with scattered hairs.

Etymology. Latin, combining long and seta, referring to the characteristic setae that cover most of the body and antenna.

Genetic Data. Six specimens sequenced for the following gene regions: 28S D2, 28S D3-5, COI NJ, and COII.

Distribution. African (Central African Republic, Kenya, Tanzania, Uganda).

Material Examined. Holotype: Central African Republic: Prefecture Sangha-Mbaéré: Parc National de Dzanga-Ndoki, Mabéa Bai, 38.6km 173° S Lidjombo, 350m, 2°21'36"N, 16°03'12"E, 22.V.2001, S. van Noort, Lowland rainforest, sweep, CAR01-S230 [♀, UCRCENT00247123; D2288], deposited in SAMC. Paratypes: Kenya: Western: Kakamega Forest, 0°14'8"N, 34°31'52"E, 23-30.IV.2000 [2, UCRC: UCRCENT00485594]. Tanzania: Tanga: West Usambara, Zigi hiuse, 462m, 5°05'60"S, 38°39'8"E, 2-3.II.2015, P. Janšta & S. Straka, T15 [2, NMPC: UCRCENT00595229; D4532]. Uganda: 20km SE Fort Portal, Makarere University Biological Field Station, 1573m, 0°33'55"N, 30°21'21"E, 4– 21.X.2001, B. & J. Gill, yellow pan trap [3, CNC: UCRCENT00505729; D0637]. Entebbe, 0°03'10"N, 32°27'54"E, 27.IX.1912, C.C. Gowdey [2, BMNH: NHMUK14582977]. Kampala, 0°18'49"N, 32°34'53"E, 4.IX.1918, C. C. Gowdey, 6489 [2, BMNH: NHMUK14582951]. Kanyawara Dist., Kibale National Park, 0°29'6"N, 30°19'55"E, S. van Noort, Malaise trap, UG05-M14 [3, SAMC: UCRCENT00247096; D7055]. Kawanda, 0°50'0"N, 31°54'59"E, X.1940, T. H. C. Taylor [2, BMNH: NHMUK14582966]. Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33'50"N, 30°21'42"E [3, SAMC: UCRCENT00560591]. Kibale National Park, Kanyawara, Makerere University Biological Field Station, 1523m, 0°33'50"N, 30°21'42"E, 6.VIII.2008, S. van Noort, primary mid altitude rainforest, sweep, UG08-KF8-S01 [3, UCRC: SAMC00086218]. Kome Island, Lake Victoria, 0°05'19"S, 32°45'0"E, 14.XII.1918, Dr. G.D.H Carpenter, forest, 1920-201 [2, BMNH: NHMUK14582956]. Mabira,

0°37′0″N, 33°09′0″E, 20.VII.1912, 4582 [♂, BMNH: NHMUK14582948]. Mityana, 0°24′21″N, 32°01′49″E, IV.1940, T. H. C. Taylor [♂, BMNH: NHMUK14582964]. Bwamba Co., Semuliki Nat. Pk., ~ 1.0 km W Ntandi, 670m, 0°50′0″N, 30°03′0″E, 15.III.2013, A. Gumovsky, palm forest, evening [♂, UCRC: UCRCENT00412201; D3913]. Semuliki Nat. Pk., 670m, 0°50′0″N, 30°03′0″E, 20.III.2013, A. Gumovsky, dry forest with palms [♂, UCRC: UCRCENT00412207; D3916].

Tutucharis punctisetosa n. sp.

(Figs 17–18, 24L–M)

Diagnosis. Distinguished from other species of *Tutucharis* by antennal flagellum of female 10-segmented with covering of short setae; head and mesosoma of with long recumbent setae; apex of head, lower face, and mesosoma punctate. Male mesoscutum anteriorly rugose to punctate; with dense long recumbent setae on head and mesosoma. Male antennal flagellum setose, without longitudinal ridges. Frenal projection rounded apically.

Female. Length, 3.1–3.9 mm. Antenna with scape pale yellow, pedicel and flagellum light brown to dark brown. Head, mesosoma, Coxa, and petiole either blue metallic with purple reflections, green metallic with gold reflections, or dark green metallic with green reflections. Femora pale yellow; tibia and tarsi pale yellow. Gaster light brown. Wings hyaline; venation light brown.

Head 1.4–1.7X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus anterior to lateral ocellus. Parascrobal area smooth, lower

face micropunctate; scrobal depression deeply impressed, smooth and narrow; occiput circularly carinate, dorsal margin rounded. Clypeus smooth, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 8 long digits. Maxillary complex large.

Antenna with 12 segments; scape 1.6–1.8X as long as broad, not reaching median ocellus; anellus absent. Antenna setose. Flagellum with 10 flagellomeres, F1L:F1W 4.6–4.7X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; multiporous plate sensilla present.

Mesosoma. Longer than broad with scattered recumbent setae. Mesoscutum punctate; notaulus inconspicuous. Axillae longitudinally carinate; scutoscutellar suture broadly carinate; mesoscutellar disc punctate; frenal process rounded and as longer that wide, with weak longitudinal carina and sharp lateral margin; axillular carina well defined; axillula mostly smooth. Coxa smooth with few setae; femora smooth with long scattered setae; tibia and tarsus setose. Fore wing 2.1X as long as broad; stigmal vein about 4.3–4.4X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Presence of posterior wing margin.

Metasoma. Petiole of female 1.1–1.4X as long as hind coxa; subcircular and laterally rugose. Gastral terga smooth and bare. Hypopygium surrounded by long erect setae.

Male. Length, 2.8 mm. Head, mesosoma, coxa, and petiole, black metallic with green and purple reflections, femora yellow. Antenna light brown and setose; scape F1L:F1W 2.4–2.7X longer than apical width and only slightly broader apically, not reaching median ocellus. Scrobal depression very wide almost reaching inner eye margin. Labrum with 8 long digits. Mesoscutellar disc rugulose. Axilla longitudinally carinate. Axillula smooth. Gaster smooth and bare. **Etymology.** Latin, combining *puncta* and *setosa*, meaning having bristly punctures referring to their characteristic punctate setae.

Genetic Data. Two specimens were sequenced for the following gene regions: 28S D2, COI NJ, and COII. Specimen D3914 was also sequenced for 28S D3-5. **Distribution.** African (Kenya, Republic of the Congo, Uganda).

Material Examined. Holotype: Republic of the Congo: Dept. Pool: Iboubikro,
Lesio-Louna Pk., 340m, 3°16'11"S, 15°28'16"E, 1.vi-18.vii.2008, Sharkey &
Braet, sweep, ROC-02 [♀, UCRCENT00408468, D3776], deposited in UCRC.
Paratypes: Kenya: Kakamega D. Yala R. Nat. Res., 1450m, 0°12'0"N,
34°52'0"E, 20.iii.2002, R. Snelling, malaise trap [♂, LACM: UCRCENT00091813,
D0707]. Republic of the Congo: Dept. Pool: Iboubikro, Lesio-Louna Pk.,
3°16'11"S, 15°28'16"E, Sharkey & Braet [♀, UCRC: UCRCENT00307704].
Uganda: nr Najjembe, Mabira forest, 1200m, 0°23'23"N, 33°00'20"E, 12.iii.2009,
A. Gumovsky [♂, UCRC: UCRCENT00412202, D3914].

Tutucharis seriata n. sp.

(Figs 19, 24N)

Diagnosis. Distinguished from other species of *Tutucharis* by the row of setae that line the lateral side of the 9-segmented antennal flagellum; mesoscutum anteriorly carinate, posteriorly mostly smooth; axilla smooth; mesoscutellar disc lightly rugose; head, mesosoma, coxae and petiole dark blue metallic with purple and green reflections; gaster and femora orange brown.

Female. Length, 4.5 mm. Antenna with scape yellow and pedicel pale yellow, flagellum dark brown. Head, mesosoma, coxa, and petiole dark blue metallic with purple and green reflections. Femora orange brown, tibia and tarsi pale yellow. Gaster orange brown. Wings hyaline; venation reddish brown.

Head 1.4X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus anterior to lateral ocelli. Face smooth with few scattered setae, scrobal depression deeply impressed and narrow; occiput smooth, dorsal margin rounded. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 10 long digits. Maxillary complex large.

Antenna with 11 segments; scape 4.3X as long as broad with no flange on ventral surface, reaching median ocellus; anellus absent. Flagellum with 9 flagellomeres, F1L:F1W 4.6X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; multiporous plate sensilla present.

Mesosoma. Longer than broad with few scattered setae. Mesoscutum faintly transversely carinate anteriorly, posteriorly smooth; notalus inconspicuous. Axillae completely smooth; scutoscutellar suture broadly carinate; mesoscutellar disc faintly rugose; frenal process rounded and as long as broad, mostly smooth with weak longitudinal carina and sharp lateral margin; axillular carina well defined. Coxa smooth with few erect setae; femora smooth with erect setae; tibia and tarsus pilose. Fore wing 2.4X as long as broad; stigmal vein about 2X as long as broad and perpendicular to wing margin; entire wing except basal area setose posterior marginal fringe present, Hind wing entirely setose, with posterior marginal fringe.

Metasoma. Petiole of female 1.6X as long as hind coxa; subcircular and laterally faintly carinate. Gastral terga smooth with scattered seatae. Hypopygium surrounded by long erect setae.

Male. Unknown

Etymology. Latin word meaning arranged in a series referring to the single row of setae on the lateral surface of their antennae.

Genetic Data. No genetic data available.

Distribution. African (Cameroon).

Material Examined. Holotype: Cameroon: J.-Albrechtshohe n. v. Kamerun-Bg., 4°39'15"N, 9°24'53"E, 1896, L. Conradt [♀, NHMUK014582971], deposited in BMNH.

Tutucharis tatianae n. sp.

(Figs 20–21, 240–P)

Diagnosis. Distinguished from other species of *Tutucharis* by the narrow frontovertex, vertex with strong longitudinal carina reaching parascrobal area; gena pectinate with strong longitudinal carina; scrobal depression deep, scrobal sulcus smooth and rounded; head and mesosoma with short recumbent setae; mesoscutum areolate-rugose and slightly apically swollen, notaulus shallow; mesoscutellar disc areolate-rugose and swollen apically; axillula shagreened in female or shallowly areolate-rugose in male, axillular carina and frenal line well defined; frenal projection squared or slightly rounded. Head, mesosoma, coxae and petiole green metallic with gold or blue reflections, black metallic with iridescence, or purple metallic with gold reflections, gaster brown; femur brown to pale yellow.

Female. Length, 3.6–4.2 mm. Antenna with scape and pedicel pale yellow, flagellum dark brown. Head, mesosoma, and petiole green metallic with gold or blue reflections or black metallic with iridescence. Coxa dark brown, femora brown; tibia and tarsi pale yellow. Gaster brown. Wings hyaline; venation light brown.

Head 1.5–1.7X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus slightly anterior to lateral ocellus. Face and vertex with covering of recumbent setae; parascrobal area and lower face with conspicuous lateral carina; scrobal depression deeply impressed; occiput circularly carinate,

dorsal margin rounded. Clypeus with few short, scattered setae, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 9 long digits. Maxillary complex large.

Antenna with 11 segments; scape 3.4–3.7X as long as broad, reaching median ocellus; anellus absent. Antennal flagellum setose with 9 flagellomeres, F1L:F1W 2.9–3.0X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length; multiporous plate sensilla not

present.

Mesosoma. Longer than broad with scattered recumbent setae. Mesoscutum areolate-rugose and swollen apically; notaulus shallow. Axillae laterally carinate; scutoscutellar suture broadly carinate, meeting transscutal articulation medially; mesoscutellar disc areolate-rugose; frenal process slightly rounded and as long as broad, with weak longitudinal carina and sharp lateral margin; axillular carina well defined. Coxa smooth with few long, recumbent setae; femora smooth with long scattered setae; tibia and tarsus pilose. Fore wing 2.2–2.4X as long as broad; stigmal vein about 3.9–4.3X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Posterior marginal fringe present.

Metasoma. Petiole of female 0.9–1.1X as long as hind coxa; subcircular. Gastral terga smooth and bare. Hypopygium surrounded by long erect setae.

Male. Length, 2.8–3.4 mm. Head, mesosoma, coxa, and petiole green metallic with gold or blue reflections or purple metallic with gold reflections, femora yellow. Antenna with 12 segments, yellow and pilose; scape F1L:F1W 1.9–2.9X longer than apical width and only slightly broader apically, not reaching median ocellus, flagellum 10 segmented. Labrum with 9 long digits.

Etymology. Named in honor of my friend, Tatiana Bush.

Genetic Data. No genetic data available.

Distribution. African (Kenya, Tanzania).

Material Examined. Holotype: Kenya: Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 4-11.vii.2000, R. Copeland, MT [♀, UCRCENT00485573], deposited in UCRC. **Paratypes: Kenya:** Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 16-23.i.2000, R. Copeland, MT [♂, ♀, UCRC: UCRCENT00485577, UCRCENT00485579]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 18-25.vi.1999, R. Copeland, MT [3♂, 2♀, UCRC: UCRCENT00485566, UCRCENT00485567, UCRCENT00485568, UCRCENT00485569, UCRCENT00485582]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 27.ii-5.iii.2000, R. Copeland, MT [♂, UCRC: UCRCENT00485585]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 3-10.vii.1999, R. Copeland, MT [♂, ♀, UCRC: UCRCENT00485570, UCRCENT00496103]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 4-11.vii.2000, R. Copeland, MT [2♂, 2♀, UCRC: UCRCENT00485571, UCRCENT00485574, UCRCENT00485576, UCRCENT00485571, UCRCENT00485574, UCRCENT00485576, UCRCENT00485581]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 5-12.vi.2000, R. Copeland, MT [♂, UCRC: UCRCENT00496098]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 7-14.v.2000, R. Copeland, MT [♂, UCRC: UCRCENT00496099]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 9-16.iv.2000, R. Copeland, MT [♀, UCRC: UCRCENT00485578]. **Tanzania:** Amani Hills, 5°06'44"S, 38°36'36"E, 23.vi-24.vii.2001, Donald Quicke, malaise trap [♀, UCRC: UCRCENT00092218].

Tutucharis troglodytes n. sp.

(Figs 22, 24F–G)

Diagnosis. Distinguished from other *Tutucharis* by the 10-segmented serrate antennal flagellum, with flagellum consisting of equal-sized segments, with covering of short setae; vertex of head with expanded region around ocelli median ocellus anterior to lateral ocelli; antennal scrobe smooth and deep, scrobal sulcus well defined; face with small scattered setiferous punctures; scutellar-axillar complex narrow; frenal projection 1.6–2.1X longer than wide and narrow. Head, mesosoma, coxa, and petiole metallic green with gold reflections to metallic black to metallic blue with green reflections, gaster brown; femora light brown to yellow.

Female. Unknown.

Male. Length, 3.2–3.9 mm. Antenna with scape and pedicel light brown, flagellum dark yellow to almost light brown. Head, mesosoma, coxa, and petiole metallic green with gold reflections to metallic black or blue; gaster brown;

femora light brown to yellow. Wings hyaline; venation pale brown, posterior margin of wings with fringe.

Head 1.3–1.7X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus anterior to lateral ocelli facing forward. Face and vertex longitudinally carinate, parascrobal area smooth; scrobal depression deeply impressed and smooth; occiput circularly carinate. Clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 8 long digits. Maxillary complex large.

Antenna with 12 segments; scape 2.7–2.9X as long as broad, not reaching median ocellus; anellus absent. Antenna setose. Flagellum with 10 flagellomeres, flagellomeres serrate and equal in length.

Mesosoma. Longer than broad with many recumbent setae. Mesoscutum entirely rugose; notaulus shallow and carinate. Scutoscutellar suture broadly carinate and large excavated pit in the center; frenal process rounded with longitudinal carina and sharp lateral margin; axillula rugose, axillular carina well defined. Coxa smooth with sparse setae; femora smooth with recumbent setae; tibia and tarsus pilose. Fore wing 2.1–2.3X as long as broad; stigmal vein about 3.5–3.9X as long as broad and perpendicular to wing margin; entire wing except basal area setose. Hind wing entirely setose. Both with posterior marginal fringe. *Metasoma*. Petiole 2.3–2.7X as long as hind coxa; subcircular and rugose. Gastral tergum smooth and bare.

Etymology. Named after their ant host, Odontomachus troglodytes.

Genetic Data. No genetic data available.

Ant Host: Odontomachus troglodytes (Ponerinae).

Distribution. African (Democratic Republic of the Congo, Kenya, Uganda). Material Examined. Holotype: Kenya: Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 5-12.vi.2000, R. Copeland, MT [3, UCRCENT00496101], deposited in UCRC. Paratypes: Democratic Republic of the Congo: Rutshuru, 1°11'8"S, 29°26'49"E, xii.1937, J. Ghesquiere [3, RMCA: UCRCENT00416956]. Kenya: Kakamega Distr.: Isecheno, Isecheno Nature Reserve, 0°14'24"N, 34°52'12"E [d, UCRC: UCRCENT00560608]. Western Prov.: Kakamega Forest, 0°14'8"N, 34°51'52"E, 18-25.vi.1999, R. Copeland, MT [3, UCRC: UCRCENT00496102]. Kakamega Forest, 0°14'8"N, 34°51'52"E, 3-10.vii.1999, R. Copeland, MT [3, UCRC: UCRCENT00485583]. Uganda: Kawanda, 0°50'0"N, 31°54'59"E, iii.1941, T.H.C. Taylor, T.729, host: Odontomachus troglodytes Santischi [3, BMNH: NHMUK14582949]. Kawanda, 0°50'0"N, 31°54'59"E, iii.1941, T.H.C. Taylor, T.730, host: Odontomachus troglodytes Santischi [2, BMNH: NHMUK14582944]. Ankole Dist.: Kichwamba, 0°42'59"N, 30°11'59"E, 23.iv.1968, PJ Spangler [3, USNM: UCRCENT00425529].

Tutucharis viridiana n. sp.

(Figs 23, 24Q)

Diagnosis. Distinguished from other species of *Tutucharis* by dense covering of recumbent setae on the vertex of the head, face, and mesosoma; parascrobal area with longitudinal carina; antennae pilose; mesosoma dorsally conspicuously areolate; frenal process either longer than wide and tapered or as long as wide and rounded; presence of deep rectangular excavation with shallow carina where scutoscutellar suture and transscutal articulation meet. Head, mesosoma, coxa, and petiole blue-green metallic with purple reflections to black metallic with purple-blue reflections, petiole brown, femora, tibia, and tarsus pale yellow.

Female. Unknown

Male. Length, 2.9–3.8 mm. Antenna with scape, pedicel and flagellum brown. Head, mesosoma, coxa, and petiole blue-green metallic with purple reflections to black metallic with purple-blue reflections, gaster brown. Femora pale yellow; tibia and tarsi pale yellow. Wings hyaline; venation brown.

Head 1.4–1.8X as broad as high. In frontal view subtriangular; eyes rounded and bare; median ocellus slightly anterior to lateral ocellus. Parascrobal area and vertex with dense covering of recumbent setae and longitudinal carina; lower face with lateral carina and micropunctate; scrobal depression deeply impressed and smooth; occiput circularly carinate. Clypeus smooth with few scattered setae, clypeal margin transverse. Genal depression absent; hypostomal lobes broadly separated. Mandibles falcate and stout with 3/2 formula. Labrum with 8 long digits. Maxillary complex large.

Antenna with 12 segments; scape 3.6–3.7X as long as broad with flange on ventral surface, reaching median ocellus; anellus absent. Antenna pilose. Flagellum with 10 flagellomeres, F1L:F1W 3.4–3.5X longer than apical width and only slightly broader apically, flagellomeres progressively decreasing in length. *Mesosoma.* Longer than broad and dorsally conspicuously areolate. Notaulus distinct. Axillae mostly smooth with few longitudinal carina; scutoscutellar suture deep and broadly carinate, meeting transscutal articulation medially; frenal process either longer than wide and tapered or as long as wide and rounded, with weak longitudinal carina and sharp lateral margin; axillular carina well defined, axillula shallowly areolate. Coxa smooth with few long setae; femora smooth with long recumbent setae; tibia and tarsus pilose. Fore wing 2.1–2.5X as long as broad; stigmal vein about 3.1X as long as broad and perpendicular to wing margin; entire wing except basal area setose, hind wing entirely setose, both with posterior marginal wing fringe.

Metasoma. Petiole 1.1–1.3X as long as hind coxa; cylindrical and laterally carinate. Gastral terga smooth and bare, except second gastral tergum micro punctate with scattered setae; gaster triquetrous; cerci present. Hypopygium with 4 long erect setae on either side.

Etymology. Latinized form of viridian meaning green, named after the Viridian Gym in the Pokémon series.

Genetic Data. Two specimens were sequenced for the following gene regions: 28S D2, 28S D3-5, COI NJ, and COII.

Distribution. African (Cameroon, Guinea).

Material Examined. Holotype: Guinea: (Conakry) Mount Nimba, Gouan camp, Gallery Forest of Zié nr "Station de Pompage Zié" canopy of trees, "Nimba 050", understory shrub layer, 1250m, 7°40'23"N, 8°22'24"W, 3.x.2011, A. Henrard & D. Van den Spiegel, fogging, (Fog 01) [♂, UCRCENT00412203, D3915], deposited in MRAC. Paratype: Cameroon: Mt. Cameroon, Bonacanda, 1040m, 4°12'55"N, 9°16'9"E, 24.viii.2013, J.Heraty, swp, H13-093 [♂, UCRC: UCRCENT00498653, D6971].

6. References

- Carmichael, A.E. 2006. The Phylogenetics and Biogeography of the Parasitoids of Large Poneromorph Ants (Eucharitini: Eucharitidae). MSc thesis, University of California, Riverside.
- Carpenter, J.M., 1922. Choosing among multiple equally parsimonious cladograms. Cladistics 4, 291–296.
- Clausen, C.P., 1928. The manner of oviposition and the planidium of *Schizaspidia manipurensis* n. sp. (Hymenoptera, Eucharidae). Proc. Entomol. Soc. Wash. 30, 80–86.
- Clausen, C.P., 1940. The immature stages of Eucharidae (Hymenoptera). J. Wash. Acad. Sci. 30, 504–516.
- Clausen, C.P., 1940. The oviposition habits of the Eucharidae (Hymenoptera). Proc. Entomol. Soc. Wash. 12, 504–516.

- Cruaud, A., Rasplus, J., Zhang, J., Burks, R., Delvare, G., Fusu, L., Gumovsky,
 A., Huber, J.T., Janšta, P., Mitroiu, M., Noyes, J.S., Noort, S., Baker, A.,
 Böhmová, J., Baur, H., Blaimer, B.B., Brady, S.G., Bubeníková, K., Chartois,
 M., Copeland, R.S., Papilloud, N.D., Molin, A.D., Dominguez, K., Gebiola,
 M., Guerrieri, E., Kresslein, R.L., Krogmann, L., Lemmon, E., Murray, E.A.,
 Nidelet, S., Nieves-Aldrey, J.L., Perry, R.K., Peters, R.S., Polaszek, A.,
 Sauné, L., Torréns, J., Triapitsyn, S., Tselikh, E.V., Yoder, M., Lemmon,
 A.R., Woolley, J.B., Heraty, J.M., 2024. The Chalcidoidea bush of life:
 Evolutionary history of a massive radiation of minute wasps. Cladistics 40, 34–63.
- Dowton, M. and Austin, A., 1997. Evidence for AT-Transversion Bias in wasp Hymenoptera: Symphyta) mitochondrial genes and its implications for the origin of parasitism. J. Mol. Evol. 44, 398–405.
- Eady, R.D., 1968. Some illustrations of microsculpture in the Hymenoptera Proc. R. Entomol. Soc. Lond. 43, 66–72.
- Evenhuis, N.L., 2020. The Insect and Spider Collections of the World Website. http://hbs.bishopmuseum.org/codens/ (accessed August 2024).

Green, P., 2009. Phrap. Version 1.3. http://phrap.org (accessed August 2024).

- Harris, R.A., 1979. A glossary of surface sculpturing. Occas. Pap. Calif. Dep. Food Agric. 28, 31.
- Heraty, J.M., 2002. A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world. Mem. Am. Entomol. Inst. 68, 1–367.

- Heraty, J.M., Hawks, D., Kostecki, J.S., Carmichael, A., 2004. Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). Syst. Entomol. 29, 544–559.
- Heraty, J.M., and Murray, E., 2013. The life history of *Pseudometagea schwarzii* with a discussion of the evolution of endoparasitism and koinobiosis in Eucharitidae and Perilampidae (Chalcidoidea). J. Hymenopt. Res. 35, 1–15.
- Heraty, J.M., Mottern, J., Peeters, C., 2015. A new species of *Schizaspidia*, with discussion of the phylogenetic utility of immature stages for assessing relationships among eucharitid parasitoids of ants. Ann. Entomol. Soc. Am. 108, 865–874.
- Heraty, J.M., 2017. World Catalog of Eucharitidae.

http://www.hymenoptera.ucr.edu/eucharitidae (accessed August 2024).

- Heraty, J.M., Burks, R.A., Gibson, G.A., (in press). External morphology of adult Chalcidoidea. In Heraty. J.M. and Woolley J.B. (eds), Chalcidoidea of the World. CABI International, London.
- Ishii, T., 1932. Some Philippine eucharids with notes on their oviposition habits. Bull. Imp. Agric. Exp. Stn. Nishigahara 3, 203–212.
- Katoh, K. and Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. and Evol. 30, 772–780.

Maddison, D.R. and Maddison, W.P., 2017. Chromaseq: A Mesquite Package for Analyzing Sequence Chromatograms. Version 1.3.

http://mesquiteproject.org/packages/chromaseq (accessed August 2024).

- Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. Grid Computing Environments DOI:10.1109/GCE.2010.5676129
- Murray, E.A., Carmichael, A.E., Heraty, J.M., 2013. Ancient host shifts followed by host conservatism in a group of ant parasitoids. Proc. R. Soc. B Biol Sci, 280, 20130495
- Narendran, T.C. and Sheela, S., 1996. A systematic study of the oriental genus *Ancylotropus* Cameroon (Hymenoptera: Eucharitidae). Uttar Pradesh J. Zool. 15, 43–47.
- Nunn, G.B., Theisen, B.F., Christensen, B., Arctander, P., 1996. Simplicitycorrelated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. J. Mol. Evol. 42, 211–223.
- Rambaut, A., 2012. FigTree. Version 1.4. <u>http://tree.bio.ed.ac.uk/software/figtree/</u> (accessed August 2024).
- Simon, C., Frati, F., Beckenbach, A., Crespi, B., Flook, P., 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Ann. Entomol. Soc. Am. 87, 651–701.

- Stamatakis, A., 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313.
- Swofford, D.L., 2003. Phylogenetic Analysis using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, MA.
- Vaidya, G., Lohman, D.J., Meier, R., 2011. SequenceMatrix: concatenation Software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics 27, 171–180.
- Zhang, J., Heraty, J.M., Darling, C., Kresslein, R.L., Baker, A.J., Torréns, J.,
 Rasplus, J., Lemmon, A., Lemmon, E., 2022. Anchored phylogenomics and
 a revised classification of the planidial larva clade of jewel wasps
 (Hymenoptera: Chalcidoidea). Syst. Entomol. 47, 329–353.485573



Fig. 1: Geographic distribution of *Tutucharis* species.



Fig. 2: Maximum likelihood tree of the Sanger dataset from RAxML. Bootstrap support values are indicated unless lower than 50. Dnumbers are molecular voucher codes. Country abbreviations for taxa are explained in Table 3.


Fig. 3: Majority rule consensus tree of 4288 unweighted parsimony trees of 1690 steps, c.i. 0.37, r.i. 0.69. MJ rule percentage above branch, bootstrap values below branches. Dnumbers are molecular voucher codes. Country abbreviations for taxa are explained in Table 3.



Fig. 4: Majority rule consensus tree of 34 successive approximations (SAW) trees. MJ rule percentage above branches, unweighted bootstrap values below branch (only reported for *Tutucharis*). Dnumbers are molecular voucher codes. Country abbreviations for taxa are explained in Table 3.



Fig. 5: *Tutucharis ashlae* $\stackrel{\bigcirc}{}$ (UCRC00595229): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 6: *Tutucharis ashlae* ♂ (UCRC00435942): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 7: *Tutucharis biimpressa* ♀ (UCRC00485572): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 8: *Tutucharis biimpressa* ♂ (UCRC00496100): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 9: *Tutucharis fabrizioi* ♀ (SAM-HYM00084155): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 10: *Tutucharis fabrizioi* ♂ (UCRC00416969): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 11: *Tutucharis krissae* ♂ (UCRC00416484): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 12: *Tutucharis leoi* ♀ (UCRC00485387): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 13: *Tutucharis leoi* ♂ (UCRC00485390): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 14: Tutucharis leoi: Planidium and egg. Tergite IX (TIX)



Fig. 15: *Tutucharis longiseta* ♀ (SAM-HYM00084155): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 16: *Tutucharis longiseta* ♂ (UCRCENT0637): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 17: *Tutucharis punctisetosa* ♀ (UCRC00408668): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 18: *Tutucharis punctisetosa* ♂ (UCRC00412202): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 19: *Tutucharis seriata* ♀ (UCRC00239478): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 20: *Tutucharis tatianae* ♀ (UCRC00485573): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 21: *Tutucharis tatianae* ♂ (UCRC00485576): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 22: *Tutucharis troglodytes* ♂ (UCRC00496101): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 23: *Tutucharis viridiana* ♂ (UCRCENT3915): A, habitus, lateral; B, mesosoma, dorsal; C, mesosoma, lateral; D, head, anterior.



Fig. 24: *Tutucharis* antennae. A–B, *T. ashlae*: A, ♂ (485385); B, ♀ (595229). C, *T. biimpressa*, ♀ (485572). D–E, *T. fabrizioi*: D, ♀ (P084157); E, ♂ (416969). F– G, *T. troglodytes*: F, ♀ (14582944); G, ♂ (496101). H, *T. krissae*, ♂ (416484). I, *T. leoi*, ♀ (92218). J–K, *T. longisetosa*: J, ♀ (247123); K, ♂ (412201). L–M, *T. punctisetosa*: L, ♀ (408468); M, ♂ (412202). N, *T. seriata*, ♀ (14582971). O–P, *T. tatianae*: O, ♀ (485573); P, ♂ (485576). Q, *T. viridiana*, ♂ (412203). Scale bars 0.5 mm.

References	C AGC-3'		3 AG-3' Nunn et al. 1996	V-3' Schulmeister 2003	GGA TTT GG-3' Simon et al. 1994	- AT-3' Dowton and Austin 1997	TGA-3' Simon et al. 1994	TGA CCA-3' Dowton and Austin 1997
Sequence	5'-CGG GTT GCT TGA GAG TGC	5'-CTC CTT GGT CCG TGT TTC-	5'-TTG AAA CAC GGA CCA AGG	5'-CGC CAG TTC TGC TTA CCA	5'-ТАТ АТТ ТТА АТТ ҮТW ССW	5'-ATT GCA AAT ACT GGA CCT	5'-ATT GGA CAT CAA TGA TAT '	5'-CCA CAA ATT TCT GAA CAT
Primer	D2-3551 F	D2Ra R	D3-4046 F	D5-4625 R	COI-NJ F	COI-D R	COII-MTD16 F	COII-MTD18 R
Gene	28S D2		28S D3-5		COINJ		COII	

Table 1. Primer oligonucleotides used in this study.

ах	axilla	om	median ocellus
ахс	axillar carina	msc	mesoscutum
axl	axillula	mss	mesoscutellum
axlc	axillular carina	not	notaulus
clm	clypeal margin	oc	occiput
cly	clypeus	000	occipital carina
CX	соха	ped	pedicel
flg	flagellum	pet	petiole
fm	femur	psa	parascrobal area
fre	frenum	sca	supraclypeal area
frl	frenal line	scd	scrobal depression
frp	frenal process	scp	scape
II	mesoscutal lateral lobe	scs	scrobal sulcus
lo	lateral ocellus	sctd	mesoscutellar disc
lof	lower face	SSS	scutoscutellar suture
lpa	lateral panel of axilla	tsa	transscutal articulation
man	mandible	vtx	vertex
mlm	mesoscutal midlobe		
triquetrous	: three sided.		
multiporou: short distaı	s plate sensilla: sensilla that are raised above a nce.	and projectin	g beyond the flagellar surface for at least a

Table 2. Morphological abbreviations and definitions.

Taxon	Locality	Voucher number	捁	Deposition	28S D2	28S D3-5	COInj	COII
Ancylotropus sp.	Kenya: Coast	UCRCENT 00103371	0964	UCRC	I	ı	ı	ı
Ancylotropus cariniscutis	Malaysia	UCRCENT 00091771	0407	UCRC	I	I	I	I
Ancylotropus cariniscutis	Malaysia: Selangor	UCRCENT 00508826	0701	UCRC	I	I	I	I
Ancylotropus cariniscutis	Singapore	UCRCENT 00237302	2836	UCRC	I	I	I	I
Ancylotropus ivondroi	Madagascar: Antananarivo	UCRCENT 00092238	0627	CASC	I	I	I	I
Ancylotropus ivondroi	Madagascar: Fiararantsoa	UCRCENT 00184057	2200	CASC	I	I	I	I
Ancylotropus ivondroi	Madagascar: Tomasina	UCRCENT 00478819	6298	UCRC	I	I	ı	ı
Ancylotropus montanus	Thailand: Phitsanulok	UCRCENT 00001428	2747	UCRC	I	I	I	I
Ancylotropus n.sp. 2	Madagascar: Fiararantsoa	UCRCENT 00468020	7070	UCRC	I	I	I	I
Austeucharis implexa	Australia: South Australia	UCRCENT 00091767	0164	UCRC	I	I	I	I
Babcokiella emaciata	Tanzania: Tanga	UCRCENT 00435911	4528	UCRC	I	I	I	I
Chalcura sp.	Australia: New South Wales	UCRCENT 00091426	0174	UCRC	I	I	I	I
Chalcura ?ramosa	Australia: South Australia	UCRCENT 00091909	0173	UCRC	I	I	I	I
Chalcura sp.1	Australia: South Australia	UCRCENT 00092100	0176	UCRC	I	I	I	I
Chalcura sp.5	Australia: New South Wales	UCRCENT 00091824	0178	UCRC	I	I	I	I
Chalcura aeginata	Australia: Queensland	UCRCENT 00091264	1010	UCRC	I	I	I	I
Chalcura deprivata	Sri Lanka	UCRCENT 00092116	0344	QDPC	I	I	I	I
Chalcura parachalcura	Fiji: E. Sigatoka	UCRCENT 00175166	1255	UCRC	I	I	I	I
Chalcura ramosa	Austalia: Queensland	UCRCENT 00091761	0630	UCRC	I	I	I	I
Chalcura samoana	USA: American Samoa	UCRCENT 00091930	0728	UCRC	I	I	I	I
Colocharis napoana	Ecuador: Orellana	UCRCENT 00091450	1102	NSNM	I	I	I	I
Eucharissa natalica	South Africa: W. Cape Province	no id#	0485	SAMC	I	I	I	I
Kapala argentina	Argentina: Salta	UCRCENT 00010184	1064	UCRC	I	I	I	ī
Kapala cuprea	Ecuador: Orellana	UCRCENT 00091807	1003	UCRC	I	I	I	I

Table 3. List of taxa used in molecular analyses, with GenBank accession numbers and deposition location.

Kapala cuprea	Ecuador: Orellana	UCRCENT 0009222	1004	NSNM	ı	ı	I	ı.
Kapala furcata	Argentina: Misiones	UCRCENT 00092093	1078	UCRC	I	I	ī	Т
Kapala iridcolor	Colombia: Magdalena	UCRCENT 00172493	0920	UCRC	I	I	ī	Т
Kapala iridicolor	Colombia: Magdalena	UCRCENT 00091816	0928-a	UCRC	I	I	I	T
Kapala ivorensis	Sao Tome	UCRCENT 00092140	0273	UCRC	I	I	I	I
Kapala izapa	Mexico: Quintana Roo	lost	0365	UCRC	I	I	T	Т
Kapala short spines	Ecuador: Orellana	UCRCENT 00092029	1173	UCRC	I	I	ī	Т
Kapala sulcifaces	Guatemala: Retalhuleu	UCRCENT 00091469	0379	UCRC	I	I	I	T
Parapsilogastrus	Australia: Queensland	UCRCENT 00092044	1370	CNCI	ı	ı	ı	ı.
Parapsilogastrus	Australia: Queensland	UCRCENT 00092043	1378	QM	I	I	I	I.
Parapsilogastrus fausta	Australia: South Australia	UCRCENT 00092134	0172	UCRC	I	I	I	I
Parapsilogastrus fausta?	Austalia: New South Wales	UCRCENT 00091905	0658	UCRC	I	I	I	Т
Parapsilogastrus skinny	Australia: Queensland	UCRCENT 00091912	0175	UCRC	I	I	I	Т
Pogonacharis browni	Indonesia: Sulawesi: Selatan	UCRCENT 00092215	1317	cuic	I	I	ī	Т
Pseudometagea bakeri	Canada: Saskatchewan	UCRCENT 00091252	0322	UCRC	I	I	I	I
Pseudometagea montana	Canada: Ontario	UCRCENT 00091473	0321	UCRC	I	I	I	Т
Pseudometagea schwarzii	USA: Missouri	UCRCENT 00091457	0274	UCRC	I	I	I	Т
Saccharissa alcocki	Thailand: Trang	UCRCENT 00161230	2032	UCRC	I	I	I	I.
Saccharissa vicina	Thailand: Trang	lost	1592	UCRC	I	I	I	Т
Schizaspidia sp.	Austalia: Queensland	UCRCENT 00091762	0663	UCRC	I	I	I	Т
Schizaspidia sp.	Austalia: Queensland	lost	0684	UCRC	I	I	ı	Т
Schizaspidia sp.	Papua New Guinea: East New Britain	UCRCENT 00092402	0993	UCRC	I	I	I	Т
Schizaspidia convergens	Sri Lanka: Central	UCRCENT 00175170	0346	UCR/QMB	I	I	ı	Т
Schizaspidia guttivipennis	Australia: Queensland	UCRCENT 00092089	0169	UCRC	I	I	I	Т
Schizaspidia nasua	Thailand	UCRCENT 00092137	0341	UCRC	I	I	ı	Т
Shizaspidia sp.	Fiji: E. Sigatoka	UCRCENT 00175165	1256	UCRC	I	I	I	Т
<i>Shizaspidia</i> sp.	India: Karnataka	UCRCENT 00092224	1423	UCRC	I	I	I	I

Shizaspidia sp.	Australia: Queensland	UCRCENT 00435919	4536	UCRC	I	I	I	Т
Thoracanthoides albispina	Australia: Queensland	UCRCENT 00241970	1860	QM	I	I	I	ī
Tricoryna iello	Australia: ACT	UCRCENT 00091449	0356	UCR	I	I	I	Т
Tricoryna reticulativentris	Australia: Queensland	UCRCENT 00091767	0163	UCRC	I	I	I	Т
Tricoryna zalates	Australia: ACT	UCRCENT 00092258	0357	CNCI	I	T	I	Т
Tutucharis ashlae	Tanzania	UCRCENT 00435942	4660	UCRC	ı	ı	ı	Т
Tutucharis ashlae	Tanzania	UCRCENT 00485385	4532	NMPC	I	I	I	Т
Tutucharis ashlae	Tanzania	UCRCENT 00435916	4533	UCRC	I	I	I	Т
Tutucharis fabrizioi	Uganda	SAM-HYM 00084155	5986	SAMC	I	I	I	Т
Tutucharis fabrizioi	Uganda	SAM-HYM 00084157	5987	SAMC	ı	I	I	Т
Tutucharis leoi	South Africa: Mpumulanga	UCRCENT 00092222	0157	UCRC	I	I	I	Т
Tutucharis leoi	Tanzania	UCRCENT 00092218	0392	UCRC	I	ī	ı	Т
Tutucharis leoi	South Africa: Mpumulanga	UCRCENT 00103372	1510	UCRC	I	I	I	Т
Tutucharis longiseta	Uganda	UCRCENT 00092023	0637	CNC	I	ı	ı	Т
Tutucharis longiseta	Uganda	UCRCENT 00412201	3913	UCRC	I	I	I	Т
Tutucharis longiseta	Uganda	UCRCENT 00412207	3916	UCRC	ı	I	I	Т
Tutucharis longiseta	Central African Republic	UCRCENT 00355341	2288	SAMC	I	I	I	Т
Tutucharis longiseta	Uganda	UCRCENT 00247096	7055	SAMC	ı	I	I	Т
Tutucharis punctisetosa	Kenya	UCRCENT 00091813	0707	LACM	I	I	I	Т
Tutucharis punctisetosa	Republic of the Congo	UCRCENT 00408468	3776	UCRC	I	ī	ī	Т
Tutucharis punctisetosa	Uganda	UCRCENT 00412202	3914	UCRC	I	I	I	Т
Tutucharis viridiana	Guinea	UCRCENT 00412203	3915	UCRC	ı	ı	ı	Т
Tutucharis viridiana	Cameroon	UCRCENT 00498653	6971	UCRC	I	I.	ı.	Т